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Plant diversity decrease and directional species turnover induced by shifting overstory dominance in the oak-hornbeam forest reserve over 50 years

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A R T I C L E I N F O

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A B S T R A C T

Due to a long history of various anthropogenic pressures, lowland forest reserves are scarce and lack historical datasets suitable for analysing long-term vegetation trends. This study investigated changes in plant diversity and species composition in the long-untouched Krakovo forest reserve, the only preserved remnant of lowland oak-hornbeam forests with primary status in Slovenia. The original vegetation sampling was conducted in the 1970s. In 2024, we resurveyed 30 semi-permanent plots capturing the natural variation in soil moisture gradient. We found the decline of *Quercus robur* in the upper tree layer and the expansion of shade-casting tree *Carpinus betulus* in the lower tree layer, a pattern mainly attributed to the lowering of the groundwater table. This shift in overstory dominance manifested in a directional change of herb-layer composition associated with high species turnover (61 %). The deterioration of light conditions at the forest floor resulted in significant decrease of species richness, accompanied by the process of taxonomic homogenization. The analysis of Ellenberg indicator values revealed a reorganization of the plant communities in response to the increasingly shaded and cooler understory environment, benefitting a limited number of perennial herbs preferring closed canopies. The change towards nutrient-demanding species was probably caused by improved litter quality, nitrogen input from agricultural areas and nutrient release from accumulated deadwood. In terms of soil moisture, the reserve still exhibits a mosaic of interchanging distribution between wetter and more mesic habitats. However, given that oak natural regeneration is very poor, we anticipate even more drastic vegetation changes in the future.

1. Introduction

Primary forests are naturally regenerated forests of native species where there are no clearly visible indications of human activities, and the ecological processes are not significantly disturbed (FAO, 2015; Sabatini et al., 2018). According to Buchwald (2005), these ecosystems occur in relatively intact forest areas that have always or at least for the past sixty to eighty years been essentially unmodified by human activity. They are characterized by certain structural and compositional features, such as continuous forest cover; presence of large, old trees; greatly varying tree dimensions and age resulting in high structural and functional complexity (multi-layered canopies); large amounts of deadwood, with various size categories and decay stages. All these factors contribute to generally higher biodiversity in long-untouched primary forests compared to managed stands (Buchwald, 2005). Current representation of remnants of primary forests is especially low in European lowland areas since humans started to alter forests millennia ago (Klimo et al., 2008; Durak and Durak, 2015).

A comparison of historic and recent vegetation surveys based on repeated sampling of semi-permanent plots has proven an effective method for evaluating long-term trajectories of plant communities in the temperate forest ecosystems, where past and present anthropogenic stressors are accumulating (Hédl et al., 2017; Knollová et al., 2024). When combined with information regarding the environmental preferences and life-history strategies of plant species, this framework can facilitate an understanding of the dynamics of communities and associated ecological processes over the course of several decades (Breton et al., 2023). However, the changes that may occur in forest vegetation within strictly protected reserves, along with the primary mechanisms that drive these shifts, remain inadequately understood. Previous studies were predominantly conducted in unmanaged beech forests across European mountains (Nagel et al., 2019; Rybar et al., 2023), whereas

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evidence from lowland oak-hornbeam forests is still scarce. In contrast to managed stands, where vegetation dynamics are strongly influenced by forest management, temporal changes in primary forests mainly reflect natural succession (Strubelt et al., 2019). Nevertheless, vegetation dynamics in primary forests can be dependent on potential legacies of forest management. Many now unmanaged forests exhibited some degree of management in the past that influence current tree species composition or richness, and these effects may reflect in trends of herb-layer vegetation (Heinrichs et al., 2022).

The issue of *Quercus robur* decline has been documented in numerous managed and unmanaged oak-hornbeam forests across Europe (Klimo et al., 2008; Čater, 2015; Čater and Levanič, 2015; Cestarić et al., 2017; Leuschner and Ellenberg, 2017). The increasing rates of crown defoliation and oak mortality observed in recent decades can be attributed to anthropogenic alterations in the hydrological regime, including a lowering of groundwater levels (Pilaš et al., 2007; Čater and Levanič, 2015; Kermavnar and Kutnar, 2024a), and an increase in the frequency of prolonged droughts, extreme heat and elevated vapour pressure deficits (Čater, 2015; Niemczyk et al., 2024). Furthermore, the aging of forest stands and the senescence of old trees in unmanaged forest reserves contribute to the progression of natural succession from optimal to terminal developmental stages, thereby promoting the ingrowth of young woody cohorts (Rybar et al., 2023). The alterations in tree composition resulting from the decline of the dominant tree species (*Quercus robur*) and the concomitant increase in the co-dominant (*Carpinus betulus*) or subordinate species have significant implications for the ground vegetation (Hofmeister et al., 2004). There is a notable knowledge gap concerning the long-term effects of increased mortality rates in foundational overstory taxa on dynamic patterns of herbaceous plants and tree regeneration (Nagel et al., 2019).

Tree species composition, the extent of canopy closure and the vertical structure of forest stands exert a profound influence on plant diversity and composition in temperate forests (Barbier et al., 2008; Balandier et al., 2022). In response to changes in the tree layer and natural stand dynamics over multiple decades, there can be a significant compositional shift in the herb-layer vegetation, with some species declining or disappearing and others becoming more abundant or newly established (Lanta et al., 2024). Consequent species turnover reflects the intricate interplay between abiotic conditions and biotic interactions. Indeed, the majority of temporal trends documented in deciduous broadleaf forests were attributed to changes in the tree layer. This is because the overstory canopy has the most significant impact on light availability, understory microclimate, soil and litter properties, decomposition rates, and nutrient cycling at the local scale (Depauw et al., 2020; Rybar et al., 2023). For example, the expansion of trees with greater shade-casting ability (e.g., *Fagus sylvatica, Carpinus betulus, Acer campestre, Tilia cordata*) in various forest types has the potential to impoverish and homogenize herb-layer assemblages (Kopecký et al., 2013; Vojík and Boublík, 2018; Cholewińska et al., 2020; Kotrík et al., 2023; Lanta et al., 2024). Such ecological trends toward shadier environments are likely to result in the proliferation of shade-tolerant, eutrophic perennials at the expense of herbs adapted to more open canopy (Vild et al., 2024). It is therefore reasonable to hypothesize that the controlling factors for plant diversity and community composition in the studied forest reserve have undergone profound change over the last decades due to the tree layer alterations triggered by oak decline.

The historical dataset based on phytosociological investigation of the oak-hornbeam forest reserve Krakovo (Slovenia), conducted in the 1970s by Milan Piskernik (Slovenian Forestry Institute), provides a unique opportunity to examine the natural dynamics of this rare and complex ecosystem. It is presumed that the vegetation is primarily influenced by altering stand characteristics, specifically a shift in overstory dominance from *Quercus robur* towards *Carpinus betulus*. Additionally, changes may indicate the presence of global change drivers, including climate warming, drying of sites or soil eutrophication. The objective of this study was to analyze changes in plant community diversity and composition in a lowland forest reserve over the last five decades using repeated vegetation surveys on a representative set of semi-permanent plots. The specific aims of this study were as follows: (i) to quantify changes in overstory composition and stand structure induced by oak decline; (ii) to examine changes in herb-layer diversity at multiple levels (alpha, beta, gamma); (iii) to test whether herb-layer vegetation has undergone significant species turnover over the last decades; and (iv) to infer potential mechanisms for observed changes based on ecological conditions, indirectly estimated by Ellenberg indicator values. In light of the considerable direct and indirect anthropogenic pressure exerted on lowland forests embedded within intensively managed agricultural landscape, we postulated that significant changes in vegetation diversity and composition would be observed.

2. Materials and methods

2.1. Study area

The Krakovo forest reserve is located in the central part of the Krakovski gozd, a 2532-hectare large area of preserved deciduous, occasionally flooded lowland forest complex in the eastern Slovenia (45° 52′ 40″ N, 15° 24′ 31″ E, 153 m a.s.l.; Fig. 1). The terrain is relatively flat and only slightly undulating, situated on the developed floodplains of the Krka River and its tributaries. The climate is temperate-continental, typical for the transitional zone between the Pre-Dinaric and Sub-Pannonian regions of Slovenia (Accetto, 1974). The mean annual temperature is 10.9 °C, and the mean annual precipitation is 1018 mm for the period 1950–2018 (climate data obtained from Škrk et al., 2021). More than two-thirds of the rainfall occur during the vegetation period. However, the precipitation regime is changing, with decreasing precipitation amounts and increasing temperatures (Appendix A). In general, the soil is characterised by a deep profile with a high clay content, a compacted structure, poor aeration, a slight acidity, a fresh to wet consistency, and the presence of waterlogging in depressions (Hočevar et al., 1980).

The Krakovo forest reserve encompasses an area of 38.6 ha. It has been protected as a strict forest reserve since 1952 and as a Natura 2000 site since 2004. Prior to this, owing to easy accessibility forest stands had been under some anthropogenic influences, including selective logging. Past evidence of human impact was also apparent in the form of hydro-ameliorative activities, namely the construction of drainage canals, which had been carried out close to the reserve. Given that studied forest reserve has some history of management, it is categorized as long-untouched primary forest (Buchwald, 2005).

The forest represents the largest and most well-preserved remnant of lowland oak-hornbeam forest in Slovenia. As a protected natural asset, it represents an exceptional case study for investigating the ecology and natural evolution of ancient forest ecosystems, while also plays a significant role in the biodiversity conservation and provides vital ecosystem services to human society, such as floodwater retention (Accetto, 1974, 1975). The Krakovo reserve is an important habitat for a few rare vascular plant species with geographically limited distribution, many of which are included on the Red List of threatened and protected taxa (e.g., *Pseudostellaria europaea, Pulmonaria dacica, Gagea spathacea, Omphalodes scorpioides*; Dakskobler et al., 2013).

In terms of broader phytosociological classification, the forest reserve is classified as a *Querco robori-Carpinetum* s. lat. association. Specifically, two similar forest associations have been described for the Krakovski gozd: *Pseudostellario-Quercetum roboris* and *Pseudostellario–Carpinetum betuli* (Accetto, 1974). On some parts, the association *Carici-Alnetum glutinosae* s. lat. (the wettest form of vegetation) can be found but covers far smaller area of the reserve. The stands are dominated by *Quercus robur* with frequent admixture of *Carpinus betulus*. The following tree species occur sporadically throughout the reserve: *Alnus glutinosa, Acer campestre, Ulmus minor, Fraxinus angustifolia, Pyrus pyraster, Prunus avium*, and *P. padus*. In the shrub layer, observations

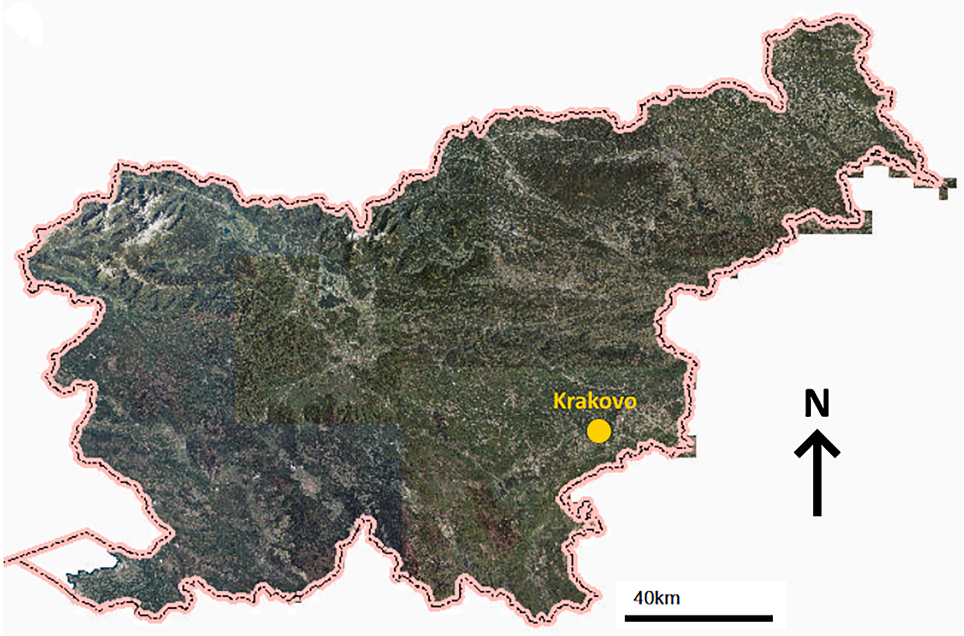

Fig. 1. Location of the studied forest reserve Krakovo in Slovenia (Map source: ARSO, 2024).

indicate the presence of *Corylus avellana* on a regular basis.

Forest stands are characterized by the prevalence of large oak trees exceeding 200 years of age, high growing stocks (730 m^3/ha), and a considerable quantity of standing and fallen deadwood (27 % of the growing stock; Hladnik and Pintar, 2017). According to Accetto (1975), *Quercus robur* constituted 91 % of the total biomass, while *Carpinus betulus* and *Alnus glutinosa* accounted for only 6 % and 3 %, respectively. Recent dendrometric measurements indicated a declining tendency of tree vitality, particularly for *Quercus robur*, resulting in gradual alterations to the vertical stand structure (Žibert, 2006; Pintar, 2016). The proportion of *Quercus robur* in the growing stock has dropped to 83 % whereas the proportion of *Carpinus betulus* has increased to 12 % (Hladnik and Pintar, 2017).

The stands exhibit vertical niche differentiation of both tree species, resulting in a two-layered structure comprising *Quercus robur* in the upper tree layer and *Carpinus betulus* and admixed broadleaves in the lower tree layer. This natural feature is more typical of unmanaged lowland oak-hornbeam forests and less so of managed stands surrounding the reserve (Žibert, 2006).

A crucial ecological factor shaping the composition of overstory and understory vegetation is soil water content. The forest reserve exhibits a mosaic pattern of plant communities, with moist microsites displaying higher water availability in shallow depressions and more mesic/dry microsites situated on slightly elevated terrain (Accetto, 1974). In general, the former occurs in periodically inundated sites and are more dominated by *Q. robur* whereas the latter exhibit greater *C. betulus* abundance due to its lower tolerance to flooded conditions. The dissimilarity of these microhabitats is largely contingent upon the groundwater level, which not only shapes the character of the vegetation but also influences its developmental dynamics. The level of groundwater in Krakovski gozd has been declining (Appendix B). It is further hypothesised that light conditions associated with canopy closure and tree species composition represent another ecological gradient that determines the diversity and composition of understory vegetation.

2.2. Vegetation sampling

Floristic survey campaigns were carried out in the period 1974–1978 as part of a comprehensive national inventory of primary forest reserves in Slovenia (Hočevar et al., 1980, 1995) using Piskernik phytosociological method. Across the entire area of reserve, 7 m × 7 m semi-permanent plots with reliable approximate location (*sensu* Kapfer et al., 2017) were placed on a systematic 100 m × 100 m grid. The plots were not permanently marked during the original survey; rather, they were drawn on detailed maps. In each plot, all vascular plants were recorded in the herb, shrub, and tree layers. The vegetation layers were defined in accordance with the Piskernik method (Hočevar et al., 1980, 1995), as follows: (1) tree layer (trees and shrubs exceeding 5 m in height), (2) shrub layer (trees, shrubs and woody vines between 0.5 and 5 m in height), (3) herb layer (all herbaceous plants, irrespective of height, and trees, shrubs and woody vines below 0.5 m in height). The tree (overstory) layer was recorded within a larger circular plot with a radius of 20 m, extending from the centre of each vegetation plot. The tree layer was further divided into two distinct height classes: the upper tree or canopy layer, comprising primarily oak trees with heights exceeding ca. 30 m, and the lower tree or subcanopy layer, which included other broadleaf species with heights ranging from 5 to ca. 25 m. The abundance of each plant species was estimated using the following scale: *e* = 1 specimen; *r* = 2–5 specimens; + = 6–10 specimens; *x* = >11 specimens and <10 % cover; 1 = 11–20 % cover; 2 = 21–40 %; 3 = 41–60 %; 4 = 61–80 %; and 5 = 81–100 %. The species nomenclature follows National Flora (Martinčič et al., 2007).

In 2024, we resurveyed 30 representative plots capturing the full spatial heterogeneity of natural conditions related to soil moisture gradient across the forest reserve. The sampling was conducted in accordance with the original protocols. Vegetation was resurveyed at the end of May, which represents the peak development period. This timing was selected to ensure comparability with the historical survey, allowing for the control of seasonal variability (Kapfer et al., 2017). Furthermore, the locations of the plots were verified to confirm that the distances and bearings between them corresponded to the original grid. It is important to note that relocation and observer errors can have a significant impact on the accuracy of resurveys of historical vegetation plots (Verheyen et al., 2018). Therefore, any interpretation of the results should be done with caution.

2.3. Data analysis

In the plot × species matrix, cover estimates for each species were first converted from the scale used in the field surveys to respective mid-point cover values (in accordance with the Piskernik method), as follows: $e = 0.05$ %, $r = 0.1$ %, $+ = 1$ %, $x = 5$ %, $1 = 15$ %, $2 = 30$ %, $3 = 50$ %, $4 = 70$ %, $5 = 90$ %. The total cover of each vegetation layer (upper tree, lower tree, shrub, herb) per plot was calculated by summing the percentage cover of all species present. Given that species may overlap within the plot, this sum can surpass 100 %. The main part of the analysis focused on the changes in the herb layer. Alpha diversity was calculated as the plot-level number of species (species richness). Additionally, the Shannon diversity index and Pielou evenness index were calculated for each plot. The diversity indices were calculated using the vegan package in R (Oksanen et al., 2022). The assessment of changes in beta diversity was conducted through the utilisation of permutation tests for homogeneity of multivariate dispersions (PERMDISP; Anderson et al., 2006). This is a distance-based procedure that employs principal coordinate axes (PCoA) to estimate the compositional variation in multidimensional space (Oksanen et al., 2022). Significance was assessed with 999 permutations. The betadisper function (vegan package) was employed to obtain the distance values of each plot to the group centroid (i.e., survey year) in a multivariate dispersion (Bacaro et al., 2012). Furthermore, a model-based approach (Baeten et al., 2014) was employed to identify species with significant contribution to taxonomic homogenization or differentiation. This method quantifies changes in community heterogeneity over time using presence/absence data, providing a general indication of community convergence or divergence. The total number of recorded plant species across all plots (i.e., species pool) was considered as gamma diversity.

To ascertain the potential mechanisms underlying the observed changes, we calculated plot-level Ellenberg indicator values (Ellenberg et al., 1992) for light, temperature, continentality, soil moisture, soil acidity/pH and soil nutrients. These indicator values are widely used as proxies for environmental conditions in applied ecology and resurvey studies, facilitating the inference of the underlying drivers of herb-layer dynamics during the survey period (Diekmann, 2003; Hédl et al., 2017). Two species-specific, expert-based metrics related to the composition of the tree layer were included: shade-casting ability (SCA) and litter quality (LQ). The first is defined as the extent to which the canopy of dominant trees reduces light availability in the forest understory, while litter quality largely determines the decomposition rate and nutrient cycling (Verstraeten et al., 2013; Bernhardt-Römermann et al., 2015). The scores for overstory species' SCA and LQ were obtained from De Lombaerde et al. (2019) and range from 1 (low shade-casting ability/decomposition rate) to 6 (high shade-casting ability/decomposition rate). It should be noted that the calculations presented here were weighted with species abundances (i.e., community-weighted means). Calculations based on the incidence data yielded comparable results.

To analyse the dynamics of species composition, we grouped species of the herb layer according to their affinity to forest habitats (Heinken et al., 2022). The categories of habitat preference included typical forest species that mainly occur in closed forests (category 1.1), plant species of edges and clearings (category 1.2), species that occur both in forests and in open habitats (category 2.1), and species that occasionally occur in forests but predominantly in open habitats (category 2.2). For each species group, a community-weighted mean was calculated.

The shift in species composition was explored using non-metric multidimensional scaling (NMDS) with two dimensions. The species cover data were $\log(x + 1)$-transformed beforehand. We explained ordination gradients using passively fit vectors based on the envfit function with its default options (Oksanen et al., 2022). A permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was applied to test for differences in species composition of the herb layer between the original and recent surveys using the adonis2 function in the vegan package with 999 iterations. Plot-level species turnover based on presence/absence data was computed using the following equation:

$$species\ turnover = \frac{species\ gained + species\ lost}{total\ species\ observed\ in\ both\ survey\ years}$$

We calculated the degree of species disappearance (lost species) and new appearance (gained species). All three parameters were calculated with the functions implemented in the codyn R package (Hallett et al., 2016). Additionally, an indicator species analysis (Dufrêne and Legendre, 1997) was performed to assess the change in species occurrences, distinguishing between decreasing (significant association with the old survey) and increasing taxa (showing a significant association with the new survey). This analysis was conducted using the indicspecies package (De Cáceres et al., 2024).

For all response variables, the differences between the old and new surveys were evaluated using the non-parametric Wilcoxon signed-rank test with Z-score statistics for paired samples, taking into account the dependence of the old and new surveys. A p-value of <0.05 was considered statistically significant. All analyses were conducted using the R software version 4.3.0 (R Core Team, 2023).

3. Results

3.1. Cover of vegetation layers

The mean cover of the upper tree layer exhibited a notable decline, from 75.3 % to 57.3 % (Z = -4.149, $p < 0.001$). This trend reflected the diminished cover of *Quercus robur*, which previously dominated the upper tree layer but was observed to have a much lesser representation in the recent survey. The mean cover of the lower tree layer increased significantly from 84.4 % to 103.8 % (Z = 4.889, $p < 0.001$). For this layer we found a significant increase in the cover of *Corylus avellana* ($p < 0.001$), *Carpinus betulus* ($p < 0.05$) and *Alnus glutinosa* ($p < 0.05$). The contrasting trends observed in the two tree layers resulted in no significant change in the tree layer (upper and lower combined) between the survey years. The proportion of *Quercus robur* in the total tree layer cover decreased from 46 % to 35 %, while the proportions of *Carpinus betulus* and *Corylus avellana* increased from 39 % to 55 % and from 3 % to 6 %, respectively (Appendix C).

The mean cover of the shrub layer exhibited a significant increase, from 14.8 % to 31.4 % (Z = 3.376, $p < 0.01$). In this vegetation layer, there was a significant increase in the cover of *Corylus avellana* and *Crataegus laevigata*, while *Frangula alnus* and *Ulmus minor* exhibited a significant decrease. The regeneration of *Quercus robur* showed a notable decline, with its presence reduced from six plots and a mean cover of 3.4 % in the old relevés to only three plots and a mean cover of 0.4 % in the new relevés. The frequency of regeneration of *Carpinus betulus* also exhibited a decline (old: 29 plots, new: 19 plots), yet the mean cover remained at a comparable level (old: 5.8 %, new: 6.0 %). The mean plot-level cumulative cover of the herb layer exhibited a significant increase (Z = 2.033, $p < 0.05$), from 159.4 % to 180.0 % (Fig. 2).

3.2. Changes in herb-layer diversity

A total of 111 vascular plant species in the herb layer were recorded across 60 relevés (Appendix D), with *Carex brizoides* exhibiting the highest mean cover in both old and new surveys. The mean number of species per plot decreased significantly from 24.6 ± 4.6 to 21.4 ± 5.3 (Z = -2.276, $p < 0.01$), representing an average reduction in species richness of 13 %. Out of the 30 resampled plots, 22 showed a decrease in herb-layer species richness, two plots demonstrated no change, and six plots exhibited an increase in species richness (Fig. 3a). No significant changes were observed for the Shannon diversity and evenness indices.

A significant ($p < 0.01$) reduction in the mean distance of samples to the group centroid (old: 0.510, new: 0.446) was observed in the PCoA multivariate space (Fig. 3b, Appendix E). This indicates a taxonomic homogenization, i.e., diminished variation in the herb-layer vegetation

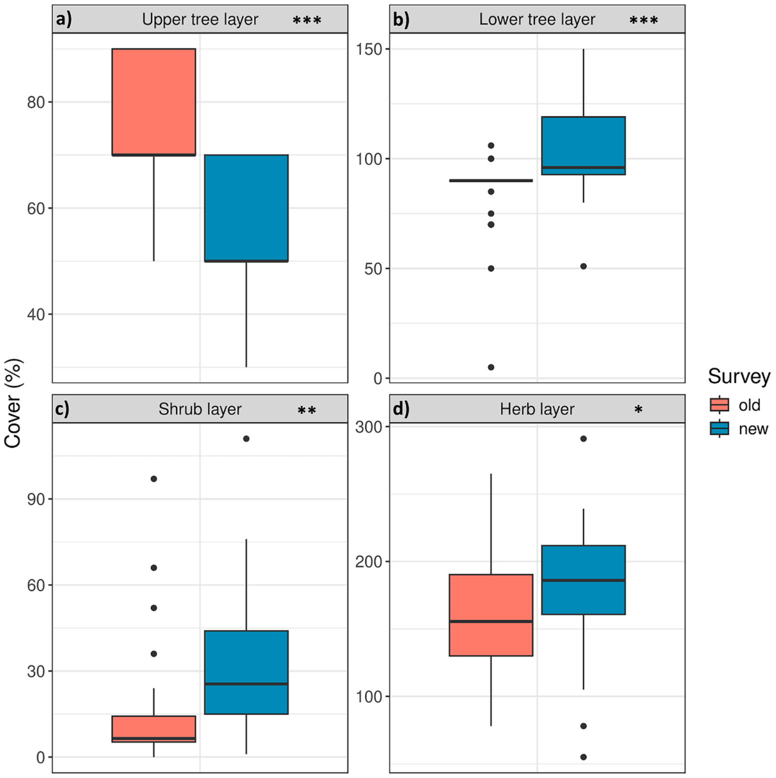

Fig. 2. The changes in the cumulative cover of four vegetation layers: a) upper tree layer, b) lower tree layer, c) shrub layer and d) herb layer. The significance between surveys is indicated with asterisks: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

composition across the sampled plots within the forest reserve. This finding was further corroborated by the model-based analysis of beta diversity, which revealed a significant convergence in community composition between the old and new survey areas (ΔD = -264; $p < 0.01$). Ten species were identified as significantly contributing to convergence (homogenization), whereas six herb-layer taxa were identified as community-divergent species (see Appendix F). The total number of species (gamma diversity) decreased from 93 in the old survey to 83 in the resurvey (Fig. 3c). Twenty species documented in the initial sampling were not observed in the subsequent sampling, while ten species were identified as new colonizers (Appendix G).

3.3. *Changes in environmental conditions*

The mean shade-casting ability of the tree layer increased significantly from 4.52 to 4.74 ($Z = 2.302$, $p < 0.05$). The mean litter quality values increased significantly from 2.11 to 2.37 ($Z = 4.884$, $p < 0.001$). Herb-layer Ellenberg values for light exhibited a significant decline, from 4.90 to 4.32 (Z = -3.652, $p < 0.001$). Similarly, the Ellenberg temperature values in the herb layer demonstrated a notable decrease, from 5.53 to 5.31 (Z = -2.942, $p < 0.01$; Fig. 4). No statistically significant changes were observed in Ellenberg values related to continentality, soil moisture and soil acidity (pH). Community-level values for soil nutrients (nitrogen) increased marginally significant ($p < 0.1$; results reported in Appendix H).

3.4. *Species composition*

The PERMANOVA results indicated a significant ($p < 0.001$) difference in herb-layer species composition between the two surveys. This finding was corroborated by a complete separation between old and new relevés along the NMDS2 axis (Fig. 5a). Among the passively fitted variables, Ellenberg light and temperature, as well as species that occur in both forest and open habitats, demonstrated a positive correlation with the NMDS2 axis. Conversely, the cover of the lower tree layer, species that predominantly occur in closed forests, and the shade-casting ability of the tree layer exhibited a negative correlation with the NMDS2 axis. The Ellenberg value for soil moisture was the only variable to demonstrate a statistically significant correlation with the NMDS1 axis (Fig. 5b). This gradient along the first axis confirms pronounced mosaic of different plant communities (*Pseudostellario-Quercetum, Pseudostellario-Carpinetum, Carici-Alnetum glutinosae* s. lat.).

The species turnover was observed to range between 38 % and 80 %, with a mean ± SD of 61 % ± 10 %. The rate of species disappearance (36 % ± 9 %) was, on average, higher than the rate of new appearances (25 % ± 9 %).

Significant temporal changes in community-weighted means for forest affinity categories were found (Fig. 6). The proportion of category 1.1 increased ($Z = 2.632$, $p < 0.01$), while the proportion of categories 2.1 and 2.2 demonstrated a decline (Z = -2.543, $p < 0.05$ and Z = -2.894, $p < 0.01$, respectively).

According to the indicator species analysis, eleven plant species in the herb layer were identified as significantly decreasing. Among these, three species (*Gentiana asclepiadea, Peucedanum palustre* and *Lysimachia vulgaris*) were not recorded in the new survey despite being relatively common in old survey (present in >20 % of plots). Conversely, six species were recognized as increasing taxa. Plant species with the most pronounced increase in frequency and mean cover were *Galeobdolon montanum* (formerly *Lamiastrum galeobdolon* agg.), *Carex remota* and *Athyrium filix-femina* (Table 1).

4. Discussion

4.1. *The shift in overstory dominance*

This study investigated long-term (1970s – 2024) changes in plant diversity and species composition in strictly protected Krakovo forest reserve, the only preserved remnant of lowland oak-hornbeam forests

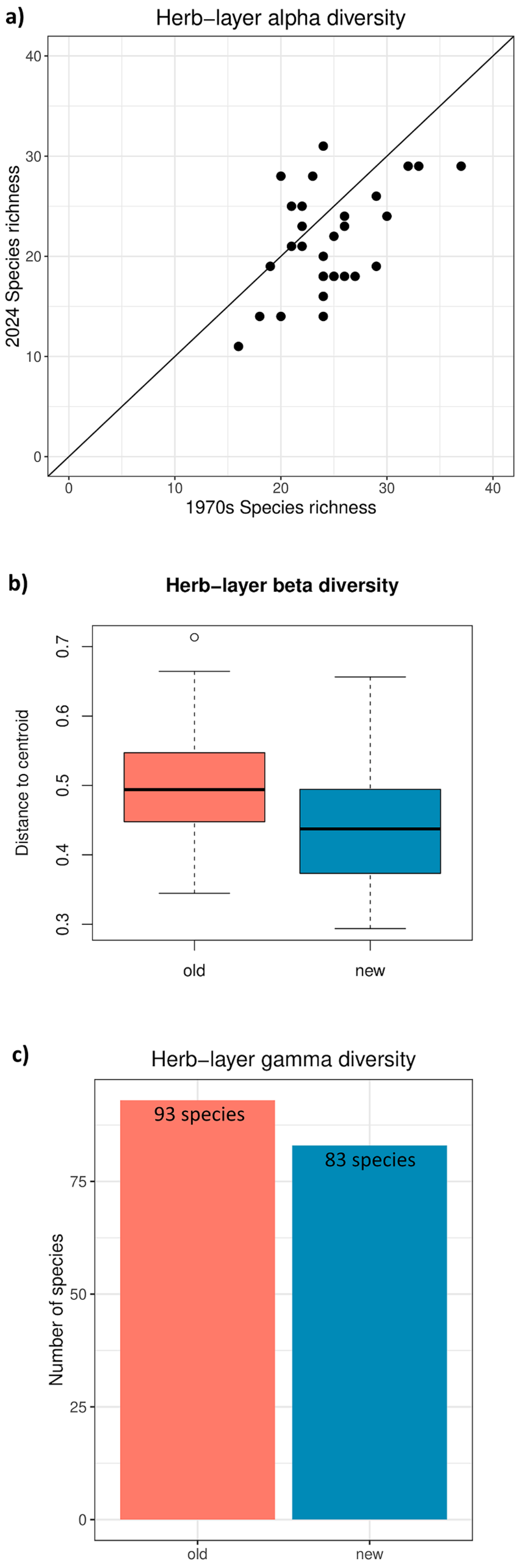

Fig. 3. The changes from old (1970s) to new (2024) surveys in the herb-layer a) species richness, measured as the plot-level number of vascular plant species; the diagonal line indicates a 1:1 relationship of no change. b) beta diversity, measured as a distance to centroid in a multivariate space. c) gamma diversity, i.e., total number of plant species recorded in each survey.

with primary status in Slovenia. Despite the common perception of strict forest reserves exhibiting greater temporal stability compared to managed forests, our research has revealed that vegetation within this long-untouched reserve has undergone significant alterations over the past 50 years. The main findings with regard to the overstory are a notable decline in the prevalence of *Quercus robur* in the upper tree layer and an increase in the abundance of *Carpinus betulus* and other subordinate broadleaves in the lower tree layer. Although the total (cumulative) tree layer cover remained constant, there was an evident shift in dominance from *Q. robur* towards *C. betulus*. Expansion of *C. betulus* can be interpreted as a general indicator of reduced flooding and soil water content (Janik et al., 2011). The shrub *Corylus avellana* exhibited significant ingrowth into the lower tree layer (height > 5 m) as well. An additional indicator of reduced site wetness can be the increase in abundance of woody regeneration in the shrub layer, which can also be caused by increased CO_2 levels (Cestarić et al., 2017; Lanta et al., 2024). Such gradual structural changes in the studied reserve have an important impact on ecological conditions in the understory, exerting strong control on herb-layer diversity and composition.

The accelerated decline of *Quercus* spp. is a commonly observed phenomenon in temperate forests across Europe (e.g., Kwiatkowska, 1994; Rohner et al., 2012; Saniga et al., 2014; Kermavnar and Kutnar, 2024a) and has been, in case of *Q. robur*, attributed to a complex combination of causal factors (Thomas et al., 2002). A change in the hydrological regime in lowland forests appears to be the primary driver of shifts in vegetation composition (Cestarić et al., 2017). Similar to alluvial forests, depth to the groundwater table is one of the most important factors explaining tree species composition in lowland oak-hornbeam ecosystems (Strubelt et al., 2017). In addition to less frequent flooding and lowering of groundwater levels (Appendix B), drought stress is also caused by seasonal and inter-annual fluctuations in groundwater table (Pilaš et al., 2007). In conditions of elevated groundwater levels, oak trees tend to develop very shallow root systems. This trait renders them susceptible to the consequences of insufficient rainfall during the summer months (Thomas et al., 2002). Old oaks are increasingly exposed to reduced water availability due to soil drainage, and overall increasing impact of recurrent summer heatwaves and prolonged periods of drought stress (Levanič et al., 2011). Such changes are manifested in reduced growth, enhanced crown defoliation or complete mortality as drought-weakened trees are more susceptible to pathogens and insect attacks due to global warming (Čater and Levanič, 2015; Bussotti et al., 2024). Another factor contributing to the decreased share of *Q. robur* in the overstory of the studied forest reserve are natural treefalls of senescent oaks, leading to the accumulation of woody biomass. It is also possible that increasing oak mortality reflects the legacy of past management (before 1952) when oak was likely favored due to higher economic value. Conversely, *C. betulus* is known to prefer sites with reduced soil water saturation and can cope better with increasing water deficit due to recurrent droughts (Cestarić et al., 2017). Therefore, we assume that lowering groundwater table, less frequent flooding, oak decline and consequent alterations in ecological conditions facilitated the expansion of *C. betulus* and other broadleaves in the tree layer at the expense of *Q. robur* (Kermavnar and Kutnar, 2024a).

This observation is very similar to reports from managed European forests (Verheyen et al., 2012; Vojík and Boublík, 2018) and from Białowieża primeval forest in Poland (Kwiatkowska, 1994). The authors documented the decline of oak forest and gradual expansion of *C. betulus* in the lower vegetation layers. The increasing occurrence and cover of subordinate, shade-tolerant tree species in lowland oak woodlands was recently reported by Lanta et al. (2024). In a permanent monitoring plot in the nearby oak-hornbeam managed forest of Krakovski gozd (air distance ~1 km from the studied forest reserve), we found similar trends in the overstory (Kermavnar and Kutnar, 2024b). From 2004 to 2020, *Q. robur* cover in the upper tree layer decreased on average from 65 % to 34 %, while *C. betulus* cover in the lower tree layer increased from 77 % to 89 %.

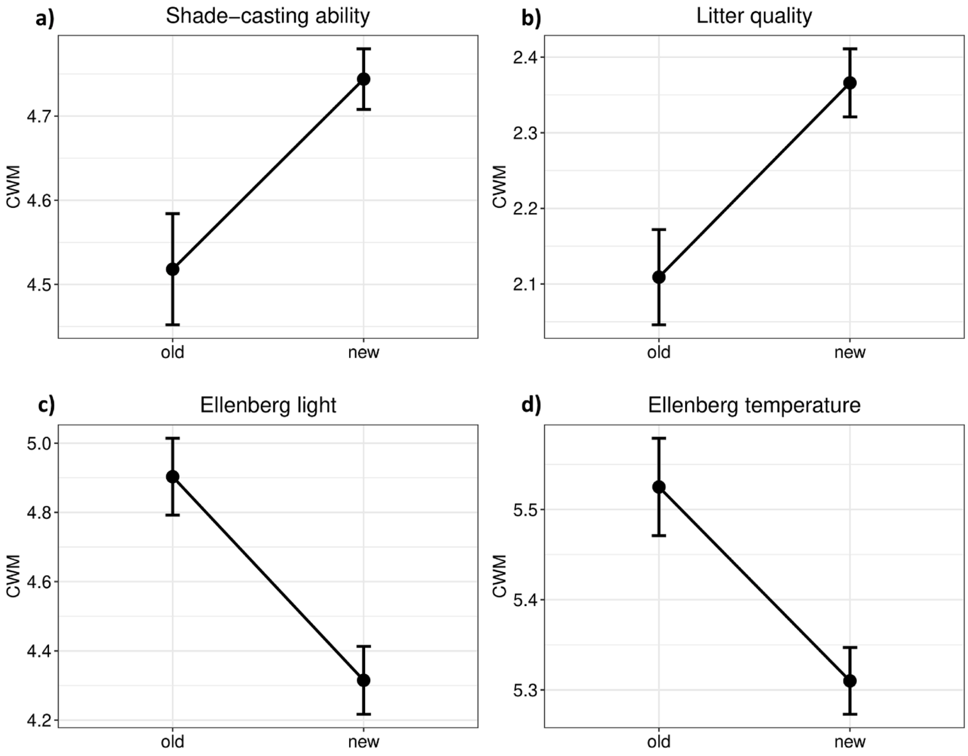

Fig. 4. The changes in community-weighted means for a) shade-casting ability of the tree layer; b) litter quality of the tree layer; c) herb-layer Ellenberg light value; d) herb-layer Ellenberg temperature value.

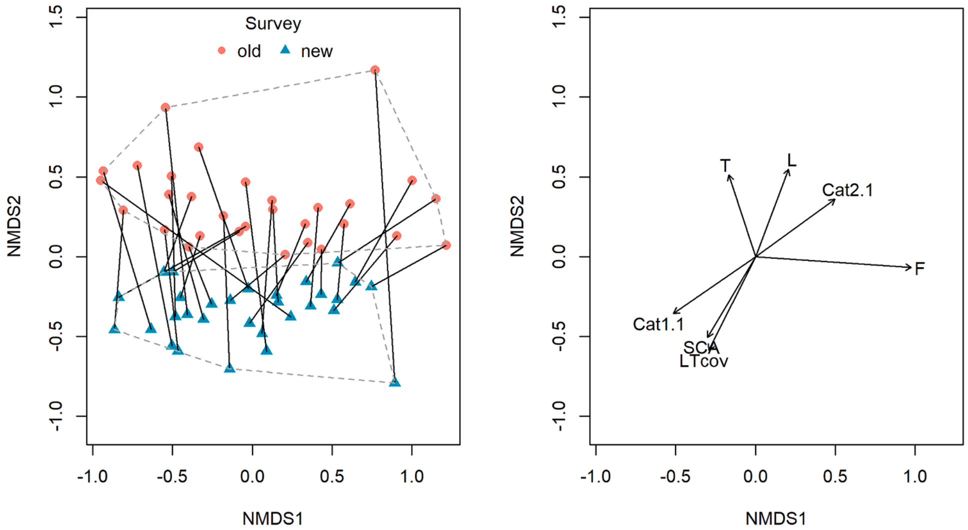

Fig. 5. a) NMDS ordination diagram illustrating the distribution of old (1970s) and new (2024) relevés, connected with lines; b) Passively fitted variables showing significant ($p < 0.05$) correlations with the ordination axes (L = Ellenberg light, Cat2.1 = species that occur both in forests and in open habitats, T = Ellenberg temperature, F = Ellenberg soil moisture, LTcov = cover of the lower tree layer, Cat1.1 = species that mainly occur in closed forests, SCA = shade-casting ability of the tree layer).

4.2. Decline in herb-layer diversity

Described changes in the forest overstory have profoundly influenced temporal trends in herb-layer diversity. We found a decrease in plant diversity on multiple levels: alpha (plot-level species richness), beta (compositional heterogeneity among plots) and gamma (species pool size) diversity, indicating floristic impoverishment and taxonomic homogenization of herb-layer plant communities. Changes in tree species composition and stand structure are causing alterations in resource availability and growing conditions at the forest floor (Barbier et al., 2008; Balandier et al., 2022). The light transmittance of the tree layer is considered one of the most important drivers shaping the understory environment and influencing the plant species richness in herb layer of temperate deciduous forests (Dormann et al., 2020).

The two tree species that dominate Krakovo forest reserve exhibit substantial variation in their crown architecture and shade-casting ability (SCA). *Q. robur* has considerably lower SCA (index 3) compared to *C. betulus* (index 6). The main consequence of this difference is a significant reduction in the amount of sunlight that reaches the forest floor beneath *C. betulus* canopies. It can be hypothesized that the gaps

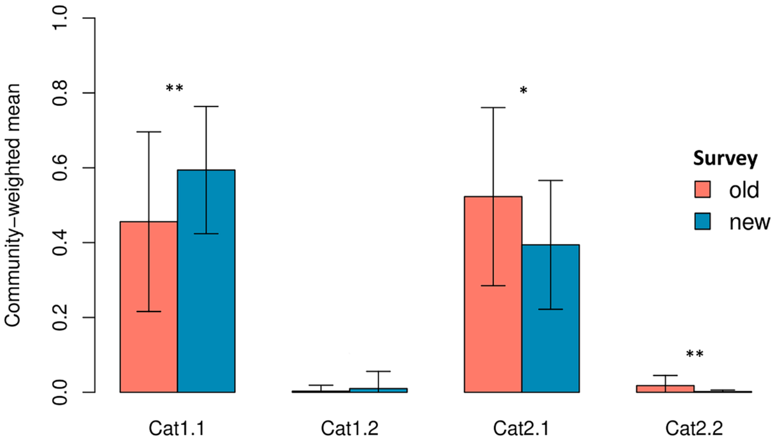

Fig. 6. Community-weighted means for different categories of plant species affinity to forest habitat. Cat1.1 = species of closed forests, Cat1.2 = species of forest edges and clearings, Cat2.1 = species occurring in forests and open sites, Cat2.2 = species of open sites (non-forest plants). Significant changes between old and new surveys are marked with asterisks: ** $p < 0.01$, * $p < 0.05$.

Table 1
The list of herb-layer indicator species significantly associated with old (11 decreasing species) and new survey (six increasing species). The order is based on indicator value produced by indicator species analysis. Frequency – proportion of plots occupied, relative to all resampled plots (30). Mean cover – averaged abundance across plots where present.

Decreasing species (losers)				
Species	Frequency_old (%)	Frequency_new (%)	Mean cover_old (%)	Mean cover_new (%)
Quercus robur	93	60	10.4	0.1
Anemone nemorosa	67	60	32.6	5.1
Ranunculus auricomus	57	27	15.4	0.1
Gentiana asclepiadea	37	0	1.0	0
Lycopus europaeus	37	10	1.0	0.1
Peucedanum palustre	23	0	6.6	0
Lysimachia vulgaris	20	0	2.7	0
Dryopteris dilatata	23	7	0.1	0.1
Cerastium sylvaticum	13	0	0.33	0
Fragaria vesca	17	0	0.28	0
Angelica sylvestris	10	0	5	0
Increasing species (winners)				
Species	Frequency_old (%)	Frequency_new (%)	Mean cover_old (%)	Mean cover_new (%)
Galeobdolon montanum	63	90	7.8	28
Carex remota	50	73	5.1	12.5
Athyrium filix-femina	93	93	14.7	22.6
Aegopodium podagraria	27	47	5.7	15.6
Rubus hirtus agg.	23	40	2.4	13.7
Milium effusum	13	27	0.3	6

created by senescent oaks were subsequently filled by the lateral growth of *C. betulus* crowns and more open canopy also stimulated the recruitment pulse of other fast-growing woody plants (e.g. *C. avellana* with SCA index 4) from the shrub to the lower tree layer. In addition to adult *C. betulus* individuals reaching a diameter of ca. 30 cm and height above 20 m, there were numerous pole-sized trees with dense crowns, contributing to increased shading of the forest understory.

The increased shading effect of the overstory canopy has been repeatedly identified as a primary driver of the decline in herb-layer species richness following natural succession, abandonment of traditional management practices or application of strict conservation measures in various forest types (Verstraeten et al., 2013; Mölder et al., 2014; Strubelt et al., 2019; Heinrichs et al., 2022). Our results confirm many resurvey studies (Vojík and Boublík, 2018; Máliš et al., 2021; Vandekerkhove et al., 2021; Kotrík et al., 2023; Lanta et al., 2024), which demonstrated that the expansion of shade-casting trees most often lead to the impoverishment of herb-layer diversity as fewer species can tolerate the low-light conditions. For instance, a gradual decline of *Abies alba* and an increase in the prevalence of *Fagus sylvatica* in old-growth forests in the Dinaric region of Slovenia were accompanied by a significant decline in herb species richness and community convergence (Nagel et al., 2019).

Filtering of heliophilous plants in the herb layer can be attributed to greater SCA in the overstory, meaning that light has become a crucial limiting resource for community assembly over the last decades (Bernhardt-Römermann et al., 2015; Máliš et al., 2021). The decline of oak-dominated plant community (*Quercetum*) and its transformation towards hornbeam-dominated community (*Carpinetum*) was an important reason for disappearance of heliophilous species typical for oak forests and overall plant diversity decrease in the study of Kwiatkowska (1994). In another study from Białowieża forest, Kwiatkowska et al. (1997) also emphasized the importance of deterioration of light conditions, induced by recruited *C. betulus* saplings, for sharp plant diversity decline. Thus, we can assume that the diversity of the herb layer was additionally reduced due to a denser cover of woody regeneration in the shrub layer.

In terms of beta diversity, we detected a process of taxonomic homogenization, i.e., significant decrease of compositional dissimilarity among plots. This observation is in line with numerous reports from temperate biome (Kopecký et al., 2013; Strubelt et al., 2017; Cholewińska et al., 2020; Máliš et al., 2021). Community convergence was driven by both (i) losses of initially rare species with higher demands for light that became less frequent or completely absent (losers), and by (ii) gains of a narrow subset of forest perennials adapted to shaded conditions but already common in the 1970s (winners), such that they contributed to a more homogeneous composition across the reserve. The loss in beta diversity is likely to result in a shrinkage of the gradient of vegetation types, blurring the distinction between them (Cholewińska et al., 2020).

In managed oak-hornbeam forest in Krakovski gozd, located in close vicinity to the studied forest reserve, Kutnar & Kermavnar (2024) observed a strong decline (38 % on average) in herb-layer richness during the 2004–2020 period. However, richness decline was not accompanied by taxonomic homogenization (Kermavnar and Kutnar, 2024b). In both cases, *Q. robur* declined in the upper tree layer and *C. betulus* expanded in the lower tree layer. In contrast, for permanent plots in managed *Quercus*-dominated lowland forests, we found an overall increase in understory diversity (herb and shrub layer combined) over the period 1992/93–2023, mainly because these stands experienced significant canopy opening triggered by oak mortality and subsequent sanitary logging, stimulating the colonization of ruderal species (Kermavnar and Kutnar, 2024a) and many neophytes as well (Kermavnar and Kutnar, 2024c). However, no neophytes were recorded in resurveyed plots in the Krakovo forest reserve, and they were already absent in the initial survey. It is likely that the shading effect impeded their colonization. In summary, the findings of this study demonstrate that long-untouched forest reserves exhibit much lower susceptibility to the invasion of neophytes in comparison to managed forests, where silvicultural interventions function as core vectors for the dispersal of invasive plants.

4.3. Directional changes in species composition

Herb-layer composition changed significantly over the study period, with an average species turnover of 61 %. Turnover was more influenced by disappearance of certain species than by colonization of new species. Compositional changes were not random because all plots shifted in similar direction triggered by alteration in overstory dominance from *Q. robur* towards *C. betulus*, resulting in changes in stand structure, available light at the forest floor, forest microclimate, and litter and soil properties.

Using vegetation-derived proxies for ecological conditions, we observed that compositional changes reflected directional reorganization of the natural plant communities in response to increasingly shaded conditions. Ellenberg indicator values (EIV) for light decreased, which corresponds well with the increase in the SCA of the overstory trees. Kopecký et al. (2013) also noted a significant decrease in EIV for light in lowland forests after change in management and associated stand structure alterations. *Carpinus*-dominated stands are in general more shaded at the forest floor than *Quercus* communities (Kwiatkowska et al., 1997; Leuschner and Ellenberg, 2017).

Light limitations act as a strong filter on plant species in the understory of temperate deciduous forests, reducing the survival chances of more light-demanding species (Verheyen et al., 2012; Máliš et al., 2021). This decline was not random as divergent trends for species with different ecological strategies (affinity to forest habitat) were noticed. Indeed, we found stronger exclusion of heliophilous plants that typically grow in both forests and in open habitats (Strubelt et al., 2017). Light-demanding taxa that require periodic disturbances or gaps in the canopy decreased or disappeared entirely over the study period. Many of these species already had low frequencies and cover at the old survey. On the other hand, the low-light environment created by expansion of shade-casting trees benefited the occurrence and abundance of shade-tolerant species that prefer closed-canopy forests (Heinken et al., 2022; Kotrík et al., 2023).

Our analysis showed that resurveyed herb-layer communities in the Krakovo forest reserve were characterized by lower EIV for temperature, suggesting cooler understory environment. This is against accelerating macroclimate warming seen on the annual and seasonal levels for studied location (Appendix A). Such discrepancy can be explained by stronger temperature buffering and elevated humidity levels beneath canopies with higher SCA (Zellweger et al., 2020). Cooler growing-season ground temperatures through increased shading may prove to be essential for the survival of forest species (Vandekerkhove et al., 2021). These results are in complement with previous conclusions that reduction of light from canopy shading can overrule the influence of climate warming on understorey communities (Depauw et al., 2020).

In contrast to evident decrease in EIVs for light and temperature, we did not detect significant changes for soil moisture and acidity, whereas increase in nutrient availability was marginal. Despite relatively stable conditions in terms of edaphic factors, significant increase in litter quality (LQ) of the overstory could offer plausible mechanistic interpretations for herb-layer changes. Tree species differ greatly in their impacts on soil fertility and acidity with consequent impacts on the herb-layer vegetation (Augusto et al., 2003; Balandier et al., 2022). *Q. robur* has low LQ (index 1) as it produces slowly decomposable leaf litter with high C:N ratio whereas two most expanding species in the overstory, *C. betulus* and *C. avellana*, have higher LQ (index 3) and faster decomposable leaves (Leuschner and Ellenberg, 2017). *Quercus*-dominated canopies can contribute to the formation of a thicker litter layer and more acid soil conditions with lower base saturation and nutrient supply (Augusto et al., 2003; Durak and Durak, 2015). Decomposition of organic material formed in the forest ecosystem constitutes an important source of soil enrichment with nutrients (Hofmeister et al., 2004). We therefore assume that the improved LQ, atmospheric nitrogen deposition and increased nitrogen release stored over decades of biomass (especially deadwood) accumulation are likely to have increased the general nutrient availability (Bernhardt-Römermann et al., 2015; Kotrík et al., 2023) in the soil, favouring species with higher EIV for nutrients and soil pH (Verheyen et al., 2012; Vojík and Boublík, 2018; Máliš et al., 2021). Moreover, in densely populated lowland areas, local sources from agricultural land can also be important contributors to soil eutrophication (Kermavnar and Kutnar, 2024a). A tendency towards more nutrient-rich and less acidic vegetation in increasingly shaded stands is similar to trends in managed forests of Central Europe (Vild et al., 2024).

Such effects may, to some extent, explain the surprising increase in plot-level cover of the herb layer. This finding contradicts the prevailing assumption that the coverage of herb layer is primarily diminished as SCA of the overstory increases (De Lombaerde et al., 2019; Depauw et al., 2020). However, soil nutrient levels can alter plant species responses to light availability. Many herb layer species need a higher nutrient supply to compete successfully with other species under shadier conditions. A possible mechanistic explanation for this phenomenon is that on more fertile soils, plants need to allocate fewer resources to roots and can therefore invest more nutrients for biomass construction of their aboveground organs (Coomes et al., 2009). This is why we suspect that increase in herb-layer cover was enhanced by greater nutrient availability, supporting local spread of eutrophic forest herbs that can efficiently utilize soil resources under low-light conditions and often exhibit marked capacity for clonal reproduction or phenotypic plasticity, in our dataset e.g. *Galeobdolon montanum* (Dong, 1993).

In the Krakovo forest reserve, soil moisture is the ecological factor that most strongly shapes the floristic differentiation of forest plant communities, creating interchanging distribution between wetter and more mesic habitats. Such mosaic enables the co-existence of species with different moisture requirements and at the scale of entire forest reserve, we found that this spatial patterning was still present in the resurvey. Due to changes in hydrology and lowering of groundwater levels causing oak mortality, we expected to also observe decrease in EIV for soil moisture. However, this was not the case here as this plant-derived variable likely relate more to the organic layer and the upper layer of the mineral soil (~10–20 cm), more relevant for the herbaceous component of understory vegetation whereas trees and shrubs with deeper roots are more influenced by groundwater table. The lack of significant changes in soil moisture in our study contrasts with Cestarić et al. (2017), Strubelt et al. (2019) and Breton et al. (2023), which all documented decreasing water level and drying of forest sites as main drivers of long-term vegetation change in the herb layer.

It could be that temporal stability in EIV for soil moisture was indirectly supported through increasing cover of shade-casting trees that amplified microclimate buffering. Greater shading likely reduced evapotranspiration rates and hence soil moisture levels in the topsoil and upper mineral soil were preserved (Vojík and Boublík, 2018), promoting species that require consistently moist soils (e.g. *Carex remota*). In return, greater soil moisture can contribute to higher humidity levels and consequently to temperature buffering due to evaporative cooling effects (Greiser et al., 2024). Furthermore, recent evidence from broadleaf forests showed that forest plant indicator values for moisture are actually more indicative of vapour pressure deficit (determined by air humidity) than of soil water content (Kopecký et al., 2024).

4.4. Future perspective of oak-hornbeam forest

Beside the multitude of pressures that threat the integrity of studied forest reserve (e.g. changes in hydrology, oak mortality, habitat fragmentation, small area of the reserve with limited buffer zone), we found that *Q. robur* is not only losing its overstory dominance but has also experienced significant decline in regeneration. In the original survey in 1970s, this foundation tree species was much more abundant in the herb and shrub layers compared to recent resurvey. Historically, more open canopies supported its natural regeneration. However, a shift towards shadier and cooler conditions in the understory have led to much lower competitiveness of oak seedlings and saplings. The decreasing light availability seems to be the most decisive factor for the poor regeneration of *Q. robur*, especially during the early stages of ontogenetic development. According to Accetto (1975), oak needs sufficient temperature for germination and seedling growth. Based on our results for EIV, the temperatures dropped in the understory, making unsuitable environment for oak regeneration which could be additionally hampered by deer browsing. Conversely, altered ecological conditions favour shade-tolerant species like *C. betulus*.

If the recent trend continues, it is probable that the studied forest reserve will undergo an accelerated transition toward a community dominated by *Carpinus*, with a high tendency for formation of even-aged, uniform stand structure and low light availability at the forest floor. Further studies are warranted to assess whether this is rather a cyclical change or more directional phenomenon that can become even more expressed in the future.

5. Conclusions

In the period from 1970s to 2024, study results indicate several key points: (i) the shift in overstory dominance due to notable *Q. robur* decrease in the upper tree layer and expansion of *C. betulus* in the lower tree layer, accompanied by increasing cover of other woody species (*C. avellana*) in the lower tree and shrub layers; (ii) a decline in herb-layer diversity and (iii) directional changes in plant community composition as a response to increased shading. A shift in dominance from oak towards hornbeam, driven by hydrological factors, exerted cascading impacts on the understory environment and herb-layer vegetation. Our results point to the conclusion that temporal trends in the herb layer of primary, long-untouched forests are driven by overstory alterations and associated changes in light conditions. This corroborates earlier studies conducted in Central Europe, which reported non-random changes and impoverished herb-layer flora following the cessation of management or the progression of natural forest succession.

Our findings underscore the pressing issues of oak mortality and its inadequate natural regeneration for the long-term integrity of this rare ecosystem. Information on changes in the herb layer of unmanaged forest reserves may be useful in assessing present-day issues related to sustainability and biodiversity in forestry and nature conservation.

CRediT authorship contribution statement

Janez Kermavnar: Writing – review & editing, Writing – original draft, Visualization, Validation, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Lado Kutnar:** Writing – review & editing, Validation, Project administration, Methodology, Investigation, Data curation, Conceptualization.

Declaration of competing interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.flora.2025.152742.

Appendix A. Long-term trends in temperature and precipitation.

Appendix B. Dynamics of groundwater table for the Krakovo forest.

Appendix C. Changes in the mean proportion of different species in the total tree layer cover.

Appendix D. Changes in frequency for all plant species recorded in the herb layer.

Appendix E. PCoA diagram for beta diversity changes (betadisper).

Appendix F. Model-based ΔD (Baeten et al., 2014) results with community-convergent and community-divergent species.

Appendix G. A list of plant species that disappeared between the two surveys and a list of newly colonized species.

Appendix H. Changes in community-weighted means of Ellenberg indicator values.

Data availability

The data that support the findings of this study will be made available from the corresponding author (JK) upon reasonable request.

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