

Urban park layers: Spatial variation in plant community structure

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Horizontal structure of natural plant communities attracted the attention of researchers for a long time, while the problem of horizontal structure of urban park plantations was not studied sufficiently. Species richness of different tiers of park plantation in the large industrial city of Dnipro (Ukraine) was revealed in this study. Also features of variation in the structure of plant communities at different spatial levels were revealed, the influence of park plantation canopy on the understory and herbaceous layer of the park. There were 30 plant species in the tree layer of the park plantation. The most common species were *Robinia pseudoacacia* L., *Acer platanoides* L., *A. negundo* L., *Gleditsia triacanthos* L., *Aesculus hippocastanum* L., *Populus carolinensis* Moench. The variance-to-mean ratio revealed that 13 tree species were randomly distributed throughout the park, and 14 species were aggregated. The number of occurrences of a given tree species per site and variance-to-mean ratio were positively correlated. The numerous tree species showed a tendency of aggregated distribution within the park. Sixteen plant species were found in the understory. Among them, the most abundant species were *Acer platanoides* L., *A. negundo* L., *A. pseudoplatanus* L., *Sambucus nigra* L., *Robinia pseudoacacia* L. Eight species were found to be randomly distributed over the park area, and eight species showed an aggregate distribution. The number of species encountered in the understory and variance-to-mean ratio were positively correlated. In the herbaceous stand, 99 plant species were found, of which *Chelidonium majus* L., *Viola odorata* L., *Impatiens parviflora* DC., *Parthenocissus quinquefolia* (L.) Planch., *Geum urbanum* L. predominated. The variance-to-mean ratio of all species was significantly less than unity, indicating regular spatial distribution. The values of alpha- and gamma-diversity of the plant community in separate layers are very different. The highest gamma diversity was found for the herbaceous stand, while the diversity of the tree stand and understory was significantly lower. Alpha biodiversity of the tree stand and the understory did not practically differ. Beta diversity values between the layers are very close, and beta diversity is practically equal for tree stand and herbaceous layer. Thus, we can assume that the mechanisms of species turnover for the plant communities of different layers are determined by the common causes. The spatial broad-scale component was able to explain 8.2% of community variation, the medium-scale component was able to explain 4.2% of community variation, and the fine-scale component was able to explain 0.7% of community variation. The understory is the most sensitive to the environmental factors, the herbaceous stand is somewhat less sensitive, and the tree stand is the least sensitive to the environmental factors. The environmental factors in this study are represented by a set of variables. The spatial variation of the stand is predominantly influenced by the factors of trophicity and moisture of the edaphotope. These same factors also act on the herbaceous stand and understory, but along with them are included the environmental variables, which are determined by the architectonics of the crown space and thus the light regime, which is regulated by the tree stand. It is important to note that the variation of the communities of the different layers of the park plantation is subject to spatial patterns. The herbaceous and understory variation is more spatially structured than the tree stand variation. The spatial patterns can arise as a result of the influence of spatially structured environmental factors and as a result of factors of a neutral nature. The latter aspect of variation is best described by the pure spatial component of community variation.

Keywords: GIS-technology; human ecology; ecological monitoring; spatial ecology; vegetation indexes; urban ecology.

Introduction

The horizontal aspect of the forest ecosystem can be divided into above-ground layers: herbaceous layer, shrub layer, understory, and canopy (Boyle et al., 2016; Luo, 2019). There are different approaches for classifying the forest on the basis of canopy stratification, which provided a basis for conceptualizing forest structure in different ways (Parker & Brown, 2000). Forest stratification is of interest for many problems in the context of forest ecosystem management, wildlife conservation, and recreation. The stratification of stands into canopy and understory layers has ecological significance for flora and fauna (Gunnarsson et al., 2009), including various insects (Ishii et al., 2004) and birds (Zimaroeva et al., 2016). In favourable conditions, the degree of differentiation and the number of horizontal forest layers may increase (Bugno-Pogoda & Durak, 2021; Matsuo et al., 2021), while in unfavourable conditions, on the contrary, the layer structure of forest is simplified (De Cáceres et al., 2019). The forest herbaceous layer consists of herbaceous (or soft-stemmed)

plants (Thrippleton et al., 2016; Wavrek et al., 2017). The vegetation in the herbaceous layer of the forest often receives little light (Gilliam, 2007), and shade-tolerant species predominate in dense canopy forests (Avalos, 2019). The area and species richness of herbaceous plants can vary greatly depending on the ecological conditions of the forest (Willie et al., 2018; Dormann et al., 2020). In temperate deciduous forests, many species of herbaceous plants flower in the spring before the trees are leafy (Gougherty & Gougherty, 2018). The tree canopy regulates the availability of understory resources such as light, nutrients and water (Mestre et al., 2017). Herbaceous diversity may depend more on factors limiting dispersion than on competition for light (Brudvig et al., 2011). The species composition of trees determines the chemical composition of water that flows down the trunks and the composition and structure of leaf litter, which strongly influences the herbaceous or shrub layer (Barbier et al., 2008; Pilon et al., 2021). The detailed-scale variability of the herbaceous stand is best explained by the mechanical resistance of the soil, electrical conductivity of the soil, litter thickness, soil temperature, moisture, density, and

aggregate structure. The broad-scale component of plant community variability is explained by stand structure (Zhukov et al., 2019). Mixed species plantations contribute more to the productivity and stability of forest ecosystems than monocultures. Understorey plant diversity is higher in mixed-species plantings than in monocultures. The positive effect of mixed plantations increased over time (Gong et al., 2021). The herb communities of urban tree plantations varied depending on various factors. The abundance and distribution of these species depended on their biological characteristics (duration of seed life in the soil), as well as on the diameter of the tree trunk, soil compaction, animal feces, solar radiation, and woody plant species (Omar et al., 2018). Biotic interactions and niche processes are the key drivers of plant community structure and species co-occurrence. The tree canopy has a strong filtering effect on the structure of understorey plant communities. Resource availability, rather than spatial heterogeneity of resources, is the main factor determining the diversity of the understorey (Zangy et al., 2021). Tree cover affects the composition of species associations of herbaceous tiers. Ecological filtration is the cause of the association of species with similar functional traits (Kohli et al., 2018). A competitive exclusion results in a low probability of co-occurrence of species with similar functional traits if competition dominates community construction (Cordero & Jackson, 2019).

The shrub layer consists of shrubs or woody plants growing relatively close to the ground surface. On a national and forest type scale, shrub species richness is largely driven by climatic and soil variables (Moreno-Fernández et al., 2021). A sufficient amount of light passing through the forest canopy is a prerequisite for the development of the shrub layer (Matsuo et al., 2021). The understorey consists of immature trees or small trees that are shorter than the main canopy level (Bohlman, 2015; Giles et al., 2022). The composition and biomass of the understorey may be variable depending on the soil depth, slope, and structure of the overstorey (Hart & Chen, 2006). Understorey communities are important because they act as determinants of overstorey succession and nutrient cycling (Hart & Chen, 2006). The understorey provides shelter for a wide range of animals (Brygadyrenko, 2015; Chaplygina et al., 2015; Zimaroeva et al., 2016; Putschkov et al., 2019). The understorey is often dimly lit and calm without much wind because of the upper protective canopy screen (Haga et al., 2022). The canopy is the layer where the crowns of most forest trees converge to form a thick layer (Kitajima, 2004). The canopy is exposed to sunlight and also forced to withstand winds (Odemark & Segalini, 2014). Trees grow tall in the struggle for access to light (Fransson et al., 2021). The herbaceous layer can reduce the species diversity of the forest stand (Royo & Carson, 2006).

The understorey is a critical feature of forest ecosystems that affects energy flow and nutrient cycling, biodiversity, and resilience (Gilliam, 2007). The composition of the understorey controls the growth, survival, and regeneration of the forest (Tonteri et al., 2016). Tree canopy determines the spatial patterns of soil macrofauna at different scales (Zhukov et al., 2018, 2019). The understorey plants are sensitive to natural and anthropogenic influences and are indicators of the sustainability, health, and conservation status of temperate forests because of their importance to ecosystem function (Lencinas et al., 2011). The understorey prevents soil erosion (Liu et al., 2022) and affects the microenvironment for the development of other species (Alasmay et al., 2020). The overstorey and understorey vegetation structure affects the understorey light environment (Messier et al., 1998). Forest understorey regulates gross photosynthetic activity of the forest floor vegetation (Kolari et al., 2006; Zymaroeva et al., 2019). The composition, structure, and distribution of the understorey community depend on the forest structure, microenvironmental conditions, and stand conditions (Márialigeti et al., 2016; Tinya et al., 2021). The composition of the understorey correlated with the structural metrics of the forest canopy rather than tree height or diameter. The structural metrics of the tree canopy reflect modifications in the light climate of the understorey (Majasalmi & Rautiainen, 2020).

Spatial and temporal patterns of forest canopy reflectance are extremely important for determining biophysical parameters of forest canopy and for modeling ecosystems (Zhukov et al., 2021). In temperate forests, the rate of development and the maximum possible biomass of the herbaceous layer depend on the relative level of light reaching the forest floor (Nabuurs, 1996). The important ecosystem functions of the understorey

attract attention to it as an object of study by remote sensing methods (Miller et al., 1997; Zymaroeva et al., 2019). The results obtained from satellite data correlate with *in situ* measured trajectories of seasonal reflection of forest understorey layers (Majasalmi et al., 2015). Plant interactions can be defined as the ways in which plants influence the growth, adaptability, survival, and reproduction of other plants, mainly by changing the environment. These interactions can be positive (facilitation) or negative (competition or exploitation) (Balandier et al., 2006). The interaction between herbaceous understorey and tree canopy is usually considered one-way. The trees of the overgrowth are seen as determining the composition of the herbaceous understorey, controlling the amount of light that reaches the forest floor (Gilliam, 2007; Li et al., 2012). However, the herbaceous understorey can significantly interfere with tree regeneration and affect the composition and dynamics of the overstorey. The herbaceous layer affects tree regeneration in different ways (Balandier et al., 2006; Royo & Carson, 2008). The herb stand acts as an ecological filter affecting the organization of the seed bank in deciduous forests. The herbaceous stand filter influenced the emergence of tree seedlings in different ways. The mechanism of the effect of the herbaceous stand filter depended on the type of trees (Thrippleton et al., 2016). It could be a change in soil properties, a change in light levels, or the attraction of predators that destroyed tree seeds. The herbaceous stand filter selectivity is due to the differential response of tree seedling species to the presence of grass cover and did not depend on the species of the herbaceous plants. The selectivity of the herb stand filter can affect the density and species composition of the seedling bank under its canopy and can determine the patterns of spatial distribution of seedlings at the canopy level (George & Bazzaz, 1999). Competition for water and nutrients can have a strong impact in dry or poor soil conditions. Light penetration is lowest in forests on moist soils that provide plenty of basic nutrients (Coomes & Grubb, 2000; Zhukov et al., 2021). The competition for light between the understorey and the forest canopy changes during the successional dynamics of the forest community. The light-demanding grasses, forbs, and shrubs dominate the open areas of the forest at the beginning of succession (Liefers et al., 1993). The abundance and diversity of understorey vegetation increases rapidly after disturbances in response to resource abundance and the influx of species adapted to disturbance. Shade-tolerant herbaceous species receive a greater advantage as the canopy closes (Hart & Chen, 2006).

During plantation establishment or natural forest regeneration after disturbance, high light levels and, sometimes, increased water and nutrient availability promote the development of opportunistic, fast-growing herbaceous and woody species that capture resources at the expense of cultivated trees (Diaci et al., 2017; Wagner et al., 2018). As a consequence, the growth and survival of cultivated trees can be drastically reduced. Within the first 15–20 years, the effect of the herbaceous layer on tree regeneration is usually considered to be strongest (Balandier et al., 2006). In conditions of pesticide application, the herbaceous layer reduces tree regeneration so much that the ecosystem is “trapped” in the herb/shrub stage and does not return to the forest (so-called “arresting succession” (Niering & Goodwin, 1974). Herbaceous vegetation significantly inhibits tree regeneration even in a closed canopy (George & Bazzaz, 1999). The biomass of herbaceous plants generally increases as canopy environments become more open (López-Carrasco et al., 2015). Windfalls and forest fires are especially significant for the grass layer because the disturbances create favourable environments for pioneer species (Turner & Gardner, 2015). Interactions between the herbaceous and tree layer are enhanced amid frequent disturbances and unstable environments (Peltzer et al., 2010). Forest plantation management practices represent a unique process of disturbance and can result in understorey plant communities that differ from those observed in natural processes (Kuuluvainen et al., 2021). The spatial and temporal context is of particular importance for understanding the interaction between overstorey and understorey (McCarthy, 2003).

Horizontal and vertical complexity are factors in the attractiveness of urban parkland for recreation (Nielsen & Jensen, 2007). The formation of a complex stratified canopy structure takes a considerable amount of time and usually occurs in mature forest stands after a long period of development (Franklin & Van Pelt, 2004). Stratified canopies are a highly valued

feature for forest recreation (Gundersen & Frivold, 2008). However, the number of strata is not a direct indicator of the attractiveness of a forest plantation for recreation (Ribe, 1989). Visual aspects vary considerably depending on plantation design and silvicultural systems. Monoculture offers the splendor of a mature columnar hall with free views and movement. Designs using succession and variations in species, age and spacing of trees offer an enhanced experience of diversity and naturalness even in the young stages (Nielsen & Jensen, 2007).

A significant body of scientific literature is devoted to the study of the horizontal structure of natural forests, while the problem of the horizontal structure of park plantations has not been sufficiently studied. Therefore, the purpose of this study was to discover the species richness of different tiers of park plantations, to reveal the features of variation in the structure of plant communities at different spatial levels, and to assess the influence of park plantation canopy on the understorey and herb layer of the park.

Material and methods

Sampling design. The study was conducted in the recreational area of the Botanical Garden of the Oles Honchar Dnipro National University (Ukraine) June 27, 2022. The sample points were located on a quasi-regular grid (Fig. 1). The highest topography point (176 meters above sea level) is in the western part of the park, and the height of the terrain decreases towards the east. The southern boundary of the Dovgaya Ravine is in the northwestern part of the park. The ravine is filled with construction debris and its level is slightly higher than the natural values. The lowest part of the terrain (153 m) on the territory of the park is in the ravine talveg. The measurements were performed at 230 sampling points. The reconstruction of the 2.8-hectare section of the park was carried out in 2019. Plant taxonomic names follow the Euro+Med Plantbase resource (<http://ww2.bgbm.org/EuroPlusMed>).

Measurement of environmental properties. The soil moisture content was measured with an MG-44 (Ukraine) at a depth of 5–7 cm. The measurement step of the device is 0.1% and the error is 1%. The soil temperature in the 7–10 cm layer was measured by a digital thermometer TC-3M (Ukraine). Air temperature and atmospheric humidity at a height of 1.5 m were measured with a HUATO HE-173 temperature and humidity logger (China). The illuminance at a height of 1.5 m was measured with a RSE-174 luxmeter (Germany). An HI 76305 sensor (Hanna Instruments, Woodsocket, RI) was used to measure the electrical conductivity of the soil in situ. This sensor works together with a portable HI 993310 tester. The tester evaluates the total electrical conductivity of the soil, i.e. the combined conductivity of air, water and soil particles. The measurement results of the device are presented in units of soil salt concentration, i.e., g/L. The comparison of HI 76305 measurements with laboratory data allowed us to estimate the unit conversion factor as $1 \text{ dS/m} = 155 \text{ mg/L}$ (Pennisi & van Iersel, 2002; Yorkina et al., 2021). The tree height was measured with an optical altimeter SUUNTO “PM-5/1520” (Finland). The diameter of the trunk of a tree at a height of 1.3 m was measured with a Mantax Precision Blue Caliper 650 mm Haglof (Sweden) as an average of measurements in two perpendicular directions. The length of the trunk diameter circle was measured with a Stanley Longtape Fiberglass 30 m × 12.7 mm tape measure when the diameter exceeded 650 mm, followed by the calculation of the diameter value.

Canopy structure and gap light transmission indices. Fisheye colour photographs were used to evaluate canopy structure. The light transmission indices of the openings were calculated using Gap Light Analyzer (GLA) software (Bianchi et al., 2017). The below indices were estimated: The proportion of open sky visible from under the forest canopy is characterized by the canopy openness percentage – COP, the effective leaf area index – LAI (Stenberg et al., 1994), the direct solar radiation transmitted by the canopy – Dr, the diffuse solar radiation transmitted by the canopy – Df.

Spectral indices based on remote sensing data. Vegetation indices were calculated based on Sentinel-2 satellite images (<https://earthexplorer.usgs.gov>): Normalized Difference Vegetation Index (NDVI) (Rouse et al., 1974), Normalized Difference Infrared Index (NDII) (Hardisky et al., 1983), Red-Edge NDVI-1 (RE NDVI-1) and Red-Edge NDVI-2 (RE NDVI-2) (Xie et al., 2018), Green NDVI (GNDVI) (Gitelson et al., 1996), Land Surface Water Index (LSWI) (Jurgens, 1997), Leaf Area

Index (LAI) (Delegido et al., 2011), MERIS Terrestrial Chlorophyll Index (MTCI) (Dash & Curran, 2004) First developed for the Medium Resolution Imaging Spectrometer (MERIS).

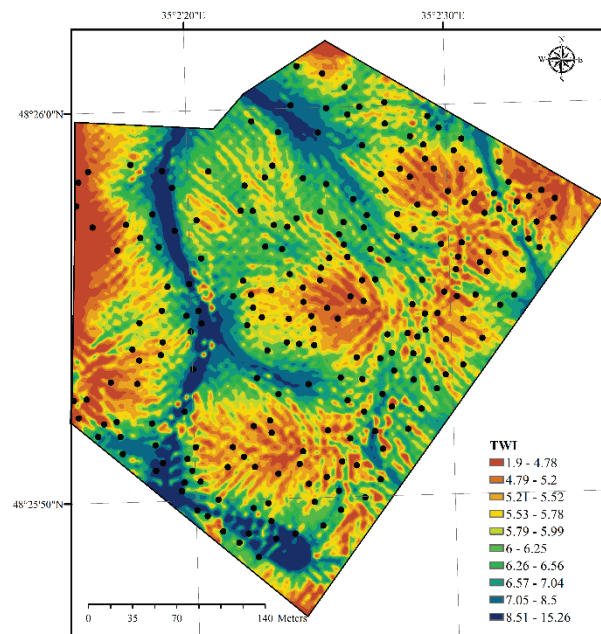


Fig. 1. Spatial variation in topographic wetness index and sampling point

Statistical calculations. The descriptive statistics and regression model parameters were calculated in the software Statistica. Partial redundancy analysis was applied to ordinate the plant communities. Applying the predictor as conditional allows us to evaluate the influence of other factors on the community if the influence of the conditional predictor is excluded. The comparison of ordinal solutions was performed using the Procrustean analysis procedure (Peres-Neto & Jackson, 2001). The ordination and partitioning of the variation of the soil macrofauna community were performed using the vegan library (Oksanen, J., 2017. *Vegan: Ecological diversity*. R Package Version 2.4-4, 1, 11. <https://cran.r-project.org/package=vegan>).

Results

There were 30 plant species in the tree layer of the park plantation (Table 1). The most common species were *Robinia pseudoacacia* L., *Acer platanoides* L., *A. negundo* L., *Gleditsia triacanthos* L., *Aesculus hippocastanum* L., *Populus carolinensis* Moench. The variance-to-mean ratio revealed that 13 tree species were randomly distributed throughout the park, and 14 species were aggregated. The number of tree occurrences of a given species per site and variance-to-mean ratio were positively correlated (Spearman's rank correlation coefficient was 0.61, $P < 0.001$). Thus, numerous tree species showed a tendency of aggregated distribution within the park.

Sixteen plant species were found in the understorey. Among them, the most abundant species were *Acer platanoides* L., *A. negundo* L., *A. pseudoplatanus* L., *Sambucus nigra* L., *Robinia pseudoacacia* L. Eight species were found to be randomly distributed over the park area, and eight species showed an aggregate distribution. The number of species encountered in the understorey and variance-to-mean ratio were positively correlated (Spearman's rank correlation coefficient was 0.64, $P < 0.002$). In the herbaceous stand, 99 plant species were found, of which *Chelidonium majus* L., *Viola odorata* L., *Impatiens parviflora* DC., *Parthenocissus quinquefolia* (L.) Planch., *Geum urbanum* L. predominated (Table 2). The variance-to-mean ratio of all species was significantly less than unity, indicating regular spatial distribution.

In the tree stand, the alpha diversity was 1.82 species and was in the range of 1.78–1.88 species 95% of the cases (Table 3). The gamma diversity of the stand was 26.85 species and 95% of the cases ranged from 25.33–27.85 species. The beta diversity of the stand was 14.81 and 95%

of the cases ranged from 13.73–15.58. In the understory, the alpha diversity was 1.72 species and ranged from 1.65–1.81 species in 95% of cases. The gamma diversity of the understory was 16.09 species and 95% of the cases ranged from 14.57–17.09 species. The beta diversity of the understory was 8.33 and 95% of the time ranged from 9.28–10.13. The alpha diversity of the herbaceous stand was 6.82 species and 95% of the case range was 6.73–6.92 species. The herbaceous gamma diversity was 99.56

species and ranged from 95.04–102.56 species 95% of the cases. The beta diversity of the herbaceous stand was 14.58 and 95% of the cases ranged from 13.94–15.04. The total alpha diversity of the community was 8.98 species and 95% of the cases ranged from 8.12–9.24 species. The total gamma diversity of the community was 142.49 species and was in the range of 135.96–145.49 species 95% of the cases. The community beta diversity was 15.07 and ranged from 15.61–16.04 in 95% of cases.

Table 1

Descriptive statistics of species abundance in the stand and understory layer

Species	Sum of individuals	Mean, individuals per sampling plot	Variance	Variance-to-mean ratio
<i>Acer negundo</i> L.	67	0.291	0.522	1.79
<i>A. platanoides</i> L.	116	0.504	1.046	2.07
<i>A. pseudoplatanus</i> L.	15	0.065	0.105	1.61
<i>Aesculus hippocastanum</i> L.	29	0.126	0.207	1.64
<i>Ailanthus altissima</i> (Mill.) Swingle	16	0.070	0.179	2.57
<i>Betula pendula</i> Roth	12	0.052	0.102	1.96
<i>Celtis occidentalis</i> L.	4	0.017	0.017	0.99
<i>Fraxinus excelsior</i> L.	1	0.004	0.004	1.00
<i>F. pennsylvanica</i> Marshall	19	0.083	0.111	1.34
<i>Gleditsia triacanthos</i> L.	37	0.161	0.284	1.77
<i>Juglans regia</i> L.	4	0.017	0.017	0.99
<i>Malus domestica</i> (Suckow) Borkh.	2	0.009	0.009	1.00
<i>Morus alba</i> L.	18	0.078	0.151	1.93
<i>Populus alba</i> L.	3	0.013	0.013	0.99
<i>P. deltoides</i> W. Bartram ex Marshall	25	0.109	0.176	1.62
<i>P. × canadensis</i> Moench	1	0.004	0.004	1.00
<i>P. nigra</i> L.	3	0.013	0.013	0.99
<i>P. nigra</i> var. <i>italica</i> (Moench) Koehne	1	0.004	0.004	1.00
<i>P. simonii</i> Carriere	10	0.043	0.085	1.97
<i>Pyrus communis</i> L.	2	0.009	0.009	1.00
<i>Quercus robur</i> L.	8	0.035	0.034	0.97
<i>Robinia pseudoacacia</i> L.	177	0.770	1.410	1.83
<i>Salix alba</i> L.	1	0.004	0.004	1.00
<i>S. cinerea</i> L.	2	0.009	0.009	1.00
<i>Sambucus nigra</i> L.	6	0.026	0.052	1.98
<i>Tilia amurensis</i> Rupr.	1	0.004	0.004	1.00
<i>T. platyphyllos</i> subsp. <i>cordifolia</i> (Besser) C.K.Schneid.	12	0.052	0.111	2.12
<i>T. × europaea</i> L.	1	0.004	0.004	1.00
<i>Ulmus laevis</i> Pall.	19	0.083	0.085	1.03
<i>U. minor</i> Mill.	4	0.017	0.017	0.99
Understory				
<i>Acer campestre</i> L.	8	0.035	0.034	0.97
<i>A. negundo</i> L.	34	0.148	0.354	2.39
<i>A. platanoides</i> L.	309	1.343	15.633	11.64
<i>A. pseudoplatanus</i> L.	11	0.048	0.081	1.69
<i>Celtis occidentalis</i> L.	4	0.017	0.035	1.99
<i>Crataegus fallacina</i> Klokov	3	0.013	0.013	0.99
<i>Euonymus europaeus</i> L.	1	0.004	0.004	1.00
<i>Fraxinus excelsior</i> L.	2	0.009	0.009	1.00
<i>Gleditsia triacanthos</i> L.	3	0.013	0.013	0.99
<i>Juglans regia</i> L.	8	0.035	0.051	1.47
<i>Ligustrum vulgare</i> L.	1	0.004	0.004	1.00
<i>Morus alba</i> L.	6	0.026	0.026	0.98
<i>Prunus spinosa</i> subsp. <i>dasyphylla</i> (Schur) Domin	1	0.004	0.004	1.00
<i>Robinia pseudoacacia</i> L.	16	0.070	0.161	2.32
<i>Sambucus nigra</i> L.	30	0.130	0.236	1.81
<i>Ulmus laevis</i> Pall.	7	0.030	0.038	1.26

Table 2

Beta distribution parameters and estimates of the mean and variance, as well as bootstrap estimates of the confidence interval for the projective coverage of herbaceous plants

Species	Shape parameters		Mean, cover per sampling plot	Variance	Variance-to-mean ratio	Confidence interval, individuals per sampling plot	
	α	β				2.5%	97.5%
<i>Acer campestre</i> L.	0.006	4.35	0.14	0.03	0.21	0.00	0.38
<i>A. negundo</i> L.	0.039	4.91	0.79	0.13	0.16	0.38	1.33
<i>A. platanoides</i> L.	0.281	5.80	4.63	0.62	0.13	3.66	5.68
<i>A. pseudoplatanus</i> L.	0.004	8.98	0.04	0.001	0.03	0.00	0.09
<i>Achillea millefolium</i> L.	0.003	3.43	0.10	0.02	0.20	0.00	0.20
<i>Aesculus hippocastanum</i> L.	0.003	2.10	0.14	0.05	0.36	0.00	0.28
<i>Agrostis capillaris</i> L.	0.003	0.53	0.48	0.31	0.65	0.00	1.30
<i>Ailanthus altissima</i> (Mill.) Swingle	0.033	4.93	0.66	0.11	0.17	0.29	1.14
<i>Alliaria petiolata</i> (M.Bieb.) Cavara et Grande	0.027	5.35	0.49	0.08	0.16	0.19	0.91
<i>Allium rotundum</i> L.	0.003	3.43	0.10	0.02	0.20	0.00	0.20
<i>Ambrosia artemisiifolia</i> L.	0.016	5.95	0.27	0.04	0.15	0.04	0.56
<i>Anisantha tectorum</i> (L.) Nevski	0.035	3.81	0.92	0.19	0.21	0.43	1.57

Species	Shape parameters		Mean, cover per sampling plot	Variance	Variance-to-mean ratio	Confidence interval, individuals per sampling plot	
	α	β				2.5%	97.5%
<i>Anthriscus sylvestris</i> (L.) Hoffm.	0.080	1.67	4.59	1.59	0.35	3.09	6.35
<i>Arctium lappa</i> L.	0.017	2.45	0.70	0.20	0.29	0.23	1.39
<i>A. minus</i> (Hill) Bernh.	0.203	4.19	4.62	0.82	0.18	3.53	5.91
<i>Artemisia absinthium</i> L.	0.004	8.98	0.04	0.004	0.10	0.00	0.09
<i>A. vulgaris</i> L.	0.016	9.08	0.17	0.02	0.12	0.00	0.30
<i>Asclepias syriaca</i> L.	0.004	6.04	0.06	0.01	0.17	0.00	0.12
<i>Asperugo procumbens</i> L.	0.003	3.43	0.10	0.02	0.20	0.00	0.20
<i>Ballota nigra</i> subsp. <i>ruderalis</i> (Sw.) Briq.	0.131	1.92	6.40	1.97	0.31	4.72	8.37
<i>Bromopsis inermis</i> (Leys.) Holub.	0.004	6.04	0.06	0.009	0.15	0.00	0.12
<i>Calamagrostis epigeios</i> (L.) Roth	0.004	8.98	0.04	0.004	0.10	0.00	0.09
<i>Campanula rapunculoides</i> L.	0.004	8.98	0.04	0.004	0.10	0.00	0.09
<i>Capsella bursa-pastoris</i> (L.) Medik.	0.027	6.21	0.44	0.06	0.14	0.17	0.79
<i>Carex acuta</i> L.	0.004	6.04	0.06	0.01	0.17	0.00	0.12
<i>C. spicata</i> Huds.	0.165	6.02	2.67	0.36	0.13	1.94	3.50
<i>Celtis occidentalis</i> L.	0.016	9.08	0.17	0.02	0.12	0.00	0.30
<i>Chaerophyllum temulum</i> L.	0.109	2.15	4.85	1.42	0.29	3.45	6.51
<i>Chelidonium majus</i> L.	0.244	1.06	18.71	6.61	0.35	15.45	21.99
<i>Chenopodium album</i> L.	0.054	1.54	3.41	1.27	0.37	2.08	5.01
<i>Cichorium intybus</i> L.	0.003	2.10	0.14	0.05	0.36	0.00	0.28
<i>Cirsium arvense</i> (L.) Scop.	0.042	1.91	2.16	0.72	0.33	1.22	3.41
<i>Clematis vitalba</i> L.	0.003	0.50	0.54	0.36	0.67	0.00	1.37
<i>Convolvulus arvensis</i> L.	0.020	5.49	0.37	0.06	0.16	0.11	0.74
<i>Cynoglossum officinale</i> L.	0.008	9.01	0.09	0.01	0.11	0.00	0.17
<i>Dactylis glomerata</i> L.	0.049	2.80	1.71	0.44	0.26	0.96	2.67
<i>Elymus repens</i> (L.) Gould	0.018	1.45	1.21	0.48	0.40	0.47	2.26
<i>Equisetum arvense</i> L.	0.005	1.46	0.34	0.14	0.41	0.00	0.88
<i>Erigeron annuus</i> (L.) Desf.	0.091	4.38	2.04	0.36	0.18	1.34	2.92
<i>E. canadensis</i> L.	0.007	4.75	0.15	0.03	0.20	0.00	0.30
<i>Euonymus europaeus</i> L.	0.004	6.04	0.06	0.009	0.15	0.00	0.12
<i>Fallopia convolvulus</i> (L.) Á. Löve	0.008	9.01	0.09	0.009	0.10	0.00	0.17
<i>Festuca valesiaca</i> Schleich. ex Gaudin	0.002	0.51	0.44	0.29	0.66	0.00	1.32
<i>Fraxinus excelsior</i> L.	0.033	5.43	0.61	0.09	0.15	0.26	1.05
<i>Galinsoga parviflora</i> Cav.	0.002	0.41	0.39	0.27	0.69	0.00	1.16
<i>Galium aparine</i> L.	0.115	3.55	3.14	0.65	0.21	2.19	4.27
<i>Geum urbanum</i> L.	0.477	4.89	8.89	1.27	0.14	7.53	10.46
<i>Glechoma hederacea</i> L.	0.004	8.98	0.04	0.004	0.10	0.00	0.09
<i>Gleditsia triacanthos</i> L.	0.049	7.33	0.67	0.079	0.12	0.33	1.07
<i>Hedera helix</i> L.	0.004	8.98	0.04	0.004	0.10	0.00	0.09
<i>Helioopsis helianthoides</i> var. <i>scabra</i> (Dunal) Fernald	0.004	8.98	0.04	0.004	0.10	0.00	0.09
<i>Hemerocallis fulva</i> (L.) L.	0.003	1.51	0.17	0.069	0.41	0.00	0.35
<i>Hordeum murinum</i> L.	0.021	0.80	2.55	1.37	0.54	1.26	4.31
<i>Hosta plantaginea</i> (Lam.) Asch.	0.003	3.43	0.10	0.02	0.20	0.00	0.20
<i>Humulus lupulus</i> L.	0.047	1.28	3.56	1.48	0.42	2.19	5.37
<i>Impatiens parviflora</i> DC.	0.198	1.24	13.76	4.87	0.35	11.02	16.69
<i>Juglans regia</i> L.	0.027	7.84	0.34	0.04	0.12	0.11	0.61
<i>Lactuca serriola</i> L.	0.085	7.81	1.08	0.12	0.11	0.66	1.56
<i>L. tatarica</i> (L.) C.A.Mey	0.008	9.01	0.09	0.009	0.10	0.00	0.17
<i>Lapsana communis</i> L.	0.039	4.93	0.78	0.13	0.17	0.39	1.33
<i>Lepidium draba</i> L.	0.004	8.98	0.04	0.004	0.10	0.00	0.09
<i>Lolium perenne</i> L.	0.013	0.67	1.92	1.12	0.58	0.76	3.55
<i>Medicago falcata</i> L.	0.013	3.80	0.34	0.07	0.21	0.06	0.73
<i>M. lupulina</i> L.	0.004	6.04	0.06	0.009	0.15	0.00	0.12
<i>Morus alba</i> L.	0.008	9.01	0.09	0.009	0.10	0.00	0.17
<i>Nonea pulla</i> DC.	0.007	5.28	0.14	0.02	0.14	0.00	0.35
<i>Oxalis dillenii</i> Jacq.	0.019	6.87	0.27	0.03	0.11	0.06	0.54
<i>Parthenocissus quinquefolia</i> (L.) Planch.	0.076	0.67	10.25	5.27	0.51	7.47	13.46
<i>Phragmites australis</i> (Cav.) Trin. ex Steud.	0.007	3.44	0.20	0.04	0.20	0.00	0.39
<i>Plantago major</i> L.	0.050	4.33	1.15	0.21	0.18	0.63	1.83
<i>Poa angustifolia</i> L.	0.092	3.53	2.55	0.54	0.21	1.69	3.61
<i>P. annua</i> L.	0.019	3.46	0.55	0.12	0.22	0.18	1.08
<i>P. nemoralis</i> L.	0.050	4.57	1.09	0.19	0.17	0.60	1.73
<i>P. pratensis</i> L.	0.007	7.04	0.11	0.01	0.09	0.00	0.27
<i>Polygonum aviculare</i> L.	0.056	4.26	1.29	0.24	0.19	0.74	2.01
<i>Populus alba</i> L.	0.016	9.08	0.17	0.02	0.12	0.00	0.35
<i>P. carolinensis</i> Moench	0.004	8.98	0.04	0.001	0.03	0.00	0.09
<i>Potentilla indica</i> (Andrews) T.Wolf	0.016	4.20	0.39	0.07	0.18	0.08	0.80
<i>Quercus robur</i> L.	0.071	9.58	0.74	0.07	0.09	0.39	1.05
<i>Robinia pseudoacacia</i> L.	0.023	8.29	0.28	0.03	0.11	0.09	0.52
<i>Rorippa sylvestris</i> (L.) Besser	0.004	8.98	0.04	0.004	0.10	0.00	0.09
<i>Rubus caesius</i> L.	0.011	6.67	0.17	0.02	0.12	0.00	0.35
<i>Sambucus nigra</i> L.	0.055	4.77	1.13	0.19	0.17	0.63	1.77
<i>Saponaria officinalis</i> L.	0.004	8.98	0.04	0.004	0.10	0.00	0.09
<i>Silene latifolia</i> Poir.	0.008	9.01	0.09	0.01	0.11	0.00	0.17
<i>Sisymbrium loeselii</i> L.	0.020	9.12	0.22	0.02	0.09	0.04	0.39
<i>Sium latifolium</i> L.	0.002	1.15	0.20	0.09	0.45	0.00	0.40

Species	Shape parameters		Mean, cover per sampling plot	Variance	Variance-to-mean ratio	Confidence interval, individuals per sampling plot	
	α	β				2.5%	97.5%
<i>Solanum nigrum</i> L.	0.036	9.27	0.39	0.04	0.10	0.13	0.61
<i>Solidago canadensis</i> L.	0.081	3.33	2.38	0.53	0.22	1.55	3.44
<i>Sonchus arvensis</i> L.	0.011	7.56	0.15	0.02	0.13	0.00	0.33
<i>S. oleraceus</i> L.	0.043	6.78	0.63	0.08	0.13	0.30	1.04
<i>Stellaria media</i> (L.) Vill	0.024	4.60	0.51	0.09	0.18	0.17	0.97
<i>Taraxacum officinale</i> agg.	0.348	8.59	3.90	0.38	0.10	3.12	4.71
<i>Trifolium pratense</i> L.	0.006	4.35	0.14	0.03	0.21	0.00	0.38
<i>Ulmus laevis</i> Pall.	0.012	9.05	0.13	0.01	0.08	0.00	0.26
<i>Urtica dioica</i> L.	0.014	2.32	0.59	0.18	0.31	0.15	1.26
<i>Viola hissarica</i> Juz.	0.007	3.44	0.20	0.04	0.20	0.00	0.39
<i>V. odorata</i> L.	0.572	2.64	17.77	3.47	0.20	15.46	20.29
<i>Vitis vinifera</i> L.	0.010	1.37	0.74	0.31	0.42	0.14	1.64

Table 3
Alpha-, beta-, and gamma-diversity of the plant community

Layer	Alpha, species			Beta, ratio			Gamma, species		
	mean	2.5%	97.5%	mean	2.5%	97.5%	mean	2.5%	97.5%
Canopy	1.82	1.78	1.88	14.81	13.73	15.58	26.85	25.33	27.85
Understory	1.72	1.65	1.81	8.33	9.28	10.13	16.09	14.57	17.09
Herb layer	6.82	6.73	6.92	14.58	13.94	15.04	99.56	95.04	102.56
Total	8.98	8.12	9.24	15.07	15.61	16.04	142.49	135.96	145.49

The stand species matrix was positively correlated with the understory matrix, and these matrices were negatively correlated with the herbaceous species matrix (Table 4). Accounting for matrices of geographic distances and ecological properties did not affect the correlation of the species matrices.

Table 4
Correlations between plant community matrices from different layers

Layers	Canopy	Understory	Herb layer
Mantel statistic			
Canopy	–	0.21, $P = 0.001$	–0.20, $P = 0.999$
Understory	–	–	–0.19, $P = 0.999$
Herb layer	–	–	–
Partial Mantel statistic conditioned on the spatial matrix			
Canopy	–	0.21, $P = 0.001$	–0.20, $P = 0.999$
Understory	–	–	–0.18, $P = 0.999$
Herb layer	–	–	–
Partial Mantel statistic conditioned on the environment matrix			
Canopy	–	0.21, $P = 0.001$	–0.19, $P = 0.999$
Understory	–	–	–0.19, $P = 0.999$
Herb layer	–	–	–

Species occurring at least 10 times in the descriptions were selected for the community ordination procedure. There were 11 such species for canopy, 9 such species for understory, and 41 such species for grass layer. The length of the first axis extracted after the Detrended correspondence analysis procedure of the canopy matrix was 1.04, the understory was 1.24, and the herb layer was 0.79. Thus, the redundancy analysis was the best alternative for community ordination. The environmental factors described 17.5% variation in canopy community structure ($F = 3.32$, $P < 0.001$), 36.9% variation in understory community structure ($F = 7.39$, $P < 0.001$), and 25.5% variation in herb layer structure ($F = 4.73$, $P < 0.001$, Fig. 2). The spatial variables described 22.7% of canopy community structure variation ($F = 1.83$, $P < 0.001$), 32.3% of understory community structure variation ($F = 2.54$, $P < 0.001$), and 30.9% of herb layer structure

variation ($F = 2.26$, $P < 0.001$). The spatial and environmental variables together described 28.3% of variation in canopy community structure ($F = 1.89$, $P < 0.001$), 48.5% of variation in understory community structure ($F = 3.12$, $P < 0.001$), and 43.1% of variation in herb layer structure ($F = 2.70$, $P < 0.001$).

A total of 81 spatial variables were extracted and ranked from broad-scale trend to fine-scale trend. The broad-scale component was represented in the stand variation, which was statistically significantly described by the spatial variables 2, 3, 4, 5, 8, 9, 10, 11, 12, and 14 (Fig. 3a) and was able to explain 8.2% of the community variation ($F = 3.03$, $P < 0.001$). The medium-scale component was described by the spatial variables 16, 17, 18, 19, 20, 22, 23, 28, 34, 35, 37, and 41 and was able to explain 4.2% of community variation ($F = 1.85$, $P < 0.001$). The fine-scale component was described by the spatial variables 48, 52, 61, and 70 and was able to explain 0.7% of community variation ($F = 1.41$, $P = 0.05$). Accounting for environmental properties led to a decrease in the explained variance. The broad-scale fraction explained 6.2% of stand community variation ($F = 2.49$, $P < 0.001$), the medium-scale fraction explained 2.5% of community variation ($F = 1.53$, $P = 0.003$). The fine-scale fraction was not statistically significant. Accounting for crown-space properties was also responsible for the reduced explained variance. The broad-scale fraction explained 7.0% of stand community variation ($F = 2.66$, $P < 0.001$), the medium-scale fraction explained 2.9% of community variation ($F = 1.61$, $P = 0.002$), and the fine-scale fraction explained 0.7% of community variation ($F = 1.40$, $P = 0.05$). Accounting for vegetation index values reduced the explained variance of the broad-scale fraction to 7.8% ($F = 2.81$, $P < 0.001$), the medium-scale fraction explained 3.1% of community variation ($F = 1.62$, $P = 0.001$). The broad-scale fraction of the pure spatial component was able to describe 4.8% ($F = 2.17$, $P < 0.001$) of community variation, the medium-scale fraction was able to describe 2.1% ($F = 1.45$, $P = 0.005$) of community variation. The fine-scale fraction of the pure spatial component of variation was not statistically significant ($F = 0.98$, $P = 0.49$).

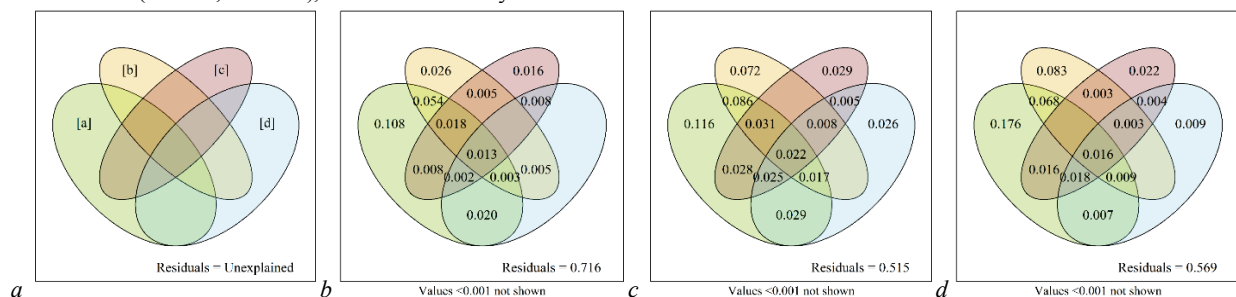


Fig. 2. Partitioning of plant community variation: a presents the influence of the (a) spatial variables, (b) environmental variables, (c) crown variables, and (d) spectral vegetation indexes: b is the partitioning of the community of canopy layer, c is the partitioning of the community of understory layer, d is the partitioning of the grass community

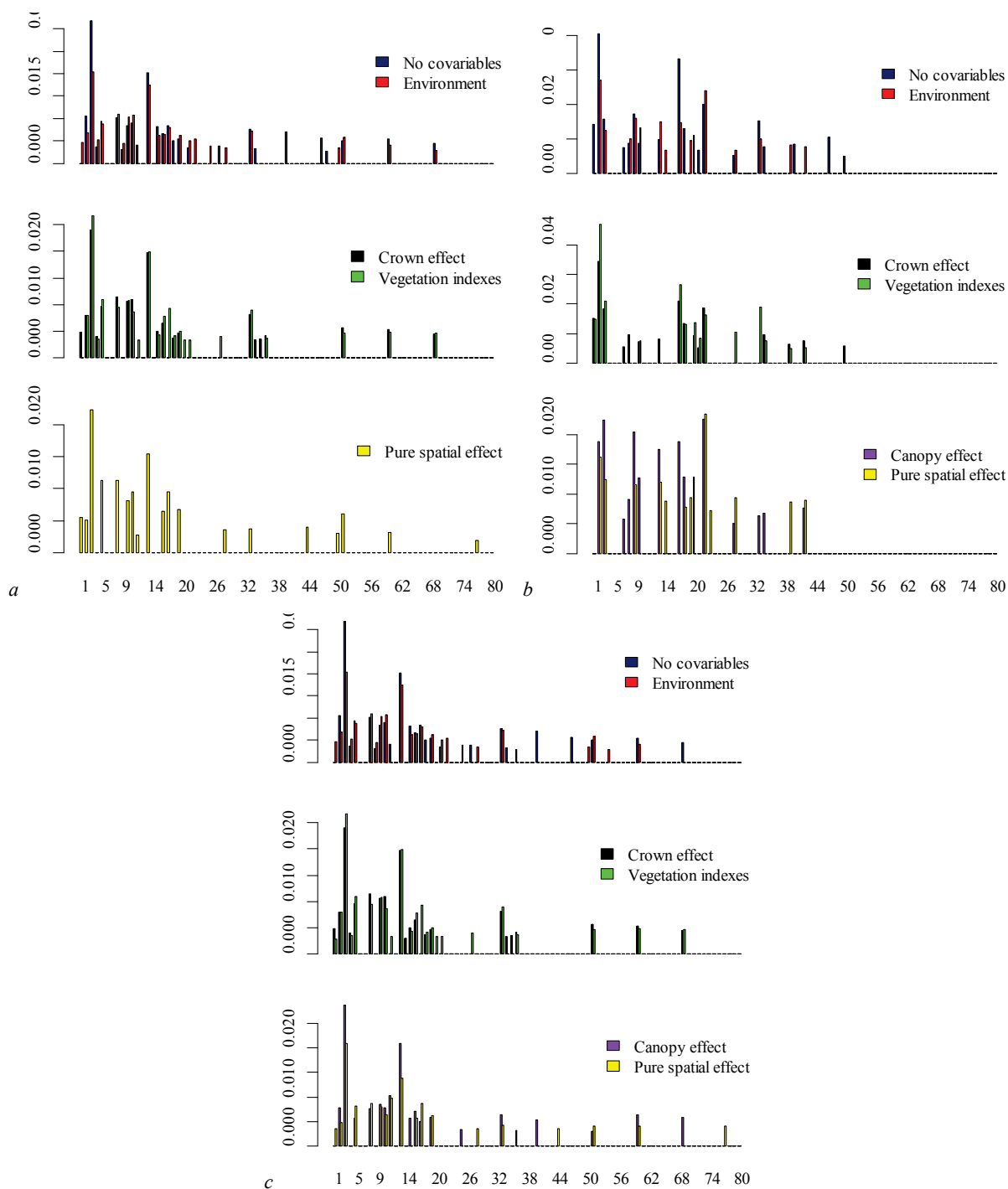


Fig. 3. Scalograms illustrating the scaling of spatially structured variation in *a* – canopy community data, *b* – understory community data, *c* – grass community data (blue bars) and residuals of the environmental models (red bars), the crown models (black bars), the vegetation indexes models (green bars), the tree canopy effect (purple bars), and the pure spatial models with environment, crown, and vegetation indexes as conditional predictors; the value of R^2_{adj} presented on the y-axis is the variation explained by individual dbMEM variables; the dbMEMs presented on the x-axis are ordered decreasingly according to the scale of spatial patterns they represent (dbMEM 1 represents the broadest scale, dbMEM 81 the finest scale)

The broad-scale component was represented in understory variation, which was statistically significantly described by the spatial variables 1, 2, 3, 7, 8, 9, 10, and 14 (Fig. 3b) and was able to explain 12.6% of community variation ($F = 5.12$, $P < 0.001$).

The medium-scale component was described by the spatial variables 18, 19, 20, 21, 22, 23, 29, 34, and 35 and was able to explain 11.8% of community variation ($F = 4.41$, $P < 0.001$). The fine-scale component was described by the spatial variables 40, 41, 43, 48, and 51 and was able to explain 3.2% of community variation ($F = 2.53$, $P < 0.001$). Accounting for environmental properties led to a decrease in the explained variance. The broad-scale fraction explained 8.4% of understory community variation ($F = 2.49$, $P < 0.001$), the medium-scale fraction explained 6.2% of

community variation ($F = 3.13$, $P < 0.001$). The fine-scale fraction explained 2.1% of community variation ($F = 2.25$, $P < 0.001$). Accounting for crown-space properties was responsible for the decrease in explained variance. The broad-scale fraction explained 9.1% of understory community variation ($F = 4.31$, $P < 0.001$), the medium-scale fraction explained 8.5% of community variation ($F = 3.73$, $P < 0.001$), and the fine-scale fraction explained 2.1% of community variation ($F = 2.09$, $P = 0.013$). Accounting for vegetation index values reduced the explained variance of the broad-scale fraction to 9.1% ($F = 4.26$, $P < 0.001$), the medium-scale fraction explained 10.8% of community variation ($F = 4.50$, $P = 0.001$), and the fine-scale fraction explained 1.4% of community variation ($F = 1.74$, $P = 0.001$). Accounting for tree stand properties was responsible for

the decrease in explained variance. The broad-scale fraction explained 8.9% of understory community variation ($F = 4.31$, $P < 0.001$), the medium-scale fraction explained 7.6% of community variation ($F = 3.52$, $P < 0.001$), and the fine-scale fraction explained 1.5% of community variation ($F = 1.85$, $P = 0.005$). The broad-scale pure spatial component fraction was able to describe 2.5% ($F = 2.20$, $P < 0.001$) of community variation, the medium-scale fraction was able to describe 3.7% ($F = 2.59$, $P = 0.005$) of community variation, and the detailed-scale pure spatial component fraction was able to describe 0.9% ($F = 1.70$, $P = 0.011$) of community variation.

The broad-scale component of the herb layer community variation was statistically significantly described by the spatial variables 2, 3, 4, 5, 8, 9, 10, 11, 12, 14, and 15 (Fig. 3c) and was able to explain 11.7% of the community variation ($F = 3.75$, $P < 0.001$). The medium-scale component was described by the spatial variables 16, 17, 18, 19, 20, 21, 22, 23, 28, 29, 34, and 35 and was able to explain 5.9% of community variation ($F = 2.21$, $P < 0.001$). The fine-scale component was described by the spatial variables 37, 41, 45, 43, 43, 48, 51, 52, 55, 61, 70, and 78 and was able to explain 3.9% of community variation ($F = 1.84$, $P < 0.001$). Accounting for environmental properties led to a decrease in the explained variance. The broad-scale fraction explained 8.4% of stand community variation ($F = 2.49$, $P < 0.001$), the medium-scale fraction explained 5.2% of community variation ($F = 3.13$, $P < 0.001$). The fine-scale fraction explained 2.1% of community variation ($F = 2.25$, $P < 0.001$). Accounting for crown-space properties was responsible for the decrease in explained variance. The broad-scale fraction explained 8.7% of the herbaceous community variation ($F = 3.38$, $P < 0.001$), the medium-scale fraction explained 4.6% of the community variation ($F = 2.09$, $P < 0.001$), and the fine-scale fraction explained 2.5% of the community variation ($F = 1.62$, $P = 0.013$). Accounting for vegetation index values reduced the explained variance of the broad-scale fraction to 10.6% ($F = 3.57$, $P < 0.001$), the medium-scale fraction explained 5.3% of community variation ($F = 2.12$, $P = 0.001$), and the fine-scale fraction explained 2.7% of community variation ($F = 1.61$, $P = 0.001$). Accounting for tree stand properties was responsible for the decrease in explained variance. The broad-scale fraction explained 9.9% of herbaceous stand community variation ($F = 3.37$, $P < 0.001$), the medium-scale fraction explained 4.0% of community variation ($F = 1.81$, $P < 0.001$), and the fine-scale fraction explained 3.1% of community variation ($F = 1.68$, $P < 0.001$). The broad-scale pure spatial component fraction was able to describe 5.3% ($F = 2.47$, $P < 0.001$) of community variation, the medium-scale fraction was able to describe 2.8% ($F = 1.70$, $P < 0.001$) of community variation, and the detailed-scale pure spatial component fraction was able to describe 2.4% ($F = 1.62$, $P < 0.001$) of community variation.

The ordination of the tree stand community with the spatial variables as predictors resulted in the extraction of two axes. The first axis was marked by the opposite dynamics of the abundance of *Tilia platyphyllos* subsp. *cordifolia* (Besser) C. K. Schneid, *Populus carolinensis* Moench, and *Acer negundo* L. on the one hand and *Gleditsia triacanthos* L. on the other (Fig. 4a).

The spatial variation of this axis indicates the predominance of maximum values along the gully slope of the northern exposure and in the eastern part of the park (Fig. 5a). The negative values of the axis prevailed in the central and western part of the park. The second axis was marked by the opposite dynamics of *Acer platanoides* L. on one side and *Robinia pseudoacacia* L. on the other. In the stand, *A. platanoides* dominated in the northwestern and central parts of the park, and *R. pseudoacacia* dominated in the eastern and western parts of the park.

Two axes were extracted from the ordination of the understory community with spatial variables as predictors. The first axis was marked by the opposite dynamics of *A. platanoides* on one side and *Sambucus nigra* L. abundance on the other (Fig. 4b). The spatial variation of this axis indicated a predominance of maximum values on gully slopes and in the eastern part of the park (Fig. 5b). The negative values of the axis prevailed in the southern part of the park. The second axis was marked by the opposite dynamics of *S. nigra* on one side and *Ulmus laevis* Pall. on the other side. In the understory, *S. nigra* was predominant in the southern and eastern parts of the park, and *U. laevis* dominated in the central part of the park.

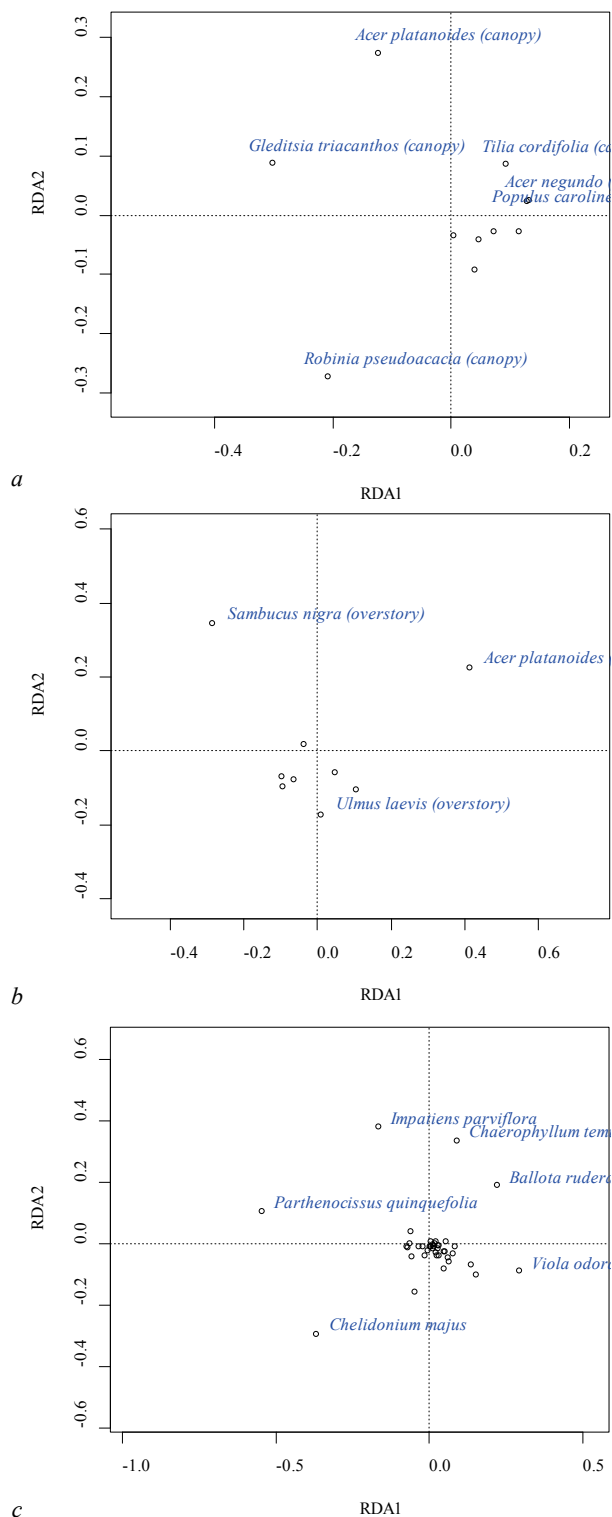


Fig. 4. Community ordination with spatial variables as predictors: the species with the highest scores on the ordination axes are shown: *a* is the stand ordination, *b* is the understory ordination, and *c* is the herbaceous ordination

Two axes were extracted from the ordination of the herbage community with the spatial variables as predictors. The first axis was marked by the opposite dynamics of the abundance of *Viola odorata* L., and *Ballota nigra* subsp. *ruderalis* (Sw.) Briq. on one side and *Parthenocissus quinquefolia* (L.) Planch. on the other side (Fig. 3c). The spatial variation of this axis indicates the predominance of maximum values in the northern part of the park (Fig. 4c). The negative values of the axis prevailed in the southeastern part of the park.

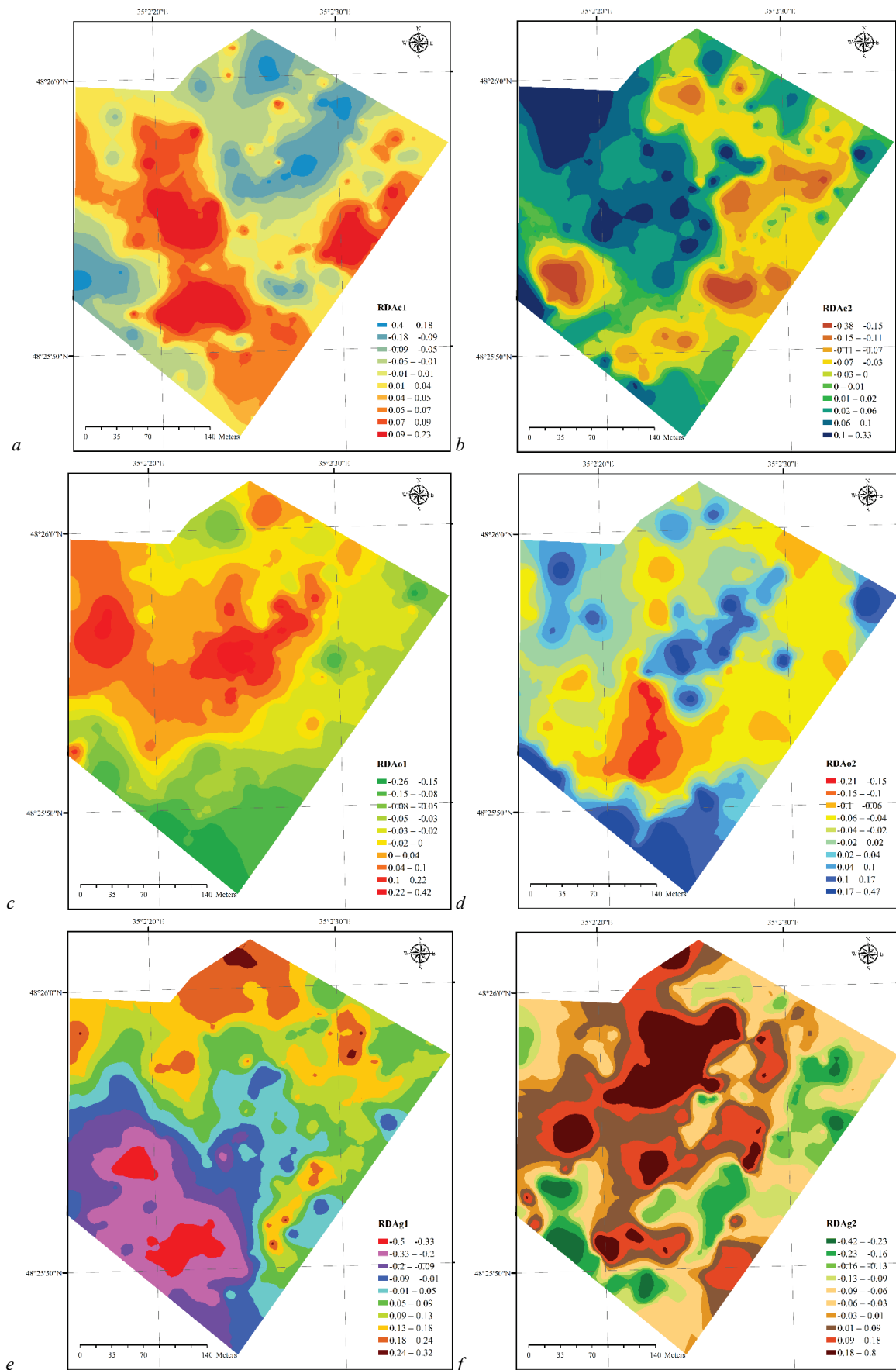


Fig. 5. Spatial variation of axes extracted after ordination of communities with spatial variables as predictors: *a* is RDA axis 1 extracted after stand community ordination, *b* is RDA axis 2 extracted after stand community ordination, *c* is RDA axis 1 extracted after understory community ordination, *d* is RDA axis 2 extracted after understory community ordination, *e* is RDA axis 1 extracted after grass community ordination, *f* is RDA axis 2 extracted after grass community ordination

The second axis was marked by the opposite dynamics of *Impatiens parviflora* DC. and *Chaerophyllum temulum* L. on one side and *Chelidonium majus* L. on the other. In the herbaceous stand *I. parviflora* and *Ch. temulum* dominated in the central part of the park, and *Ch. majus* dominated in separate sites in the eastern and western parts of the park.

Accounting for the influence of axes extracted after tree community ordination for understory and herbaceous communities resulted in shifts of the ordination solutions for these communities (Fig. 6). The largest biases were found for understory species *A. platanoides*, *A. campestre*, and *M. alba*. The herbaceous species most sensitive to stand influence were *V. odorata*, *Ch. majus*, *P. quinquefolia*, and *L. perenne*. The understory was most sensitive to stand influence in the northwestern and central part of the park, and the herbaceous stand was least sensitive to stand influence in the southwestern part of the park.

The effect of the stand on the understory and herbaceous stand was accompanied by a change in environmental properties. The effect of the stand led to a decrease in soil temperature and an increase in soil moisture and electrical conductivity (Table 5). The decrease in temperature and

increase in moisture also increased the effect of the stand on the underlying tiers of the ecosystem. The stand effect responded positively to the height and projective cover of the herbaceous stand. The understory was insensitive to crown-space properties, while the herbaceous stand, by contrast, was very sensitive to crown architectonics. The vegetation indices were sensitive markers of the influence of the stand on the undergrowth. Only NDII and LAI were so sensitive in terms of their influence on herbage.

Discussion

An urban park is an important element of urban infrastructure that performs a wide range of ecosystem functions (Mexia et al., 2018). The park's plant communities are under intense anthropogenic influence (Bao et al., 2022). This influence is due to both the application of plantation management tools (Chan et al., 2014; Hajzeri, 2021) and the complex anthropogenic influence of the urban environment (Sarah et al., 2015).

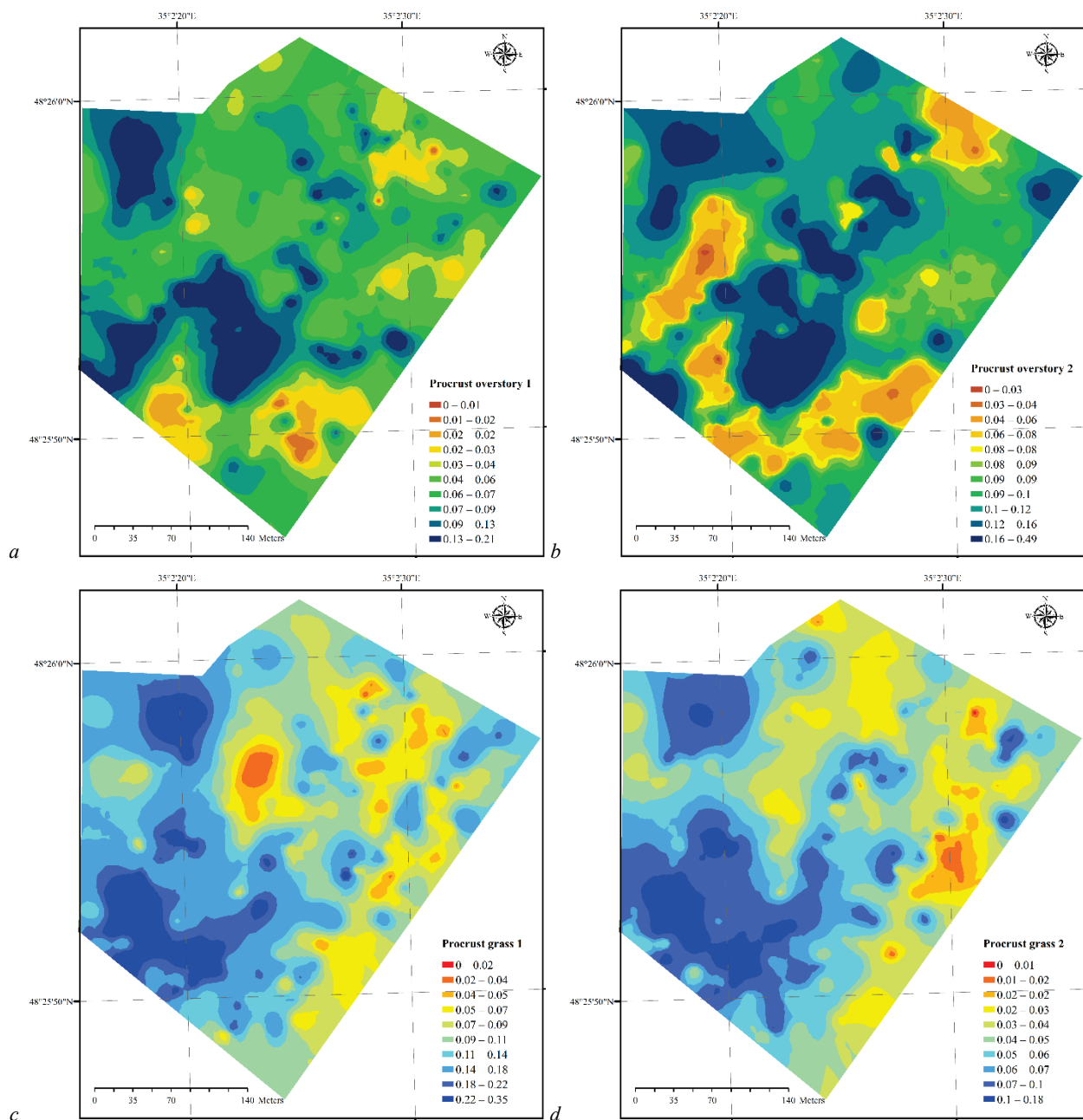


Fig. 6. Spatial variation of Procrustes distances resulting from rotation of ordination solutions for understory communities (a, b) and herbaceous stand communities (c, d) with spatial variables as predictors and RDA axis 1 (a, c) RDA axis 2 (b, d) extracted after forest stand community ordination as conditional predictor

Table 5Correlation of ordination axes and procrustean distances with predictors (the statistically significant Pearson correlation coefficients for $P < 0.05$)

Predictor	Ordination axes						Procrustean distances			
	Canopy1	Canopy2	Understory1	Understory2	Grass1	Grass2	Understory1	Understory2	Grass1	Grass2
Environment variables										
TWI	–	0.14	–0.16	0.15	–0.17	–	–	–	0.20	0.21
Soil T	–	–	–0.13	0.17	0.49	–	–0.23	–0.19	–	–0.21
Soil moisture	0.18	–0.13	–	–0.21	–0.42	–0.17	0.21	0.17	0.20	0.27
EC	0.24	–	–	–0.16	–0.31	–	0.41	0.40	0.16	0.20
Lighting	–	–0.14	–0.29	–	0.26	–	–	–	–	–
Air temperature	–	–0.20	–0.19	–0.14	0.35	–	–	–0.29	–	–0.19
Atmospheric humidity	0.20	–	0.16	–	–0.48	–	–	0.18	0.19	0.27
Grass, cm	–	–	–0.16	–0.14	–0.14	0.17	–	–	0.13	–
Cover	–	–0.21	–0.39	–0.14	–0.29	–	–	–	0.28	0.24
Crown space variables										
COP	0.22	–	–0.26	–	–	–0.21	–	–	0.26	–
LAI	–0.19	–	0.32	–	–	0.29	–	–	–0.21	–
TDr	0.20	–	–0.18	–	–	–0.24	–	–	0.25	–
TDF	0.19	–	–0.25	–	–	–0.23	–	–	0.24	–
Vegetation indices										
NDVI	–	–	0.42	–0.20	–0.14	0.16	0.15	–	–	–
NDII	–	–	0.20	–0.13	–0.42	0.15	0.19	0.19	–	0.17
Red-Edge NDVI-1	–	–	0.25	–	–0.30	0.14	0.18	–	–	–
Red-Edge NDVI-2	–	–	0.28	–	–0.29	0.16	0.18	–	–	–
GNDVI	–	–	0.32	–	–0.28	0.17	0.17	–	–	–
LSWI	–	–	0.35	–0.22	–0.30	0.20	0.17	–	–	–
LAI	–	–	–	0.17	–0.35	–	0.19	–	–	0.18
MTCI	–	–	0.31	–0.31	0.15	–	–	–	–	–

Undoubtedly, the recreation activity is an important source of anthropogenic influence in urban parks (Bertram et al., 2017; Zhang & Zhou, 2018). A compromise between the intensification of ecosystem services and the recreational function can be seen as the goal of optimal parkland management. These aspects of park function do not always coincide and are sometimes in conflict. The layer structure of the park is the result of the efficient exploitation of resources by plant species, their competition, and also significantly improves the aesthetic perception of park plantations (Aboufazel et al., 2021). In natural old-growth forests, the number of layers can be very large. In the studied park we distinguished three layers: forest canopy, understory, and herbaceous stand. The understory and shrub layer in the park plantation were not differentiated, so in our work we considered as a single layer, which was designated as the understory layer.

Species diversity of the park plantation is quite high. The park was created on the site of a natural oak forest, fragments of which are still preserved in the form of individual old-growth oaks (Yorkina et al., 2022). However, the main part of the plantation was planted by man, or arose as a result of dispersal of planted species (Solonenko et al., 2021). The species diversity of the park community is increased by adventive species. Some of them are planted in the park as more resistant to the conditions of living in an urban environment, and some are planted for reasons of better aesthetic properties.

The trees are distributed throughout the park either randomly or aggregated. The regular distribution of individuals across the park was not found for any single tree species. It is important to note that regular distribution occurs when there is a strong antagonistic relationship between spatial objects, or in the case of artificial placement (Luambua et al., 2021). Considering that a large part of the park plantation arose artificially, regular placement of woody plants would be quite expected. The lack of a regular pattern of spatial placement can be explained by the process of naturalization of the forest plantation. During the growth and development of an artificial forest stand, the originally regular pattern of spatial arrangement is replaced by a random or aggregated pattern. This is facilitated by different living conditions within the park and different rates of self-renewal of the tree stand. Also, during the functioning of the park, additional planting of trees in separate locales of different species composition took place in the park, which also contributed to the heterogeneity of the park plantation. The spatial distribution of plants in the understory is also either aggregated or random. The structure and dynamics of an understory is highly dependent on the species composition of the stand. The species of the forest stand form the understory as a result of generative or vegetative reproduction. This explains the similarity of the spatial patterns of tree stand and understory. Also, the composition and structure of

the tree canopy influences the growth dynamics of the understory, which is also the reason for the consistency of the spatial structure in the two layers. The spatial placement of herbaceous species is fundamentally different from that of stand and understory. The herbaceous species are placed in a regular manner. The herbaceous stands in the park were not specifically planted, so their spatial arrangement is the result of complex population processes and interspecific interactions. Competitive relationships may be the cause of regular patterns of spatial arrangement of herbaceous species (Getzin et al., 2006).

The values of alpha- and gamma-diversity of the plant community in separate layers are very different. The highest gamma diversity was found for the herbaceous stand, while the diversity of the tree stand and understory was significantly lower. Alpha biodiversity of the tree stand and the understory did not practically differ. Beta diversity values between the layers are very close, and beta diversity is practically equal for tree stand and herbaceous layer. Thus, we can assume that the mechanisms of species turnover for the plant communities of different layers are determined by common causes. The overall level of beta diversity (8.33–14.81) indicates a high degree of plant community heterogeneity, which may be a consequence of both a high degree of heterogeneity of conditions in the park and a high degree of competitive relationships between community species. The variability of the tree layer and understory is consistent, as confirmed by Mantel's statistics. The herbaceous stand community matrix has an opposite correlation with the tree stand and understory matrices. This effect is a consequence of redistribution of solar radiation by the tree canopy (Konarska et al., 2014). In treeless or sparse canopy areas, the species diversity, density, and height of the herbaceous stand increase. In shady conditions, the diversity and abundance of herbaceous plants decreases. This pattern is universal and does not depend on location or other ecological conditions, which is confirmed by the partial correlation coefficients.

The understory is the most sensitive to the environmental factors, the herbaceous stand is somewhat less sensitive, and the tree stand is the least sensitive to the environmental factors. The environmental factors in this study are represented by a set of variables. The spatial variation of the stand is predominantly influenced by the factors of trophicity and moisture of the edaphotope. These same factors also act on the herbaceous stand and understory, but along with them are included the environmental variables, which are determined by the architectonics of the crown space and thus the light regime, which is regulated by the tree stand. It is important to note that the variation of the communities of the different layers of the park plantation is subject to spatial patterns. The herbaceous and understory variation is more spatially structured than the tree stand variation. The spatial patterns can arise as a result of the influence of spatially struc-

tured environmental factors and as a result of factors of a neutral nature (Legendre et al., 2009). The latter aspect of variation is best described by the pure spatial component of community variation (Gazol & Ibáñez, 2010; Chang et al., 2013).

The spatial aspect of community variation has a hierarchical structure and is divided into broad-, medium-, and fine-scale components. The importance of these components decreases in the direction from broad-scale to fine-scale components. The role of environmental factors decreases in the opposite direction: the environmental factors are most important for the generation of fine-scale stand patterns. The effects due to crown-space structure and vegetation indices are generally medium-scale in origin. The pure spatial component of tree stand structure variation is broad-scale. Such a feature can be explained by the artificial origin of the tree stand. The equalization of the values of the spatial components of variation of different scale levels can be a marker of the degree of naturalization of the tree stand.

The broad- and medium-scale components of the spatial variation of understory are practically equivalent. The environmental factors induce predominantly the medium-scale component. The crown space properties are represented predominantly by the broad- and medium-scale components of variation, but their role is not significant. The vegetation indices are sensitive to the broad- and fine-scale components of understory variation. The tree stand generates the predominantly fine-scale components of understory variation. The pure spatial component, which reflects the effect of factors of a neutral nature, is predominantly medium-scale. An important feature of the spatial variation of the herbaceous vegetation is the predominant significance of the broad-scale component on the one hand, and the high contribution of the fine-scale component on the other hand. The environmental factors are of the greatest importance in the generation of fine-scale patterns. The crown structure plays an important role at all hierarchical levels, but is most important for the formation of the fine-scale pattern. The role of vegetation indices is insignificant for explaining the spatial patterns of the herbaceous stand, but it is the greatest for the fine-scale component. The tree stand structure largely determines the medium-scale component of the spatial variation of the herbaceous vegetation.

The markers of the main trends of tree stand structure variation are adventive plant species, which once again emphasizes the role of the anthropogenic factor in the formation of the park stand. The axes extracted as a result of stand community ordination were used as predictors to describe the variation of understory and herbaceous stand communities. The tree stand varies coherently and the influencing factors on the other layers of the plant community are not the individual trees, but the result of the coherent variability of all tree species, which is characterized with the help of ordination axes. The main drivers of variation in stand structure are the trophicity ordinate and the humidity ordinate. Our results are fully consistent with this general position, as evidenced by the fact that ordinal axis 1 correlates strongly with electrical conductivity, and ordinal axis 2 correlates with soil wetness and the topographic wetness index. The electrical conductivity of soil is a marker of soil solute concentration by dissolved salts, on which the trophicity of the edaphotope directly depends. It is important to note that ordination axis 1 strongly correlates with crown structure indices. Thus, the typological features of the tree stand, which are driven by the trophicity gradient, determine the features of the crown space structure as well. The spectral indices are not sensitive to variation in tree stand community structure. This means that for a given level of spectral index, the characteristics of crown space can vary. Obviously, the resolution of space images does not allow us to distinguish the differences in the structure of crown space. The ordination axis 2 is sensitive to the soil moisture and illumination and atmospheric temperature. It can be assumed that this axis reflects variability in the composition of the stand in the gradient of light conditions in the crown zone. Its structure is also difficult to differentiate on space images, due to which the ordinate axis 2 has no statistically significant correlation with vegetation indices.

The ordination axes extracted after the analysis of the understory community are strongly correlated with the vegetation indices. Apparently, the variability of crown-space density recorded from space is largely due to changes in the structure of the understory. The understory also influences crown-space structure indices and light regime. An increase in the abundance of *A. platanoides* and a decrease in *S. nigra* of the understo-

ry contribute to a decrease in light and temperature under the canopy of the park plantation. Logically, the decrease in light induced by the density of the understory leads to a decrease in the height and projective cover of the herbaceous stand. The tree stand induces a rotation of the ordination axes of the understory community, on the basis of which the mechanisms of the effect of the stand on the understory can be identified. The ordination shift of the understory community induced by the tree stand is associated with changes in the soil temperature, moisture, and electrical conductivity, as well as spectral properties of the vegetation cover. Ordination axis 2 also reflects the effect of canopy on soil temperature and moisture. The shift of this axis induced by the tree stand also indicates changes in atmospheric moisture and temperature.

The ordination axes distinguish two trends in the variability of herbaceous community structure induced by the environmental properties (axis 1) and by the properties of the crown space (axis 2). It is worth noting that the variability of both of these axes is reflected in the variability of spectral indices. The effect of the stand on herbage is associated with changes in the properties of the environment for the trends described by both axes. The effect of stand on herbage is virtually unaffected by the spectral indices. The influence of tree stands on axis 1 is associated with changes in the structure of the crown space, to which this axis is initially insensitive. The influence of stand on axis 2 is not associated with changes in the structure of crown space, to which this axis is sensitive.

Thus, the layer structure of the park plantation influences the variability of environmental properties, on which the formation of favourable conditions for recreation depends. Reduced temperature in summer and increased humidity create more comfortable conditions for park visitors (Cheung et al., 2021). The high species diversity of different layers is a condition for the formation of a stable ecosystem (Hu et al., 2017), which stabilizes the performance of ecosystem functions of the city park. Our results allowed us to establish that the spectral indices are not sensitive to the species structure of the forest stand of the city park, but they are sensitive to the structure of the understory and herbaceous layer. This result is quite surprising, since the understory and herbaceous layer are hidden by the forest canopy. It can be assumed that such a spectral response may be formed by tree stands with different species composition. Also, the high species diversity of the tree stand can explain the sensitivity of the spectral indices to vegetation density but not to the species composition of the stand. The spectral characteristics of vegetation density can be complemented by understory or herbaceous stands. The high level of competition for light resources can be a significant structuring factor that significantly changes the structure of shade-loving and light-loving communities of undergrowth or herbaceous stands. Thus, the composition of communities that fill light gaps in the canopy will differ from those in the shade. Accordingly, the communities that fill the gaps will increase the spectral estimate of the park's plantation density.

Conclusion

Park vegetation is represented by three layers of vegetation: stand, undergrowth, and herbaceous stand. The herb layer has the greatest species richness (99 species), much less species diversity of the tree stand (27 species) and the understory (16 species). The spatial distribution of trees and understory plants is random or aggregated, while the distribution of herbaceous species is regular. The beta diversity of all layers of vegetation is at the similar level. The understory is the most sensitive to the environmental factors, the herbaceous stand is somewhat less sensitive, and the tree stand is the least sensitive to the environmental factors. The environmental factors are most important for the generation of fine-scale tree stand patterns. The effects due to crown space structure and vegetation indices are generally medium-scale in origin. The main drivers of tree stand structure variation are trophicity and moisture. The spectral indices are not sensitive to the variation in tree stand community structure. The effect of tree stand on the understory is related to changes in soil temperature, moisture, and electrical conductivity as well as the spectral properties of the vegetation cover. The influence of the tree stand on the herbaceous layer is practically not reflected in the spectral indices, but is associated with changes in the structure of the crown space.

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