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Urban landscape organization is associated with differences in avian-mediated regulating ecosystem services

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HIGHLIGHTS

- Urban landscape organization affects avian-mediated regulating ecosystem services (RES).
- Land-sharing provides more bird-mediated scavenging, seed dispersal and pest control.
- There are seasonal differences in the provision of avian-mediated RES.
- Green cover and fruit-bearing plants enhance the provision of avian-mediated RES.
- Higher levels of built cover and pedestrians decrease several avian-mediated RES.

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ABSTRACT

Urbanization alters ecosystems through multiple biotic and abiotic changes that directly affect urban biodiversity. However, we still lack information on how urban areas influence the ecosystem services provided by wildlife, particularly regulating ecosystem services (RES) such as seed dispersal, pollination, pest control, and scavenging. Recent studies have shown marked differences in animal communities depending on urban landscape configuration, which ranges from land-sharing (low-density housing with small, fragmented green areas) to land-sparing (high-density housing with large, unfragmented green areas). Because this gradient affects animal communities, we expect it to also influence potential ecosystem service provision. In addition, several local urban attributes may influence these communities and, consequently, could also affect RES provision. To address these research questions and their potential temporal variation, we collected bird assemblage data from nine European cities during the breeding and non-breeding seasons. We used bird diets and abundances to identify the main species providers of the four avian-mediated RES mentioned above and analyzed their variation in potential service provision along the urban landscape organization gradient. Land-sharing areas provided higher potential scavenging (both seasons), seed dispersal (non-breeding), and pest control (non-breeding). Several urban attributes (e.g., abundance of fleshy fruit-bearing plants) significantly enhanced RES, while others (e.g., built cover) reduced them, although these effects varied seasonally. These findings provide new insights into the debate on how cities can be more biodiversity-friendly and can help to implement measures based on local urban attributes that promote RES provision, both of which are vital for urban ecosystems and citizens' well-being.

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1. Introduction

The rapid expansion of urban areas, added to the fast growth of the human population living in cities, has become one of the most important socio-ecological challenges for the globe (Liu et al., 2018; United Nations, 2023). This intense human-induced landscape change is known to drive several impacts on ecosystems, such as habitat loss and fragmentation of natural habitats with the consequent generalized reduction in biodiversity levels (Li et al., 2022; Newbold et al., 2015; Piano et al., 2020). These impacts have severe consequences in ecosystem functioning and the provision of ecosystem services (ES) (Elmqvist et al., 2013, 2016), defined as the processes by which nature provides benefits to humans (Levine & Chan, 2011). In fact, ES have gained increasing importance in conservation since the establishment of the Millenium Ecosystem Assessment in 2005, which also comprises urban areas (Elmqvist et al., 2013; Millennium Ecosystem Assessment, 2005; O'Farrell, 2020). However, despite the importance of urban ES, there are still several important gaps in our knowledge, particularly regarding those mediated by wildlife and how urbanization-driven changes in animal communities influence their provision (Pejchar et al., 2025; Soulsbury & White, 2015).

Animals provide ecosystem services vital for human well-being (Pinho et al., 2017; Soulsbury & White, 2015). Hence, identifying the key ES providers is critical for good management and planning (Kremen & Ostfeld, 2005). Birds stand out in urban environments as providers of multiple ecosystem services, helping to maintain important functions for the ecosystem (Sekercioglu et al., 2016; Whelan et al., 2008). Among all ES, several studies highlight the relevance of birds in the provision of Regulating Ecosystem Services (RES). According to the classification provided by Michel et al. (2020), RES are important for controlling insect pests, carrion removal (and, indirectly disease transmission), pollinating flowers (particularly, but not only, in tropical areas) and dispersing seeds (Sekercioglu et al., 2016; Wenny et al., 2011). This also applies to urban areas with several studies supporting the important role of urban birds in the provision of these RES (e.g. Cruz et al., 2013; Inger et al., 2016; Maruyama et al., 2019, 2024). However, we still lack information on how and which urbanization factors modulate avian-mediated RES, with recent studies indicating that it is a clearly understudied topic (Luna et al., 2021). Furthermore, studies on the topic are mainly local (e.g. Cruz et al., 2013; Inger et al., 2016; Maruyama et al., 2019), providing useful information at that local scale but preventing generalizations of results. Large-scale (multi-city) studies would provide a broader perspective, although to the best of our knowledge no study has evaluated avian-mediated RES in more than one city simultaneously.

Functional traits (such as diet) and species abundance could be very useful for the evaluation of animal-mediated RES (Barros et al., 2019), as these variables are highly related to ecosystem service provision (Cadotte et al., 2011; Carlucci et al., 2020; Gaston et al., 2018). Bird functional traits and community composition could be very useful to understand animal-mediated RES in urban areas even if they only give us information on the potential provision of RES. One of their advantages is the detailed information on bird functional traits including seasonal variation in diet and bird abundance that would allow for the rarely explored temporal effects. Several recent studies highlighted the importance of this temporal component to fully comprehend the impact of urbanization on wildlife (Ibáñez-Álamo et al., 2020; Leveau et al., 2021).

Interestingly, bird community composition varies depending on the urban design (Cristaldi et al., 2023; Ibáñez-Álamo et al., 2020; Lerman et al., 2021). Urban areas are not homogenous and could be organized in several ways (Forman, 2014; Norton et al., 2016). Urban areas can be developed along an urban landscape configuration gradient that ranges between two extremes: land-sharing and land-sparing. The land-sharing/sparing urban gradient concept has been increasingly investigated to analyze the socio-ecological impacts of within-city variability (Geschke et al., 2018; Lin & Fuller, 2013). On one extreme of the gradient, land-sharing urban areas are characterized by low-density housing (mostly family houses), low population density, and small and fragmented green patches. On the other extreme, land-sparing urban areas have high-density housing and high population density surrounding large green patches (Lin & Fuller, 2013). According to recent studies, land-sharing urban areas show higher bird taxonomic and functional diversity levels than land-sparing areas, although these effects change seasonally (Assandri et al., 2025; Ibáñez-Álamo et al., 2020; Lerman et al., 2021). Thus, the potential provision of RES by birds would differ depending on changes in community assembly between seasons and urban landscape organizations. To the best of our knowledge, this possibility has not been explored yet, although several studies indirectly support this assumption. On the one hand, a recent study indicates that seed dispersal, pollination, and pest control are highly related to habitats with large green patches (i.e., land-sparing areas) and strong connectivity (Wu et al., 2024), pest control being the most affected by landscape structure and urbanization levels (Máthé & Batáry, 2015; Wu et al., 2024). On the other hand, land-sharing urban areas hold more corvids (Jokimäki et al., 2020), which are the main scavengers in cities (Inger et al., 2016). Despite this suggestive information, little is known about the variation in avian-mediated RES according to the urban landscape organization gradient. This information will be particularly interesting in the current debate on how to create more biodiversity-friendly cities.

Specific local modifications in the urban design could also affect avian-mediated RES through changes in community composition (Beninde et al., 2015; Morelli et al., 2021). For example, built cover is negatively associated with avian diversity (Ibáñez-Álamo et al., 2020; Morelli et al., 2021), as built cover would reduce the potential provision of avian-mediated RES. In contrast, vegetation attributes (presence and cover of trees, bushes, or grass) favor biodiversity levels in multiple taxa, and tend to promote species displaying specific traits, influencing the animal-mediated RES (Morelli et al., 2021; Pena et al., 2023).

Studying the impact of local urban attributes is particularly interesting from an applied and management point of view as they can be modified in the short term whereas changes in urban landscape type require longer-term planning (Campos-Silva & Piratelli, 2020; Soga et al., 2014). Therefore, the main aims of this study were: (1) to identify whether the urban landscape organization gradient (i.e. land-sharing/land-sparing gradient) is associated with a different potential provision of avian-mediated RES; and (2) to investigate which local urban attributes (e.g., bushes, trees, built cover) promote their provision, allowing recommendations for city planners and practitioners. We propose that urban landscape organization influences the potential provision of avian-mediated RES by altering community assembly. Furthermore, given the impacts of urbanization on avian communities (see above), we expect seed dispersal, pollination, and pest control to be higher in land-sparing urban areas, while scavenging would show the opposite trend. We also predict that several site-scale attributes that enhance bird diversity (e.g., water and vegetation cover, fleshy fruit-bearing plants or bird feeders) will promote RES provision, whereas others (e.g., built cover, presence of pedestrians or mammals) will reduce it. To investigate the general applicability of our findings, by using a trait-based approach, we quantified multiple potential avian-mediated RES simultaneously (fruit dispersal, scavenging, pollination, and pest control) and used data obtained from **a** large spatial scale (i.e., several European cities) and two temporal scales (i.e., two seasons) to account for changes in community assembly.

2. Methods

2.1. Study area

We used data from nine European cities (Rovaniemi, Turku, Poznan, Groningen, Prague, Munich, Madrid, Toledo, and Granada; Fig. 1) along a wide (3700 km) latitudinal gradient from the north of Finland to the south of Spain. City size ranged between 64,000 to 3,170,000 inhabitants, and they are located in three different European vegetation zones (i.e. Mediterranean forest, Temperate deciduous forests and Boreal coniferous forests), to capture a good representation of the variation in urban areas in Europe (see Ibáñez-Álamo et al., 2020; Suhonen et al., 2022 for further details about the cities selected). In each city, we selected ten paired 500 m x 500 m squares located 570 ± 65 (mean ± SD) m apart to ensure independence. We initially selected the squares by visual inspection of satellite images ensuring that half of these ten squares corresponded to a land-sharing urban landscape organization, and the other half to a land-sparing type. Then, we confirmed the urban landscape organization gradient value of each square by calculating an index developed by Ibáñez-Álamo et al. (2020). This index quantifies the level of sparingness/sharingness of each square and ranges between −4 and 4, where negative values indicate land-sharing urban areas and positive values correspond to land-sparing areas. The calculation of the index consists in the principal component of a PCA performed using landscape variables measured at the 500-m square level (i.e. percentage of high vegetation cells, number of green patches, percentage of built cells of all vegetated cells, and other variables. See Ibáñez-Álamo et al., 2020 for details). The size of green areas or the overall level of urbanization could influence bird communities (Beninde et al., 2015; Ibáñez-Álamo et al., 2017; Pena et al., 2023), and, thus, we ensured that paired land-sharing and land-sparing squares had comparable proportions of green cover and built surfaces. To do so, we first verified that paired squares had similar proportions of green areas (see Ibáñez-Álamo et al., 2020 for details). Then, we calculated a commonly used urbanization index (Liker et al., 2008) for each selected square and confirmed that paired squares did significantly differ in either green areas cover or urbanization index (Ibáñez-Álamo et al. 2020). Together, these procedures ensured that, we specifically assessed the effect of urban landscape configuration gradient avoiding these potential confounding factors. More details about the selection of squares are available from Ibáñez-Álamo et al. (2020).

2.2. Bird censuses

We randomly selected seven-point count stations with a fixed radius of 50 m in each square, all keeping at least 100 m between them and with the border of the square. However, landscape configuration constraints (e.g. restricted areas) forced us to include only six-point counts in 28 out of the final 90 squares. We designed the study to minimize detection issues by implementing a reduced census radius (50 m) and conducting repeated visits (twice per season) at each point count (Voříšek et al., 2008). This methodology is consistent with other studies on avian-mediated ecosystem services (e.g., Barros et al., 2019). Ornithologists, with over a decade of bird survey experience (all included as co-authors) performed the census to mitigate potential sources of data heterogeneity related to skill differences (van Heezik & Seddon, 2017). We detected all the birds by sight and sound for 5 min in each point count. We conducted point counts only under good weather conditions (no rain or heavy wind) to increase the detectability of the birds. Because of the seasonality of urban bird assemblages (Leveau et al., 2021; Moreno-Contreras et al., 2024), we carried out censuses both during the breeding season of 2016 (i.e. spring: April–June) and the non-breeding season of 2016–2017 (i.e. winter: December-February), with two visits per season separated by a month. We conducted the censuses from sunrise to a maximum of three hours after daybreak. At northern latitudes, where the sun does not set in mid-summer, breeding season surveys started between 02.00 and 03.00 (local time), and finished within three hours of starting time, i.e. timed on the peak of the “dawn” chorus time of the birds. The maximum number of individuals per species in the two visits was the estimate of each species’ abundance per season. We used all the species encountered within the 50-meter radius to estimate RES values.

2.3. Local urban attributes

Within the 50-m radius point count, we estimated the percentage (to the nearest 10 %) of cover with buildings and paved surfaces (i.e., roads), water and vegetation at three levels (trees, bushes and grass) in the field. Additionally, during the non-breeding season, we collected data on the number of bird feeders and the abundance of fleshy fruit-bearing plants as they can influence the avian urban community (Morelli et al., 2021; Tews et al., 2004). We classified the abundance of fruit-bearing plants as follows: 0 indicates the absence of plants with fleshy fruit-bearing; 1 indicates the presence of fleshy fruit-bearing plants whose size is shorter than 1.75 m in height (i.e. the average human height-size in Europe; WorldData 2025); and 2 indicates the presence of plants with berries that were larger than 1.75 m in height (WorldData, 2025). Finally, during the 5 min. counts and within 50 m of the census point, we also measured the number of potential mammal predators (red squirrels [*Sciurus vulgaris*], dogs [*Canis lupus familiaris*], cats [*Felis catus*]) and pedestrians seen as a proxy for predator pressure and human disturbance, respectively. We averaged the number of mammals or pedestrians recorded in both visits to obtain a value for each predictor per season.

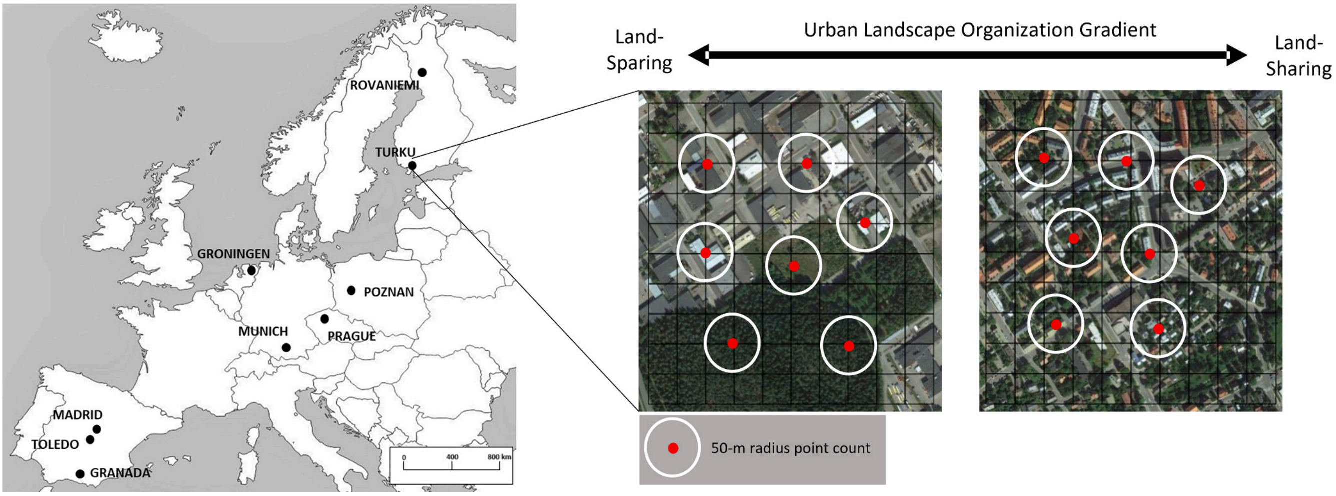

Fig. 1. Map showing the location of the nine European cities (left) and the bird census design (right). On the right, two 500 × 500 m study squares represent the two extremes of the urban landscape organization gradient. The red points with a 50-m census radius (white) indicate the locations of the survey stations.

2.4. Estimation of ecosystem services

We used species-specific traits of bird species as a proxy for the study of avian-mediated RES. The link between these functional traits and the ecosystem service provision is well studied for birds (Barros et al., 2019; Goodness et al., 2016; Luck et al., 2012). The estimation of avian-mediated RES (seed dispersal, scavenging, pollination, and pest control) followed the procedure used by Barros et al. (2019). First, we calculated an estimate of the provision of each ecosystem service per each species using bird diets as a proxy, given that avian-mediated RES results mostly from their foraging behavior (Wenny et al., 2011). We used the percentage of invertebrates, fruits, nectar, and carrion in diets as estimates to the potential provision of pest control, seed dispersal, pollination, and scavenging services, respectively. Diet data were extracted from SAviTraits 1.0, a recently published and comprehensive dataset (Murphy et al., 2023). This dataset also contains information about the seasonal variation in diet of all the species surveyed, allowing us to estimate RES for each season. We used the mean percentages from April to June for the breeding bird community and from December to February for the non-breeding season. Second, we calculated the value of each RES at the assemblage level (point count census) by multiplying each species' estimates by its abundance to obtain a corrected measure per species, and then summing all the corrected values for the species present in each point count.

2.5. Statistical analyses

We carried out generalized linear mixed models (GLMM) to test the association between each avian-mediated RES and urban landscape organization as well as the potential effect of local urban attributes.

Prior to these analyses, we carried out a spatial correlation test for each response variable in each season to check whether our point counts can be used as independent observations for RES values. We took a similar approach as Sanllorente et al. (2023) and we did a Mantel test (Legendre & Fortin, 2010) based on Monte Carlo permutations with 9999 randomizations and two matrices: the spatial distance matrix (geographic UTM coordinates to indicate the distance among point counts) and another for the differences in seed dispersal, scavenging, pollination or pest control among point counts (response variable distance matrix). We conducted these analyses for both seasons (8 correlation tests in total). We found a spatial correlation in all the analyses (see Table S1 for further details), except for pollination in the breeding season ($r = -0.007$, $p = 0.716$, $N = 593$) and pest control in the non-breeding season ($r = -0.034$, $p = 0.848$, $N = 555$). Thus, we included the interaction term (Latitude x Longitude) in the posterior GLMM analyses to control for spatial correlation in the six affected analyses (Dormann et al., 2007).

Secondly, we visually identified and eliminated the outliers in each dependent variable (Aguinis et al., 2013). We confirmed the absence of outliers after running the subsequent analyses using the test for outliers available in the R package "performance" (Lüdecke et al., 2021). We also scaled and centered all independent continuous variables by using the "scale" function before running the analysis to allow easier comparison of the estimates (Schielzeth, 2010). Thirdly, we run one model (GLMM) for each RES type (i.e., pest control, seed dispersal, pollination, and scavenging) and each season (breeding and non-breeding season). We initially assumed a Poisson distribution based on the distribution of the data. However, we detected overdispersion in all models. Thus, we ultimately ran negative binomial GLMM models to control for it by using the R package "glmmTMB" (Magnusson et al., 2019). The structure of these models consisted of using the RES values per point count as the dependent variable and the following predictors: urban landscape organization gradient (forced to be in all analyses in the posterior selection of models), built cover, tree cover, bush cover, grass cover, water cover, number of pedestrians, number of mammals, number of feeders (non-breeding season), the abundance of fleshy fruit-bearing plants (non-breeding season) and Latitude x Longitude (when needed; see above) (Table 1). We also included the following interactions in all analyses: (1) urban landscape organization and built cover, as land-sparing areas are known to have a more intense form of building cover compared to land-sharing areas (Lin & Fuller, 2013); and (2) urban landscape organization and mammals because of the possible differences in mammal community composition between areas, potentially leading to differences in predator pressures and species interactions between areas (Jokimäki et al., 2020; Villaseñor et al., 2017). We also included the interaction between feeders and urban landscape organization in the non-breeding season analyses because the bird feeding behavior may differ between areas (Fuller et al., 2008). To account for consistent differences among cities and due to the presence of different squares as spatial replicas, we included square ID nested within city ID as a random factor to all models. We tested for model assumptions and multicollinearity issues in all models by checking the VIF values using the R package "performance" (Lüdecke et al., 2021). No variable was dropped due to low values of VIF (values always lower than 4.29). Finally, we chose the predictors that best explain the variation in the response variables (i.e., RES types) using model selection and averaging approach available in the R package "MuMIn" (Symonds & Moussalli, 2011; Zuur et al., 2009). The terms urban landscape organization gradient and Latitude x Longitude were forced to be in all models through the selection (see above). Then, we averaged the models using the commonly used $\Delta\text{AIC} < 2$ criteria (Symonds & Moussalli, 2011). See Tables S2 and S3 for more information about the models selected. Additionally, we calculated the sum of weights of each term (Tables S4 and S5) as they reflect robustly the importance of each variable in the analyses (Cade, 2015; Giam & Olden, 2016).

To evaluate possible relationships of urban landscape organization with the different local urban attributes and the other fixed terms, we fitted several models using each urban attribute as the predictor and urban landscape organization gradient as the fixed term (see Table S8 for further details). To do so, we run linear mixed models assuming Gaussian distribution for all variables except for abundance of fleshy fruit-bearing plants for which we assumed a Poisson distribution.

Additionally, we used the function *interact_plot* available in the R

Table 1
Table summarizing the variables used for the avian-mediated RES analyses.

Variable	Description	Season
Urban landscape organization	Gradient indicating the level of land-sharing or land-sparing of a surveyed square. More negative values indicate more land-sharing urban design while more positive values indicate more land-sparing values.	Both
Built cover	Percentage (to the nearest 10 %) of cover with buildings and paved surfaces (i.e. roads)	Both
Tree cover	Percentage (to the nearest 10 %) of cover with trees	Both
Bush cover	Percentage (to the nearest 10 %) of cover with shrubs	Both
Grass cover	Percentage (to the nearest 10 %) of cover with grass	Both
Water cover	Percentage (to the nearest 10 %) of cover with water	Both
Pedestrians	Average of number of pedestrians encountered during the 5 min point-count in the two visits per season	Both
Mammals	Average of number of mammals (red squirrels [*Sciurus vulgaris*], dogs [*Canis lupus familiaris*], cats [*Felis catus*]) encountered during the 5 min point-count in the two visits per season	Both
Feeders	Number of bird feeders within the point count	Non-breeding
Fleshy fruit-bearing plants	Abundance of fleshy fruit-bearing plants (0 to 2 code, from absence of plants with berries to an abundance of berries higher to the size of a human)	Non-breeding

package "Interactions" (Long, 2024) to visually check the significant interactions of the models. Given that this function cannot run results from averaging models, we employed a negative binomial glmer using the same fixed terms obtained in the results from the averaging model.

Finally, we wanted to obtain information about the importance of species providing each of the RES. To do so, we carried out multiple regressions using each RES and season and calculating the variance explained by each species. We added this information by including several barplots in the supplementary material (Figs. S1 and S2).

3. Results

We identified 115 bird species during the breeding period, of which the most common were: Eurasian blackbird (*Turdus merula*; present in 70 % of all point counts), great tit (*Parus major;* 67 %), house sparrow (*Passer domesticus*; 63 %), common wood-pigeon (*Columba palumbus*; 56 %) and common swift (*Apus apus*; 48 %). In contrast, during the non-breeding season, we identified 72 species and the most common were: great tit (67 %), house sparrow (51 %), rock pigeon (*Columba livia*; 51 %) and **Eurasian** blackbird (45 %). Full statistical outputs for all models are provided in Tables S6 and S7.

3.1. Seed dispersal

The most important species providing seed dispersal were common wood-pigeon, Eurasian jackdaw (*Coloeus monedula*) and European greenfinch (*Chloris chloris*) in both seasons (Figs. S1 and S2). Seed dispersal increased along the urban landscape organization gradient during the non-breeding season (Estimate ± SE = −0.164 ± 0.08, Z = 2.04, p = 0.041; Fig. 2).

Local urban attributes showed seasonal patterns: during breeding, seed dispersal species providers were favored by tree cover (Estimate ± SE = 0.114 ± 0.04, Z = 2.62, p = 0.009) and grass cover (Estimate ± SE = 0.101 ± 0.04, Z = 2.52, p = 0.012). Non-breeding season analyses showed that the potential provision of seed dispersal was negatively related to built cover (Estimate ± SE = −0.394 ± 0.06, Z = 6.29, p < 0.001) and positively influenced by the abundance of fleshy fruit-bearing plants (Estimate ± SE = 0.237 ± 0.06, Z = 4.30, p < 0.001), mammals (Estimate ± SE = 0.126 ± 0.06, Z = 2.18, p = 0.030) and feeders (Estimate ± SE = 0.220 ± 0.05, Z = 4.11, p < 0.001). Seed dispersal during the non-breeding season was further mediated by an interaction between feeders and the urban landscape organization gradient (Estimate ± SE = 0.141 ± 0.07, Z = 2.07, p = 0.039; Fig. 3).

3.2. Pest control

Common swift, western house-martin (*Delichon urbicum*) and spotless starling (*Sturnus unicolor*) were the most important bird species regarding pest control during the breeding season, whereas black-headed gull (*Chroicocephalus ridibundus*), spotless starling and fieldfare (*Turdus pilaris*) were the most important pest controllers during the non-breeding season (Figs. S1 and S2). Potential pest control provision

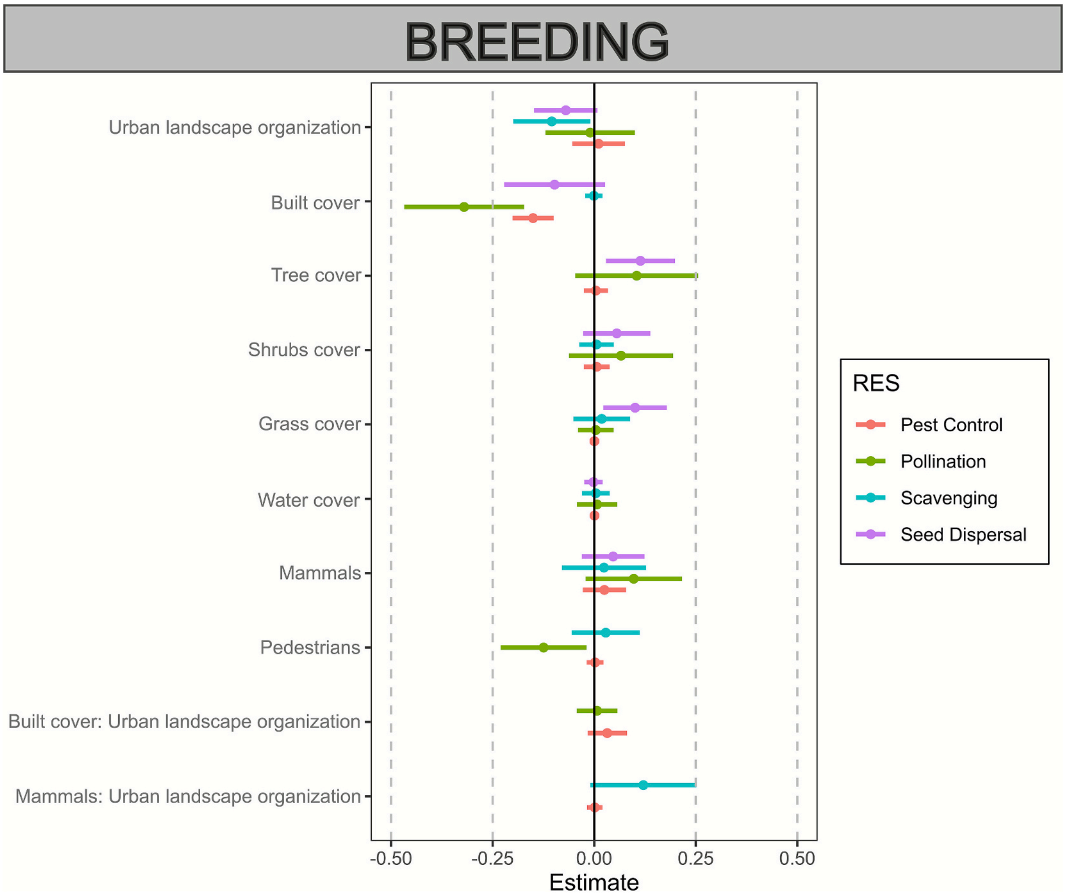

Fig. 2. Plots summarizing the results of the best models from the model selection and averaging on the generalized linear mixed models (GLMM) for the four RES for the breeding season (A) and the non-breeding season (B). The results are expressed as the estimates of each variable with the standard errors. If the individual variable level standard error intervals do not overlap zero, it indicates a significant effect. For the variable "Urban landscape organization" negative values imply more land-sharing areas while positive values indicate more land-sparing areas. To simplify the plots, the term Latitude x Longitude was not included in the visualization. Please note that the predictors selected for each RES component (i.e., response variable) are different according to the selection model averaging procedure used.

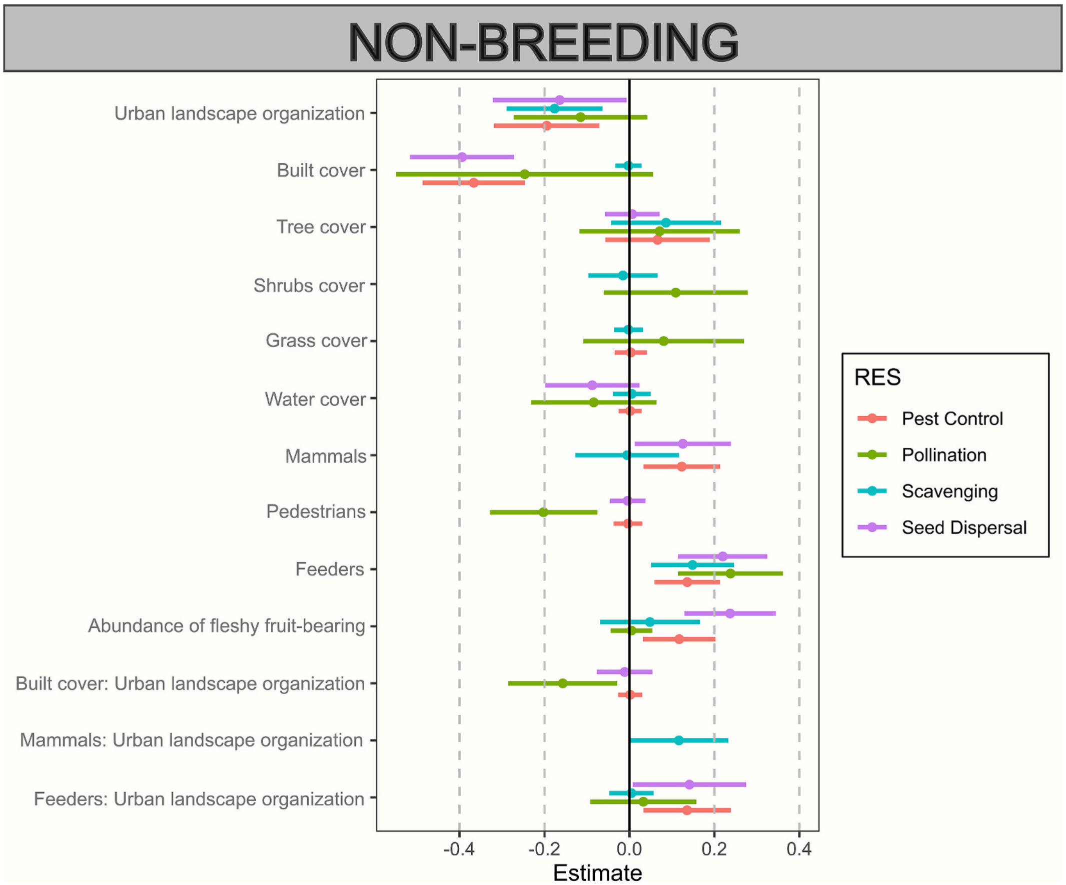

Fig. 2. (*continued*).

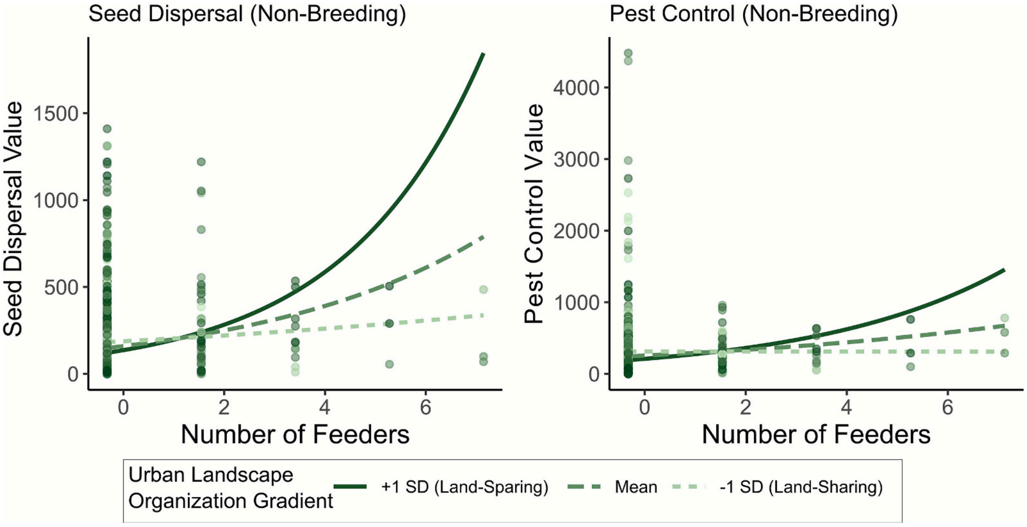

Fig. 3. Graphs with the result of the interaction between urban landscape organization gradient and number of feeders for the seed dispersal and pest control services during the non-breeding season. On the left we can see the results of the seed dispersal analysis and on the right part the results of the pest control analysis. The variable number of feeders is scaled. The variable urban landscape organization gradient is divided into three parts: "+1 SD" implies an increase of the values (more land-sparing areas), "Mean" corresponds to mean values of the variable and "-1 SD" implies a reduction in the values of the variable (more land-sharing areas).

increased along the urban landscape organization gradient (Estimate ± SE = −0.195 ± 0.06, Z = 3.07, p = 0.002; Fig. 2).

Additionally, built cover were negatively associated with potential pest control in the breeding (Estimate ± SE = −0.150 ± 0.03, Z = 5.82, $p < 0.001$) and non-breeding seasons (Estimate ± SE = −0.367 ± 0.06, Z = 5.96, $p < 0.001$). Furthermore, our analyses for the non-breeding season also indicated that mammals (Estimate ± SE = 0.123 ± 0.05, Z = 2.67, p = 0.008), the abundance of fleshy fruit-bearing plants (Estimate ± SE = 0.117 ± 0.04, Z = 2.69, p = 0.007) and feeders (Estimate ± SE = 0.136 ± 0.04, Z = 3.45, p = 0.001) promote species that perform pest control. However, the later association was mediated by urban landscape organization gradient (Estimate ± SE = 0.136 ± 0.05, Z =

2.58, p = 0.010; Fig. 3).

3.3. Pollination

The most important pollinators in both seasons were Eurasian blue tit (*Cyanistes caeruleus*) and Eurasian blackcap (*Sylvia atricapilla*), with great tit also contributing during the breeding season and spotless starling during the non-breeding season (Figs. S1 and S2). Potential pollination values showed no significant association with the urban landscape organization gradient.

Regarding local urban attributes, the potential provision of pollination was significantly (negative) associated with built cover (Estimate ± SE = −0.320 ± 0.07, Z = 4.25, p < 0.001) and pedestrians (Estimate ± SE = −0.125 ± 0.05, Z = 2.31, p = 0.021) during the breeding season. The former association was mediated by the urban landscape organization gradient during the non-breeding season (Estimate ± SE = −0.157 ± 0.07, Z = 2.39, p = 0.017; Fig. 4). Such analyses also showed that bird feeders support species that perform pollination (Estimate ± SE = 0.238 ± 0.06, Z = 3.77, p < 0.001), whereas human presence (i.e. pedestrians) reduces the occurrence of species providers (Estimate ± SE = −0.202 ± 0.07, Z = 3.12, p = 0.002).

3.4. Scavenging

The most important scavengers in both seasons were house sparrow, Eurasian magpie (*Pica pica*) and carrion crow (*Corvus corone*) (Figs. S1 and S2). Potential scavenging values increased along the urban landscape organization gradient during both the breeding (Estimate ± SE = −0.104 ± 0.05, Z = 2.15, p = 0.031; Fig. 2) and the non-breeding season (Estimate ± SE = −0.176 ± 0.06, Z = 3.05, p = 0.002; Fig. 2).

No local urban attribute significantly influenced scavenging RES during the breeding season. In contrast, feeders were positively associated with scavenging species during the non-breeding season (Estimate ± SE = 0.149 ± 0.05, Z = 3.00, p = 0.003).

4. Discussion

Our results showed that the urban landscape organization strongly influences the potential provision of avian-mediated Regulating Ecosystem Services (RES), and that these patterns vary substantially between seasons. Our findings also indicate that these differences in the potential provision of RES along the urban landscape organization gradient depends on changes in bird community composition. Such communities are composed of species with high diet-based contribution scores for a given service (e.g. common swift during the breeding season for pest control), together with high abundances of species with lower individual contribution scores (e.g. house sparrow for scavenging). Furthermore, our study emphasized the importance of considering seasonality when investigating the provision of ecosystem services in urban areas and the ecological effects of urban landscape organization (e.g., Graves et al., 2019; Ibáñez-Álamo et al., 2020).

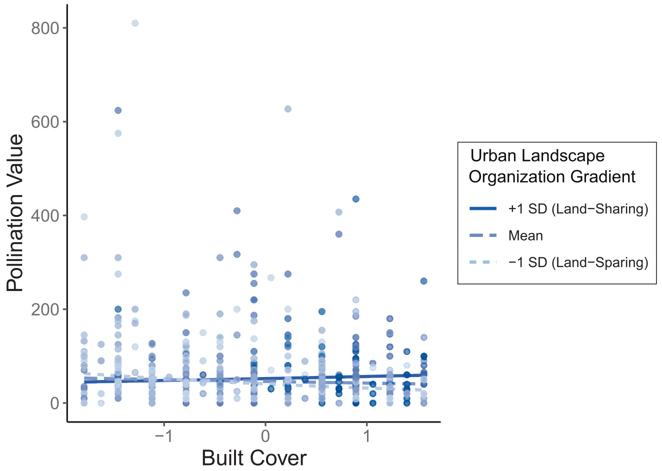

Fig. 4. Result of the interaction between urban landscape organization gradient and built cover for the pollination regulation ecosystem services during the non-breeding season. The variable built cover is scaled. The variable urban landscape organization is divided into three parts: "+1 SD" implies an increase of the values (more land-sparing areas), "Mean" corresponds to mean values of the variable and "-1 SD" implies a reduction in the values of the variable (more land-sharing areas).

4.1. Seed dispersal and pest control

Our results show that the species providers of seed dispersal and pest control followed a similar pattern regarding their relationship with local urban attributes, especially during the non-breeding season. This is probably because both RES were provided by the same pool of species (e.g. spotless starling, *Turdus* spp., great tit).

Our findings indicated that the most extreme form of land-sharing urban areas was potentially related to higher levels of potential seed dispersal and pest control RES values, especially during the non-breeding season. Our results contrast with the only study on ecosystem services across urban landscape organization gradient, which favored land-sparing areas (Stott et al., 2015). This discrepancy may be attributed to differences in taxa (insects vs. birds) or the specific services analyzed. Our findings also contradict our initial predictions, as Wu et al. (2024), reported that large green areas (land-sparing) support more services like pest control and seed dispersal. One possible explanation for this discrepancy is that the proportion (or distribution) of specialist/generalist species differs between our study and theirs. Specialist forest species, that are very sensitive to human disturbance are more typical from land-sparing urban areas (Assandri et al., 2025; Suhonen et al., 2022), and they can be key-providers of these RES (Máthé & Batáry, 2015; Wu et al., 2024). However, urbanization filters out many of these sensitive taxa (e.g., forest-dependent species such as warblers, tits; Jokimäki et al., 2016; Palacio et al., 2018), promoting communities dominated by generalist providers species (Mubamba et al., 2022; Schneiberg et al., 2020). However, although generalists could contribute less to the provision of RES at the individual level, their high abundances may compensate for this and still substantially contribute to RES provision. This is precisely what is suggested by our data, which show higher abundances of generalist RES providers in European land-sharing urban areas. (e.g. spotless starling or common wood-pigeon; see Tables S9 and S10).

Interestingly, our results show that land-sharing areas are associated with higher levels of built cover compared to land-sparing areas (see Table S8). Built cover and other local urban attributes associated with human disturbance are known to reduce avian-mediated RES (Palacio et al., 2018; Swartz et al., 2023). This apparent contradiction may be clarified by considering species' habitat sensitivity. Built cover might mainly impact forest-specialists, while generalists (less affected by these disturbances) continue to provide key ecosystem services. This could partially explain our findings, including the observed negative relationship between built cover and potential pest control values in both seasons, and between built cover and potential seed dispersal in the non-breeding season. Conversely, these forest species benefit from other local urban attributes. For example, we found that species providers of seed dispersal are favored by the percentage of trees and grass during the breeding season. These attributes, linked to green patches, are known to improve general biodiversity levels (Beninde et al., 2015; Morelli et al., 2021; Pena et al., 2023), potentially leading to positive changes in the RES provision.

Furthermore, our results show clear seasonal differences in the relationship between the landscape variables and the species providers of RES. This could be because many urban birds change their diet preferences between seasons (Leveau et al., 2021). During the breeding season, European urban bird communities are dominated by insectivorous species (see Jokimäki et al., 2016), potentially explaining our (lack of) results regarding pest control RES. In contrast, non-breeding bird species, which are more generalist in their diet, could benefit from certain local urban attributes, such as the presence of fleshy fruit-bearing plants. Land-sharing urban areas are mainly privately managed, integrating green spaces with ornamental vegetation depending on the gardening preferences (Paker et al., 2014), potentially leading to more fleshy fruit-bearing plants (Table S8). This management would lead to higher fruit availability in these areas, increasing the species providers of both RES in these locations. Consequently, urban design practices should include this local landscape attribute (i.e. vegetation with fleshy fruit-bearing) to increase the number and abundance of bird species providers, enhancing the provision of RES within the city.

The fact that species during the non-breeding season are more generalists could also explain the positive relationship between the species providers of all RES and the presence of feeders. Bird feeders alter the composition of urban bird communities (Fuller et al., 2008; Jokimäki & Kaisanlahti-Jokimäki, 2012a). In many northern European areas, urban birds need these additional food sources during the non-breeding season to cope with the hard environmental conditions, which increases their densities around bird feeders (Jokimäki & Kaisanlahti-Jokimäki, 2012b; Jokimäki & Suhonen, 1998). Our findings about the importance of feeders in promoting RES provide information in the current debate on whether citizens should use bird feeders based on their associated ecological problems via ecosystem disservices (e.g., spread of diseases, dispersal of harmful plant species) (Reynolds et al., 2017; Robb et al., 2008). In this context, it is important to highlight that we found an interaction between feeders and urban landscape organization gradient for the potential provision of pest control and seed dispersal. More precisely, the positive association between feeders and the species providing pest control and seed dispersal becomes stronger as the urban landscape organization gradient moves toward a land-sparing configuration. One possible explanation can be that land-sharing feeders concentrate lower densities of providers because they can find other food sources in these areas (e.g. vegetation with fleshy fruit-bearing).

Contrasting our predictions, we found that the species providers of seed dispersal and pest control were favored by the presence of mammals (e.g. red squirrels, dogs, cats) in the non-breeding season. We expected that mammals such as pets would negatively affect the provision of these two RES by their negative influence on bird diversity levels (Beliniak & Krauze-Gryz, 2024; Paker et al., 2014). However, it could be that these mammals, especially predators, only reflect the presence of high concentrations of their bird prey. Additionally, it could be possible that, during the non-breeding season, some mammals are attracted to the same feeding sites, potentially explaining the significant association between these species providers and mammals. For example, the red squirrel is attracted to feeders during the non-breeding season (Jokimäki et al., 2017). Also, some carnivores are attracted to places with high density of fruits in the non-breeding season (Guitián & Munilla, 2010) when their prey abundances are lower.

4.2. Pollination

Contrasting our predictions, we did not find a relationship between urban landscape organization gradient and potential pollination values. This RES is normally provided by specialist species (Maruyama et al., 2019; Pauw & Louw, 2012). Nevertheless, in the case of Europe, only a few bird species are considered pollinators, being also more abundant in the Mediterranean region. These European species are mainly forest species such as tits and warblers (da Silva et al., 2014), and they are not affected by urban landscape organization (see Assandri et al., 2025 and supplementary material in Ibáñez-Álamo et al., 2024). However, these species are sensitive to human disturbances (see above; da Silva et al., 2014), being more affected by other urban local attributes (i.e. built cover in breeding season and pedestrians in both seasons). This could also explain our result on the interaction between built cover and urban landscape organization gradient. We found that the negative effect of built cover on potential bird pollinators was stronger in more land-sparing than land-sharing urban areas. Thus the more intense urbanization mode typical of land-sparing urban areas could affect pollinators deeply. These findings are important, considering that European bird pollination is still poorly studied (Sekercioglu et al., 2016; Whelan et al., 2008).

4.3. Scavenging

Finally, in agreement with our predictions, we found that land-sharing urban areas promote avian-mediated scavenging species during both the breeding and non-breeding seasons. Scavenging in urban environments is mainly provided by generalist species with high tolerance to human disturbances (Inger et al., 2016; Mateo-Tomás et al., 2015), like corvids and the house sparrow in our case. Thus, our results could be explained by the higher abundance of corvids found in European land-sharing urban areas (Jokimäki et al., 2020). Also, the fact that scavenging is provided by generalist species could also explain the lack of results regarding urban local attributes, which agrees with the results found by Inger et al. (2016). However, our results are restricted to birds, and do not mean that scavenging is absent in land-sparing urban areas. This ecological function could be carried out by other non-avian species, such as mammals, in land-sparing urban areas as they seem to be favored by large (and less disturbed) green areas typical of this urban landscape organization (Villaseñor et al., 2017).

4.4. Study limitations

Despite our findings providing the first estimation of the effect of urban landscape organization gradient on avian-mediated RES, we would also like to acknowledge some limitations. Firstly, our results might not be directly applicable for continents outside Europe as it depends on bird community composition. Also, probably the most important limitation is that our approach provides a proxy for the potential provision of avian-mediated RES rather than a direct measurement of the provision. Because our estimates are based on diet data, they may over- or underestimate the real value provided by certain species (Pejchar et al., 2025; Sebastián-González et al., 2023). Therefore, more precise studies directly evaluating these RES will provide useful complementary information, especially in urban environments, where there is an important knowledge gap regarding the actual provision of avian RES (Pejchar et al., 2025; Pena et al., 2023). Another important consideration for future studies on the topic is the need to investigate also other ecosystem services that affect human well-being (e.g. cultural) as well as ecosystem disservices (e.g. zoonotic diseases, plant damages) (Lyytimäki, 2015). This approach is relevant in our aim for an integrative and biodiversity-friendly urban planning.

5. Conclusions

Overall, our study provides new knowledge on the growing debate on how to develop cities. Although a land-sharing urban organization seems to be better for bird diversity and the provision of ecosystem services, land-sparing urban areas could also be essential for improving biodiversity of other taxa such as mammals (Caryl et al., 2016; Youngsteadt et al., 2023). Therefore, city planners should design urban areas integrating both urban landscape organizations types (or at least mixed configurations within this gradient), ensuring high levels of biodiversity of different taxa and high levels of ecosystem service provision and ecosystem functioning. They can also promote these outcomes by modifying some local urban attributes. In this way, there are some specific measures that could help to promote avian Regulating

Ecosystem Services (RES). Urban planners could try to minimize built cover by increasing the number of green patches and total green cover (e.g. street vegetation or small public gardens; Lerman et al., 2021, 2023). Also, establishing restricted or semi-restricted areas could provide refuges for key bird species, reducing disturbance from pedestrians. Furthermore, using fleshy fruit-bearing plants, as well as plants with traits that can enhance other sources of food for RES species providers (e.g. improving insect diversity), will promote avian-mediated pest control and seed dispersal during the non-breeding season. The addition of some grassy areas within the urban green patches (e.g. in urban parks) could also help to promote seed dispersal during the breeding season. We hope that these recommendations and other findings from our study can help us find an equilibrium between urban development and biodiversity conservation, guarantee the provision of avian-mediated RES, and consequently, human well-being (Hernández-Blanco et al., 2022; Lerman et al., 2023).

CRediT authorship contribution statement

Lucía Izquierdo: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Data curation, Conceptualization. **Mario Díaz:** Writing – review & editing, Investigation. **Yanina Benedetti:** Writing – review & editing, Investigation. **Jukka Jokimäki:** Writing – review & editing, Investigation. **Marja-Liisa Kaisanlahti-Jokimäki:** Writing – review & editing, Investigation. **Federico Morelli:** Writing – review & editing, Investigation. **Tomás Pérez-Contreras:** Writing – review & editing, Investigation. **Enrique Rubio:** Writing – review & editing, Investigation. **Philipp Sprau:** Writing – review & editing, Investigation. **Jukka Suhonen:** Writing – review & editing, Investigation. **Piotr Tryjanowski:** Writing – review & editing, Investigation. **Juan Diego Ibáñez-Álamo:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of Competing Interest

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2025.105540.

Data availability

Data will be made available on request.

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