

Gardeners' Contributions to Urban Biodiversity: A Multi-Taxa Assessment of α - and β -Functional and Taxonomic Diversity in a Densifying City

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Abstract

Urban ecosystems are playing a growing role in conserving and enhancing biodiversity and ecosystem functioning, yet ongoing urban densification can challenge them by reducing urban green spaces, including urban gardens, limiting their contribution to achieving conservation targets. However, it is first critical to understand how different biodiversity metrics and facets, which might show contrasting responses, are affected by local and landscape factors in gardens. Here, we use a large, multi-taxa invertebrate diversity dataset from 85 urban gardens in the city of Zurich, Switzerland, to investigate their role in supporting multifaceted urban invertebrate biodiversity, both currently and considering future urban densification. To do so, we use a combination of social-ecological factors, including management practices, urban density, vegetation and habitat diversity. We sampled 264'972 individuals belonging to 756 species from eight taxonomic groups of invertebrates, including pollinators, herbivores, predators and decomposers, as well as functional traits related to abiotic tolerances, trophic preference, life history, mobility, morphology, reproduction and phenology for all species. We found that gardens' γ -diversity was mostly driven by α -diversity. We found urban density to be the main driver negatively impacting invertebrate α and β taxonomic and functional diversity across groups in a non-linear way, followed by plant diversity, with a positive effect, and management intensity, with a negative one. Thus, local gardens may partly compensate for the effects of landscape urban density on invertebrate diversity, both by increasing local plant diversity and by indirectly increasing habitat diversity and reducing management intensity through human actions. Finally, future urban densification led to species losses across taxa. Overall, our study showed that urban gardens represent an important asset for multifaceted urban biodiversity, yet urban densification represents a major threat. Measures to reconcile urban development with biodiversity preservation are critically needed, especially by improving local garden conditions via biodiversity-friendly management.

INTRODUCTION

Reconciling human activities and needs with biodiversity conservation is a critical research topic. Land-use changes are a major driver of biodiversity decline and loss of ecosystem functioning (Wagner et al., 2021; Simkin et al., 2022; Jaureguiberry et al., 2022). Yet, human-dominated ecosystems, such as cities, can play an important role in conservation as they retain part of the existing biodiversity and the functions they perform, including rare and endangered species (Soanes & Lentini 2019; Ong et al., 2022; Lepczyk et al., 2023), through their network of urban green spaces, spanning highly managed green infrastructure to remnant patches of native vegetation (Aronson et al., 2017; Spotswood et al., 2021). These patterns have sometimes been seen as paradoxical, particularly under conservation paradigms that focus on native vegetation or "biodiversity hotspots" only (i.e., "nature by itself"; Dunn et al., 2006; Mace 2014). Moreover, most urban green spaces are typically small (e.g. Gaston et al., 2013) and often perceived as highly isolated. This poses a main question regarding how to overcome scale mismatches between human land use units (e.g., urban green spaces) and the spatial scales at which high-extinction-risk species or communities live (Goddard et al., 2010). At the same time, the recognition of small habitat patches are crucial for biodiversity is adding some nuance and providing opportunities for

integrating urban ecosystems within regional and global conservation frameworks (IPBES, 2019; Okey et al., 2021). Specifically, small habitat patches, when diverse and well-connected, can act as stepping-stones and refugia (Riva & Fahrig 2022; Riva et al., 2024). Overall, cities are increasingly regarded as important areas for contributing achieving large-scale conservation goals, and provide ecosystem functioning and services through the communities and populations they harbour (Kowarik et al., 2025).

However, the importance of biodiversity conservation in cities and their urban green spaces is spatially and temporally dynamic (Kowarik & von der Lippe 2018; Uchida et al., 2021; Kowarik et al., 2025) and remains controversial. Particularly, analogous to agroecosystems, urban ecosystems can undergo land use intensification via increasing urban densification: a process through which per capita land use, and sometimes but not always urban population, increases while the existing urban area is maintained, often involving an expansion of built-up space horizontally and vertically (Chen et al., 2020), which leads to denser and more compact cities (Soga et al., 2014; Geschke et al., 2018; Bibri et al., 2020). While few densification scenarios exist, often they involve loss and reduction of urban greenspaces and vegetation, resulting in the remaining urban greenspaces to be surrounded by a denser and compact matrix (Erlwein & Pauleit, 2021; Brynildsrud et al., 2025). Consequently, urban densification often has major negative effects on biodiversity (Olivier et al., 2020). Densification has shaped and will be affecting European cities (Cortinovis et al., 2022; Kauer et al., 2025). Under these circumstances, one might ask whether actions of local stakeholders can compensate for landscape-scale urban land-use intensification.

The intermediate landscape-complexity hypothesis (Tschardt et al., 2012) predicts that targeted patch-level management and design to favor biodiversity and ecosystem functioning can, at least partly, compensate the negative effects of intensive land use in the surrounding of a patch, particularly in simplified and intensified landscapes with intermediate proportions of (semi-)natural habitat. In urban ecosystems, this may occur by enhancing local urban greenspace features, such as those that satisfy the niche demands of targeted species or communities that increase overall diversity by increasing niche availability and partitioning (McIntyre 2006; Ong et al., 2022). For example, local plant diversity has been found to boost pollinators (Casanelles-Abella et al., 2023), herbivores (Helden & Leather 2004), and decomposers (Tresch et al., 2019a). Moreover, differences in plant communities and habitat structure can also enhance community differentiation (i.e. β -diversity) in cavity-nesting wasps (Martínez-Núñez et al., 2024). Overall, this suggests that urban green spaces can mitigate to a certain degree the landscape-scale impact of urban densification. Thus, enhancing biodiversity in patches of urban green space could serve as an offset in cities. For example, and depending on the type of urban green space, through targeted restoration, rehabilitation, and design (Klaus 2013; Fabián et al., 2021; Klaus & Kiehl 2021; Kowarik et al., 2025), targeting plant communities, habitat and management regimes.

However, it remains unclear whether the local compensatory effect of certain urban areas would affect different diversity dimensions that are relevant for conservation (Pollock et al., 2020). Particularly, different biodiversity dimensions might be impacted differently by urban landscape and local scale drivers. At the landscape scale, if urban density remains similarly large, urban animal communities are expected to become similar and homogeneous, likely with an overall impoverishment of functional and

taxonomic diversity (Luck & Smallbone, 2010). Strong differences in urban density between sites increases nestedness between animal communities, and thus, also contributes to homogenisation. On the one hand, regarding local management, when similar, more intensive management regimes are applied uniformly across multiple sites, they can reduce β -diversity by homogenizing species composition and functional traits (reference). On the other hand, a larger diversity of management styles and types, specially when less intensive, is expected to increase habitat heterogeneity and boost overall gamma diversity (Fournier et al., 2020). However, concerning biodiversity facets, Fournier et al., (2020) found that bee and carabid beetle α and β taxonomic diversity was high and maintained due to differences between and among urban green spaces (e.g., because of specific management practices and design), but functional diversity remained more homogeneous, stressing the need for stronger management efforts to boost functional diversity and contribute to conservation. The discrepancies in biodiversity patterns among metrics and scales in relation to urban drivers, and their different contributions to conservation (e.g., overall species, uniqueness, functionality, Pollock et al., 2020) still remains unclear. Consequently, the extent of the operational space within which urban ecosystems can densify while maintaining their biodiversity (Haaland & van den Bosch 2015; Amaya-Espinel et al., 2019) remains to be assessed.

Urban gardens serve as an excellent model system for examining existing trade-offs in current and future urban densification and biodiversity conservation. Urban gardens (sometimes referred to as urban agriculture (Jha et al., 2023)) encompass both public (e.g., allotments) and domestic (e.g., domestic) (Ong et al., 2022) gardens and can make up a large extent of existing greenspace (e.g., Switzerland: 25% (Young et al., 2020), Europe: 20% (Goddard et al., 2010)). Urban gardens have been found to support diverse communities of certain taxa, particularly pollinators (Baldock et al., 2019; but see Theodorou et al., 2020). For example, urban gardens can host species of high conservation priority, emerging as significant opportunities for biodiversity conservation (Smith et al., 2006a; Goddard et al., 2010; Egerer et al., 2024). As products of gardener preferences and consequently, local management choices, urban gardens can exhibit substantially different local features, such as plant and habitat diversity (Kendal et al., 2012a, 2012b; Seitz et al., 2022). Urban densification might affect urban gardens more than other urban greenspace types; they may have a significantly higher risk of being lost because they are less economically profitable compared to other land uses (Tappert et al., 2018). Hence, urban densification threatens major loss in urban biodiversity, nature contributions to people and ecosystem functioning that is maintained and harboured in urban gardens, making impact assessments critically needed (Tappert et al., 2018).

Several local features influence how urban gardens can support biodiversity. Such local features are proxies of habitat amount, heterogeneity, disturbance and resource availability. For example, urban gardens are generally regarded as heterogeneous green spaces with high plant diversity (Loram et al., 2008; Frey & Moretti 2019; Sexton et al., 2025; Seitz et al., 2022), although considerable variation exist (e.g. Young et al., 2020). Consequently, they have the potential to fulfil the niche requirements of several taxa (Majewska & Altizer 2020). Nonetheless, while previous studies have investigated the responses of several invertebrate guilds in localised context (Owen, 2010; Smith et al., 2006b) there are still remaining

gaps, particularly in understanding their responses across broader spatial scales, different environmental gradients, and under varying management regimes. Particularly, gardeners directly influence biodiversity through their management practices by cultivating, facilitating or excluding species or functional groups (e.g. pollinators, pest species) shaping community assembly (Aronson et al., 2016; Avolio et al., 2021; Swan et al., 2021). Although the role of management in shaping biodiversity is widely recognised, its assessment remains challenging due to the complexity of quantifying and summarising diverse practices. Nevertheless, management intensity has been shown to explain patterns in species diversity (Tresch et al., 2019a; Casanelles-Abella et al., 2023), ecosystem functions (Tresch et al., 2019a, b), and biotic interactions (Martínez-Núñez et al., 2024).

Here, we investigate the social-ecological drivers of urban biodiversity in urban gardens. We achieve this by conducting a large, multi-taxa study that includes 264,972 individuals belonging to 756 species from eight taxonomic groups, including pollinators, herbivores, predators, and decomposers, sampled in 85 urban gardens in the city of Zurich, Switzerland. By integrating different invertebrate groups, multifaceted diversity metrics, detailed social-ecological predictors, temporal estimates of past urban densification, and random forests, our study provides a comprehensive assessment of the drivers of urban biodiversity in urban gardens under current conditions, as well as considering future urban densification based. Specifically, we ask: (1) How do urban gardens support α and β taxonomic and functional diversity across invertebrate groups? (2) What is the contribution of selected landscape and local social-ecological predictors, that is, urban density, garden management intensity, habitat diversity, and plant diversity, in shaping biodiversity responses in urban gardens? (3) Do invertebrate guilds (eight main groups representing soil, ground, and flying invertebrates) exhibit distinct responses to urban social-ecological predictors? (4) To what extent do local features compensate for landscape urban density in maintaining urban garden diversity? (5) What consequences will future densification have on urban garden diversity?

METHODS

Study area and design

The study area and sampling design uses the data from the BetterGardens project, explained in Frey & Moretti (2019), Tresch et al., (2019a), and Martínez-Núñez et al., (2024). Specifically, the study was carried out in the city of Zurich, Switzerland (Fig. 1). We selected 85 urban gardens (43 allotment gardens, public land rented or used usually for food production and leisure; 42 domestic gardens, private land attached to a house, used mostly for recreation). Gardens were selected based on a double, quasi-orthogonal gradient of urban density at the landscape scale and local structural vegetation complexity. To maximise independence, gardens were distributed widely across the city, ensuring representation of all urban districts. Additional details can be found in Frey & Moretti (2019), Tresch et al., (2019a), and Text S1.

Invertebrate sampling

We sampled surface-dwelling invertebrates and flying insects in all gardens (following Casanelles-Abella et al., 2021; Tresch et al., 2019).

Surface-dwelling arthropods. Within each garden, surface-dwelling arthropods (e.g., ground beetles, spiders) and terrestrial gastropods were caught using six 72-mm diameter pitfall traps level with the ground and covered with transparent plastic roofs as rain protection at 10 cm. Pitfall traps were placed in two garden habitat types: an uncultivated habitat (such as a lawn or meadow) and a cultivated habitat (e.g., flowerbeds, vegetable beds, or berry cultivations). We selected the most extensive habitats when multiple options were available. Within each garden habitat, pitfall traps were arranged in two equilateral triangles with a side length of 1 m. In cases in which the arrangement in triangles was not possible, the pitfall traps were arranged in rows of 1 m length. Pitfall traps were emptied weekly between May 18th and August 19th 2015, for 13 consecutive weeks.

Flying insects. Flying insects were sampled with 3-colour sets of pan traps fixed on a 1.5-m tall triangular wooden pole (Buri et al., 2014). One pan trap set was placed in a central and unshaded position in each garden, i.e., the lawn or meadow. Each 1-litre pan trap was sprayed with either UV-bright blue, white, or yellow paint (Sparvar Leuchtfarbe, Spray-Color GmbH, Merzenich, Germany (Westphal et al., 2008)). Both pitfall and pan traps were filled to three-quarters with 0.2% Rocima solution (bactericide and fungicide from Acima, Buchs, Switzerland). All traps were continuously open from May to August 2015 and emptied weekly.

Trapped invertebrates were stored in 70% alcohol, sorted in the laboratory, and sent to specialists for species identification (see Acknowledgements). Individuals were identified to the lowest taxonomic level possible, in the vast majority of cases to species level, and when not possible, to genus level. We selected eight invertebrate groups to encompass a broad spectrum of invertebrates reflecting different ecological functions: hoverflies and bees as pollinators, leafhoppers and true bugs as herbivores, spiders and carabid beetles as predators, and snails as decomposers. Finally, due to their low number of species, for modelling we combined the taxa from the subphyla Myriapoda and Crustacea (i.e., isopods, diplopods, and chilopods) into a single group named other soil fauna (hereinafter soil fauna), as it includes soil-dwelling species.

Functional traits

For each invertebrate group, we collected taxon-specific functional traits (sensu Violle et al., 2007), which are considered key for growth, reproduction, and survival of individuals. In particular, we selected abiotic tolerances, feeding preference, life history, mobility, reproduction strategy, and phenology (Text S2) following Hahs et al., (2023) and Moretti et al., (2017). Traits were quantitative (numerical), semi-quantitative (ordered categories) and qualitative (categories), depending on the information available (Text S2).

Biodiversity metrics

To assess multifaceted biodiversity, we computed the α and β taxonomic and functional diversity components for each taxonomic group. For α diversity, we computed species richness for the taxonomic dimension and functional richness (Ricotta et al., 2014) for the functional one.

Regarding taxonomic and functional β -diversity, we computed the local community contribution to taxonomic and functional β -diversity (hereinafter, LCBD), with Legendre & De Cáceres approach (2013). Briefly, this approach provides a measure of the uniqueness of each urban garden (site) in terms of community composition and has been applied to understand the effects of ecological gradients on diversity (e.g., Casanelles-Abella et al., 2023b). High LCBD values indicate sites with distinctive species assemblages, meaning their species composition is markedly different from that of sites with lower LCBD values, either through unusual species combinations, strong differentiation, or both (Legendre, 2014). Taxonomic β -diversity (taxonomic LCBD) was calculated from the species abundance matrix using the Bray–Curtis dissimilarity and partitioned into turnover and nestedness components using the function `beta.pair.abund` in the `betapart` package (Baselga et al., 2012). Functional β -diversity (functional LCBD) was computed using species trait data and presence–absence community matrices using Sorensen index.

Finally, we also assessed the contributions of the α and β -diversity components to gamma biodiversity for each taxonomic group, for taxonomic and functional diversity. Furthermore, for taxonomic diversity, we partitioned β -diversity into its nestedness and turnover components, using species abundances and the Sorensen distance, and following Baselga et al., (2010). Concerning functional diversity, we did not further decompose β -diversity as many gardens contained too few species in several taxonomic groups (e.g., ground beetles, hoverflies, snails), making the decomposition not feasible for a large proportion of sites.

Predictors

For each garden, we quantified several variables at the local (i.e., garden) scale and at the landscape scale surrounding the gardens. Specifically, the different variables were related to four main categories: garden properties, plant diversity, management intensity, urban density, and urban densification.

Garden properties. Using publicly available aerial photographs as templates, we manually mapped garden features, land-use types, and the boundaries of each garden, excluding the buildings in domestic gardens. These features were then digitalized using ArcMap software (v. 10.3; ESRI, Redlands, CA, USA) to calculate the garden area. Moreover, we assessed garden structure by estimating the relative cover of 7 main habitat types: open ground, herb layer, shrub layer, tree layer, highly managed areas (e.g., lawn), paved areas (e.g. parking place, gravel path), detritus (e.g. dead wood), and water (e.g. pond). The habitat diversity was calculated using the Shannon diversity index of the number of habitat types found

in a garden and their respective area. Finally, we used the garden type identity, that is, whether a garden was an allotment or a domestic garden.

Plant diversity. A comprehensive inventory of all vascular plants, both spontaneous and cultivated, was carried out in each garden through repeated visits over the entire growing season in 2015 as occurrence (presence/absence). On average, 268 plant species were recorded per garden, with a range of 151 to 402 species. Further methodological details are explained in Frey & Moretti (2019). Specifically, we calculated the Shannon diversity of the plant community per garden.

Management intensity. As gardens are actively managed urban green spaces, we calculated a composite index variable based on 29 Likert-style questionnaire items based on the approach by Smith et al., (2006b). These items measured the frequency of traditional gardening and horticultural practices on five-point scales (Tresch et al., 2019a). To account for the varying number of garden features and questionnaire items across sites, we calculated a composite management index using a nested normalization approach (Eq. 1). First, we calculated a relative intensity score for each garden feature by dividing the sum of its items by the maximum achievable score for that specific feature. We then averaged these scores across all features present within the garden. This procedure ensures that the final index, bounded between 0 and 1, represents the mean intensity of practice rather than a cumulative total influenced by garden complexity:

$$MI = \frac{1}{n} \sum_{i=1}^n \left(\frac{\sum_{j=1}^{k_i} s_{ij}}{5k_i} \right)$$

Where:

n is the total number of garden features present in the garden.

k_i is the number of questionnaire items associated with land-use type i .

s_{ij} is the score (1–5) for the j -th item within garden feature i .

$5k_i$ represents the maximum possible score for garden feature i (based on the 5-point Likert scale)

Urban density. We define urban density as a measure of the proportion of built-up structures within a given area. To assess it, we employed a multiscale analysis of the landscape surrounding each garden to investigate the impact of urban intensity on invertebrate communities in urban gardens. We used the ‘High Resolution Layer Imperviousness’ from the Copernicus monitoring program for the year 2015 (Imperviousness Density 2015). The raster is set at 10 m resolution. We calculated the degree of imperviousness at four spatial scales: 50, 100, 250, and 500 m radii centered on the garden centroid, an

established and validated approach in the same sites (e.g. Frey et al 2018). The use of multiple spatial scales accounted for differences in how organisms perceive and interact with landscape features, depending on their activity ranges, including several small (i.e. 50–250 m) and one large (i.e. 500 m) spatial scales and was based on a large body of work in both Zurich and cities of similar size (e.g. Braaker et al., 2014; Winfree et al., 2014; Litteral & Shochat, 2017; Turrini & Knop, 2015, Casanelles-Abella et al., 2023a, Perrelet et al., 2025). As adjacent buffers were highly correlated, we focused on the 500 m scale as it encompasses the surrounding landscape and for comparability as it is a common buffer used in urban biodiversity studies with invertebrates (e.g., Casanelles-Abella et al., 2023a, 2024; Martínez-Núñez et al., 2024).

Past and future urban densification. We define urban densification as the process aimed at increasing urban densities by overlapping uses, often leading to an expansion of built infrastructure (Tappert et al., 2018b) and resulting in compact cities (Wolff et al., 2018; Bibri et al., 2020). We considered the temporal change in urban density in the past (i.e., densification) as a potential driver of our animal communities. To assess densification, we followed the approach of the ‘High Resolution Layer Imperviousness’ from the Copernicus monitoring program. Specifically, we calculated the % of change between 2006 and 2015 using as input raster the respective Imperviousness Density layer for 2006 and 2015. Similar to the urban density measure, we calculated the change in a 500 m radius centered on the garden centroid. Furthermore, we also wanted to assess the effects of future densification. There are not available densification scenarios at a suitable resolution for our study city to inform us which areas of the city will densify and what urban green spaces will be loss. Consequently, we develop two approaches to assess, in a simplified way, the effects of future densification: (1) a space-for-time substitution to account for increasing urban density in the surrounding landscape based on the predictions of our models while assuming no garden loss, and (2) we simulated loss of gardens via modified SAC as species loss curves (see details in the following section ‘Statistical Analyses’).

Statistical analyses

All analyses were conducted in R 4.2.0 (R Core Team 2022).

Drivers of biodiversity metrics

Furthermore, we analysed the effect of urban density, garden properties, plant diversity, and management intensity on multi-taxa biodiversity, that is, on α and β taxonomic and functional diversity metrics. To do so, we used random forests because of their ability to handle complex, high-dimensional data, along with their interpretability through, e.g., feature importance. We modelled each response variable (species richness, functional richness, LCBF taxonomic, and LCBF functional). We used as predictors proxies of urban density (proportion of imperviousness within 500 m), garden habitat diversity, plant diversity management intensity index, and taxonomic group identity. By also including taxonomic group as a predictor, the model could learn both general biodiversity-environment relationships and taxon-specific responses (see below). This approach thus leverages information

across all taxa to identify shared biodiversity-environment relationships while explicitly accounting for taxonomic identity.

Random forests were trained on 75% of the data and evaluated on the remaining 25%. Model training and parameter tuning were done using 30-fold spatial cross-validation. Specifically, we created 30 spatial folds for cross-validation using the function “CreateSpacetimeFolds” from the package “CAST” (Meyer H et al., 2025) to maximise the spatial transferability of model results and avoid potential overfitting. Parameter tuning used 10 random values of the number of variables to be sampled at each split time. The best model was chosen based on Root Mean Square Error (RMSE), mean absolute error (MAE), and R^2 measured on the trained dataset. The performances of the selected model were further evaluated on the test dataset using the same metrics. Potential overfitting was double-checked by comparing the model evaluation metrics between the train and test sets.

To assess the importance of the drivers of changes in urban garden biodiversity (i.e., variable importance), we computed model prediction loss as the ratio between the MAE before and after shuffling each explanatory variable. This process was repeated 50 times, and average model prediction losses were computed to obtain more accurate and stable results. This analysis was done using the “FeatureImp” function of the package “iml” (Molnar et al., 2018) based on Fisher et al., (2018).

To assess the changes in biodiversity metrics induced by explanatory variables, we used partial dependence plots (using the package PDP, Greenwell 2017). PDPs help visualise the relationship between a subset of the features and the response while accounting for the average effect of the other predictors in the model (see Fig. 2). This analysis was done using the “FeatureEffects” function of the package “iml”.

Taxa-specific responses

To assess differences in the response to our predictors among the eight studied taxa groups (i.e., taxa-specific responses), we computed the interaction between the explanatory factor representing the 8 taxonomic groups and all other explanatory variables. A strong interaction indicates important differences in the effect of the target variables on individual taxonomic groups. The interaction is measured by Friedman's H-statistic (Friedman & Popescu 2008) and takes on values between 0 (no interaction) to 1 (100% of the standard deviation of $f(x)$ due to interaction). This analysis was done using the “Interaction” function of the package “iml” based on Friedman & Popescu (2008).

Landscape moderation by local features

We aimed at investigating which local features could compensate for landscape-scale urban density. We performed random forests using the total invertebrate richness per garden as the response variable, the landscape urban density within 500 m and one of the two following local garden variables: plant diversity and management intensity. Models were done separately for allotments and domestic gardens. To

assess the potential mitigation, we computed the Friedman's H interaction term between local plant diversity and landscape urban density within 500 m. Finally, we plotted the interaction surface between the landscape urban density and local garden features. Finally, we performed random forests for the responses species richness, functional richness, taxonomic LCBD and functional LCBD. Models were build separately for allotments and domestic gardens, including the taxonomic group, the landscape urban density within 500 m and one of the two following local garden variables: plant diversity and management intensity.. As in total invertebrate richness, we used the Friedman's H interaction. Finally, we tested for the association between plant diversity and management intensity in domestic gardens and allotments separately.

Future urban densification

Concerning the space-for-time substitution approach, we analyse the effect of increasingly dense landscapes surrounding our sites by using the predictions from our models based on the urban density within 500 m. To simulate the effect of losing gardens under increasing urban densification, we first generated species accumulation curves (SACs) separately for each of the eight invertebrate groups and for the combined community. For each group, we built a species-by-garden abundance matrix and computed sample-based accumulation curves using the *random* method implemented in the function "specaccum" from the package *vegan*, which repeatedly randomizes the order of sampled gardens to obtain mean richness and its variability across permutations. To characterize the shape of each accumulation pattern, we fitted a logistic growth model to the observed SAC using non-linear optimization. The model estimates three parameters: (i) S_{max} , the asymptotic species richness; (ii) k , the rate at which species accumulate; and (iii) x_0 , the inflection point where accumulation changes most rapidly. For each taxonomic group, we extracted the fitted parameters as well as the full set of permuted species-accumulation values, which were subsequently used to visualize uncertainty via boxplots and to compare accumulation behaviour across groups. SACs were then transformed to species loss curves by transforming the species richness to species loss and the number of retained gardens to garden loss (Ney-Nifle & Mangel, 2000; Triantis et al., 2010). While this approach has limitations (under or overestimating species loss, see Fattorini & Borges, 2012, He & Hubbell, 2011), it remains appropriate because our objective was not to make precise quantitative predictions or mechanistic forecasts of extinction, but to provide a comparative assessment of overall species-loss patterns and their variability among taxonomic groups.

RESULTS

Garden biodiversity overview

We sampled 264,972 individuals belonging to 714 species and 44 morphospecies (at the genus level) from eight groups across 85 urban gardens (Fig. 1). This included 112 bee species, 60 ground beetle species, 48 hoverfly species, 115 spider species, 44 snail species, 188 true bug species, 103 leafhopper species and 33 species from the other soil fauna (i.e., 15 isopods, 12 chilopods, 6 millipedes) (Fig. 1C,

Table S1). Rank abundance distributions revealed widespread, pronounced dominance patterns across taxonomic groups (Fig. 1B), with only 17 species accounting for more than 10% of the total number of individuals captured within their respective taxonomic groups. Private and allotment gardens had similar numbers of species (Figure S1), but domestic garden species richness decreased more pronouncedly along the urban densification gradient (Fig. 1D).

Partitioning the contributions of α and β -diversity to γ taxonomic diversity for each taxa revealed a major contribution of α -diversity (species richness) for all groups (Table S2). However, the contribution of α -diversity varied widely across groups (Figure S2). For bees and soil-dwelling fauna, α diversity contributed over 80%, whereas for snails and carabid beetles, the contribution was slightly above 50% (Figure S2). Furthermore, the contribution of β -diversity was mainly driven by the turnover component, with the nestedness component consistently having a minimal contribution (Figure S2).

Effects of urban drivers

Random forests revealed a major contribution of urban density in shaping α taxonomic and functional diversity responses (Fig. 3, Figure S3, Table S3). Urban density at 500 m, measured as the degree of imperviousness, had the highest variable importance for both α taxonomic and functional diversities (Fig. 3), as well as for functional LCBD (functional β -diversity). Particularly, urban density decreased both species richness and functional richness. Conversely, urban densification increased taxonomic and functional LCBD (Fig. 3). Plant diversity and management intensity metrics influenced α species richness mostly and played a minor role in the remaining responses, with varying directions. First, plant diversity positively affected both species richness and functional richness (Fig. 3). Second, management intensity had a moderately negative effect on species richness and a more neutral effect on the other response metrics. Finally, habitat diversity was the most important predictor for taxonomic LCBD (taxonomic β -diversity), with a moderately negative effect (Fig. 3). Other habitat and garden features had a generally low importance for all responses.

Taxa-specific responses

For α taxonomic diversity, all taxonomic groups except snails responded to the studied predictors in a similar way (Fig. 4, Figure S4-S8). Concerning α functional diversity, taxon-specific responses were evident for urban density (Fig. 4) and were mostly driven by carabid beetles, which exhibited strong declines with increasing density (Figure S4). We also detected some taxa-specific responses for both taxonomic and functional β -diversity (Fig. 4), which were mostly driven by snails (Figure S4-S8). Concerning taxonomic β -diversity, we found main taxa-specific responses for urban density within 500 m, and for functional β -diversity, we found taxa-specific responses particularly prominent for plant diversity (Fig. 4, Figure S5).

Moderation of the effect of landscape urban density by local garden conditions

Friedman's interaction H between landscape urban density and local plant richness was 0.215 for domestic gardens and 0.339 for allotments. Friedman's interaction H between landscape urban density and local management intensity was 0.163 for domestic gardens and 0.357 for allotments. Predicted total animal species richness peaked for high levels of plant diversity (Fig. 5A) and lower management intensity (Fig. 5B) independently of the urban density at the landscape context for both allotment and domestic gardens (Fig. 5A-B). Moreover, our random forests per taxonomic group revealed higher Friedman's interaction H between landscape urban density and local garden conditions on allotments than in domestic gardens for α taxonomic, α functional, and β functional diversities, ranging between 0.377 and 0.499 in allotments and 0.241 and 0.381 in domestic gardens (Table S3). Conversely, Friedman's interaction H was larger in domestic gardens than allotments for taxonomic β -diversity (Table S4). Finally, plant diversity was larger in allotments than in domestic gardens (allotments, mean $\pm$ SD, min-max: 3.83 ± 0.20 , 3.40–4.36; domestic gardens, mean $\pm$ SD, min-max: 3.74 ± 0.28 , 3.15–4.22; Fig. 5C). In addition, management intensity lower in allotments than in domestic gardens (allotments, mean $\pm$ SD, min-max: 0.51 ± 0.09 , 0.35–0.72; domestic gardens, mean $\pm$ SD, min-max: 0.52 ± 0.10 , 0.27–0.75; Fig. 5C). Within garden group variability was also lower in allotments than in domestic gardens (Fig. 5C).

Future urban densification

We assessed the effects of future densification using a space-for-time substitution to account for increasing densification in the surrounding landscape, and simulated garden loss via modified SAC as species-loss curves. Regarding the simulated loss of gardens, the species loss curves exhibited an inflexion point around 92% garden loss after which the rate of species loss increased exponentially (Fig. 6), corresponding to the rapid saturation of species richness observed in the SACs for all animal taxa (Figure S9). Furthermore, the degree of biodiversity decline resulting from the loss of urban gardens was highly variable across taxa. Specifically, the largest species losses were observed for herbivores (Fig. 6), that is, true bugs and leaf hoppers whereas bees and carabids showed the lowest losses (Fig. 6, Table S5). For example, assuming a loss of 50% of the gardens, true bugs lost a median value of $21.1 \pm 2.92\%$ of the species and leafhoppers lost a median value of $21.81 \pm 3.31\%$ of species, whereas bees lost a median value of $12.5 \pm 2.62\%$ of the species and carabid beetles lost a median value of $16.4 \pm 5.57\%$ of species (Fig. 6, Table S5).

DISCUSSION

Our results support the view that gardens underpin urban biodiversity across diverse taxonomic groups and animal guilds, including pollinators, herbivores, decomposers, and predators. There is compelling evidence on the role of gardens in supporting biodiversity for specific taxa, such as bees and wasps (Smith et al., 2006b; Philpott & Bichier, 2017; Neumann et al., 2024). Here, we demonstrate that the biodiversity role of urban gardens is transferable across multiple invertebrate faunal groups, making urban gardens critical for preserving and promoting urban biodiversity and fulfilling the conservation role that cities are increasingly committing to (Shaffer 2018; Oke et al., 2021; Kowarik et al., 2025). Thus,

even though urban ecosystems do filter taxa and specifically traits (Fournier et al., 2020), within a city urban gardens can still support taxa across multiple trophic levels, mobility types, and feeding behaviours, such as central-place foragers, mobile generalists and mobile specialists (*sensu* Hahs et al., 2023).

Our study supports the view that biodiversity can be harboured in many small habitat patches, as increasingly observed in other non-urban ecosystems, due to heterogeneity between patches (Szangolies et al., 2022). This heterogeneity can be expected to be particularly large in green spaces created and maintained by humans, such as gardens, which are prone to being subjected to specific behaviours and preferences, resulting in plant communities that can be highly diverse (Frey & Moretti 2019; Seitz et al., 2022; Sexton et al., 2025). Ultimately, these effects also translate to fauna, enhancing their diversity (Tasker et al., 2020; Mata et al., 2021). Finally, given the significant contribution of species richness to total diversity, our results suggest a degree of redundancy in the composition of faunal assemblages, which might contribute to the resilience and stability of the overall garden network, as observed in other systems (Walker 1992; Naeem 1998). Naturally, this is also influenced by habitat abundance, heterogeneity, and resource availability at relevant spatial scales, all of which are main determinants of biodiversity (Fahrig 2001, 2013).

We found that urban density around the gardens had a profound negative effect on overall diversity metrics for almost all taxa studied. The degree of urban density, which we inferred horizontally as the amount of impervious surfaces within a given area, is negatively associated with habitat, heterogeneity, and resource availability (Theodorou 2022; Casanelles-Abella et al., 2024). Higher urban density is expected to reduce the size and number of available habitat patches, and while the remaining patches may still exhibit some heterogeneity, the overall habitat area is reduced (Soga et al., 2014). This occurs due to the greater dominance of the built infrastructure, which includes buildings, roads, and other elements of the cityscape. Such a loss of habitat area can be expected to isolate gardens, thus reducing their potential to sustain viable populations due to limited individual dispersal and constrained foraging (Jha & Kremen 2013; Olivier et al., 2020), and to increased susceptibility to stochastic events (Sattler et al., 2010). Worldwide, habitat loss has been identified as a major driver of biodiversity decline (Melian & Bascompte 2002; McWilliams et al., 2019), with well-documented effects on invertebrates (Biesmeijer et al., 2006).

Interestingly, we found a U-shaped relationship between β -diversity and urban density. This indicates that, above a specific urban density threshold, gardens make a greater contribution to overall β -diversity, suggesting they become more unique. There is some evidence of such patterns for both plant (Avolio et al., 2020; Swan et al., 2021) and animal (Gordon & Kerr 2025) communities, indicating that α and β -diversity do not respond to urban drivers in the same way. A main reason for this pattern could be that gardens in high-density areas tend to contain a subset of species (i.e., high nestedness), with a greater presence of synanthropic species at the expense of species more vulnerable to urban drivers (Martin & Bonier 2018; Collado et al., 2019). However, our results showed that β -diversity was driven by turnover rather than nestedness. In that regard, our study aligns with an increasingly large body of published

literature showing that, when investigating community assembly within cities, often there is a major replacement of taxa among local communities (Fournier et al., 2020), as it happens in other ecosystems characterised by strong ecological gradients (Casanelles-Abella et al., 2021; O'Sullivan et al., 2021). Furthermore, in highly dense parts of the city, urban gardens might serve as refuges to maintain populations. This has been found to be the case for urban hymenopterans, which, as central place foragers, can maintain their diversity in dense urban areas if local resources within their nesting sites are sufficient (Egerer et al., 2024b; Berger et al., 2024; Ranalli et al., 2025). Whether this extends to our system and to different taxonomic groups and guilds requires population-level monitoring of urban species.

Other factors also contributed to the development of urban biodiversity in urban gardens. Garden type was a main factor, as allotment gardens had lower values of urban density and hosted more diverse communities. The reasons are likely linked to inherent differences between allotments and domestic gardens from a land-use and urban-planning perspective. Specifically, allotments are not normally found alone, but within large areas composed of several other allotments placed together contiguously, thus reducing the influence of landscape urban density. Furthermore, domestic gardens and allotments do not necessarily have the same purpose and can be managed and designed differently, thus influencing microhabitat and resource availability (Tresch et al., 2018, 2019a; Home et al., 2019). Plant diversity and management intensity also influenced animal diversity, as plants serve as the trophic baseline for animal taxa, whereas management intensity is negatively associated with plant diversity. Similar effects have been detected in soil diversity and functioning (Tresch et al., 2019), predation (Frey et al., 2018), pollination (Reji Chacko et al., 2025) and host-enemy interactions (Martínez-Núñez et al., 2024). Finally, past densification had a minor importance and often had a small positive effect. The reasons behind this are that past densification was generally low in the landscapes surrounding our gardens. Hence, it had not been a major factor in our study system for the considered period.

Our results on Friedman's interaction between landscape urban density and local garden conditions provide certain support for the intermediate landscape-complexity hypothesis (Tscharntke et al., 2012) in urban gardens. We found that local garden conditions, particularly those shaped by gardeners' decisions and actions (i.e. management intensity and plant diversity), play a role in determining the extent to which urban gardens can contribute to maintaining and enhancing urban invertebrate diversity under increasing urban density. Specifically, this can happen if urban gardens are managed to boost local habitat heterogeneity and plant diversity (as discussed in Fournier et al., 2020). Under such conditions, improving the local conditions of existing urban gardens could represent a partial compensatory action for ongoing densification, with actions that enhance local habitat as a potential biodiversity offset in urban ecosystems. In fact, while biodiversity offsets generate debate (Mancini et al., 2024), performing local compensation may still be preferable to taking no action (Riva et al., 2024). This might be particularly true in circumstances when drivers of change, such as urban densification, are expected to occur and cannot be feasibly prevented.

In urban gardens, which are urban green spaces heavily influenced by humans, actions could be aimed at adapting management and design efforts to boost habitat amount via increasing heterogeneity and plant diversity, as seen in other cases (Ulrich & Sargent 2025). Available approaches to achieve these goals vary according to the focus on restoring a certain degree of historical habitats (Hobbs et al., 2009), ranging from restoration and rehabilitation (Klaus & Kiehl 2021) to the general diversification of plant communities via a combination of native and non-native, as well as spontaneously occurring and cultivated plants (Niinemets & Peñuelas 2008; Segar et al., 2022). The preference for one approach or another is complex, and changing management and design requires outreach efforts and co-creation approaches to combine different types of expertise (Ostrom 1990, 2008; Karleowski et al., 2024). Not less important, urban gardens do not necessarily serve a primary ecological and biodiversity role, but rather a social one, with gardeners having different motivations, including production, psychological restoration, and leisure (Home et al., 2019; Di Fiore et al., 2021; Murtagh & Frost 2023; Karleowski et al., 2024). Finally, local features compensate only to a limited extent for surrounding urban density; gardens in more heterogeneous, less dense urban landscapes are expected to sustain higher levels of biodiversity (Hahs et al., 2023). Thus, from a broader perspective, urban biodiversity strategies in the face of densification should not limit themselves to maintaining and improving existing urban green spaces but also seek to increase the amount of habitat and landscape complexity (Soga et al., 2014; McDonald et al., 2023; Ranalli et al., 2025).

Our study shows that future densification—whether through increasing building density or the loss of garden spaces—is likely to negatively affect garden biodiversity. Regarding simulated loss of gardens, our results indicate general losses across taxa, with variation among taxonomic groups, likely linked to their distribution patterns (Casanelles-Abella et al., 2021) and their underlying trait syndromes (Hahs et al., 2023). A key limitation of our investigation is the absence of spatially explicit future densification scenarios, which are urgently needed to refine projections. Nonetheless, using a space-for-time substitution, the strong negative influence of current urban density on garden taxa suggests that gardens embedded within more densely urbanised landscapes are likely to experience further declines in biodiversity. While space-for-time substitutions should be interpreted with caution because they may oversimplify future outcomes, the well-documented negative effects of increasingly intensified urban landscapes on biodiversity (Concepción et al., 2015; Guenat et al., 2019; Hahs et al., 2023) indicate that future densification should be viewed with concern.

Simultaneously, the role of urban gardens in promoting biodiversity and benefiting people might be strengthened within densifying landscapes, serving as a green hub in increasingly urban areas. In such circumstances, urban gardens may be regarded as small yet powerful (Egerer et al., 2024a) green spaces that contribute to preserving biodiversity and functioning (Jha et al., 2023; Neumann et al., 2024), providing NCPs (Jha et al., 2023), and enabling human-nature interactions in cities (Čepić et al., 2024). However, continuous landscape densification surrounding the gardens, without further additions of habitat patches (e.g., MacDonald et al., 2023) and securing the connectivity of the remaining habitat patches (e.g., Küffer & Vega, 2022), may eventually lead to the gardens becoming too isolated to sustain viable populations. The consequences of this scenario are difficult to predict but may be more

dramatic than anticipated. First, the thresholds at which land-use changes, such as urban densification, trigger isolation-related negative effects on local populations are expected to be species-specific, making general cutoff thresholds unreliable and likely to underestimate the negative effects on species (Hartlieb et al., 2025; O'Brien et al., 2025). Second, the consequences of isolation on local populations and communities may exhibit lagged responses, resulting in extinction debts that remain undetected until population declines become severe (Kindsvater et al., 2018). Such dynamics can lead to local extinctions that persist unless counterbalanced by adequate immigration rates (MacArthur & Wilson 1967). As our study was temporally restricted to a single year, we were unable to capture these potential lagged responses. Long-term monitoring of urban gardens will therefore be essential for detecting trends in biodiversity, assessing the impacts of ongoing densification, and evaluating the effectiveness of mitigation measures.

CONCLUSION

Overall, urban gardens can help protect urban invertebrate biodiversity (Tresch et al., 2019; Eggerer et al., 2024). In our study, we found that urban density is a major negative force shaping urban biodiversity patterns. In this regard, local garden features related to habitat amount, resource availability, and management intensity can compensate for surrounding densification; it is not only landscape factors but also individual actions and decisions of gardeners (Fournier et al., 2020). A stronger focus on management approaches aimed at maximising overall biodiversity is thus critical to urban conservation (Fournier et al., 2020). However, the contribution of urban gardens has limits. Several decades of research in cities have revealed a common pattern: that in denser cityscapes with fewer habitats, urban biodiversity is reduced (Hahs et al., 2023; Kowarik et al., 2025), which aligns with well-documented knowledge on biodiversity-area relationships (Riva et al., 2024). Thus, the ongoing densification, already evident in several cities, including Zurich (Tappert et al., 2018b), makes it urgent to identify a safe operational space that meets both human and natural needs (Rockström et al., 2009). The solution to densifying cities is complex and not necessarily, nor purely, an ecological one, as it may involve revisiting current living standards and urban planning decisions, along with their associated economic, social, and political dimensions. Overall, reconciling the pressures of densification with the imperative of conserving urban biodiversity demands a coordinated effort that extends beyond ecology alone. Prioritising biodiversity-supportive design, informed governance, and socially acceptable urban futures will be essential to ensure that cities remain livable for both people and wildlife.

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Figures

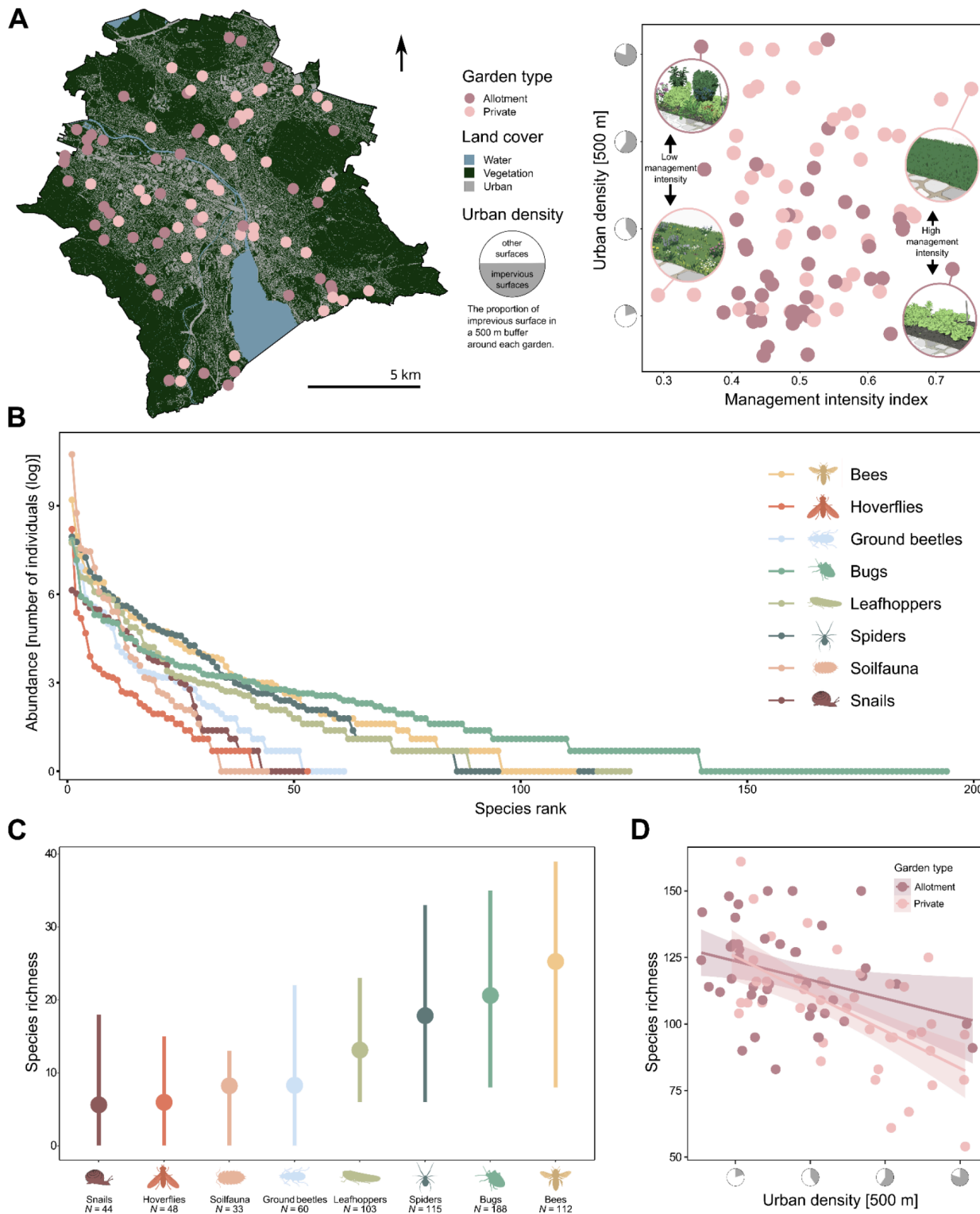


Figure 1

Overview of the study design and diversity patterns. (A) Distribution of the 85 urban gardens (i.e., allotments and domestic gardens) in the city of Zurich, Switzerland, within urban density and management intensity gradients (reference). (B) Rank-abundance distribution of the eight groups considered. (C) Mean species richness of the eight groups considered, with the whiskers representing the minimum and maximum across the gardens. Total species richness of each group (N) is listed under

the taxonomic name. (D) Relationship between overall species richness and urban density gradients in the two types of urban gardens considered.

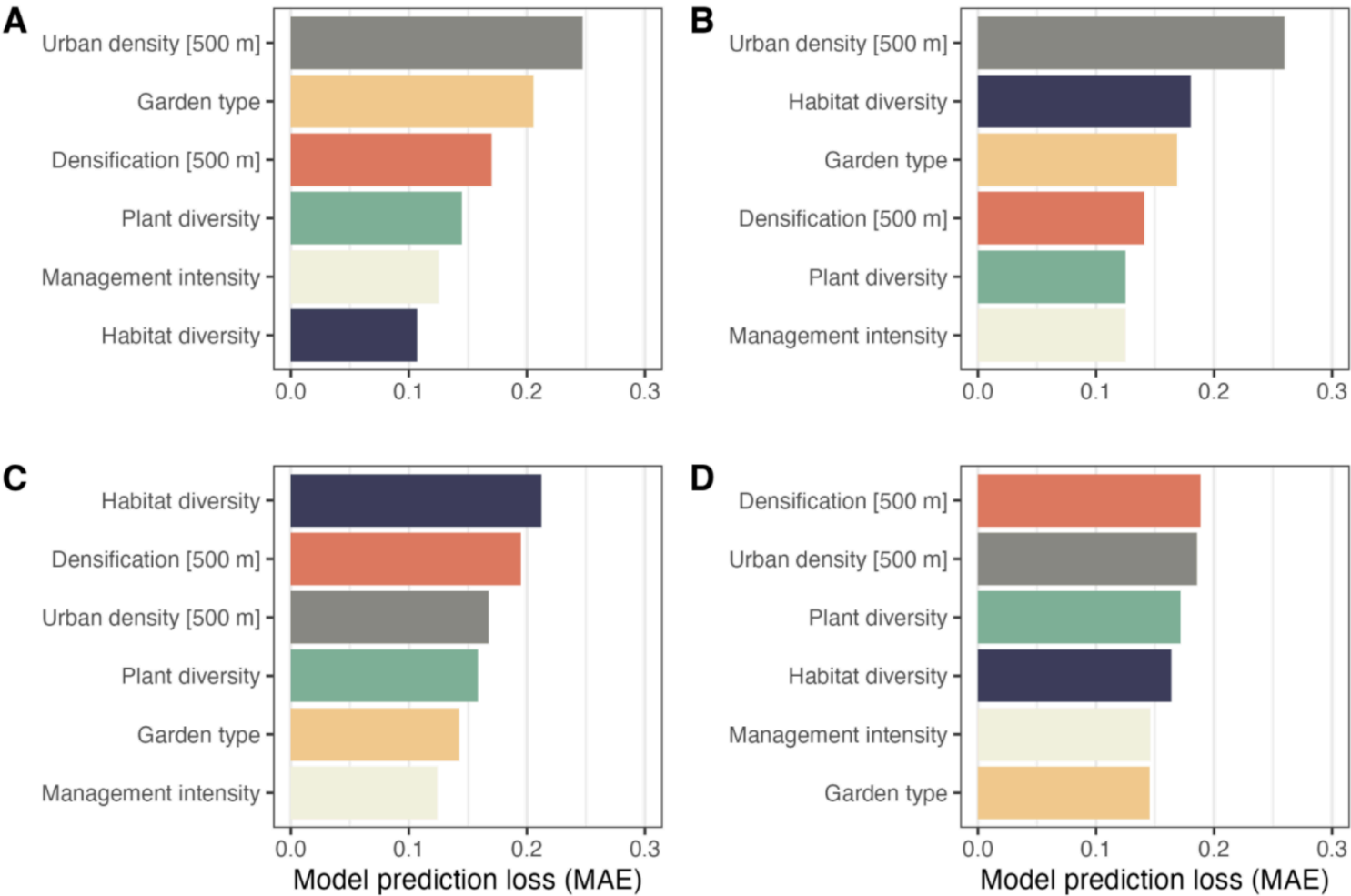


Figure 2

Variable importance of the included predictors depicting current urban density within 500 m, plant Shannon diversity, management intensity, urban densification between 2006-2015 (change in impervious surface) within 500 m and garden type (i.e., allotment or domestic garden) on (A) α species richness, (B) α functional richness, (C) local contributions to taxonomic β -diversity, and (D) local contribution to functional β -diversity. Variable importance was estimated using the residual sum of squares from random forest models. Longer bars indicate more important predictors for model predictions.

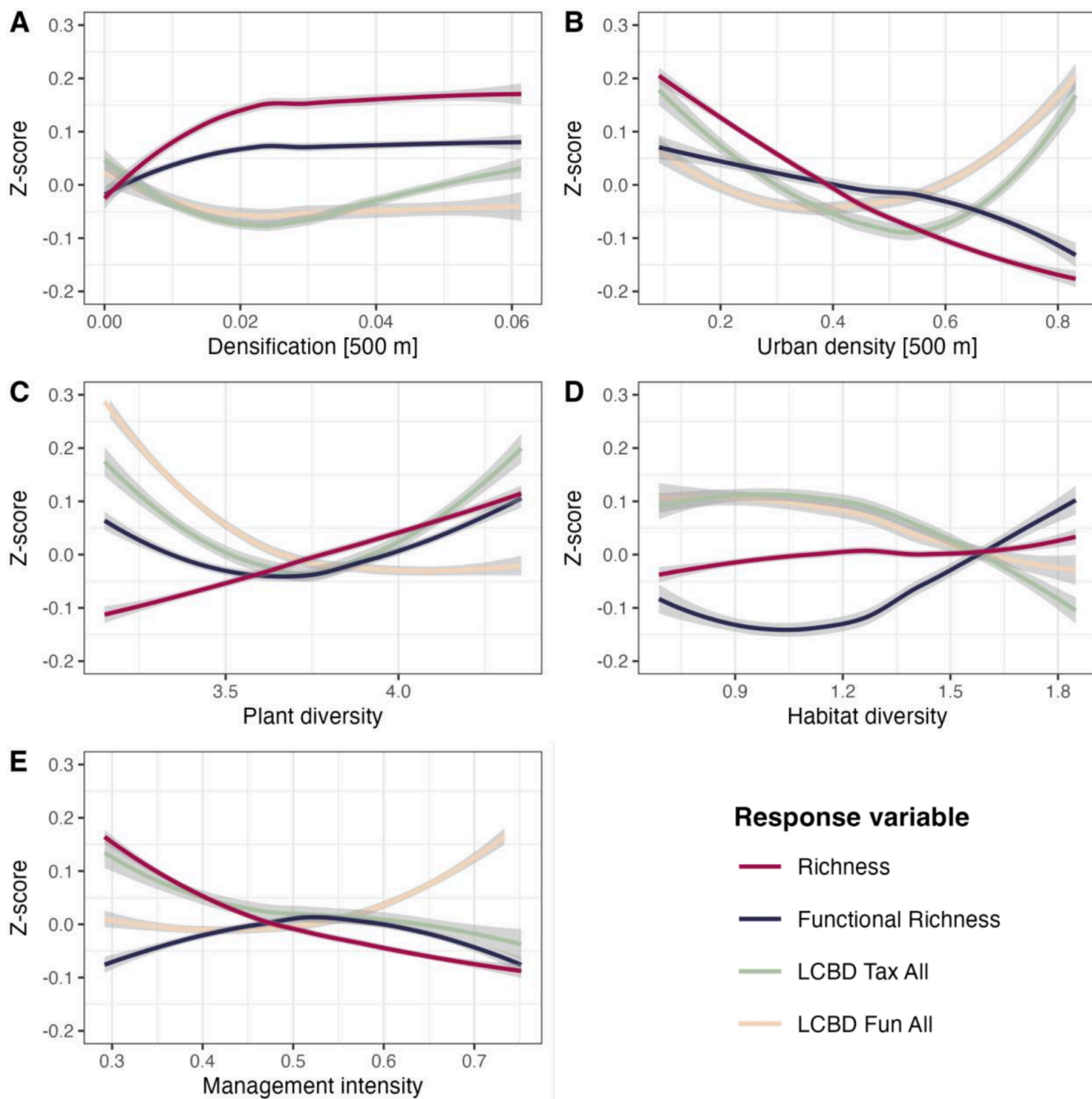


Figure 3

Partial dependence plots depicting the relationships between the four responses depicting selected α and β taxonomic and functional dimensions, and (A) urban densification (% change in impervious surfaces 2006-2015) within 500 m, (B) urban density (% impervious surfaces) within 500 m, (C) plant Shannon diversity, (D) habitat diversity and (E) management intensity. Response variables are standardized using the Z-score transformation for comparability. Shaded bands indicate the 95% confidence interval. Range of values (mean $\pm$ SD; minimum-maximum): species richness (14 $\pm$ 8; 1-39);

functional richness (0.39 ± 0.17 ; 0.00-0.83), taxonomic LCBD (0.01 ± 0.004 ; 0.005-0.034), and functional LCBD (0.01 ± 0.006 ; 0.004-0.06).

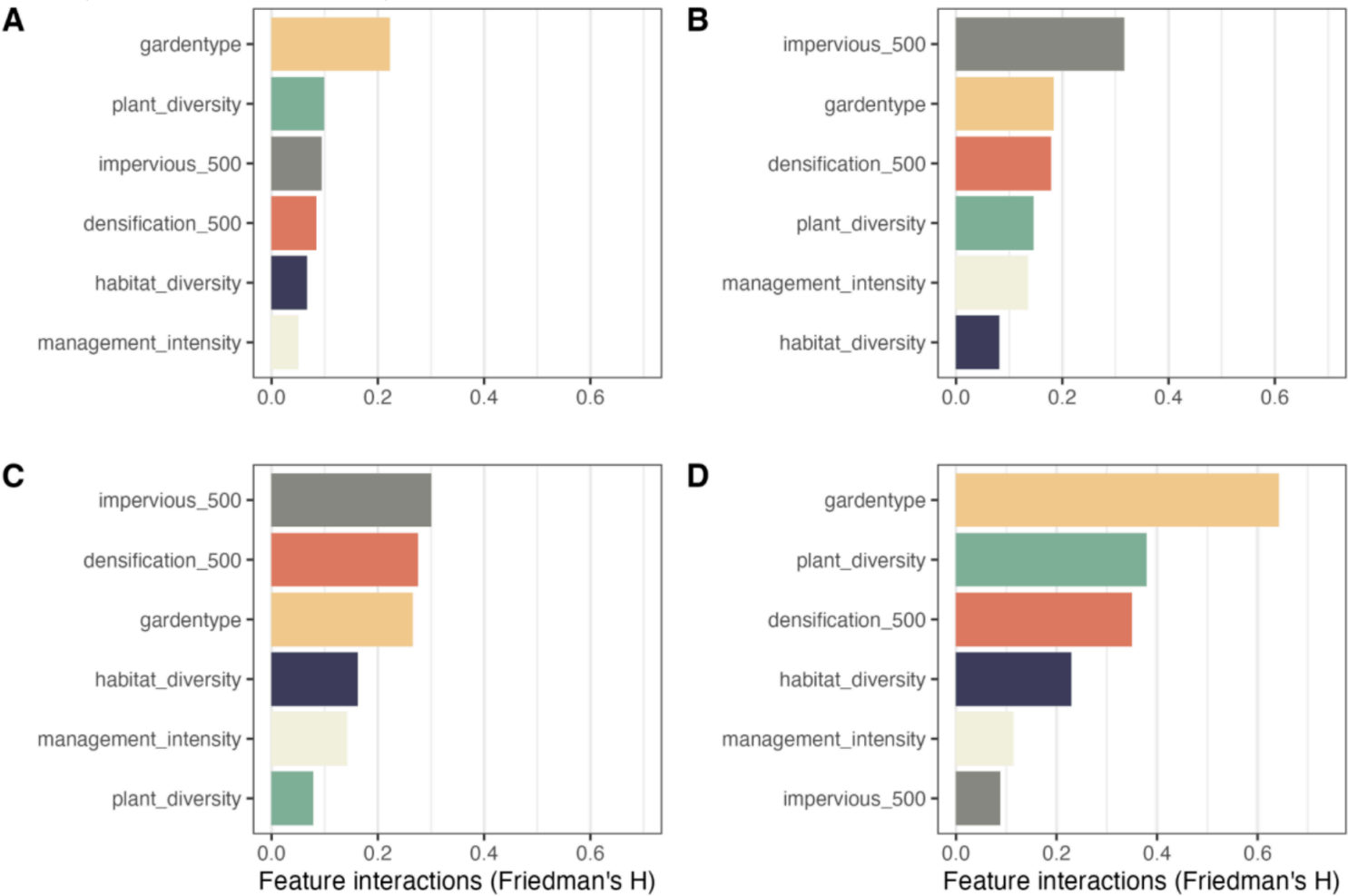


Figure 4

Taxon-specificity of predictor effects based on Friedman’s H statistic. Barplot of Friedman’s H statistics calculated using taxonomic group as the grouping variable for (A) α species richness, (B) α functional richness, (C) local contributions to taxonomic β -diversity, and (D) local contributions to functional β -diversity. Higher H values indicate predictors whose effects on invertebrate diversity differ more strongly among taxa, while lower values indicate similar responses across taxa.

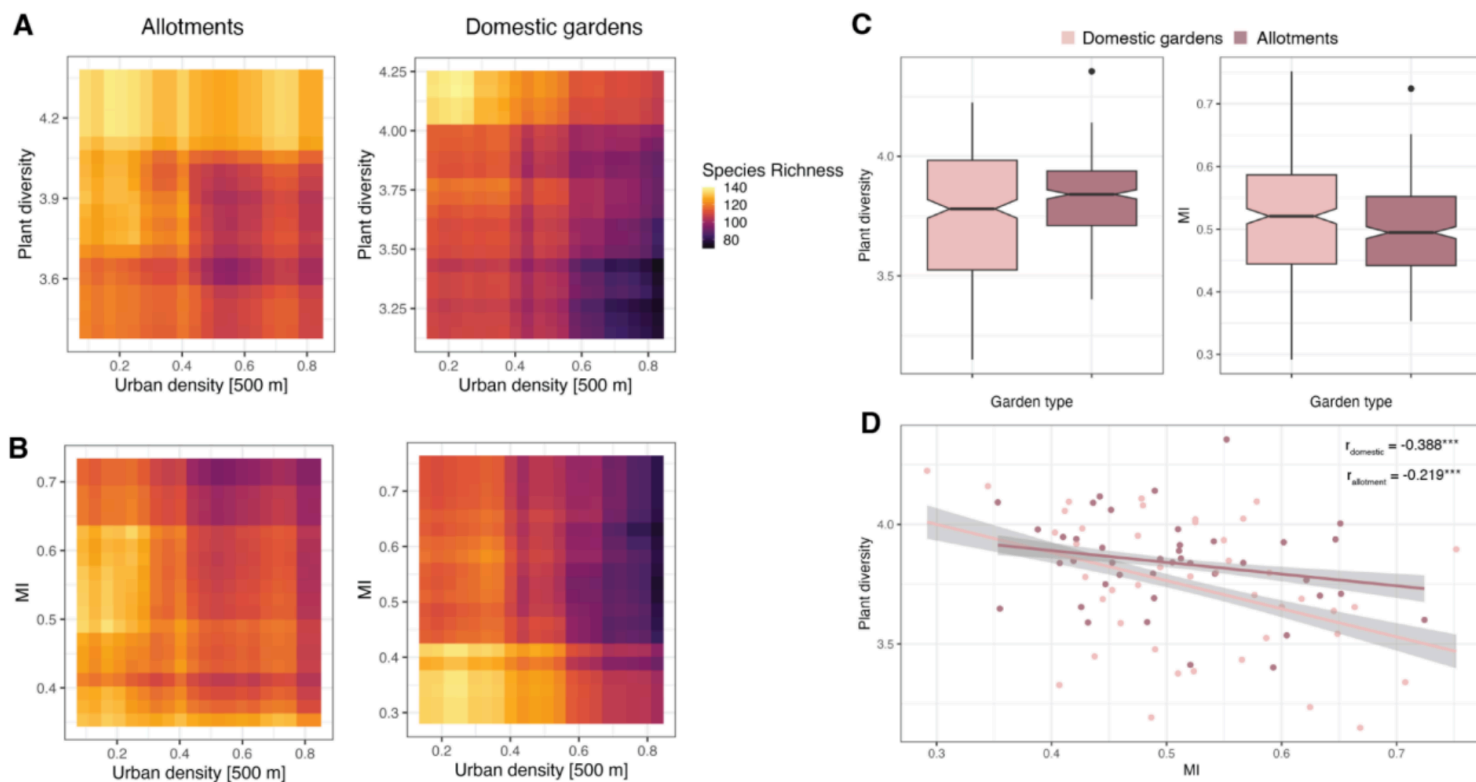


Figure 5

Landscape moderation by local site features (based on the intermediate landscape complexity hypothesis, Tscharrntke et al., 2012). A-B. Heatmaps of the predicted total animal α species richness (including all taxonomic groups sampled together) in relation to the landscape urban density measured within 500 m and two local garden features, the plant diversity (B) and the management intensity (MI) (B), separately for allotments and domestic gardens. C. Boxplots depicting differences in plant diversity and management intensity between domestic gardens and allotments. D. Relationship between plant diversity and MI in domestic gardens and allotments. Shaded bands indicate the 95% confidence interval. The correlation and association tests are provided. ***: $p < 0.001$

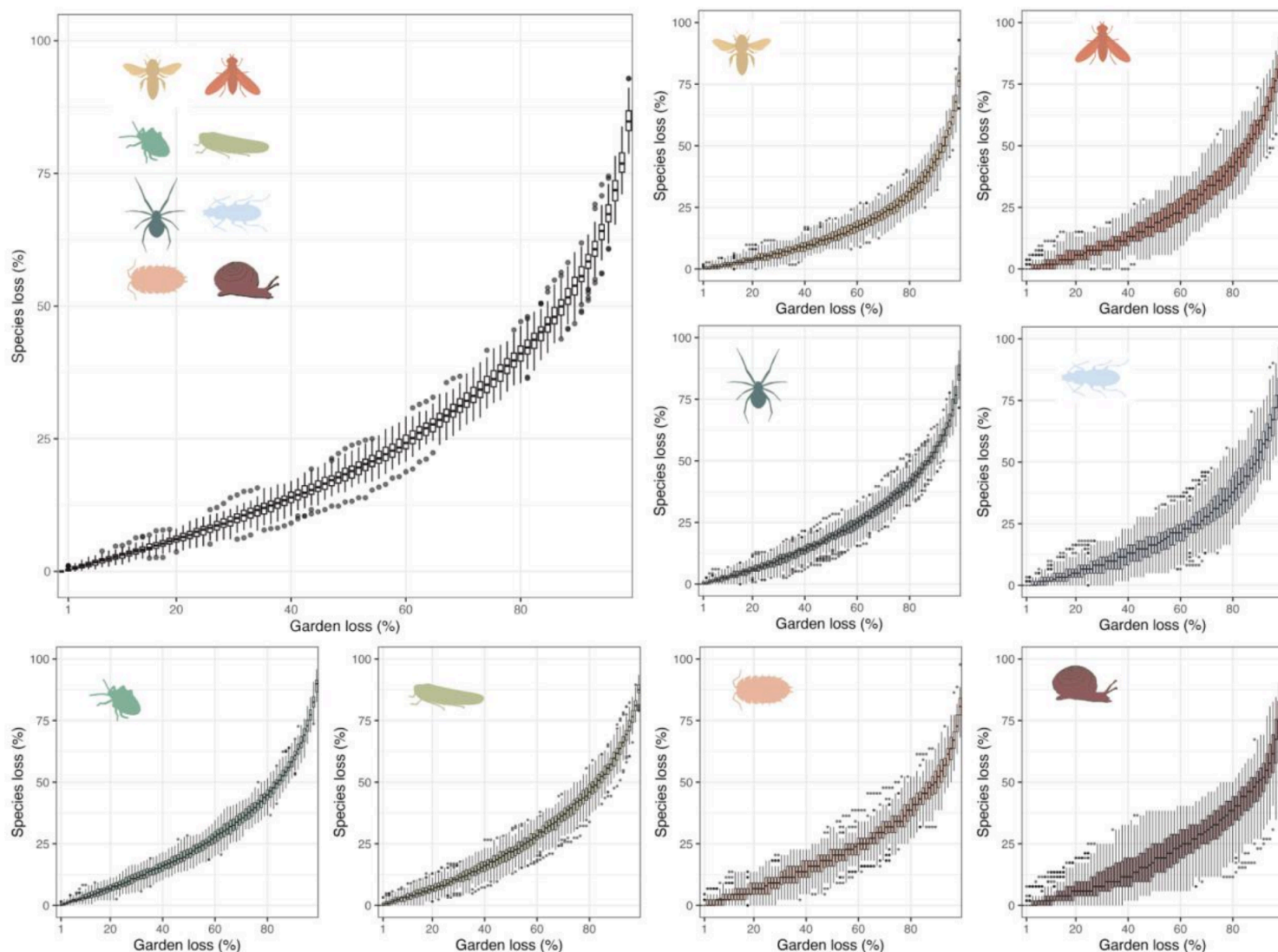


Figure 6

Species loss curves for all taxa combined and for the eight specific groups studied, depicted using animal silhouettes. For a given percentage of lost gardens (X-axis), boxplots show the range of species loss across all potential combinations of gardens