

Exploring the biotic homogenization and diversity resistance hypotheses: The understorey of non-native and native woodland canopies in three urban areas of Europe

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Abstract

Aim: Exploring the biotic homogenization and diversity resistance hypotheses by assessing the effect of non-native black locust canopy on understorey species turnover.

Location: Berlin, the Venetian metropolitan area, and Rome.

Methods: We modelled the zeta (ζ) expression of diversity to compare the understorey species turnover between the non-native black locust and native woodland canopies across multiple sites and through predictors of anthropogenic pressure (road and built-up density) and interior conditions (tree basal area and mean height).

Results: In Rome, black locust showed the lowest survivability and cover and did not produce any homogenization of the understorey. In Berlin and in the Venetian metropolitan area, black locust caused understorey homogenization, although with a lower intensity in Berlin. Under black locust canopies, distance between sites and road density was more consistently associated with species turnover, across urban areas and multiple sites. Under native canopies in Berlin, factors prominently associated with species turnover were road and built-up density and mean tree height, while in the Venetian metropolitan area it was road density.

Main conclusions: Evidence in support of the biotic homogenization in contrast to the diversity resistance hypothesis varied across urban areas. Species turnover was influenced by land use patterns more evidently under native tree canopies and where the non-native tree had higher survivability. Similar analyses in other urban areas may confirm these relationships with other types of landscapes.

KEYWORDS

alien species, invasion ecology, invasive tree, land use pattern, *Robinia pseudoacacia*, spatial species turnover, urban biodiversity, urbanization, wild urban woodland, zeta diversity

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1 | INTRODUCTION

Land use patterns determined by city growth are among the main drivers of urban plant diversity at the landscape scale. At the local scale, land use patterns interact with habitat features in determining the diversity of urban vegetation. Urban vegetation is rich in non-native plant species spread by trade, traffic and horticulture (Hulme et al., 2008, 2018; Padayachee et al., 2017). Habitat fragmentation and introductions of non-native species may filter out individuals according to their functional traits. Such filtering reduces specialist species and replaces them with common generalist species (Gámez-Virués et al., 2015), a process known as biotic homogenization (McKinney & Lockwood, 1999; Olden & Rooney, 2006; Winter et al., 2009).

Biotic homogenization can occur with or without changes in species richness within a site (α diversity) (Olden & Poff, 2003), but it always implies a loss of diversity among sites (β diversity). Beta diversity has been often decomposed into two components: nestedness and turnover. Nestedness refers to differences in composition deriving from differences in species richness, where the species pool of a site is a subset of the species pool of a site richer in species. Species spatial turnover, which accounts for biotic homogenization, is the substitution of species from one site to another along a spatial gradient (Baeten et al., 2012).

Woodland patches are important in restoring and maintaining biodiversity within the boundaries of urban areas. If they regenerate spontaneously, they are defined wild urban woodlands to emphasize their high degree of self-regulation in ecosystem processes where direct human impact is negligible. Here, we focus on wild urban woodlands developed on vacant or abandoned urban land uses (Kowarik, 2021), and their plant communities are affected at the landscape scale by anthropogenic pressures from the surrounding built-up areas and road networks (Kowarik, 2005; Kowarik et al., 2019; Trentanovi et al., 2013). Species composition of these woodlands also correlates with stand factors, such as density and height of the tree canopy, indicators of interior conditions. Frequently, invasive non-native trees dominate wild urban woodlands because of their strong propagule pressure and because they disperse more easily than native trees into open disturbed habitats (Alston & Richardson, 2006). In urban areas with very scarce woodland cover, non-native trees play pivotal roles as builders of novel ecosystems (Hobbs et al., 2006), providing habitats for plant and animal species (Kowarik et al., 2019). For this reason, the ability of some non-native tree species to spread on disturbed soils is regarded as a key for initiating ecological restoration in urban areas (Trentanovi et al., 2021). Indeed, not just native, but also non-native wild woodlands, have been considered as potential habitat patches for biodiversity restoration in urban areas for many years (Hare, 1988).

Although wild urban woodlands dominated by non-native trees can be beneficial for biodiversity, their long-term homogenization effects on plant diversity remains a major current focus in urban ecology (Gaertner et al., 2017). A tree species that has received

great attention is black locust (*Robinia pseudoacacia* L.). It is one of the most common non-native invasive tree species in cities from Central to Southern Europe. It easily disperses into open urban habitats, causing changes in light, microclimate and soil conditions, and in turn in biodiversity (Campagnaro, Brundu et al., 2018; Cierjacks et al., 2013; Vítková et al., 2020). For example, a study in the city of Berlin compared invaded sites to nearby uninvaded sites (Trentanovi et al., 2013). A canopy dominated by black locust per se did not result in a higher biotic homogenization of the understorey when compared to canopies dominated by the native trees, since homogenization was mediated by differences in the land cover of the surrounding matrix. However, this result was obtained from a pairwise measure of β diversity that, by definition, is limited to species shared by two sites, and hence overestimates the contribution of rare species. Moreover, this study was referred to one city, while it would be relevant to know whether results can be extrapolated to other cities for both scientific and practical reasons. In fact, the European Union biodiversity strategy for 2030 promotes the restoration of urban biodiversity through tree planting while calling local and regional authorities to control invasive non-native species (European Commission, 2020). Hence, the role and fate envisaged by this strategy for wild urban woodlands remain unclear.

We aimed to fill this gap by assessing the homogenization effect of black locust on understorey species spatial turnover in three European urban areas at different latitudes: Berlin, the Venetian metropolitan area, which consists of the urban functional areas of Padua and Venice (hereafter Padua-Venice), and Rome. Species spatial turnover was measured through zeta (ζ) diversity, the number of shared species by multiple communities, increasingly distant from each other. This metric enables composition patterns to be compared between multiple sites and across spatial scales (McGeoch et al., 2019). We applied a spatially paired sampling design. A non-native dominated canopy and a close native counterpart formed each pair. Therefore, the values of ζ diversity in the understorey could be consistently compared between the two types of canopies.

Compared to native tree canopies, black locust canopies are known to level out topsoil variability, by increasing available phosphorus and phenols and lowering the carbon to nitrogen ratio. Under black locust, shade-tolerant forest species are out-competed by species adapted to disturbance, soil fertility and weedy habitats (Sitzia et al., 2018). Native canopies are usually composed by several tree species, across more variable site conditions. When tree species diversity is low, their understorey might be invaded by opportunistic plants (Chabrerie et al., 2008). In both cases, the understorey of native tree woodlands is expected to have a higher spatial species turnover than black locust woodlands that act as sources of biotic homogenization. An opposite scenario emerges if we accept the classic diversity resistance hypothesis (Levine & D'Antonio, 1999). According to this hypothesis, the understorey of black locust is more susceptible to the propagule pressure of casual species from nearby cultivated plants and hence maintained in a state of permanent succession. Thus, the understorey of black locust canopies should

TABLE 1 Climate type (Cfb: temperate oceanic, Cfa: humid subtropical, Csa: hot-summer Mediterranean climate), area of land cover classes (1: artificial surfaces, 2: agricultural areas, 3: forests and semi-natural areas, 4: wetlands, 5: water bodies), woodlands with participation of black locust, anthropogenic pressure and interior conditions in the three urban areas under study

| Urban area | Climate type ⁽¹⁾ | Area (km ²) | Land cover classes (%) ⁽²⁾ | | | | | Woodlands with black locust (%) | Average survivability of black locust ⁽⁶⁾ | Mean (min-max) values of the variables collected ⁽⁷⁾ | | | |
|--------------|-----------------------------|-------------------------|---------------------------------------|----|----|---|---|---------------------------------|--|---|----------------------|------------------|------------------------------|
| | | | 1 | 2 | 3 | 4 | 5 | | | Road density (%) | Built-up density (%) | Mean height (m) | Basal area (m ²) |
| Berlin | Cfb | 1,075 | 70 | 9 | 16 | 0 | 5 | 0.63 ⁽³⁾ | 0.74 | 12 (4–27) | 30 (5–54) | 13.4 (8–22.1) | 0.4 (0.1–1.4) |
| Padua-Venice | Cfa | 1,283 | 34 | 60 | 2 | 1 | 3 | 0.52 ⁽⁴⁾ | 0.40 | 8 (4–13) | 39 (20–54) | 15.7 (11.1–21.8) | 0.3 (0.1–0.7) |
| Rome | Csa | 1,285 | 43 | 48 | 8 | 0 | 1 | 0.24 ⁽⁵⁾ | 0.18 | 3 (1–6) | 16 (2–44) | 13.2 (10–16.9) | 0.3 (0.2–0.8) |

Note: Sources: (1) Peel et al. (2007); (2) Copernicus Programme (2020); (3) SenStadt (2014) and Landesamt für Umwelt Brandenburg (2009); (4) Del Favero (2006); (5) Regione Lazio (2015); (6) Sitzia, Cierjacks et al. (2016); (7) $n = 66$ in Berlin, $n = 20$ in Padua-Venice, $n = 10$ in Rome.

have a higher spatial species turnover than native tree canopies and should not be homogenized.

Biotic homogenization, however, does not only depend on stand conditions, but also reflects landscape structure and composition. Urban regions are mosaics of built infrastructures, agricultural fields, semi-natural habitats and sparse natural habitats, including wild urban woodlands, whose arrangement may influence the effect of non-native canopies on biotic homogenization (Kühn & Klotz, 2006). Dispersal processes and the ability of the non-native tree to homogenize habitat conditions are strongly dependent on the mean patch size and the heterogeneity of the landscape (Skelsey et al., 2013). The urban land mosaic of Berlin is characterized by compact, but heterogeneous urban agglomerations, and large woodland patches (von der Lippe et al., 2020). A high proportion of species belonging to semi-natural habitats, particularly woodland species, is dispersed by human-aided vectors, like vehicles (von der Lippe & Kowarik, 2007). Among the three urban areas, the Venetian metropolitan area has the greater share of agricultural land (Tempesta, 2010), in which woodlands are limited to small patches within vacant lots, brownfields (Sitzia, Campagnaro et al., 2016), or around hedgerows (Sitzia et al., 2014). The matrix of this land mosaic is expected to produce a diffuse barrier to dispersal, rapidly changing growing conditions, and relevant edge effects for the few wild woodlands present. Finally, the urban sprawl of Rome is characterized by a star-shaped pattern, persistence of woodlands and agricultural field patterns, with benefits for ecological connectivity and vegetation recovery potential (Capotorti et al., 2013; Frondoni et al., 2011).

Here, we aimed at identifying the drivers of understory spatial species turnover across three urban areas that differed in black locust survivability and in land use patterns. We suggest that both the biotic homogenization and the diversity resistance hypothesis could explain any of the differences we may find between the understory of the two canopy types. Moreover, we expect that the association of anthropogenic pressure and interior conditions with spatial species turnover at the landscape and at the local scale will differ across the three urban areas.

2 | METHODS

2.1 | Study urban areas

The urban areas under study were spatially identified as the core of the functional urban area of Berlin, the functional urban areas of Padua and Venice, and the municipality of Rome. The survivability of black locust reflected the precipitation and temperature regimes of the three urban areas. Artificial areas mostly cover Berlin; Padua-Venice and Rome are mixed urban-agricultural areas. Forests and other semi-natural areas are common in Berlin and Rome, while in Padua-Venice they are scarce and dispersed (Table 1).

By the end of the 18th century, black locust started to be cultivated and used as a forestry or ornamental tree, also due to its ability to fix nitrogen. The species became naturalized in the following decades, across all the studied urban areas. Since the 1950s, black locust has spontaneously expanded and it is currently considered invasive (Galasso et al., 2018; Kowarik, 1990; Montelucci, 1950). The sampled stands originated spontaneously, after the cessation of urban and agricultural land uses. Therefore, the stands met the definition of wild urban woodlands codified by Kowarik et al. (2019), although some of the canopy trees might have been occasionally planted.

2.2 | Sampling design

We surveyed plots from nearby paired stands. One stand of the pair had a canopy dominated by the non-native black locust tree and the other a canopy dominated by a native tree species (Figure 1).

Stands within the same pair had a maximum distance of 500 m, while different pairs were at least 1 km distant. Therefore, the same land mosaic was shared by the stands in the same pair, but not by different pairs. Built-up areas covered not more than half of the total surface of land in a 500m buffer around each pair. Mean tree height of the stands should be more than 8 m. Assuming a medium class of fertility, this meant a minimum age of 10 years for black locust and higher for the other tree species (Giordano, 1949; Rédei et al., 2014).

The sampling effort in each urban area was proportional to the observed cover of black locust woodlands. Hence, while in Berlin we sampled 23 pairs, in Padua-Venice and Rome we surveyed the total number of available pairs, respectively, 10 and 5.

Stands dominated by a non-native canopy had a density of black locust, expressed as a cumulative proportion of basal area, the cross-sectional area of trees at breast height, higher than 90%. The native canopies were dominated by birch (*Betula pendula*) (88%) in Berlin; by white poplar (*Populus alba*) (35%), black poplar (*Populus nigra*) (23%), field elm (*Ulmus minor*) (20%) and honeyberry (*Celtis australis*) (10%) in Padua-Venice, and by cork oak (*Quercus suber*) and Turkey oak (*Quercus cerris*) (both 41%) and field elm (9%) in Rome.

2.3 | Data collection

In each stand, we measured stand density and mean tree height and assessed understorey composition in a 10 m × 10 m plot placed at least 5 m away from the stand edge. Stand density was described by basal area. Trees were counted if their diameter at breast height was larger than 5 cm.

Understorey included all herbaceous species and woody plants <2 m in height. Plant surveys were carried out between May and July 2010 in Berlin, between June and July 2017 in Padua-Venice, and in May 2018 in Rome.

For each pair, we assessed the built-up and the road density as a share of the total surface of land in a 500m buffer area. These data were retrieved from existing maps in Berlin or visually recognized and mapped from recent aerial photos in Padua-Venice and Rome.

2.4 | Data analysis

The understorey species turnover was measured by ζ diversity, a concept based on the average number of species shared by any given

number of communities. Zeta diversity improves the description of communities that can be achieved considering α and β diversity. The ζ order i is the number of communities from which the number of shared species is calculated. Zeta diversity at order 1 corresponds to α diversity and at order 2 to β diversity. Differences in the number of shared species at low orders of ζ are driven by rare species and the contrary happens for high orders. Therefore, by increasing the number of sites being compared ($i > 2$), the contribution to turnover of rare and common species can be distinguished along a continuum (further details in Hui & McGeoch, 2014).

The turnover along a single gradient was not of concern in this study. Rather, we were interested in comparing the multidirectional turnover realized by two canopy types in a spatial continuous area. Therefore, we selected the $i-1$ nearest neighbours from each canopy type within each urban area dataset and used them as spatial clusters. In fact, these clusters were subsamples of the whole set of stands of which we calculated the turnover. The number of possible spatial clusters of the $i-1$ nearest neighbours and, in turn, the number of subsamples inevitably decreased with ζ order. As a result, only two combinations and obtainable ζ values were possible for $i = 4$ in Rome. Given that we wanted to compare the ζ diversity of three urban areas at the same orders of ζ , we analysed composition patterns until $i < 5$ through the following three analyses.

We described the pattern of ζ diversity decline as a result of an increase of ζ order. The decline of ζ is slower when the difference between the frequency of rare species with discontinuous ranges, specialist or casual, and common generalist species, is smaller. This trend is due to the fact that rare species are, by definition, shared only by a few sites. We calculated ζ_{1-4} diversity of the understorey under non-native and native canopy separately and compared their raw values. Along ζ_{2-4} , we calculated also the normalized values ζ_i / ζ_{i-1} . Moreover, we used the ratio $(\zeta_{\text{non-native}} / \zeta_{\text{random non-native}}) / (\zeta_{\text{native}} / \zeta_{\text{random native}})$ as a homogenization rate related to the non-native canopy. In line with Roigé Valiente (2017), the random values were generated from randomized occurrence matrices comprising the same

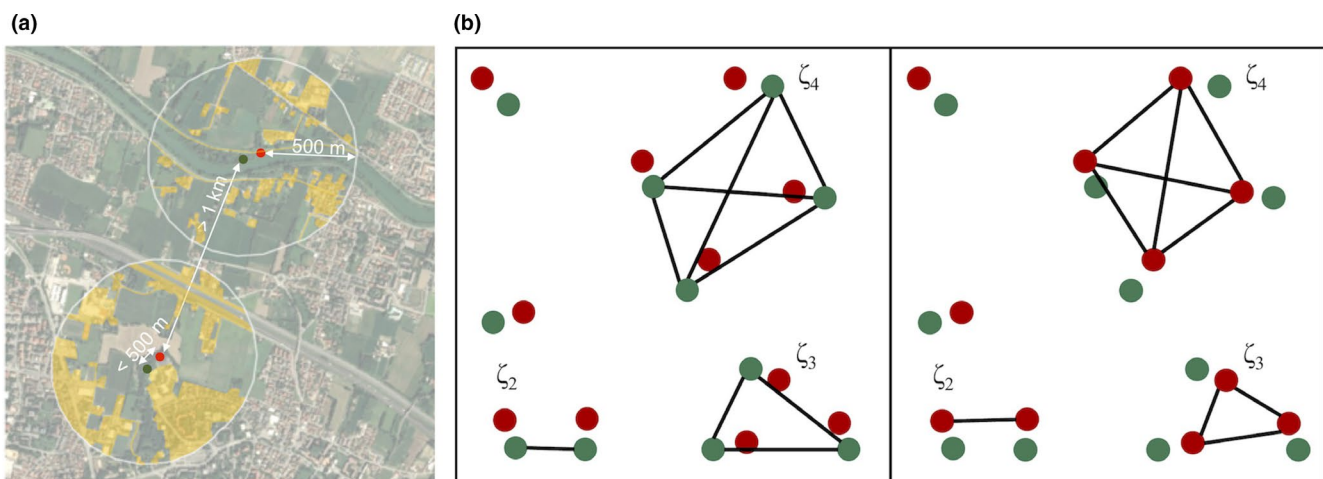


FIGURE 1 Paired plots study design with built-up areas and roads, in yellow, used as predictors of anthropogenic pressure (a) and theoretical scheme displaying how sites are combined for the calculation of ζ diversity at different ζ orders with the nearest neighbour nondirectional scheme (b)

number of presences and absences as in the non-native and native occurrence matrices, respectively.

The mean geographical distance among the sites differed in each of the subsamples that defined the spatial clusters. We analysed if and how the spatial turnover (ζ diversity) decayed with increasing mean geographical distance. This was assessed for each ζ order separately since ζ diversity distance decay from lower to higher orders occurs together with a gradual transition to a greater contribution of common species. The distance decay was computed through a generalized linear model with the parameters suggested by the function `Zeta.ddecay` from the package “zetadiv” of the R software (Latombe et al., 2018).

We used a multi-site generalized dissimilarity model (MS-GDM) to compare the amount of ζ diversity between non-native and native canopies associated with predictors of anthropogenic pressure and interior conditions. The modelling technique is called multi-site because it is an extension of generalized dissimilarity modelling (GDM) to encompass ζ diversity, indeed a multi-site measure of turnover. The rate of change and variation of a given predictor along its observed gradient and the corresponding relative (to the other predictors) effect on ζ diversity was described by a combination of I-splines and generalized linear models (GLM). We did this separately for non-native and native canopies for ζ_2 , ζ_3 and ζ_4 in each urban area. Built-up and road density were used as indicators of anthropogenic pressure, tree basal area and mean height as indicators of interior conditions. Geographical distance was also included. For $i > 2$, the pairwise I-splines differences and distances were combined through their means, and in Berlin, a random sample of 1,000 among the total number of possible combinations (for ζ_4 , $n = 8,855$) was used. In the other cities, all combinations (for ζ_4 , $n = 210$ in Padua-Venice and $n = 5$ in Rome) were used. The values of ζ were normalized dividing the number of shared species by the minimum richness (Simpson version) to emphasize the drivers of richness-independent turnover. Readers unfamiliar with the properties and definitions of the generalized dissimilarity modelling (GDM) can find excellent explanations in Ferrier et al. (2007) and their multi-site application to ζ diversity through I-splines and GLM in Latombe et al. (2018) and Krasnov et al. (2020).

The I-splines provided insight into the total magnitude of species differentiation as a function of each gradient and where, along each gradient, those changes were most pronounced. In particular, MS-GDM provided two information: (a) the relative importance of each predictor in explaining ζ diversity within the same ζ order given by its amplitude, that is the maximum value of the I-splines (the sum of the coefficients of the I-splines), and (b) the rate of turnover and its change across the range of a predictor given by the variation in slope (Ferrier et al., 2007; Latombe et al., 2017). In practical terms, a flat I-spline indicates that the given variable does not influence species turnover. We used the functions `Zeta.msgdm` and `Plot-ispline` from the package “zetadiv” of the software R. Apart from those here explicitly mentioned, we adopted the default parameters suggested by this package. Further details are given in Latombe et al. (2018).

3 | RESULTS

3.1 | Alpha diversity patterns

In Berlin, most of the paired stands (93%) had more understorey species under native than under non-native canopies, but in Padua-Venice six stands (60%) with non-native canopy hosted more species than the paired native canopies. In Rome, three out of five pairs had higher species richness under native canopies. In Berlin, the average species richness per stand decreased from 32.2 under native to 20.6 under non-native canopy, while the differences were negligible in the other two cities, respectively, 11.5 versus 12.6 in Padua-Venice, and 22.2 versus 22.0 in Rome.

3.2 | Biotic homogenization by non-native canopy

The mean number of species shared between the understorey of any two stands with native canopy (ζ_2) ranged between 11.9 in Berlin and 3.4 in Padua-Venice, while under non-native canopy it ranged between 7.5 in Berlin and 4.9 in Padua-Venice. Relative to the total species numbers, under native and non-native canopies the proportion of shared species was nearly the same in Berlin (36.4 vs. 36.9%) and Rome (32.4 vs. 33.6%) but showed a contrasting pattern in Padua-Venice (29.5 vs. 38.9%).

At increasing ζ order, the proportion of understorey species shared between any three and four stands (ζ decline) decreased faster under native canopy in Padua-Venice, while the opposite happened in Rome and Berlin (Table 2).

These patterns are reflected in pairwise homogenization ratios of 1.16, 1.11 and 0.95, in Berlin, Padua-Venice and Rome, respectively. Higher orders of zeta (ζ_{3-4}) showed that the homogenization patterns observed in Padua-Venice and Rome became more marked as more stands were included, while in Berlin they remained stable (Table 3).

3.3 | Patterns of species turnover at increasing distance

The maximum distance between two stands was approximately 30 km both in Berlin and in Padua-Venice, while it was around 20 km in Rome. When four stands were compared, maximum distance decreased to 25 km in Berlin and Padua-Venice and to 13 km in Rome.

By plotting ζ diversity against distance (decay curves) we described patterns of species turnover over increasing study extents, and hence larger spatial scales, within the same ζ order. Order 2 decay curves are shown in Figure 2, and orders 3 and 4 in Figure S1.1 and Figure S1.2 of the Supporting Information, respectively.

Regression slopes of the decay curves for understorey of non-native canopy were statistically significant for all ζ orders only in Padua-Venice, where ζ diversity substantially decreased with increasing distance. Under non-native canopies in Berlin, slopes were

| ζ orders | Berlin | | Padua-Venice | | Rome | |
|----------------|--------|------------|--------------|------------|--------|------------|
| | Native | Non-native | Native | Non-native | Native | Non-native |
| 2 | 36.9 | 36.4 | 29.5 | 38.9 | 32.4 | 33.6 |
| 3 | 58.8 | 50.7 | 32.3 | 61.2 | 66.7 | 64.9 |
| 4 | 67.1 | 50 | 63.6 | 86.7 | 79.2 | 62.5 |

TABLE 3 Mean homogenization ratios between i stands (ζ orders) on understorey plant communities given by the replacement of a native canopy with a non-native canopy in the three urban areas under study

| ζ orders | Berlin | Padua-Venice | Rome |
|----------------|--------|--------------|------|
| 2 | 1.16 | 1.11 | 0.95 |
| 3 | 1.19 | 1.78 | 0.86 |
| 4 | 1.07 | 2.05 | 0.62 |

significant only for $i < 4$. Under native canopies, across all urban areas, values of ζ diversity did not significantly or substantially vary with distance (Table S1).

3.4 | Predictors of species turnover

The patterns of ζ diversity association with anthropogenic pressure and interior conditions differed between Berlin and Padua-Venice and between native and non-native canopies (Figures 3–4). In Rome, the absolute (for $i < 2$) and mean (for $i > 2$) differences among values of predictors for any set of combinations converged to the value for the overall distribution. As explained by Latombe et al. (2017), this produced singularity problems and meant that, across the woodlands sampled in Rome, the MS-GDM model cannot explain deviance because anthropogenic pressure and interior conditions had no evident association with ζ diversity.

The deviance explained by the models was relatively higher in Padua-Venice and under non-native canopies. Compared to anthropogenic pressure and interior conditions, the relative effect of geographical distance was very weak under native canopies for all ζ orders, while the opposite happened under non-native canopies, except for pairwise comparisons ($i = 2$). Among the predictors of interior conditions, mean tree height was consistently associated with species turnover in Berlin, while in Padua-Venice, all the indicators of interior conditions played a lower role under both canopies at all ζ orders. In Berlin, built-up density had lower relative effects under non-native than under native canopies at all orders, the opposite happened under native canopies with built-up density having always the highest amplitude, whereas mean tree height and road density had the highest amplitudes at all orders under non-native canopies, together with geographical distance at $i > 2$. In general, predictors of anthropogenic pressure and interior conditions had similar relative effects in Berlin under both canopies. On the contrary, road density

TABLE 2 Zeta decline: mean per cent shared (ζ_i/ζ_{i-1}) understorey species between i stands in the three studied urban areas, under native versus non-native canopies, with i being the ζ order

had a prominent role compared to the other predictors in Padua-Venice, particularly under native canopies at $i > 2$.

When the effect of a predictor was relatively important, the species turnover was faster at lower values of the predictor under both canopies, particularly for the indicators of interior conditions. The only exception was road density under native canopies in Berlin, which more uniformly influenced the turnover across the whole range of its values.

In Berlin, under native canopies, the role of mean tree height and road density increased with ζ order, and tree basal area had negligible role in shaping ζ diversity. Under non-native canopy, built-up density had a similar pattern, but with increasing ζ order, its role was shared with other predictors. More evidently that with other predictors, increments of tree height in the lower range of values were related to greater changes in shared species between two stands, whereas short to medium geographical distances showed higher changes in shared species between three stands. Instead, ζ diversity between four stands showed strong changes with increments of road density (Figure 3 and Table S2).

As previously mentioned, in Padua-Venice, road density was the most important factor shaping ζ diversity in stands with native canopy, whereas distance was still the most relevant factor for stands with non-native canopy. The variation in species shared by three or four stands under native canopy was only explained by road density with a strong increase in the effect of this variable when shifting from small to medium values across its range. Road density was important also for patterns of turnover under non-native canopy, but most of the variation was still explained by geographical distance, especially if large. In general, with increasing ζ order, species turnover was associated only with one or two factors (Figure 4 and Table S2).

4 | DISCUSSION AND CONCLUSION

Our results provided insights into the homogenization brought by black locust, the most invasive tree non-native to Europe, on the understorey of wild woodlands of three urban areas. We deepened the understanding on how changes in the rate of species turnover, the process that drives homogenization, are influenced by anthropogenic disturbance, interior conditions, spatial scale and level of species commonness. In particular, we focused on how the influence of these factors varies under black locust as opposed to native tree canopies. We suggested that both the biotic homogenization and the diversity resistance hypothesis could explain differences between

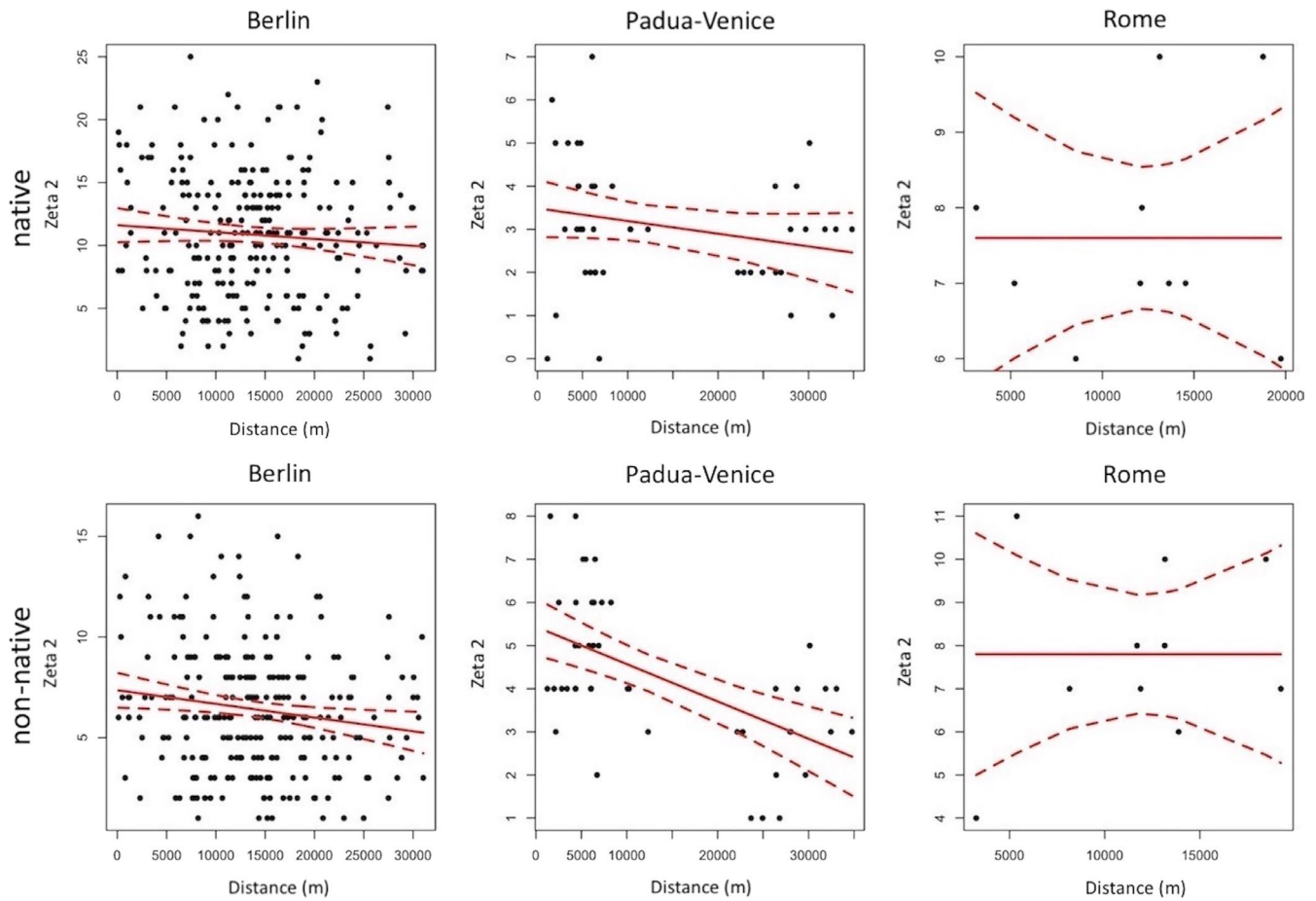


FIGURE 2 Zeta diversity decay over distance (in m) for ζ order 2 in native and non-native stands. ζ -decay shows variation in the number of shared species with increasing distance between sites considered by the chosen ζ order. Dashed lines represent 95% confidence intervals

the understorey of the two canopy types. The two hypotheses were explored by assessing the effect of non-native black locust canopy on understorey species turnover in three European urban areas. We applied a sampling design and the ζ expression of diversity that made it possible to study species turnover at comparable scales between non-native and native canopies and across multiple sites.

Assuming the biotic homogenization hypothesis to account for non-native trees' negative effects on urban plant species turnover, black locust canopies should level out environmental heterogeneity and filter out specialist species, showing a simpler and more stable composition. Under this scenario, black locust canopies must produce biotic homogenization of the understorey and show weaker association of anthropogenic pressure and interior conditions with species turnover. On the contrary, the diversity resistance hypothesis should be accepted in the case that black locust canopy is more susceptible to the propagule pressure of casual species and, hence, its understorey is more variable and subject to faster species turnover and to the effect of outside conditions. Under this scenario, there should be no negative, weak or even positive effect of the non-native tree on urban plant species turnover. The three urban areas under comparison were representative of different climates and floras and showed contrasting land mosaic patterns. For this reason,

we expected that the influence of anthropogenic pressure and interior conditions at the landscape and at the local scale on spatial species turnover would differ across the three urban areas under study.

In the urban area where black locust had the lowest survivability and cover, Rome, the results conformed to the diversity resistance hypothesis. In the other two urban areas, black locust homogenized the understorey, but the intensity of the process was very weak in Berlin. Under black locust canopies, distance between sites and road density were more consistently associated with species turnover, across urban areas and multiple sites, irrespective of the rarity of the species considered. Under native canopies of Berlin, factors prominently associated with species turnover were road and built-up density and mean tree height, while in the Venetian metropolitan area it was road density. In fact, anthropogenic pressure gave an important contribution to ζ diversity, relative to distance, under native canopies, while decreasing similarity in environmental conditions with distance seemed to be a prominent factor in reducing shared species under non-native canopies. This conforms to the biotic homogenization hypothesis.

Previous studies comparing average α and β pairwise diversity between stands dominated by native versus non-native trees focused on individual cities (Aronson et al., 2014; Gaertner et al., 2017;

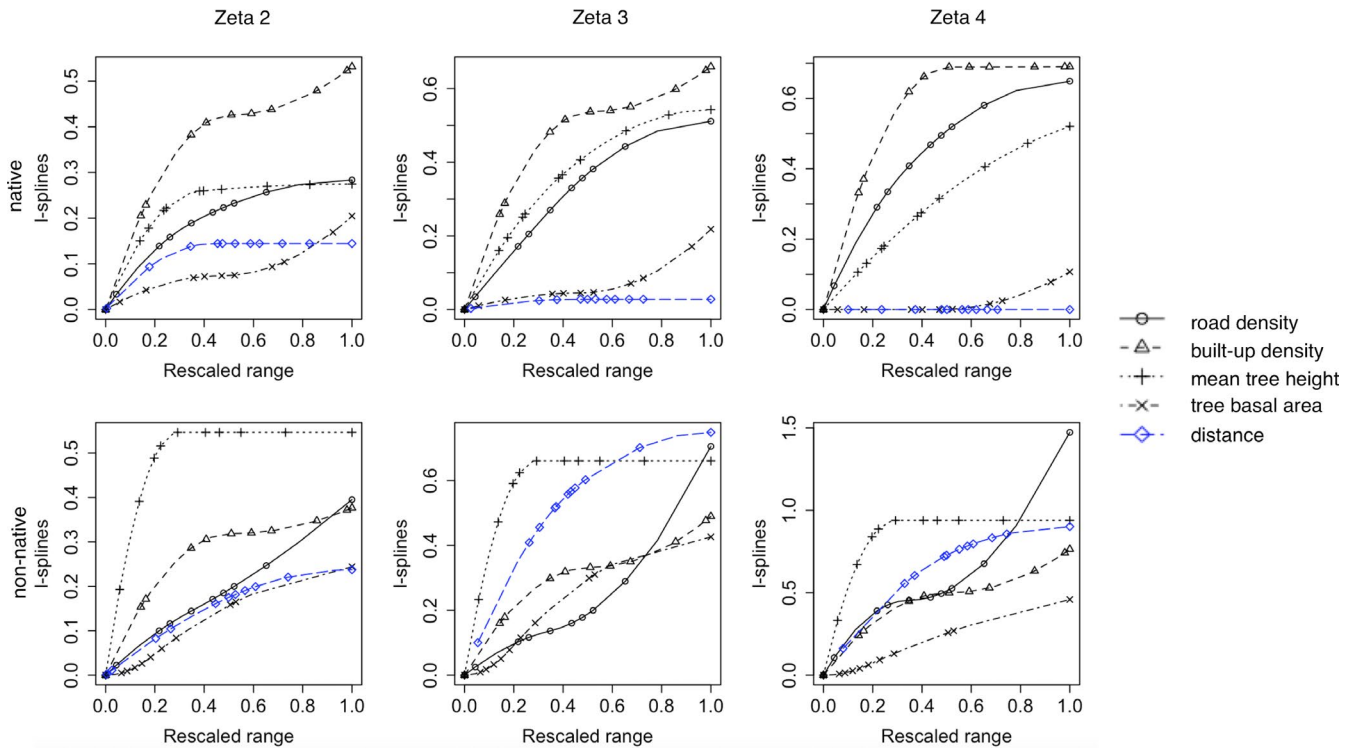


FIGURE 3 I-splines showing the contribution of anthropogenic pressure and interior condition on ζ diversity under native and non-native canopies of Berlin. All variables were rescaled between 0 and 1 for comparison, and changes in slope of the I-splines correspond to changes in rate of compositional dissimilarity with variations of the values of the variable

Kowarik, 2011) and produced contrasting results. Woodland stands with a black locust canopy were found to contribute to the replacement component of β diversity at the landscape scale (Campagnaro, Nascimbene et al., 2018), and black locust canopy did not result in clear homogenization of understorey in rural landscapes (Sitzia et al., 2012). Other studies pointed out that under black locust canopies forest specialists, occurring under native canopies, are replaced by nitrogen demanding species (Benespero et al., 2012), or by an understorey richer and more abundant in non-native species (Von Holle et al., 2005). Micro-environmental conditions under plantations of black locust were found to be highly homogeneous, hence reducing the heterogeneity of the understorey pool of species (Šibíková et al., 2019). In urban areas, canopy dominance by non-native trees reduced α but not β diversity of total species, with changes also influenced by anthropogenic pressures (Trentanovi et al., 2013). Given these contrasting results, it is not surprising that, by encompassing multiple urban areas, our study found that the invasion by a non-native tree determined different patterns of species turnover and did not uniformly conform to a scenario of biotic homogenization. Understorey turnover patterns diverged among cities under both native and non-native canopies.

The homogenization effect due to the non-native canopy was particularly evident only in Padua-Venice. The number of shared species decreased with distance at a markedly faster rate under non-native than under native canopies. As a consequence, the relative effect of spatial distance on understorey turnover compared to the other predictors was weaker under native canopies.

Under black locust canopies, geographical distance had a strong relative effect particularly at lower values of its range, suggesting that the distance decay of similarity in species composition of the understorey was due to rare, casual, species. Understorey of non-native canopies was rather affected by random dispersal of generalist, opportunist plant species. The role of distance reflects some underlying ecological processes that hinder dispersal, such as in our case increased numbers of barriers, like roads. Indeed, the steepest initial slope for anthropogenic disturbance, particularly road density, followed by a plateau, indicated that changes in species composition occurred already at low levels of disturbance. Under native canopies, local factors, such as being closer to dispersal barriers that may disrupt their otherwise more stable composition, must have played a more prominent role (Soininen et al., 2007).

Weak homogenization effects by black locust were observed in Berlin. Native and non-native canopies showed similar patterns of distance decay in ζ diversity that were slower in Berlin than in Padua-Venice. Consequently, the barrier effect must be less pronounced in Berlin than in Padua-Venice, explaining the slower ζ diversity decrease with distance (Soininen et al., 2007). It is also remarkable that under non-native canopies, distance was relatively less important than the other predictors only for the pairwise comparisons in Berlin. We may conclude that the patterns observed by Trentanovi et al. (2013) using pairwise β diversity measures are only partially retained across multiple sites. Instead, in both canopy types of Rome, we recorded wide changes of ζ diversity across different

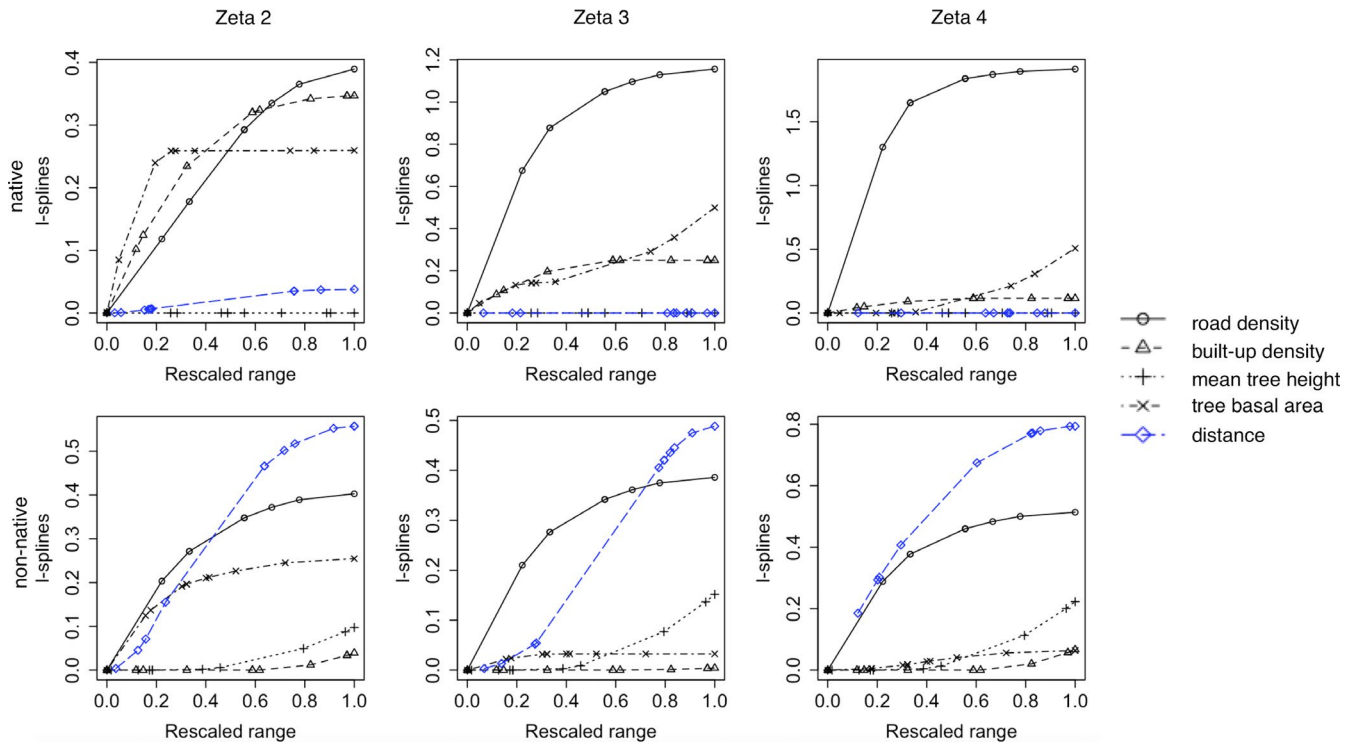


FIGURE 4 I-splines showing the contribution of anthropogenic pressure and interior condition on ζ diversity under native and non-native canopies of Padua-Venice. All variables were rescaled between 0 and 1 for comparison, and changes in slope of the I-splines correspond to changes in rate of compositional dissimilarity with variations of the values of the variable

combinations of stands, however these changes did not show correlation with distance between sites. Moreover, the black locust communities in Rome had a distinct composition, with several characteristic and differential species that may alternate between several stands (Allegrezza et al., 2019). In Rome, anthropogenic pressure and interior conditions did not have any effect, an expected consequence of the narrow fluctuation of ζ diversity and a lack of any evident homogenization effect and distance decay.

We conclude that biotic homogenization effects by non-native trees cannot be generalized across urban areas. Species turnover is influenced by land use patterns more evidently under native woodland canopies and where the non-native tree has higher survivability. It would be interesting to widen the approach here used to other cities, other landscape patterns, and increase the maximum number of site combinations.

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CONFLICT OF INTEREST

Authors declare no conflict of interest.

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BIOSKETCH

Tommaso Sitzia is a forest scientist who pursues a multidisciplinary approach for the management of natural resources. He aims at contributing to an effective integration between biodiversity conservation and the use of natural and semi-natural habitats through teaching, researching, and consulting. His interest in wild urban woodlands originated from a visiting period at the Institute of Ecology of the Technische Universität Berlin.

Author contributions: TS conceived the idea; GT, AC, ML and TS conducted the fieldwork in Berlin; SB, LCG, CB, TS and SI in Rome; SI, TC and TS in the Venetian metropolitan area, with additional material from collaborators; TS and SI analysed the data; AC, IK and ML jointly inspired the idea; SB and CB designed the sample in Rome, and TS coordinated the work and led the writing with major assistance from SI, TC, GT and SB. Every author reviewed the writing, with personal contributions.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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