Applied Vegetation Science IAVS

RESEARCH ARTICLE

Measuring plant functional specialization in urban environments with Grime's CSR strategies

Mara Di Giulio[1] | **Zdeňka Lososová**[2] | **Marta Carboni**[3] | **Carlo Ricotta**[4]

[1]CREA-Council for Agricultural Research and Economics, Research Centre for Agriculture and Environment, Rome, Italy

[2]Department of Botany and Zoology, Faculty of Science, Masaryk University, Brno, Czech Republic

[3]Department of Sciences, University 'Roma Tre', Rome, Italy

[4]Department of Environmental Biology, University of Rome 'La Sapienza', Rome, Italy

Correspondence
Carlo Ricotta, Department of Environmental Biology, University of Rome 'La Sapienza', Rome, Italy.
Email: carlo.ricotta@uniroma1.it

Abstract

Question: Specialization refers to the degree of niche breadth of a species. Generalist species are able to persist in a broad range of habitats, whereas specialist species are adapted to a restricted range of environmental conditions. Cities host a great heterogeneity of habitats with variable degrees of human impact. This is generally reflected in the functional composition of the urban floras. The aim of our study is thus to explore whether the degree of functional specialization of urban plant assemblages varies among habitats subject to different degrees of human impact and disturbance regimes.

Location: Thirty-two cities in Central Europe with more than 100,000 inhabitants.

Methods: We used a data set containing plots of urban floras sampled in seven habitat types within each city: historical city square, boulevard, residential area with a compact building pattern, residential area with an open building pattern, city park, early successional site, and mid-successional site. These habitats differ in the level of human impact, ranging from moderately urbanized suburban habitats to the most urbanized habitats in the city center. For each plot, we calculated a recently introduced specialization index, which is based on the application of concentration measures to Grime's community-level mean CSR strategies.

Results: Along the urbanization gradient, from peripheral to central habitats, we observed a marked intensification in the degree of functional specialization of urban habitats, which is primarily attributable to an increase in the selection of ruderal species.

Conclusions: Urban ecosystems are characterized by a wide variety of human impacts that affect the functioning of the resident species. Considering cities as heterogeneous systems is thus of paramount importance for understanding the mechanisms that drive the assembly of urban floras.

KEYWORDS
concentration measures, CSR ternary diagram, disturbance regimes, extent of trait variation, human impact, species-level specialization, urban habitats

1 | INTRODUCTION

The notion of specialization refers to the niche breadth of an individual, species, or community (Clavero & Brotons, 2010; Devictor et al., 2010; Carboni et al., 2016; Carscadden et al., 2020). At the species level, generalist species can exploit a broad spectrum of resources across diverse habitats, whereas specialized species tend to exhibit more restricted niches (Devictor et al., 2010; Carboni et al., 2016; Morelli et al., 2019). According to MacArthur (1984), the restricted ecological niche breadth of specialist species results from the evolutionary trade-off between the range of the resources a species can exploit and the efficacy of exploiting a specific resource. This hypothesis implies that specialist species should theoretically invest in becoming more competitive in a restricted ecological space where conditions are limiting for most species at the expense of their performance in other habitats (Futuyma & Moreno, 1988; Wilson & Yoshimura, 1994; Jasmin & Kassen, 2007). As a consequence, specialist species are expected to be most abundant in stressful environments such as high elevations, wetlands, and halophytic, coastal or xeric habitats, whereas generalist species should be dominant in less extreme environments (Thompson et al., 1998; Lavergne et al., 2004; Carboni et al., 2016; Ricotta et al., 2023).

Indeed, variation in the degree of specialization has been previously observed along natural environmental gradients. Analyzing 570 vegetation plots of coastal dune systems in central Italy at varying distances from the sea, Carboni et al. (2016) found significant variation in the degree of specialization along the gradient. Environments closer to the sea, subject to more extreme environmental conditions, show a higher proportion of specialized species. By contrast, sheltered back dune habitats were dominated by generalists. Likewise, in a study aimed at estimating specialization for approximately 1,200 plant species in the French Alps, Boulangeat et al. (2012) observed that specialist species were mainly found in extreme habitats, such as wetlands, cold alpine environments, and dry heathlands. These species were usually geographically restricted but relatively dominant in their local communities.

Functional traits have often been used to understand how plants with distinct levels of specialization utilize resources in habitats with varying degrees of environmental stress. The position of plants within the functional trait space (sensu Díaz et al., 2016) characterizes species survival, growth, and colonization ability. Therefore, trait information can also potentially be summarized to define the level of functional specialization of species and plant assemblages. Ricotta et al. (2023) proposed a method to quantify the functional specialization of plant species and communities based on Grime's (1974) CSR strategies. According to this method, a plant species that can be exclusively assigned to a single CSR strategy is considered a specialist, because it adopts only one adaptive strategy to access resources. By contrast, species that exhibit functional characteristics of multiple CSR strategies are considered generalists. This measure of functional specialization is expected to vary along environmental gradients, including those found in urban environments.

Urban floras are also subject to strong environmental filters that are mostly related to the severity and frequency of human impact, including disturbance, artificialization, soil sealing, etc. (Ricotta et al., 2009; Williams et al., 2009; Aronson et al., 2016). Nonetheless, it has been repeatedly demonstrated that, because of the high diversity of habitats, urban floras are generally species rich, harboring more species than the surrounding landscapes (Kowarik, 1985).

The affinity of several plant species toward urban areas has been shown by a number of authors. For example, an urbanity scale (i.e., tendency to occur in cities) ranging from urbanophilic to urbanophobic depending on the species presences in cities has been developed by Klotz et al. (2002) and Kühn et al. (2004) for 3,659 taxa of the European flora, and by Hill et al. (2002) for the flora of central England. However, if we want to improve our knowledge of urban plant ecology, we should not consider cities as homogeneous entities, but rather as a mosaic of more or less distinct habitats with varying levels of human impact; for example, residential areas of diverse types and densities, parks, industrial and agricultural areas. In spite of this, studies comparing the effects of different urban habitats on species assemblages are scarce, and most are limited to a single city (Godefroid & Koedam, 2003, 2007; Zerbe et al., 2003; Muratet et al., 2008; Godefroid & Ricotta, 2018) or a few cities (Celesti-Grapow & Blasi, 1998; Maurer et al., 2000). Lososová et al. (2011, 2012, 2016) were among the first to use a standardized sampling protocol to examine plant species diversity of different urban habitats in a large number of cities across Central Europe, Belgium, and the Netherlands. Using the same data set, the aim of this study is to explore the degree of functional specialization of urban plant communities in habitats with varying levels of urbanization. In accordance with the general expectation that specialist species are most abundant in stressful environments, we hypothesize that highly urbanized habitats, because of their more extreme conditions, will harbor a higher proportion of specialized plants, whereas generalist species will be dominant in the less extreme suburban habitats. For this purpose, we used the specialization index recently introduced by Ricotta et al. (2023), which is based on the application of concentration measures to Grime's (1974) CSR strategies, which represent the main adaptive responses of plants to environmental pressure.

2 | DATA

We used the data set compiled by Lososová et al. (2011) containing presence–absence data of 1,136 spontaneous vascular plant species sampled from 32 Central European cities with more than 100,000 inhabitants. Seven urban habitat types that differed in their degree of human impact were sampled in each city (Lososová et al., 2011):

1. Historical city square, usually with pre-19th century houses, and with paved or sealed area > 90%
2. Boulevard, with 19th-century houses, lines of trees, small lawns, and paved or sealed area > 70%

3. Residential area with compact building pattern, consisting of family houses at least 50 years old and private gardens
4. Residential area with open building pattern, consisting of blocks of flats built in the 1960s–1980s, with lawns and scattered trees and shrubs
5. City park, with old deciduous trees (tree cover 10%–50%) and frequently mown lawns.
6. Early successional site, strongly disturbed 1–3 years ago, with prevailing bare ground and scarce vegetation cover, usually within or around construction sites
7. Mid-successional site, abandoned for 5–15 years, dominated by perennial grassland, with scattered shrubs and young trees.

In each city, all spontaneous vascular plant species for each habitat were recorded in one square plot of 1-ha size. Because of restricted access to private gardens in residential areas with compact building patterns, street sections of 500 m in length were sampled instead of 1-ha plots in this habitat. For a detailed description of the sampling protocol, see Lososová et al. (2011, 2012).

3 | METHODS

To quantify the functional specialization of urban plant assemblages, we employed the approach of Ricotta et al. (2023), which consists in applying concentration measures (the opposite of evenness) to Grime's (1974) mean CSR strategies at each sampling site.

Environmental filters, such as different land uses or disturbance regimes, select species with advantageous functional traits and ecological niche requirements (Kalusová et al., 2017). Specialization is thus a multidimensional concept that can be measured by considering different functional traits reflecting the species' ability to use a certain range of resources (Devictor et al., 2010; Morelli et al., 2019; Benedetti et al., 2022). In this framework, Grime's (1977, 2001) CSR theory aims to explain the main adaptive responses of plants that have evolved under the influence of different intensities of stress, disturbance, and competition (Pierce et al., 2013). According to Grime's CSR model, competitors (C) are species of stable and productive habitats in which competition is the major selective pressure. Competitor species invest in relatively rapid and continued growth of large individuals, which allows them to maximize the capture of resources. Stress-tolerators (S) are species of habitats with variable productivity. Such species retain resources in persistent reserve tissues that buffer metabolic rates from environmental fluctuations. Ruderals (R) allocate a substantial proportion of resources in propagules, from which the individuals can regenerate despite repeated disturbances (Pierce et al., 2017).

Based on Grime's CSR model, one can compare the adaptive strategies of plants within and across communities using ternary diagrams. These strategies can be recognized by examining a number of features related to resource allocation, morphology, phenology, or response to stress (Grime, 1974, 1977). At the community level, the mean CSR strategies of plants can be used to provide a functional overview of the vegetation and to compare communities of different habitats (Pierce et al., 2017; Zanzottera et al., 2020; Mastrogianni et al., 2023; Ricotta et al., 2023).

In this paper, we assigned Grime's CSR plant strategies using the classification method of Pierce et al. (2017). This method assigns species a position in the ternary diagram of CSR strategies based on the trade-offs between three easily determined leaf traits associated with the two main dimensions of plant variation: the leaf economic spectrum and the plant size spectrum (Díaz et al., 2016). High values of leaf dry matter content (LDMC) and specific leaf area (SLA) represent the two extremes of conservative and acquisitive leaf economics, whereas, orthogonal to leaf economics, leaf area (LA) reflects the species ability to intercept light (Díaz et al., 2016; Pierce et al., 2017).

The values of LA (mm^2), LDMC (%) and SLA (mm^2/mg) of 832 species were collected from the TRY database (https://try-db.org). Trait values were calculated as the average of all available trait records for each species in TRY. Next, we classified the species according to Grime's CSR functional strategies using the StrateFy classification tool of Pierce et al. (2017). For this purpose, we employed fuzzy-coded values ranging from 0 to 1 such that for each species $C + S + R = 1$ (Chevenet et al., 1994). The CSR functional strategies of an additional 45 species were directly extracted from Pierce et al. (2017, table S1), resulting in a total of 877 analyzed species. Presence–absence data for the 877 species across the 224 plots (32 cities × 7 habitat types) used in this study are reported in Appendix S1, along with the CSR strategies of each species.

To assess differences in Grime's functional strategies among the distinct urban habitats, we first calculated the mean of single-species CSR scores (C_k, S_k, R_k) at each sampling site k.

$$C_k = \frac{\sum_{j=1}^{N_k} C_{jk}}{N_k} \quad (1a)$$

$$S_k = \frac{\sum_{j=1}^{N_k} S_{jk}}{N_k} \quad (1b)$$

$$R_k = \frac{\sum_{j=1}^{N_k} R_{jk}}{N_k} \quad (1c)$$

where C_{jk}, S_{jk}, and R_{jk} are the CSR scores of species j in plot k, and N_k is the number of species in plot k. The mean distribution of the CSR scores for plot k: $P_k = (C_k, S_k, R_k)$ is thus an aggregated indicator that summarizes community-level functional responses to environmental drivers (Garnier et al., 2004; Violle et al., 2007).

According to Morelli et al. (2019) and Ricotta et al. (2023), we calculated the degree of specialization for each urban plot by applying the concentration index of Williams (see Kvålseth, 2015) to their distribution of CSR scores. Let $P_k = (C_k, S_k, R_k)$ be the

mean distribution of the CSR scores for plot k. Further, let $P_1 = (1/3, 1/3, 1/3)$ and $P_0 = (1, 0, 0)$ be the most extreme distributions for a CSR classification. P_1 corresponds to a maximally generalist species for which $C_k = S_k = R_k = 1/3$, whereas P_0 represents a specialist species associated with a single CSR strategy (Ricotta et al., 2023). The Williams concentration is expressed as the Euclidean distance $d(P_k, P_1)$ between the actual CSR proportions P_k and the most even distribution P_1 normalized by the distance between the most extreme distributions P_1 and P_0. This is the distance for which $d(P_k, P_1)$ is expected to take on its extremal values (Kvålseth, 2015). Accordingly, the index of specialization for plot k can be expressed as:

$$\sigma_k = \frac{d(P_k, P_1)}{d(P_0, P_1)} \tag{2}$$

The values of σ_k range from zero to one. For a given plot, specialization is maximal if the corresponding point falls close to any of the corners of the CSR triangle, which refers to a situation in which the value of a CSR strategy is one and the other two values are zero. Specialization gradually decreases as the point approaches the center of the ternary diagram, which represents a uniform distribution of the CSR strategies. The principle behind this method is that a species with a single adaptive strategy to access resources can be defined as a specialist species. By contrast, species that possess intermediate functional characters between the main CSR strategies can be considered more generalist (Ricotta et al., 2023). From a more technical viewpoint, among the many concentration measures available in the ecologist toolbox, we used the index of Williams because of its linear relationship to changes in the distribution of CSR scores (for details, see Molinari, 1989; Kvålseth, 2015; Ricotta et al., 2023).

For each plot, the values of σ_k were calculated with the R function available in Ricotta et al. (2023, Appendix 2). The ternary diagram of CSR strategies for the distinct urban habitats was plotted with the R package *composition* (Van den Boogaart et al., 2018). Next, using the R package *PERMANOVA* (Vicente-Gonzalez & Vicente-Villardon, 2021), we tested for significant differences in the CSR ternary composition among the urban habitats with distance-based multivariate analysis of variance (db-MANOVA; Anderson, 2001) and the Bray–Curtis dissimilarity. The p-values were obtained by 9,999 random permutations of individual plots among the distinct habitats. db-MANOVA is a multivariate extension of traditional analysis of variance that is used to test for differences between two or more groups of plots based on any possible dissimilarity measure of choice (Anderson, 2001). Using permutation methods, db-MANOVA compares the within-group dissimilarities between plots with the between-group dissimilarities. The larger the dissimilarities observed between groups compared with the dissimilarities within groups, the more likely it is that the distinct groups of plots have different CSR compositions (Anderson, 2001). At least for exploratory data analysis, Ricotta et al. (2023) considered this procedure appropriate for handling compositional data with a constant sum constraint. Finally, we used standard univariate analysis of variance (ANOVA) to test for pairwise differences in the values of plot-level specialization σ_k and single CSR strategies. Even in this case, p-values were obtained by 9,999 random permutations of single plots among habitat types.

4 | RESULTS

The ternary diagram in Figure 1 displays the average CSR strategies for all plots within the selected habitat types. In this diagram, the urban habitats are located along an urbanization gradient, ranging from the less impacted mid-successional plots to the heavily impacted boulevards and squares. From a functional perspective, the results of db-MANOVA (Table 1) show a significant difference in the CSR ternary composition among the urban habitat types (overall $F = 31.9$, $p = 0.0001$). In terms of single CSR strategies, the results of standard ANOVA (Table 2) show that the distinct habitat types exhibit significant differences in their mean CSR scores, mainly along the R–S axis (R-strategy: overall $F = 46.7$, $p = 0.0001$; S-strategy: overall $F = 29.2$, $p = 0.0001$), whereas C-selection was the least discriminating strategy (overall $F = 8.6$, $p = 0.0001$).

The functional shift along the gradient of increasing human impact is marked by a gradual rise in ruderal species, which are more adapted to urban disturbances, at the expense of more stress-tolerant species. This strategy variation also corresponds to a progressive increase in specialization (overall $F = 43.9$, $p = 0.0001$). Less urbanized and disturbed mid-successional plant communities showed the lowest degree of functional specialization. At the opposite end of the urbanization gradient, the vegetation of squares and boulevards, which is usually subject to stronger environmental filters, showed the highest levels of specialization (Table 2; Figure 2).
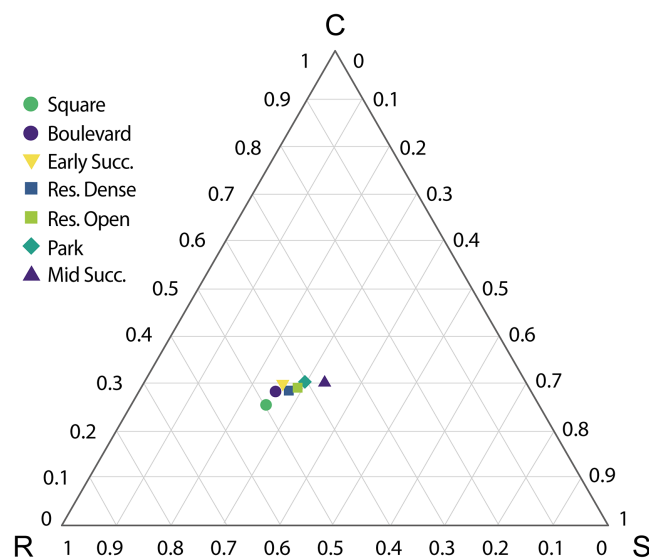
FIGURE 1 Ternary diagram of the mean CSR strategies of the urban habitat types. The habitat types are ordered along an urbanization gradient from the most urbanized to the less urbanized habitat.

TABLE 1 Results of the db-MANOVA for pairwise differences in plot-level CSR strategies among the urban habitat types (Bray–Curtis dissimilarity, 9,999 permutations).

| Habitat type	Square	Boulevard	Early succession	Residential compact	Residential open	Park	Mid succession
Square		0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
Boulevard	12.8		0.2498	0.0085	0.0002	0.0001	0.0001
Early succession	15.1	1.4		0.2707	0.1160	0.0188	0.0001
Residential compact	27.7	5.4	1.3		0.6521	0.0175	0.0001
Residential open	32.7	9.0	2.3	0.4		0.1562	0.0001
Park	42.4	15.5	4.6	4.2	1.9		0.0001
Mid succession	127.2	105.0	50.7	81.5	66.2	46.7	

Note: F-values are shown in the lower half-matrix and p-values in the upper half-matrix. The p-values of the pairwise comparisons between habitat types are shown without adjustment for multiple testing (overall $F = 31.9$; $p = 0.0001$). The habitat types are ordered along an urbanization gradient from the most urbanized to the less urbanized habitats.

db-MANOVA: distance-based multivariate analysis of variance.

TABLE 2 Mean (SD) values of specialization σ_k, and single C, S and R strategies in each habitat type.

	Habitat type						
	Square	Boulevard	Early succession	Residential compact	Residential open	Park	Mid succession
σ_k	0.238 (0.059)[a]	0.186 (0.031)[b]	0.172 (0.061)[bc]	0.160 (0.023)[c]	0.152 (0.033)[cd]	0.139 (0.033)[d]	0.073 (0.038)[e]
C	0.264 (0.029)[a]	0.289 (0.023)[b]	0.294 (0.019)[b]	0.289 (0.018)[b]	0.291 (0.021)[b]	0.296 (0.022)[b]	0.299 (0.020)[b]
S	0.246 (0.033)[a]	0.258 (0.023)[a]	0.263 (0.041)[ab]	0.273 (0.022)[b]	0.277 (0.017)[b]	0.281 (0.022)[b]	0.329 (0.025)[c]
R	0.489 (0.040)[a]	0.453 (0.022)[b]	0.443 (0.041)[bcd]	0.438 (0.015)[c]	0.432 (0.022)[cd]	0.423 (0.022)[d]	0.372 (0.029)[e]

Note: For each indicator, habitat types denoted by the same letter do not differ significantly at $p < 0.01$. Pairwise differences between habitat types were tested using standard analysis of variance and 9,999 permutations of individual plots.
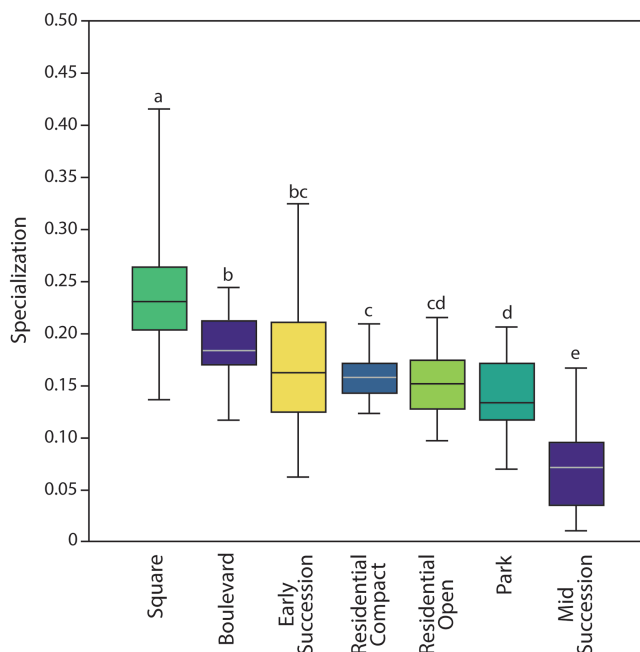
FIGURE 2 Box plots (mean and SD) of the specialization levels σ_k for the urban habitat types. Habitat types denoted by the same letter do not differ significantly at $p < 0.01$. Pairwise differences between habitat types were tested with a standard analysis of variance and 9,999 permutations of individual plots.

5 | DISCUSSION

The rapid pace of urbanization is expected to continue in the future, with more than two-thirds of the world's population residing in urban areas by 2050 (United Nations, 2018). Large cities usually host rich floras, which colonize a variety of distinct habitats, each with distinct levels of urbanization, environmental conditions, and specific species pools. Despite being the result of complex factors, where the frequency and severity of human impacts are among the main drivers, these habitats are similar among cities from different regions, making it possible to apply a comparative approach involving multiple cities across large geographic areas (Lososová et al., 2011).

Our results indicate that the extent of functional specialization of plant communities varies across different urban habitats. These habitats reflect the distinct human impacts along the rural–urban gradient, which filter species with appropriate life strategies, traits, and ecological niche requirements (Angold et al., 2006; Celesti-Grapow et al., 2006; Godefroid & Koedam, 2007; Lososová et al., 2011; Kalusová et al., 2017; Toffolo et al., 2021).

From the moderately impacted suburban habitats to the most urbanized habitats in the city center, there is a marked intensification in plant specialization, which is primarily due to a gradual increase in the selection of ruderal species. In our study, city squares and boulevards, which are usually affected by a high proportion

of impervious areas, frequent trampling, and deliberate removal of vegetation, are the most urbanized and stressful habitat types. This condition constrains the assemblage of species that appear to be the most specialized in terms of CSR strategies, supporting the observation that the extent of specialization of urban plant assemblages is greater in habitats subject to more intense and long-lasting human pressure, leading to increased levels of habitat homogenization.

Our results suggest that plants of strongly urbanized habitats tend to be highly specialized by having traits that enable them to establish new populations through massive seed production and by avoiding frequent disturbances with a rapid life cycle (Grime & Pierce, 2012). At the other extreme of the gradient, mid-successional peri-urban habitats usually experience lower levels of human impact and less uniform disturbance regimes resulting in less pronounced homogenization and therefore greater availability of microhabitats. These habitats are generally colonized by less specialized assemblages where species variability is less constrained by human impact and hence with a greater presence of more stress-tolerant species. By contrast, the presence of competitive species remains rather limited, thus highlighting the general absence of highly productive habitats in urban environments. Several studies highlight these peri-urban areas as hotspots of urban biodiversity (Schadek et al., 2008; Kattwinkel et al., 2011).

Overall, the low differences in CSR values among the selected urban habitat types contrast with the corresponding high variation in species richness (Lososová et al., 2011). From an ecological viewpoint, this implies that the urban flora is generally subject to strong management, reducing the whole functional spectra of urban assemblages (Lososová et al., 2016). From a more "technical" viewpoint, working with species presence and absence data, the same weight is assigned to rare and abundant species in the calculation of the mean CSR values of the urban plots. However, while common species are generally better adapted to the abiotic conditions of the distinct urban habitat types, rare species are much more variable in their functional traits (see Grime, 1998). Accordingly, assigning the same weight to rare and abundant species leads to an underestimation of the role of abundant species in community-level ecosystem functioning, and to an overestimation of the more functionally heterogeneous species, thus reducing the functional differences between the distinct urban habitats.

In conclusion, regardless of the data format, urban ecosystems are characterized by a great heterogeneity of environmental conditions that influence the structure and composition of the resident assemblages by imposing filters that select more specialized species in some central urban habitats and more generalist species in peri-urban habitats. Understanding the peculiarities of these habitats and how they influence the assembly and specialization of species that inhabit them is of fundamental importance for the correct management and conservation of the biodiversity present in these systems.

AUTHOR CONTRIBUTIONS

MDG: conceptualization, methodology, writing – original draft; ZL: data collection, data analysis, writing – review & editing; MC: data analysis, writing – review & editing; CR: conceptualization, methodology, writing – original draft.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

The list of species sampled in the urban habitat types, along with their CSR strategies, is included in an electronic Supplementary Information to this paper (Appendix S1). The plot-level functional specialization values were calculated using the R function provided in Ricotta et al. (2023, Appendix 2).

ORCID

Mara Di Giulio 🔟 https://orcid.org/0009-0002-1519-0647
Zdeňka Lososová 🔟 https://orcid.org/0000-0001-9152-7462
Marta Carboni 🔟 https://orcid.org/0000-0002-9348-4758
Carlo Ricotta 🔟 https://orcid.org/0000-0003-0818-3959

REFERENCES

Anderson, M.J. (2001) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, 26, 32–46.

Angold, P.G., Sadler, J.P., Hill, M.O., Pullin, A., Rushton, S., Austin, K. et al. (2006) Biodiversity in urban habitat patches. *Science of the Total Environment*, 360, 196–204.

Aronson, M.F., Nilon, C.H., Lepczyk, C.A., Parker, T.S., Warren, P.S., Cilliers, S.S. et al. (2016) Hierarchical filters determine community assembly of urban species pools. *Ecology*, 97, 2952–2963.

Benedetti, Y., Morelli, F., Callaghan, C.T. & Fuller, R. (2022) Distribution and protection of avian specialization in Europe. *Global Ecology and Biogeography*, 31, 10–24.

Boulangeat, I., Lavergne, S., Van Es, J., Garraud, L. & Thuiller, W. (2012) Niche breadth, rarity and ecological characteristics within a regional flora spanning large environmental gradients. *Journal of Biogeography*, 39, 204–214.

Carboni, M., Zelený, D. & Acosta, A.T.R. (2016) Measuring ecological specialization along a natural stress gradient using a set of complementary niche breadth indices. *Journal of Vegetation Science*, 27, 892–903.

Carscadden, K.A., Emery, N.C., Arnillas, C.A. & Cadotte, M.W. (2020) Niche breadth: causes and consequences for ecology, evolution, and conservation. *The Quarterly Review of Biology*, 95, 179–214.

Celesti-Grapow, L. & Blasi, C. (1998) A comparison of the urban flora of different phytoclimatic regions in Italy. *Global Ecology and Biogeography Letters*, 7, 367–378.

Celesti-Grapow, L., Pyšek, P., Jarošík, V. & Blasi, C. (2006) Determinants of natives and aliens species richness in the urban flora of Rome. *Diversity and Distributions*, 12, 490–501.

Chevenet, F., Dolédec, S. & Chessel, D. (1994) A fuzzy coding approach for the analysis of long-term ecological data. *Freshwater Biology*, 31, 295–309.

Clavero, M. & Brotons, L. (2010) Functional homogenization of bird communities along habitat gradients: accounting for niche multidimensionality. *Global Ecology and Biogeography*, 19, 684–696.

Devictor, V., Clavel, J., Julliard, R., Lavergne, S., Mouillot, D., Thuiller, W. et al. (2010) Defining and measuring ecological specialization. *Journal of Applied Ecology*, 47, 15–25.

Díaz, S., Kattge, J., Cornelissen, J.H.C., Wright, I.J., Lavorel, S., Dray, S. et al. (2016) The global spectrum of plant form and function. *Nature*, 529, 167–171.

Futuyma, D.J. & Moreno, G. (1988) The evolution of ecological specialization. *Annual Review of Ecology and Systematics*, 19, 207–233.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M. et al. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, 85, 2630–2637.

Godefroid, S. & Koedam, N. (2003) How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context? *Global Ecology and Biogeography*, 12, 287–298.

Godefroid, S. & Koedam, N. (2007) Urban plant species patterns are highly driven by density and function of built-up areas. *Landscape Ecology*, 22, 1227–1239.

Godefroid, S. & Ricotta, C. (2018) Alien plant species do have a clear preference for different land uses within urban environments. *Urban Ecosystems*, 21, 1189–1198.

Grime, J.P. (1974) Vegetation classification by reference to strategies. *Nature*, 250, 26–31.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist*, 111, 1169–1194.

Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, 86, 902–910.

Grime, J.P. (2001) *Plant Strategies, Vegetation Processes and Ecosystem Properties*. Chichester, UK: Wiley.

Grime, J.P. & Pierce, S. (2012) *The evolutionary strategies that shape ecosystems*. Chichester, UK: Wiley.

Hill, M.O., Roy, D.B. & Thompson, K. (2002) Hemeroby, urbanity and ruderality: bioindicators of disturbance and human impact. *Journal of Applied Ecology*, 39, 708–720.

Jasmin, J.N. & Kassen, R. (2007) Evolution of a single niche specialist in variable environments. *Proceedings of the Royal Society of London, Biological Sciences*, 274, 2761–2767.

Kalusová, V., Čeplová, N. & Lososová, Z. (2017) Which traits influence the frequency of plant species occurrence in urban habitat types? *Urban Ecosystems*, 20, 65–75.

Kattwinkel, M., Bidermann, R. & Kleyer, M. (2011) Temporary conservation for urban biodiversity. *Biological Conservation*, 144, 2335–2343.

Klotz, S., Kühn, I. & Durka, W. (2002) BIOLFLOR—Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde*, 38, 1–334.

Kowarik, I. (1985) Grundlagen der Stadtökologie und Forderungen nach ihrer Berücksichtigung bei der Stadtgestaltung am Beispiel Berlins. *Schriftenreihe DBV-Jugend*, 3, 22–39.

Kühn, I., Brandl, R. & Klotz, S. (2004) The flora of German cities is naturally species rich. *Evolutionary Ecology Research*, 6, 749–764.

Kvålseth, T.O. (2015) Evenness indices once again: critical analysis of properties. *Springerplus*, 4, 232.

Lavergne, S., Thompson, J.D., Garnier, E. & Debussche, M. (2004) The biology and ecology of narrow endemic and widespread plants: a comparative study of trait variation in 20 congeneric pairs. *Oikos*, 107, 505–518.

Lososová, Z., Chytrý, M., Danihelka, J., Tichý, L. & Ricotta, C. (2016) Biotic homogenization of urban floras by alien species: the role of species turnover and richness differences. *Journal of Vegetation Science*, 27, 452–459.

Lososová, Z., Chytrý, M., Tichý, L., Danihelka, J., Fajmon, K., Hájek, O. et al. (2012) Native and alien floras in urban habitats: a comparison across 32 cities of Central Europe. *Global Ecology and Biogeography*, 21, 545–555.

Lososová, Z., Horsák, M., Chytrý, M., Čejka, T., Danihelka, J., Fajmon, K. et al. (2011) Diversity of central European urban biota: effects of human-made habitat types on plants and land snails. *Journal of Biogeography*, 38, 1152–1163.

MacArthur, R.H. (1984) *Geographical ecology: patterns in the distribution of species*. Princeton, NJ: Princeton University Press.

Mastrogianni, A., Kiziridis, D.A., Karadimou, E., Pleniou, M., Xystrakis, F., Tsiftsis, S. et al. (2023) Community-level differentiation of Grime's CSR strategies along a post-abandonment secondary successional gradient. *Flora*, 308, 152399.

Maurer, U., Peschel, T. & Schmitz, S. (2000) The flora of selected urban land-use types in Berlin and Potsdam with regard to nature conservation in cities. *Landscape and Urban Planning*, 46, 209–215.

Molinari, J. (1989) A calibrated index for the measurement of evenness. *Oikos*, 56, 319–326.

Morelli, F., Benedetti, Y., Møller, A.P. & Fuller, R.A. (2019) Measuring avian specialization. *Ecology and Evolution*, 9, 8378–8386.

Muratet, A., Porcher, E., Devictor, V., Arnal, G., Moret, J., Wright, S. et al. (2008) Evaluation of floristic diversity in urban areas as a basis for habitat management. *Applied Vegetation Science*, 11, 451–460.

Pierce, S., Brusa, G., Vagge, I. & Cerabolini, B.E.L. (2013) Allocating CSR plant functional types: the use of leaf economics and size traits to classify woody and herbaceous vascular plants. *Functional Ecology*, 27, 1002–1010.

Pierce, S., Negreiros, D., Cerabolini, B.E.L., Kattge, J., Díaz, S., Kleyer, M. et al. (2017) A global method for calculating plant CSR ecological strategies applied across biomes world-wide. *Functional Ecology*, 31, 444–457.

Ricotta, C., Dalle Fratte, M., Pierce, S., Carboni, M., Cerabolini, B.E.L. & Pavoine, S. (2023) Quantifying the extent of plant functional specialization using Grime's CSR strategies. *Ecological Indicators*, 148, 110066.

Ricotta, C., La Sorte, F.A., Pyšek, P., Rapson, G.L., Celesti-Grapow, L. & Thompson, K. (2009) Phyloecology of urban alien floras. *Journal of Ecology*, 97, 1243–1251.

Schadek, U., Strauss, B., Bidermann, R. & Kleyer, M. (2008) Plant species richness, vegetation structure and soil resources of urban brownfield sites linked to successional age. *Urban Ecosystems*, 12, 115–126.

Thompson, K., Hodgson, J.G. & Gaston, K.J. (1998) Abundance-range size relationships in the herbaceous flora of central England. *Journal of Ecology*, 86, 439–448.

Toffolo, C., Gentili, R., Banfi, E., Montagnani, C., Caronni, S., Citterio, S. et al. (2021) Urban plant assemblages by land use type in Milan: floristic, ecological, and functional diversities and refugium of railway areas. *Urban Forestry & Urban Greening*, 62, 127175.

United Nations, Department of Economic and Social Affairs, Population Division. (2018) World urbanization prospects: the 2018 revision, Online Edition. Available at: https://population.un.org/wup/Download/

Van den Boogaart, K.G., Tolosana-Delgado, R. & Bren, M. (2018) Compositions: compositional data analysis. R package version 2.0-4. https://CRAN.R-project.org/package=compositions

Vicente-Gonzalez, L. & Vicente-Villardon, J.L. (2021) PERMANOVA: multivariate analysis of variance based on distances and permutations. R package version 0.2.0. https://CRAN.R-project.org/package=PERMANOVA

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. et al. (2007) Let the concept of trait be functional! *Oikos*, 116, 882–892.

Williams, N.S.G., Schwartz, M.W., Vesk, P.A., McCarthy, M.A., Hahs, A.K., Clemants, S.E. et al. (2009) A conceptual framework for predicting the effects of urban environments on floras. *Journal of Ecology*, 97, 4–9.

Wilson, D.S. & Yoshimura, J. (1994) On the coexistence of specialists and generalists. *American Naturalist*, 144, 692–707.

Zanzottera, M., Dalle Fratte, M., Caccianiga, M., Pierce, S. & Cerabolini, B.E.L. (2020) Community-level variation in plant functional traits and ecological strategies shapes habitat structure along succession gradients in alpine environment. *Community Ecology*, 21, 55–65.

Zerbe, S., Maurer, U., Schmitz, S. & Sukopp, H. (2003) Biodiversity in Berlin and its potential for nature conservation. *Landscape and Urban Planning*, 62, 139–148.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. List of species sampled in the urban habitat types, together with their CSR strategies.