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Three decades of understorey vegetation change in *Quercus*-dominated forests as a result of increasing canopy mortality and global change symptoms

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Abstract

Questions: The long-term response of understorey vegetation to increasing tree mortality has rarely been addressed in resurvey studies. For two *Quercus*-dominated forest types, we asked: (a) How did overstorey alterations, induced by canopy mortality, affect understorey diversity and composition? (b) Is there a signal of global change effects on understorey communities? (c) Are these assemblages experiencing a homogenization process?

Location: Five sites in *Quercus robur* (QR) and four sites in *Q. petraea* (QP) forests, Slovenia.

Methods: We studied changes in vascular plants in the understorey layer from 1992/1993 to 2023 across 45 permanent 20 m × 20 m plots in QR and QP forests, respectively. Vegetation surveys were carried out following the standard Braun-Blanquet method. We compared original surveys with recent resurveys using multivariate analysis, ecological indicator values (EIV), plant traits and methods that quantify changes in individual species.

Results: Since the early 1990s, tree layer cover decreased from 95% to an average of 55% in QR, whereas it remained relatively high (77%) in QP plots. This resulted in denser understorey vegetation and a significant increase in plot-level species richness in QR forests, but a slight decrease in QP forests. The extensive loss of canopy cover and disturbance effects in QR forests caused significant changes in species composition. Species turnover in QR was driven by colonization of new disturbance-tolerant taxa characterized by ruderal traits, whereas the compositional shift in QP was to a greater extent due to species losses. We detected a process of vegetation thermophilization (increase in EIV-temperature), suggesting an effect of rapid climatic warming. Understorey communities are now more similar to each other than 30 years ago, indicating a decrease in beta-diversity (floristic homogenization).

Conclusions: Despite some common trends, vegetation responses were forest type-specific. Our study presents evidence of understorey vegetation changes triggered by increased canopy mortality (a strong local driver particularly in QR plots) and also

points to the signal of global change symptoms (thermophilization, homogenization), which acted rather independently from the observed decline in tree layer cover.

KEYWORDS

floristic homogenization, forest disturbances, permanent vegetation plots, *Quercus robur* and *Q. petraea*, resurvey study, Slovenia, thermophilization, tree layer cover

1 | INTRODUCTION

Pedunculate oak (*Quercus robur*; hereafter QR) and sessile oak (*Quercus petraea*; hereafter QP) are common broad-leaved tree species widely distributed across Europe (Eaton et al., 2016). Mixed deciduous forest ecosystems dominated by these two oak species have traditionally been valued for their significant economic importance and high biodiversity (Mölder et al., 2019). However, oak forests have faced severe human pressure for centuries, primarily because of their proximity to settlements in lowlands and hilly regions with gentle topography (Kotrík et al., 2023). The historical development and current state of QR forests have been strongly influenced by interventions in the hydrological regime (regulation of riverbeds, construction of embankments, dams and hydroelectric power plants), leading to significant drainage of natural forest sites. In addition, land-use changes, unfavorable management practices (conversion to stands dominated by *Carpinus betulus*, artificial introduction of less adapted tree species) and air and soil pollution have further contributed to their overall degradation (Klimo et al., 2008). Similarly, QP forests have been characterized by extensive exploitation and activities adapted to agricultural needs, such as deforestation, habitat fragmentation, coppicing, litter raking, wood pasture and other non-timber forest uses (Durak & Durak, 2015; Bou & Vilar, 2019; Kotrík et al., 2023).

Oak forests dominated by QR and QP are vegetation types that are highly susceptible to various threats posed by environmental changes of both natural or anthropogenic origin (e.g., habitat loss and degradation, pollutants and nutrient loads, climate change). The problem of increasing canopy mortality in Europe has important consequences for habitat functioning and the provision of ecosystem services (Senf et al., 2021). Lowland QR forests in particular have been experiencing widespread tree mortality and consequent canopy cover decline for an extended period (Čater, 2015; Eaton et al., 2016; Mölder et al., 2019). These changes are reflected in a decline in vitality and failures in forest regeneration (Dakskobler et al., 2013; Čater, 2015). One of the main causes of QR mortality is desiccation due to a lowering of the groundwater table and its interannual oscillations caused by human interventions. In addition, the increasing trend of forest dieback has recently been attributed to climate change (Anderegg et al., 2012). Rising temperatures, prolonged dry periods in spring and summer, extreme weather events and others stress factors have contributed to a massive oak decline in recent decades (Dakskobler et al., 2013; Čater, 2015). Global warming and

drying are also expected to have significant influence on QP forest stands. Such pressures are causing significant alterations in the diversity and floristic composition of the understorey layer in oak forests (Bhatta & Vetaas, 2016).

The understorey vegetation of temperate forests harbors a major proportion of vascular plant diversity and plays a vital functional role (Gilliam, 2007; Wen et al., 2022). This stratum may serve as an indicator of long-term changes in abiotic site conditions. Over the past decades, forest understorey communities have been observed to change in species diversity and composition in response to both anthropogenic and natural impacts, yet the underlying mechanisms are not fully understood (Verheyen et al., 2012). Observational studies have summarized these findings into a few driver–response relationships, which have contributed to the formation of a predictive framework conceptualizing patterns and processes of long-term vegetation dynamics at the European scale (Chudomelová et al., 2017; Closset-Kopp et al., 2019). Observed changes have largely been attributed to several external drivers that promote macroecological processes such as thermophilization (increase in thermophilous species due to climate warming; De Frenne et al., 2013; Seliger et al., 2023), eutrophication (nitrogen enrichment of soil favoring nitrophilous species; Heinrichs et al., 2012) and biotic homogenization (decrease in beta-diversity, i.e., spatial variation in species composition; Rolls et al., 2023). Such directional trajectories of vegetation changes in the understorey layer, steered by global or regional drivers, are a cause for concern from a conservation perspective because these factors can potentially lead to a decline in plant species and trait diversity (Prausová et al., 2020). Despite this generality, contradictory results in the scientific literature suggest that trends are not universal, because local factors interact with environmental drivers operating at larger spatial scales (Naaf & Kolk, 2016). For example, changes in canopy cover in mature forests can amplify, neutralize or even counterbalance the effects of global drivers (De Frenne et al., 2013). In addition, temporal trends can vary greatly among forest vegetation types (Wrońska-Pilarek et al., 2023; Kermavnar & Kutnar, 2024).

The resurvey of historical vegetation plots has become a well-established tool for understanding the long-term dynamics of plant communities (Hédl et al., 2017; Kapfer et al., 2017; de Bello et al., 2020). However, resurvey studies often used semi-permanent plots with inherent bias (relocation errors), permanent plots with a shorter time span between the initial survey and the resurvey (e.g., Valerio et al., 2021) and were mainly conducted in

beech (Heinrichs & Schmidt, 2017; Prausová et al., 2020; Scherrer et al., 2024) or mixed forests (Helm et al., 2017). Conversely, forest communities dominated by QR and QP are relatively underrepresented, with studies often focusing on the effects of the cessation or complete abandonment of historical management practices (Becker et al., 2017; Klynge et al., 2020). In addition, less is known about the effects of increasing canopy mortality on the long-term dynamics of understorey vegetation. Beside gradual autogenic changes in forest structure and composition (von Oheimb & Brunet, 2007), vegetation responses to disturbance events and tree losses induced by either abiotic or biotic agents (Nagel et al., 2019; Brunet et al., 2023) have been identified as important drivers of long-term understorey dynamics. The tree canopy strongly influences the taxonomic and functional composition and diversity of the understorey vegetation, mainly through changes in light availability, microclimate regulation and soil conditions (Su et al., 2019; Valerio et al., 2021). Consequently, canopy mortality and forest disturbances play a pivotal role in shaping the dynamics of understorey vegetation in temperate forests over time. By creating canopy gaps, altering microclimatic conditions, and changing soil nutrient levels, tree canopy changes influence plant community composition and successional processes in forest ecosystems. Understanding these dynamics is essential for managing forests to maintain biodiversity, resilience and ecological function in the face of natural and anthropogenic disturbances, because their frequencies and intensities are predicted to increase with ongoing climate change (Anderegg et al., 2012; Seidl et al., 2017; Kutnar et al., 2021).

A network of permanent research plots in QR and QP forests in Slovenia was established in the early 1990s (Smole & Kutnar, 1994). Understorey records included the full inventory of plant species across five sites dominated by QR and four sites in QP forests. Previous research related to the decline of oak stands has focused on crown defoliation assessment and problems with natural regeneration (Čater, 2015). However, less is known about the impact of environmental changes on understorey vegetation. Because of the strong interconnectedness between overstorey and understorey vegetation, changes in the overstorey are presumably reflected in the diversity and composition of understorey communities. Here, we aimed to analyze the effects of environmental changes on the understorey vegetation layer. Our research questions were as follows: (a) Has canopy mortality increased in the studied forest stands, and how have overstorey alterations affected understorey diversity and composition in response to an altered light regime? (b) Do the results indicate a signal of climate change and nutrient enrichment in the long-term dynamics of understorey communities? (c) Are plant assemblages becoming less diverse in terms of alpha- and beta-diversity? We hypothesized that understorey vegetation changes would reflect the increasing canopy mortality of oak trees and associated management disturbances. In parallel with the anticipated overstorey decline, our objective was to test whether vegetation shifts reflect the impacts of global change symptoms (climate change and nitrogen deposition; Wrońska-Pilarek et al., 2023). More

gradual autogenic changes of forest structure and composition (natural stand dynamics) were expected to play a less dominant role.

2 | METHODS

2.1 | Study area

The study area encompasses nine *Quercus*-dominated sites in semi-natural managed forests, mainly located in the eastern and southeastern parts (Sub-Pannonian phytogeographic region) of Slovenia (Figure 1). At five sites, *Quercus robur* is the dominant tree species, whereas at the remaining four sites, the main species is *Quercus petraea*. These sites were selected in the early 1990s as part of an international project for monitoring crown defoliation in oak forests (Smolej & Hager, 1995), its causes and its effects on forest vegetation and soil conditions. All sites featured stands that were more than 80 years old, with homogenous ecological conditions and high canopy closure, exhibiting almost no signs of disturbances (minor crown defoliation; Smole & Kutnar, 1994; Kutnar, 2006).

Most of the lowland QR sites are located on the floodplains of rivers where deep hydromorphic soils prevail. These soils developed under the influence of either waterlogging above less-permeable soil layers (pseudogley soils) or a high groundwater table (amphigleys and hypogleys) (Kutnar, 2006). The potential natural forest vegetation is *Querco roboris-Carpinetum* s.l. According to the EUNIS habitat classification (Chytrý et al., 2020; https://floraveg.eu/habitat/), QR-dominated forests can be classified as Temperate Hardwood Riparian Forest (code T13) and *Carpinus* and *Quercus* Mesic Deciduous Forest (T1E). Many QR sites exhibit a two-layered stand structure; i.e., pedunculate oak in the upper tree layer and hornbeam and other broad-leaved trees in the lower tree layer. In the original survey, the average proportion of QR in the growing stock was 80%, with notable admixtures of *Carpinus betulus* and *Picea abies* (Table 1). The selected QP sites were placed on permeable hilly terrain (ranging from undulating topography to relatively steep slopes) with various types of forest soils formed on different parent materials (limestone, flysch, sandy clay). According to the EUNIS habitat classification, QP-dominated forests can be classified as *Carpinus* and *Quercus* Mesic Deciduous Forest (T1E) and Acidophilous *Quercus* Forest (T1B). The average share of QP in the stand growing stock was nearly 90%, with *Quercus cerris* and *Fagus sylvatica* being the species with the highest admixture in the growing stock (Table 1). During the 1992/1993 survey, all selected sites in both forest types were characterized by closed stands with high tree layer canopy cover and a more or less uniform understorey microclimate in the preserved forest interiors.

2.2 | Sampling design and vegetation survey

At each site, a 1-ha (100 m × 100 m) permanent research area with homogenous stand conditions was established in the central part of the forest complex. The stands were at least 80 years old and
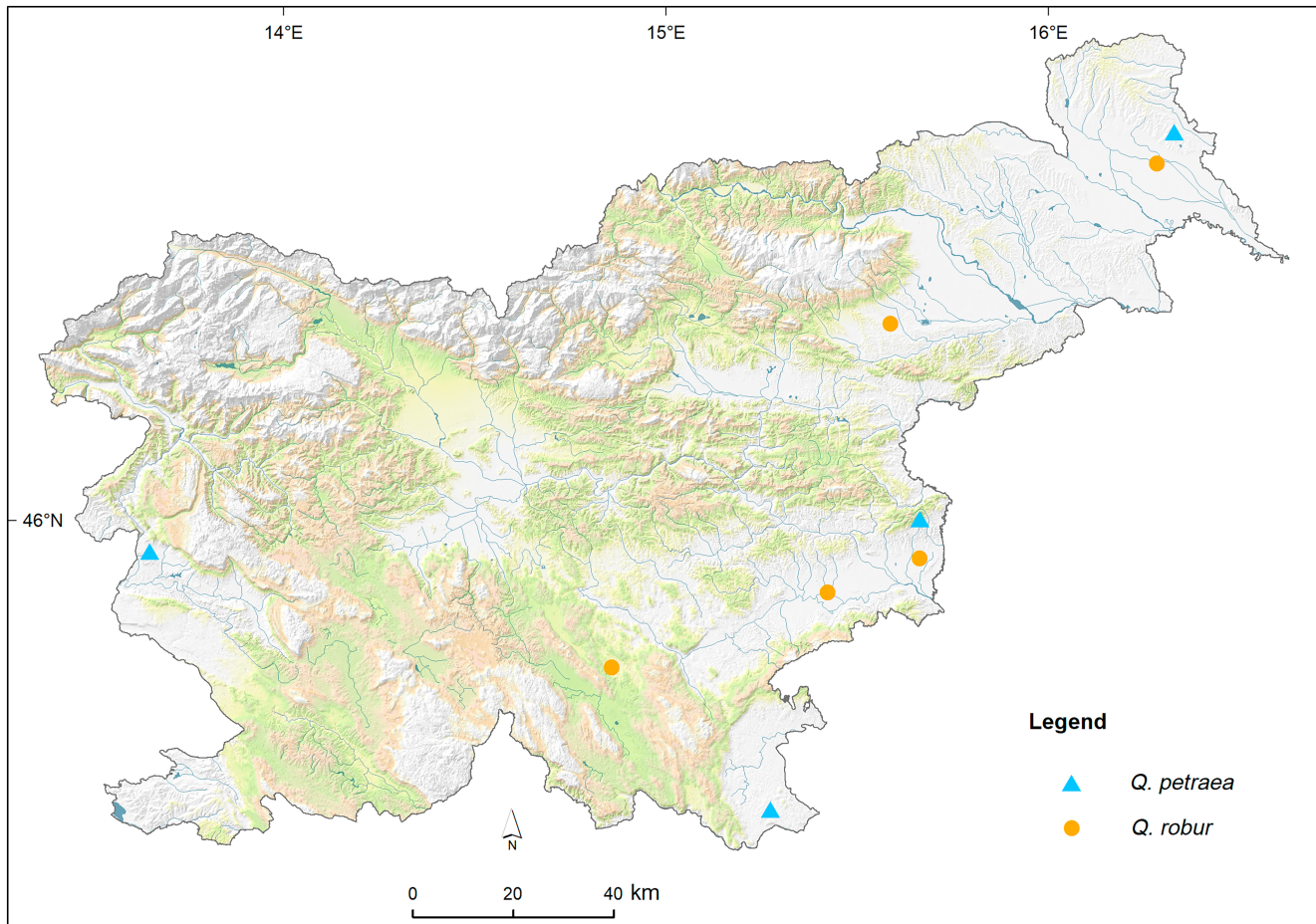
FIGURE 1 Locations of permanent vegetation plots in five *Quercus robur* and four *Q. petraea* forest sites in Slovenia (map creation: Erika Kozamernik, Slovenian Forestry Institute).

featured closed tree canopies (Smole & Kutnar, 1994; Smolej & Hager, 1995). The research area was divided into 25 sampling plots/quadrants each measuring 20 m × 20 m. In the initial survey (1992/1993), all living trees with a diameter ≥ 10 cm, measured at 1.3 m above the ground, were measured, numbered (Figure 2) and mapped, providing a detailed spatial scheme of the stand situation (Appendix S1).

Complete floristic surveys (phytosociological relevés) of all vascular plants in the understorey layer were conducted in 1992/1993. In this study, understorey vegetation was defined as all herbaceous species and woody plants in the herb and shrub layers (≤5 m height). The surveys were carried out according to the standard Central European phytosociological method. The percentage cover of each vascular plant species in the shrub and herb layers was estimated using the Braun-Blanquet seven-degree cover class scale (Braun-Blanquet, 1964). In addition, the overall cover percentages of the tree layer (all woody species taller than 5 m), shrub layer (all woody species with height between 0.5 m and 5 m) and herb layer (comprising all herbaceous vascular plants and woody species <0.5 m) were visually estimated in each plot. The frequency of each understorey species was measured by the number of plots in which it was present.

In the summer of 2023, the permanent plots in QR and QP forests were revisited. Vegetation resurveys were carried out following the original sampling protocols (Smole & Kutnar, 1994) in precisely located permanent plots, ensuring no relocation error and maintaining the integrity of ecological inference. Reconstruction on more disturbed plots was still possible based on existing marked trees and tree stumps. At each site, vegetation data were collected from five plots; i.e., the central plot and four corner plots (Appendix S1). This resulted in a total of 25 plots across QR sites and 20 plots across QP sites, totaling 45 pairs of historical and resampled plots. Field sampling was conducted at the peak of the growing season to capture the typical state of understorey vegetation.

The source for the species nomenclature was Martinčič et al. (2007). Plot-level vegetation data are available in Appendix S2.

2.3 | Data analysis and statistics

First, we explored the patterns in variables that were expected to most strongly affect vegetation changes; i.e., canopy mortality and climate change. The change in estimated tree layer cover (TLC) was used as a proxy for canopy mortality and overall disturbance

TABLE 1 Site and stand characteristics of the two forest vegetation types based on data from the original inventory in 1992/1993.

	Quercus robur			*Quercus petraea*		
	Min	Avg	Max	Min	Avg	Max
Elevation (m a.s.l.)	150	224	370	140	280	470
Mean annual temperature (°C) 1961–1990[a]	9.1	9.9	10.3	9.4	10.3	12.3
Mean annual precipitation (mm) 1961–1990[a]	793	1,023	1,252	771	1,199	1,493
Stand density (DBH ≥10 cm)	305	421	623	305	474	648
Growing stock – GS (m³/ha)	299.4	528.0	680.3	307.2	446.1	588.7
Quercus in GS (%)	70.5	79.8	87.2	78.1	88.6	98.4
Tree species richness	2	2.5	4	1	2.4	5
Other tree species in GS	*Carpinus betulus (8.6%), Picea abies (6.4%), Tilia cordata (1.4%), Alnus glutinosa (0.7%), Acer campestre (0.5%)*			*Quercus cerris (5.5%), Fagus sylvatica (4.9%), Carpinus betulus (0.1%), Acer campestre (0.1%), Tilia cordata (0.1%)*		

[a]A reference 30-year period prior to the start of evident climate change. Climate data obtained from the SLOCLIM database (Škrk et al., 2021).

FIGURE 2 Numbered oak trees in one of the resurveyed *Quercus petraea* stands. Permanent markings on the trees, still very visible after three decades, allowed for precise reconstruction of the historical plots.

intensity in plots. To illustrate how climatic conditions have changed, the mean monthly temperature and precipitation deviations for the period 1993–2022 relative to the period 1961–1990 were determined for each study site based on daily data from the SLOCLIM database (Škrk et al., 2021).

For vegetation data, different plot-level diversity metrics were calculated. Species richness represents the total number of understorey species in a plot. The total cumulative cover of the understorey layer per plot was calculated by summing the cover percentages of all species present (often exceeding 100%). The Shannon–Wiener index was used as a measure of alpha-diversity. Evenness (species equitability) was calculated based on Pielou's formula (Pielou, 1975).

Changes in gamma-diversity were evaluated by species accumulation curves.

The shift in species composition was explored by Non-metric Multidimensional (Distance) Scaling (NMDS; Oksanen et al., 2022) with two dimensions. Abundance data estimated by the Braun-Blanquet cover class scale were converted to respective mid-point values as follows: $r=0.1\%$; $+=0.5\%$; $1=3\%$; $2=15\%$, $3=37.5\%$; $4=62.5\%$; $5=87.5\%$. These percentages were then $\log(x+1)$-transformed to down-weight the cover of dominant species. Before running NMDS, rare plant taxa present in only one plot were excluded. Differences in species composition between the original survey and the recent resurvey were analyzed for the

entire data set and separately for QR and QP plots, respectively. We explained ordination gradients using passively fitted vectors implemented in the *vegan* package version 2.6-4 (Oksanen et al., 2022). For the whole data set, the dominant tree species (QR and QP) and TLC (%) were fitted. For both subsets of plots, the time of the survey and TLC were taken as explanatory variables. Permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) was applied to test for differences in species composition of the understorey layer between the original survey and resurveyed plots using the "adonis2" function in the *vegan* package with 999 iterations. Plot-level species turnover based on presence/absence data was computed as follows: (species gained + species lost)/total species observed in both survey years. We additionally 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* package in R (Hallett et al., 2016).

Changes in beta-diversity (between-plot dissimilarity in species composition) were assessed by permutation tests for homogeneity of multivariate dispersions (PERMDISP; Anderson et al., 2006), a distance-based procedure that uses principal coordinate axes to estimate the variance in multidimensional space (Oksanen et al., 2022). Significance was assessed with 999 permutations. With the "betadisper" function (*vegan* package), distance values of each plot to the group centroid (i.e., survey year) in a multivariate dispersion were obtained. This distance is defined as a measure of beta-diversity (Bacaro et al., 2012). In parallel, the Bray–Curtis dissimilarity index ("vegdist" function in the *vegan* package) was calculated for independent pairwise comparisons. This was done in two ways: (a) among pairs of five plots within each site (resulting in 50 pairwise comparisons for QR and 40 comparisons for QP), and (b) among all plot pairs across the sites within each forest type (a total of 300 pairwise comparisons for QR and 190 comparisons for QP). A decrease in the compositional dissimilarity index suggests floristic homogenization (Kermavnar & Kutnar, 2024).

We compiled data for ecological indicator values (EIVs) of vascular plants for light availability, thermal conditions (temperature), soil moisture content, soil reaction (pH) and soil nutrients (nitrogen). We employed EIVs as plant community indicators of resources and conditions, which are widely used in resurvey studies to identify the main environmental drivers behind the observed changes in vegetation (Diekmann, 2003; Scherrer et al., 2024). Data from the newly established EIVE 1.0 database (Dengler et al., 2023) were used, resulting in all species having complete data (no missing values). We calculated community-weighted means of EIVs using the *weimea* package (R version 0.1.18; R Core Team, R Foundation for Statistical Computing, Vienna, AT).

We investigated the changes in frequency and abundance for single understorey species, separately for each oak forest type. Frequency was calculated as the number of plots in which a specific species was recorded. Plant species with cover values >1% and present in more than 20% of all plots (a minimum of six plots for QR and a minimum of five plots for QP) in at least one of the two samplings were included in this analysis.

We tested whether species colonizations and local disappearances are related to species traits. Analyzing trends in mean trait values of sample plots is a common approach in studying the effects of environmental drivers on the temporal dynamics of forest understorey plant communities (Naaf & Wulf, 2011; Hedwall & Brunet, 2016). As increasing canopy mortality was assumed to induce colonization of disturbance-tolerant taxa, we used disturbance indicator values for European plants (Midolo et al., 2023). We opted for three indicators: disturbance severity in the herb layer, disturbance frequency in the herb layer and soil disturbance. In addition, we considered traits of ecological importance belonging to the well-established L–H–S scheme (Westoby, 1998)—specific leaf area (SLA), plant height and seed mass. These traits were analyzed for the herbaceous component of the understorey layer (excluding woody species). Trait values for SLA, plant height and seed mass were sourced from the FloraVeg. EU database (Database of European Vegetation, Habitats and Flora; www.floraveg.eu), and the community-weighted mean for each plot and survey period was calculated.

For all explanatory (TLC) and response variables (diversity indices, community-weighted means of EIVs and plant traits, Bray–Curtis dissimilarity, abundance data of single species), the statistical significance of the difference between two time points was tested using the Wilcoxon signed-rank test for paired data as the normality and heteroscedasticity assumptions were violated. For the 30-year time series of monthly temperature and precipitation data, unpaired tests were used. Because the temporal change in TLC (proxy for canopy mortality) was hypothesized to show a strong impact on understorey trends, we additionally performed correlation tests between ΔTLC (percentage in the 2023 resurvey minus percentage in the 1992/1993 survey, expressed in percentage points) and diversity metrics, species turnover and its components, community-weighted means of EIVs and plant traits (18 variables in total). We calculated absolute changes in these responses over time by subtracting the value of the understorey variable at the initial 1992/1993 survey from the value of that variable at the 2023 resurvey. Relationships of ΔTLC with changes in the aforementioned understorey variables were analyzed using Spearman's rank correlation coefficient. Sampling plots ($n=25$ for QR and $n=20$ for QP) were used as input data points in all statistical analyses performed in R statistical software (version 4.3.0; R Core Team, R Foundation for Statistical Computing, Vienna, AT).

3 | RESULTS

3.1 | Changes in tree layer cover and climatic parameters

The average TLC in QR plots in the 1992/1993 survey was 95.0%, ranging from 90% to 100% (Figure 3). In the 2023 resurvey, it decreased to an average of 54.7%, ranging from 0% to 95%. The average TLC in QP plots in the 1992/1993 survey was 94.6%, ranging from 90% to 99%. In the 2023 resurvey, it dropped to an average of
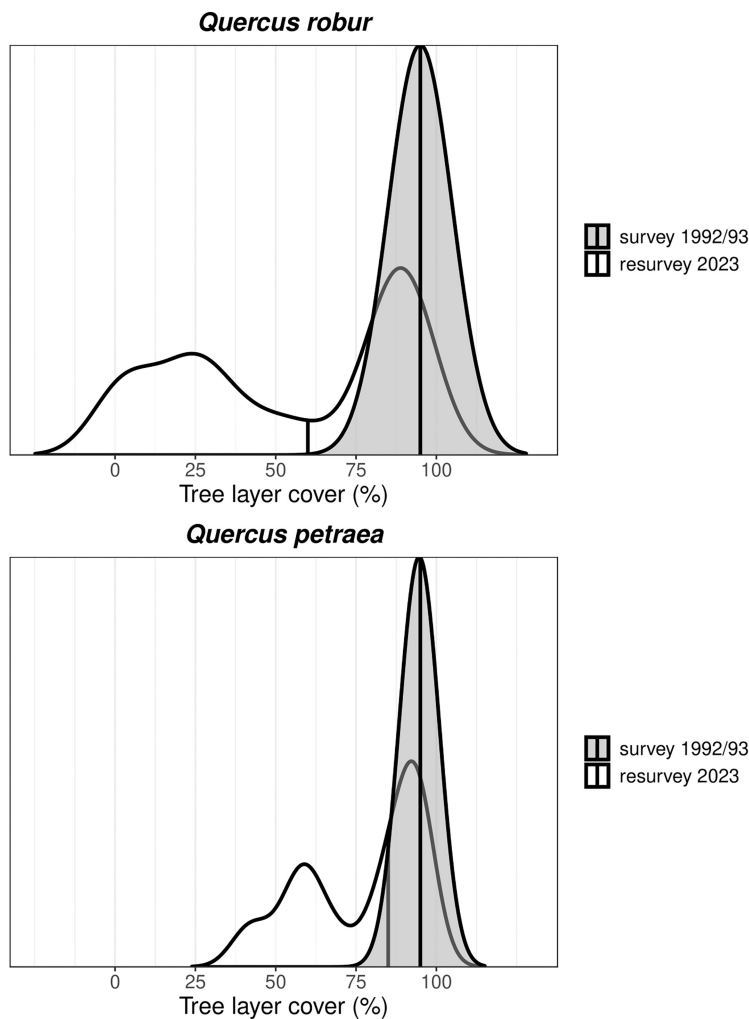
FIGURE 3 Density curves for tree layer cover (TLC; %) estimated in the 1992/1993 survey and the 2023 resurvey. The change in TLC was used as a proxy for canopy mortality. Vertical lines show median values across all plots for each forest type; i.e., *Q. robur* (top) and *Q. petraea* (bottom). The photo on the right depicts the canopy mortality of mature oak trees in a *Quercus robur* plot with reduced crown foliage and massive accumulation of dead branches.

76.8% (min: 40%, max: 97%). The decrease in TLC was highly significant in both forest types (Wilcoxon test; QR: $p < 0.001$, QP: $p < 0.01$). Plots in both forest types experienced varying levels of canopy mortality, yielding a wide gradient of TLC across the resurveyed plots (Figure 3).

In the 1993–2022 study period, air temperatures were higher than the long-term mean from 1961 to 1990 in all months (Appendix S3). The average annual temperature deviation was significant for both forest types (Wilcoxon test, QR: $p < 0.001$, QP: $p < 0.001$) and was larger in QR sites (1.49°C) than QP sites (1.15°C). For QR sites, we found significant differences in mean monthly temperatures for all months except September. For QP sites, temperature increases were significant for January, April–August and November (Appendix S4). Precipitation patterns suggest climatic drying, because precipitation amounts were lower during the 1993–2022 period than the 1961–1990 period, with the highest precipitation deviations observed during the summer and spring months (Appendix S5). For QR and QP sites, significantly lower monthly amounts of precipitation were

detected for March and June. For QR sites, mean annual precipitation decrease was marginally significant (past period: 1,027 mm, recent period: 957 mm; $p < 0.1$), whereas the decrease was significant ($p < 0.05$) for QP sites, with on average 100 mm less precipitation (past period: 1,199 mm, recent period: 1,099 mm) (Appendix S4). These changes in climatic parameters clearly indicate warmer and drier conditions in recent decades.

3.2 | Species diversity changes

Across all studied plots, 319 different vascular plant species (244 herbaceous and 75 woody) in the understorey layer were recorded over both sampling periods and forest types (Appendix S2). In the QR plots, the total species number increased from 159 species in 1992/1993 to 234 species in 2023. *Quercus robur* was the most frequent species in the understorey layer in the initial survey, whereas *Athyrium filix-femina* and *Carpinus betulus* were the

most frequent species in the resurvey. In the QP plots, the species pool also increased but to a far lesser degree, from 141 species in the initial survey to 152 species in the resurvey. The most frequent species in the understorey layer in the initial survey was *Prunus avium*, whereas *Quercus petraea* and *Carpinus betulus* were the most common species in the resurvey. Species accumulation curves for each forest type and sampling period are shown in Appendix S6.

Plot-level species richness in QR forests increased significantly ($p < 0.001$) from an average of 29 species in the original survey to 44 species in the recent resurvey (Figure 4). By contrast, QP plots showed an insignificant decrease in plot-level species richness. The cumulative cover of the understorey layer increased significantly ($p < 0.001$) in both forest types, more in QR (from an average of 104.3% to 212.0%) than in QP plots (from 90.8% to 175.0%). The Shannon diversity index in QR plots increased significantly ($p < 0.001$) from 1.82 in the original survey to 2.63 in the recent resurvey. In QP plots, the Shannon diversity index decreased insignificantly. Similar patterns were observed for plot-level species evenness, which increased significantly ($p < 0.001$) from 0.56 to 0.71 in QR plots but decreased insignificantly in QP plots (Figure 4). For QR plots, we found a significant negative correlation between absolute change in TLC (ΔTLC) and species richness, Shannon diversity index and species

evenness, whereas for QP plots, the cumulative cover of understorey correlated negatively with ΔTLC (Appendix S7).

3.3 | Compositional shifts and species turnover

QR and QP plots were well-differentiated in the NMDS ordination space (Appendix S8). The variation in understorey species composition of the whole data set (final stress: 0.113) was better explained by dominant tree species ($r^2 = 0.81$, $p < 0.001$) than by TLC ($r^2 = 0.15$, $p < 0.01$), with the time of sampling being insignificant. In addition, TLC showed higher explanatory power ($r^2 = 0.55$, $p < 0.001$) than the time of sampling ($r^2 = 0.28$, $p < 0.01$) for QR plots (Appendix S8), suggesting that differences in species composition between the 1992/1993 survey and 2023 resurvey were substantial and driven by changes in TLC (stress: 0.141, $R^2 = 27.7\%$). Changes in species composition for QP forests were not explained by TLC or the time of sampling ($p > 0.05$; vectors not projected in the ordination space in Appendix S8; stress: 0.144, $R^2 = 1.0\%$). This was also confirmed by the PERMANOVA test. Species composition changed significantly between the two surveys in QR ($p < 0.01$, $R^2 = 0.0721$) but not in QP plots ($p > 0.05$, $R^2 = 0.0480$).
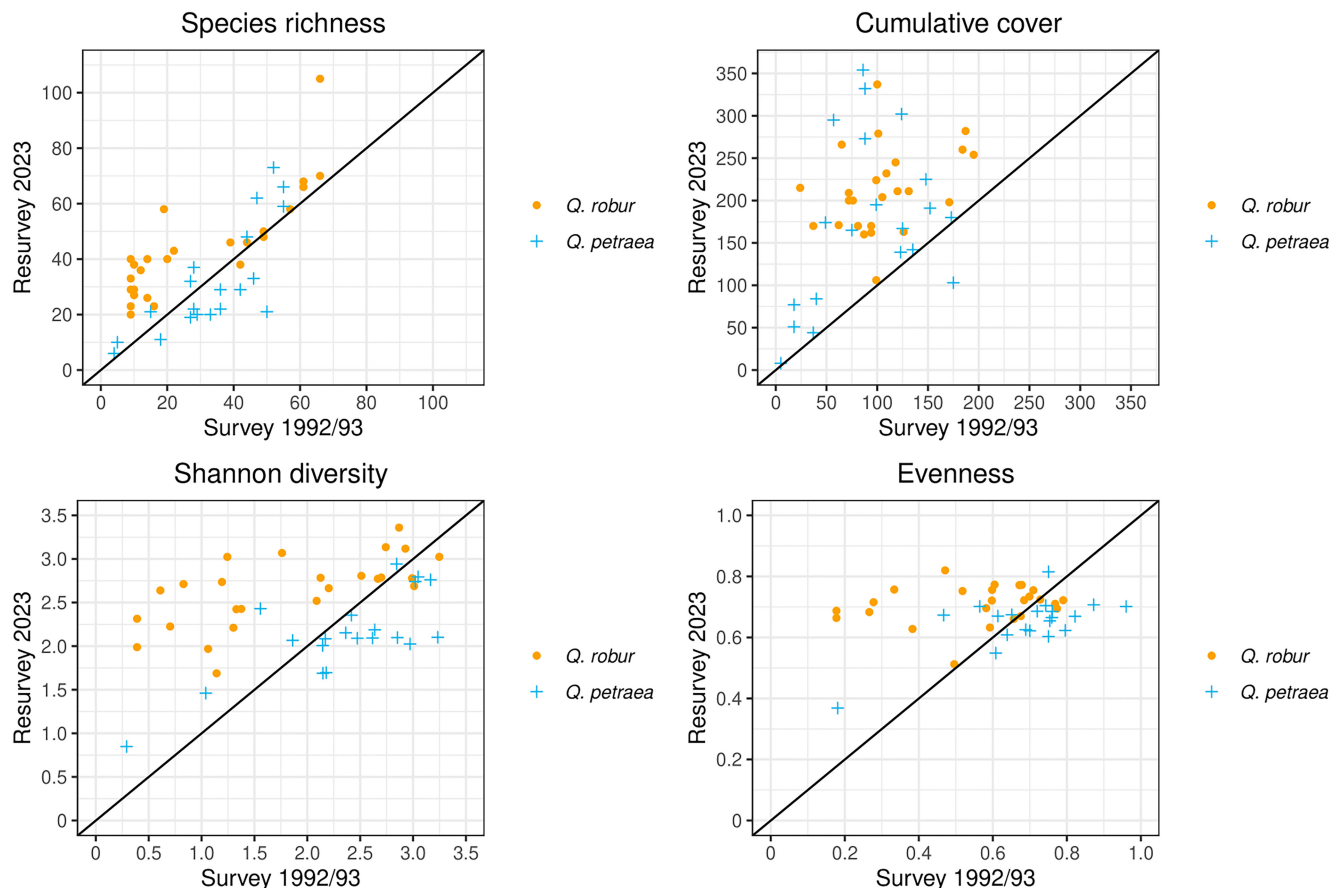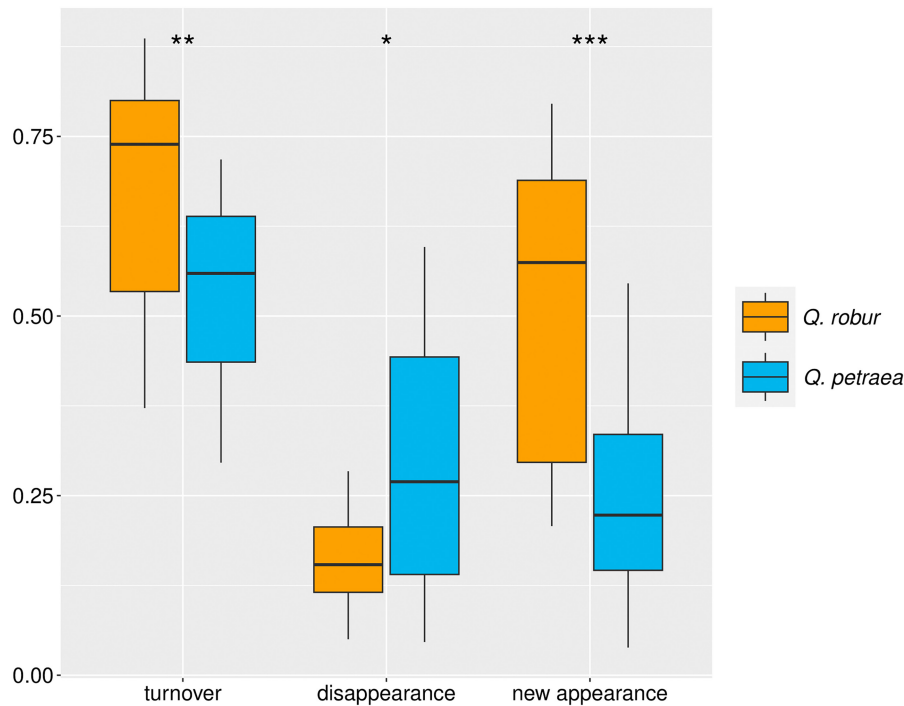

FIGURE 4 Plot-level changes in understorey diversity indices: species richness, cumulative cover, Shannon diversity index and evenness. The diagonal line corresponds to no change in the diversity metric.

FIGURE 5 Species turnover, disappearance and new appearance for *Quercus robur* and *Q. petraea* forests. The significance level from the Wilcoxon test is indicated above the boxplots: $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

The pattern of greater changes in understorey composition in QR forests compared with QP forests was supported by species turnover values (Figure 5). In QR plots, the average species turnover was 0.67 ± 0.17, whereas it was significantly lower in QP plots (0.53 ± 0.13). We found that the two forest types differed significantly in other parameters, suggesting that species turnover was driven by different processes (gained vs lost taxa). Species disappearance showed a significantly higher contribution to turnover in QP forests (0.29 ± 0.17) than in QR forests (0.16 ± 0.07), but the reverse was true for new appearance rates (QR: 0.51 ± 0.21, QP: 0.25 ± 0.14; $p < 0.001$) (Figure 5). We found a significant negative correlation between ΔTLC and species turnover and the rate of new species appearances in QR plots (Appendix S7). No significant correlations were detected for QP plots.

3.4 | Beta-diversity patterns

In both studied forest types, beta-diversity decreased from the original survey to the recent resurvey, suggesting floristic homogenization. According to the PERMDISP outputs, this decrease was significant in QP plots and marginally significant in QR plots ($p < 0.1$). The distance to the centroid in the multivariate space decreased (Figure 6, middle). According to the model of homogeneity of multivariate dispersions for QR plots, the average distance to the centroid in the 1992/1993 survey was 0.581, and it decreased to 0.551 in the 2023 resurvey (difference: −0.030). In the case of QP plots, the average distance to the centroid decreased from 0.587 in the 1992/1993 survey to 0.543 in the 2023

resurvey (difference: −0.044). The Bray–Curtis dissimilarity index for within-site pairwise comparisons dropped insignificantly in QR and significantly for between-site pairwise comparisons (from 0.88 to 0.84). Both within-site and between-site site comparisons decreased significantly in QP forests, from 0.57 to 0.43 and from 0.91 to 0.85, respectively (Figure 6, lower). Lower compositional variability in 2023 compared with 1992/1993 is also visible on NMDS diagrams (Appendix S8).

3.5 | Changes in ecological indicator values, species abundances and plant traits

Community-weighted means of EIVs changed significantly in the case of light (EIV-L), temperature (EIV-T), soil moisture (EIV-F), soil reaction (EIV-R) and nutrients (EIV-N), with differences between QR and QP plots (Figure 7). The mean EIV-L in QR increased significantly from 5.44 to 5.69. The mean EIV-T increased more significantly in QP, from 5.90 to 6.17. The direction of change in mean EIV-F differed between the two forest types. It increased non-significantly in QR but decreased significantly in QP (from 5.19 to 5.07). The mean EIV-R increased significantly in QR (from 5.19 to 5.56) but not in QP. A contrasting pattern was detected for EIV-N, with a highly significant increase in QR forests, from 4.50 to 4.90 (Figure 7). In QR plots, ΔTLC was significantly negatively correlated with changes in EIV-L, EIV-F, EIV-R and EIV-N. No significant correlations were identified for QP plots (Appendix S7).
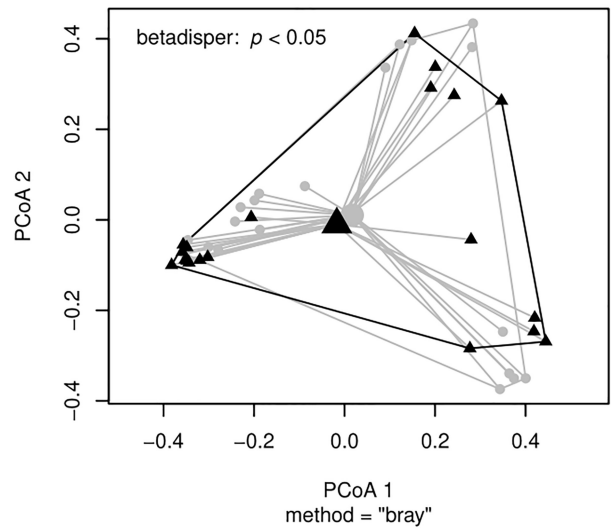
In QR plots, 30 understorey species exhibited a significant increase in mean cover and/or frequency (Table 2), including
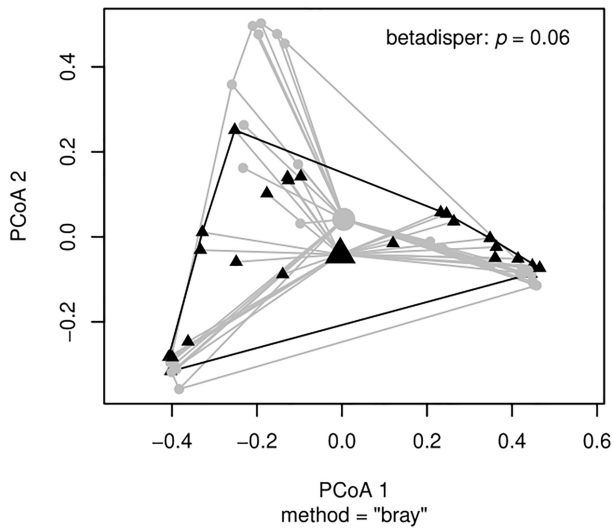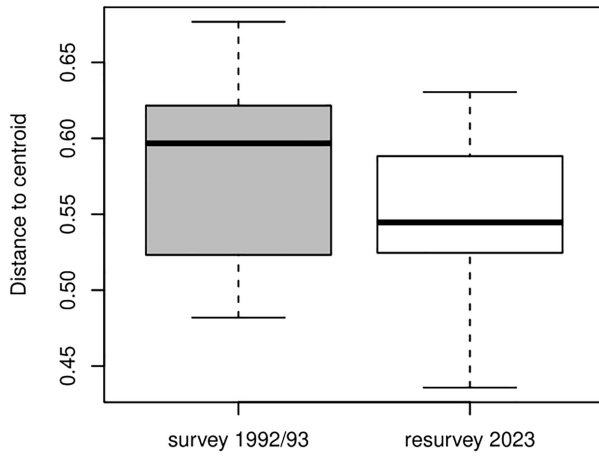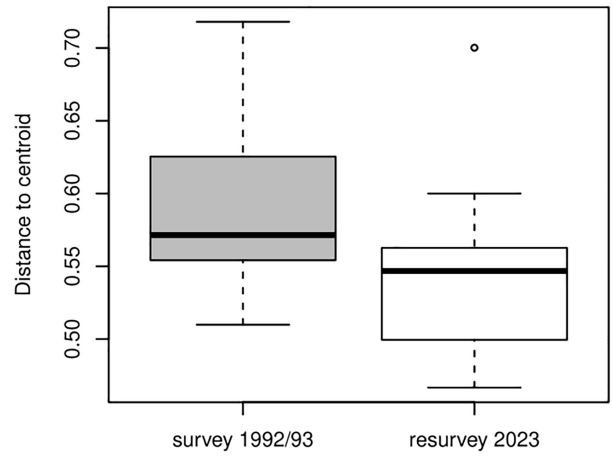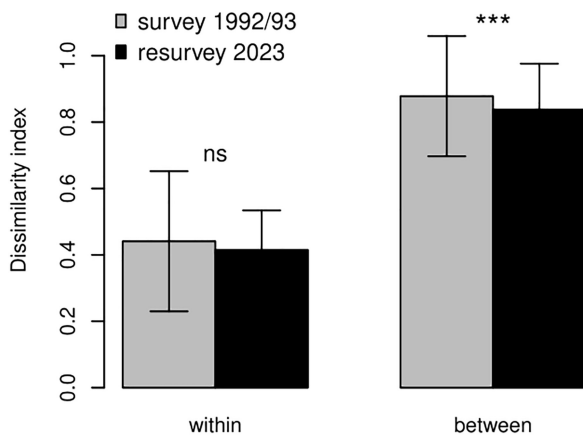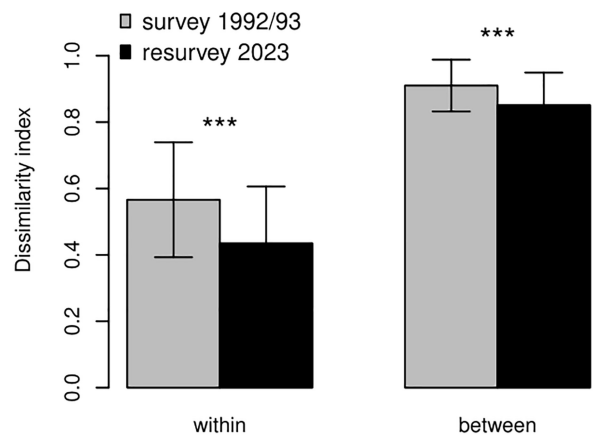
FIGURE 6 Principal coordinate axes (PCoA) diagrams, distance to centroid and dissimilarity index for *Quercus robur* (QR; left column) and *Q. petraea* (QP; right column) forests. In the PCoA (upper), gray symbols represent the original 1992/1993 survey, and black symbols represent the recent 2023 resurvey. For the dissimilarity index (lower), the "within" category represents pairwise comparisons for plots within each site (a total of 50 comparisons in QR and 40 in QP), whereas the "between" category is for plot pairwise comparisons between different sites (a total of 300 in QR and 190 in QP). Statistical significance is coded as: ***$p < 0.001$, ns, non-significant.
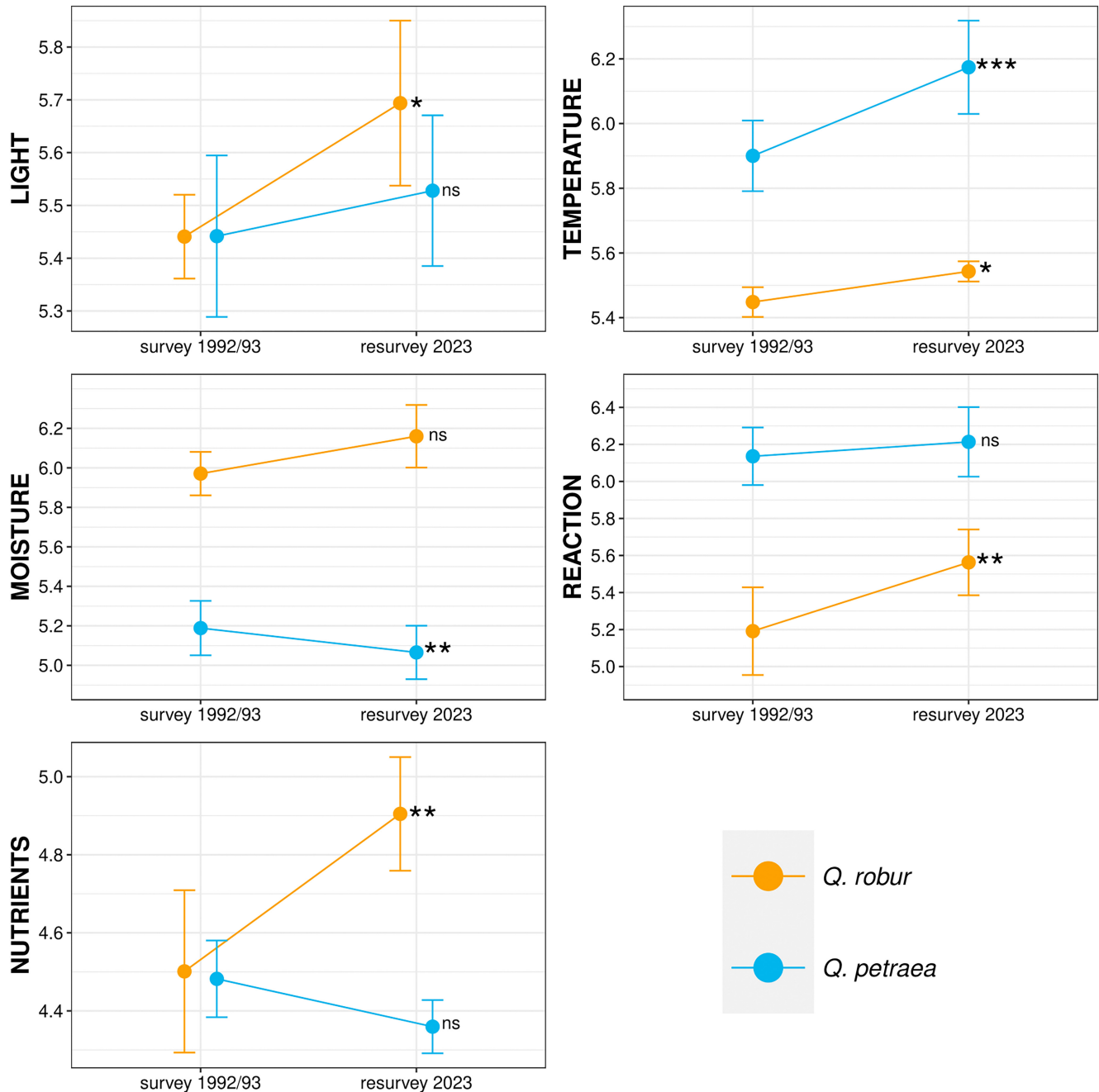
FIGURE 7 Changes from 1992/1993 to 2023 in ecological indicator values for studied *Quercus robur* and *Q. petraea* forests. Statistical significance: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ns, non-significant. Error bars represent standard deviations around the mean values.

seven woody species. Some species remained relatively stable in frequency but exhibited a significant increase in mean cover. Among the species with a profound increasing trend in frequency were also non-native herbaceous species. By contrast, two species in QR plots showed significant decreases in mean cover and frequency.

Species	Frequency difference	Mean cover difference	Significance
Increase			
Impatiens parviflora	14	5.1	***
Juncus effusus	12	19.0	**
Solidago gigantea	12	7.2	**
Urtica dioica	11	1.4	**
Scrophularia nodosa	12	1.1	***
Calamagrostis epigejos	11	3.4	**
Carex sylvatica	9	2.9	**
Galeopsis speciosa	8	3.4	*
Salix caprea	8	1.5	*
Fraxinus excelsior	8	1.2	*
Dryopteris filix-mas	8	0.5	**
Polygonum hydropiper	7	8.2	**
Erechtites hieraciifolius	7	1.6	*
Poa trivialis	7	0.6	*
Hedera helix	7	0.3	*
Galium aparine	7	0.3	*
Erigeron annuus	6	7.5	*
Cirsium palustre	6	3.8	*
Stellaria holostea	6	3.1	*
Stachys sylvatica	6	2.1	*
Agrostis canina	5	14.2	*
Galeobdolon montanum	5	5.5	*
Acer pseudoplatanus	5	1.2	*
Carpinus betulus	4	14.3	**
Alnus glutinosa	4	1.6	*
Brachypodium sylvaticum	4	0.8	*
Deschampsia cespitosa	3	19.5	**
Crataegus laevigata	2	8.6	*
Acer campestre	1	11.6	***
Frangula alnus	1	11.0	*
Decrease			
Picea abies	−8	−2.2	*
Anemone nemorosa	−1	−17.2	**

TABLE 2 Understorey species with significant increases or decreases in *Quercus robur* plots between the 1992/1993 survey and 2023 resurvey.

Note: Differences in frequency and mean cover are reported, and significance was tested with the Wilcoxon signed-rank test (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$).

In QP plots, 14 understorey species exhibited significant increases in mean cover and/or frequency (Table 3), with the majority being woody species. By contrast, eight herbaceous species in QP plots showed significant decreases in mean cover and frequency. Increasing species mostly changed in abundance, while decreasing species showed declines in frequency.

In QR plots, we found significant changes for disturbance indicators, plant height and seed mass (Table 4). Community-weighted means in QR plots for disturbance severity, disturbance frequency, soil disturbance and plant height increased from the original survey to the recent resurvey, whereas seed mass significantly decreased (became more negative on the logarithmic scale). In QP plots, temporal changes were significant for mean SLA, which decreased from 27.9 to 25.2 mm^2/mg (Table 4). For both QR and QP plots, we found strong negative correlations between ΔTLC and community-weighted mean for disturbance severity, disturbance frequency and soil disturbance. Changes in TLC in QR plots showed a significant negative correlation with community-weighted mean for plant height and a positive correlation with community-weighted mean for SLA. In QP plots, there was a significant positive correlation between ΔTLC and community-weighted mean for seed mass (Appendix S7).

TABLE 3 Understorey species with significant increases or decreases in *Quercus petraea* plots between the 1992/1993 survey and 2023 resurvey.

Species	Frequency difference	Mean cover difference	Significance
Increase			
Carpinus betulus	5	2.1	*
Hedera helix	5	1.2	**
Bromopsis ramosa	5	0.6	*
Fagus sylvatica	4	11.2	**
Fraxinus ornus	3	21.8	**
Quercus petraea	3	4.0	*
Crataegus monogyna	3	3.4	**
Vinca minor	2	3.8	*
Carex flacca	1	20.4	*
Sorbus torminalis	1	3.0	**
Ilex aquifolium	1	1.5	*
Prunus avium	1	1.3	**
Ruscus aculeatus	0	30.7	*
Ligustrum vulgare	0	24.7	*
Decrease			
Melampyrum pratense	−8	−1.3	**
Galium sylvaticum	−7	−0.5	*
Hieracium umbellatum	−6	−0.9	**
Luzula pilosa	−6	−0.6	*
Primula vulgaris	−6	0.0	*
Vicia oroboides	−6	0.0	*
Sanicula europaea	−4	−0.5	*
Polygonatum multiflorum	−4	−0.1	*

Note: Differences in frequency and mean cover are reported, and significance was tested with the Wilcoxon signed-rank test ($*p<0.05$, $**p<0.01$).

TABLE 4 Significant changes in community-weighted means (± standard deviation) of plant traits for *Quercus robur* and *Q. petraea* between the 1992/1993 survey and 2023 resurvey.

Trait	Survey 1992/1993	Resurvey 2023	Significance
Quercus robur			
Disturbance severity	0.25 ± 0.05	0.28 ± 0.09	**
Disturbance frequency	1.39 ± 0.05	1.43 ± 0.09	*
Soil disturbance	0.12 ± 0.01	0.15 ± 0.03	**
Plant height (m)	0.37 ± 0.12	0.52 ± 0.17	***
Seed mass (log-scaled)	−0.05 ± 0.47	−0.23 ± 0.50	**
Quercus petraea			
Specific leaf area (mm^2/mg)	27.91 ± 6.10	25.16 ± 4.38	*

Note: Significance levels according to the Wilcoxon signed-rank test: $*p<0.05$, $**p<0.01$, $***p<0.001$.

4 | DISCUSSION

4.1 | Canopy mortality as the main driver

In this study, we revisited permanent vegetation plots established in the early 1990s in two oak-dominated forest types in Slovenia. The study period from 1992/1993 to 2023 coincided with a protracted increase in oak mortality in the canopy layer, predominantly impacted by anthropogenic pressures and climate change, although natural succession (aging of stands) may also be the cause for the observed dieback of large, old QR trees. Increasing canopy mortality emerged as the key driver of observed vegetation changes in QR forests, whereas its effect in QP forests was less pronounced. Overall, QR forests exhibited greater changes in diversity and larger

compositional shifts compared with QP, because canopy mortality was more pronounced in QR stands, although trends were highly variable among individual plots. This confirms that understorey community changes in temperate deciduous forests are strongly linked to the dynamics of the forest stand characteristics and overstorey conditions (Su et al., 2019; Valerio et al., 2021).

The magnitude of change in understorey vegetation was generally proportional to the degree of overstorey canopy mortality. Plots with the highest level of mortality were additionally disturbed because of management interventions and recent storm damage (e.g., salvage logging causing soil disturbance), shifting vegetation towards early successional communities in canopy openings dominated by disturbance-adapted species. The resulting increase in light availability in the understorey (Čater, 2015) is likely the main reason for the observed increase in the number of non-forest species and generalists with higher EIV-L scores and consequently overall plant diversity (richness, cover, Shannon index) in QR plots. Soil disturbance in canopy gaps creates suitable niches for the establishment of ruderal species from the seed bank or colonization via long-distance dispersal (Förster et al., 2017; Kermavnar et al., 2019). Habitats with higher resource availability and heterogeneity in abiotic conditions normally host a greater number of plant species (Su et al., 2019; Helbach et al., 2022), and species gains due to increased resource supply were greater than species losses. In addition, the significant decrease in the community-weighted mean for seed mass is an indicator of an increase in ruderal species. Such trends point to the synanthropization (sensu Czerepko et al., 2021) of understorey communities in QR stands.

Tree mortality triggered by repetitive droughts and temperature stress has become a widespread phenomenon (Anderegg et al., 2012). Canopy mortality in Slovenia is increasing, affecting not only oak stands, but also other forest types (e.g., beech; Ogris & Skudnik, 2021), which are under pressure from crown defoliation, storm damage and salvage logging (Kutnar et al., 2021). In a recent study on increasing canopy mortality in European forests from 1985 to 2018 (Senf et al., 2021), Slovenia was ranked first among 35 countries. The increasing impact of disturbances on long-term understorey dynamics has been reported in previous studies (Helm et al., 2017; Closset-Kopp et al., 2019). Forest disturbances have been identified as one of the leading drivers of temporal dynamics in Slovenian forests (Kutnar et al., 2019). Canopy mortality has also been responsible for long-term understorey changes also in old-growth forests (Nagel et al., 2019).

In the early 1990s, permanent research plots were established in mature forests with preserved forest interiors and almost no sign of disturbance (only some trees showed minor crown defoliation). In the 2023 resurvey, the level of mortality varied greatly among sites and even among plots within the same site. High variability in the degree of crown defoliation and damage yielded a broad spectrum of canopy conditions across the resurveyed plots, spanning from closed forest stands to almost completely treeless communities in QR forests. Plots also exhibited a great variety in time since the last natural or management-related disturbance. Some plots were recently affected by an opening of the canopy, while others exhibited a more gradual decline of the oak overstorey with the ingrowth of sub-canopy trees and shrubs. The most open sites were recently disturbed by windthrows and salvage logging. In contrast to disturbed stands, resurveyed plots with minor changes in canopy cover can provide some insight into the gradual transition of vegetation change associated with natural stand maturation and development towards late-successional stages (Scherrer et al., 2024). In the absence of profound overstorey mortality, local stand dynamics have progressed in a different direction, with a denser sub-canopy and shrub layer compared with plots with disturbance-induced pulses in resource availability. In some cases, intense recruitment and ingrowth of subordinate broad-leaves in the lower tree and shrub layers occurred, similar to the results observed by Szwagrzyk et al. (2018). Even in plots with moderately defoliated crowns, these effects created small gaps that tend to close rapidly following the lateral growth of different broad-leaved trees and shrubs. The sub-canopy layer increased, including a shading effect on the understorey vegetation (Nagel et al., 2019), resulting in elimination of herbaceous species and lower species richness as observed in QP forests. Thus, some communities exhibited the opposing direction of change compared with disturbed plots.

4.2 | Climate change effects

The climate in Slovenia is becoming warmer and drier (Kutnar et al., 2021). In QR and QP forests, monthly temperatures over the past three decades were significantly higher compared with the period 1961–1990. The mean summer temperature in the studied plots has increased by nearly 2°C, and the frequency and intensity of heatwaves and drought events have increased significantly (Anderegg et al., 2012; Čater, 2015; Kutnar et al., 2021).

Our results confirm the direct effects of climate change on two levels. First, the increasing canopy mortality of oaks was likely caused by warming and precipitation deficits during the growing season (Čater, 2015). Climate change predisposes oak forests to drought-induced tree mortality events in many parts of the world, and future climate models predict a greater recurrence of these perturbations (Saura-Mas et al., 2015; Petritan et al., 2021). Changes in the precipitation regime may have played an important role in progressive tree crown defoliation and dieback, because both Quercus species are also very sensitive to interannual fluctuations in rainfall (Čater, 2015). Second, substantial changes in understorey community composition toward more thermophilic conditions have occurred. A significant increase in EIV-T (thermophilization) was observed in both forest types. A decrease in EIV-F (indicating a decline in drought-sensitive species and an increase in plants with lower moisture demands) suggests a decrease in the moisture content of topsoil layers, providing additional evidence of climate change effects in QP forests. Moreover, the effects of climate change can be inferred from trait-based responses. A significant decrease in community-level values of SLA (observed in QP) is indicative of the

thermophilization process because plants producing more resource-conservative leaves (lower SLA) are better adapted to warmer and drier climates (Harrison et al., 2015; Stevens et al., 2015). Considering the reduced precipitation in spring and summer, in combination with increased temperatures, soil moisture and magnified evaporative demand can also become limiting factors for the growth of understorey herbs in the future (Heinrichs et al., 2012).

Another signal of climate change effects is an increase in the frequency and abundance of evergreen species and woody lianas. Understorey species such as *Ruscus aculeatus*, *Vinca minor* and *Ilex aquifolium* were detected as winners in QP plots, whereas woody vines such as *Hedera helix* significantly increased in both studied forest types. The increase in these species, benefiting from drier summers and milder winters, was recently termed the "laurophyllization" of temperate forest flora (Heinrichs et al., 2012). An increase in the proportion of woody components might be indicative of climate change effects because woody species in the understorey layer have better developed root systems compared with herbaceous plants and are thus less prone to desiccation during drought events. Such trends align with empirical studies (Becker et al., 2017) as well as model-based predictions of future scenarios (Wen et al., 2022). In QR plots, a significant increase in the ingrowth and regeneration of *Carpinus betulus*, which has a larger amplitude for soil moisture and temperature compared with *Quercus robur*, can be interpreted as an indication of the lowering of the groundwater table.

Thermophilization of species assemblages is frequently reported in temperate forest resurveys (Helm et al., 2017; Kermavnar & Kutnar, 2024; Scherrer et al., 2024). For example, climate warming was identified as the most significant environmental driver of changes in the herb layer of *Quercus petraea* forests in the Western Carpathians (Kotrík et al., 2023). In forests with a closed canopy and preserved forest interior, microclimatic buffering effects create time lags in understorey vegetation responses (De Frenne et al., 2013). However, the opening of the tree canopy increases the susceptibility of understorey communities to climate warming, as a decline in canopy cover reduces the thermal buffer on lower vegetation strata (Dietz et al., 2020). In our study, more disturbed forest stands did not exhibit greater thermophilization, which contrasts with the common assumption that disturbances amplify the abundance of thermophilous species (Stevens et al., 2015) because of changes in microclimatic conditions. The communities in QP forests, which were less affected by canopy mortality, showed a stronger thermophilization signal compared with the communities in QR stands. In fact, the mean EIV-T changes were not related to changes in TLC (Appendix S7), suggesting that the thermophilization process acted independently from the increasing disturbances. This finding is in agreement with those of Helm et al. (2017).

Furthermore, our analysis revealed that there was no discernible correlation between site-level changes in EIV-T and macroclimate warming rate during the study period of 1993–2022 (calculated as °C/decade; QR: Spearman correlation coefficient=0.5, $p > 0.05$; QP: correlation=0.4, $p > 0.05$). Sites that exhibited the highest rates of macroclimate warming did not necessarily demonstrate elevated levels of vegetation thermophilization. This can be corroborated by comparing the two forest types (QR vs QP). The average macroclimate warming rate across QR sites was 0.414, whereas it was 0.386 in QP sites. However, the mean delta EIV-T was much higher in QP sites (0.274) than in QR sites (0.095). These results support the conclusion that observed floristic changes acted independently from macroclimate changes. However, it should be noted that EIVs are a coarse approximation for the thermal preferences of the species and can be easily masked by other effects associated with local factors, such as topography. For example, some lowland QR sites could function as terrain depressions with the accumulation of colder air. Alternatively, changes in soil moisture may also be a contributing factor. In QP forests, precipitation decreased to a greater extent, and EIV-moisture values decreased significantly (mean delta EIV-F for QP was −0.123, whereas it increased in QR for 0.189). The occurrence of droughts and overall drier conditions may have contributed to a stronger thermophilization signal in QP plots, as a result of the lowered microclimate buffering and evaporative cooling effects (Greiser et al., 2024). A substantial body of research has highlighted the pivotal role of water availability and soil moisture levels in influencing forest vegetation responses to future global warming (Davis et al., 2019).

4.3 | Other temporal trends

Apart from evident canopy mortality and climate change effects, one of the strongest patterns observed in both forest types was the significant decrease in the dissimilarity of species composition among plots, suggesting a decline in beta-diversity. This led to plots becoming more homogenous, indicating a narrowing of ecological space in terms of species composition (Klynge et al., 2020; Kermavnar & Kutnar, 2024). Floristic homogenization trends are increasingly reported in temperate forest understories (Seliger et al., 2023; Wrońska-Pilarek et al., 2023), potentially leading to a simplification of both taxonomic and functional diversity of vegetation (Olden et al., 2018). It relates to the convergence in species composition over time, which could lead to lower levels of differentiation and distinctiveness among forest types. Floristic homogenization is most often interpreted with respect to the local extinctions of rare species and the disappearance of habitat specialists or functionally distinct taxa, and their replacement by more ubiquitous species that can exploit increased resource availability in altered conditions; i.e., native generalists or non-native invasives (Durak & Durak, 2015; Prach & Kopecký, 2018; Kutnar et al., 2019; Wrońska-Pilarek et al., 2023). Previous studies have offered reasonable evidence for the underlying mechanisms of floristic homogenization. Several factors have been suggested as key contributors of vegetation homogenization in forests, including pollution (nitrogen deposition), climate warming, deer browsing and changes in forest management, such as the abandonment of traditional practices (Naaf & Wulf, 2010; Chudomelová et al., 2017; Heinrichs & Schmidt, 2017). However, homogenization

is not a universal trend, and temporal changes in beta-diversity can be highly context-dependent (Brunet et al., 2023). For example, Kotrík et al. (2023) and Scherrer et al. (2024) showed increased spatial heterogeneity of understories in *Quercus petraea* and *Fagus sylvatica* forests, respectively, during the past multi-decade periods.

The combined effects of canopy mortality and climate change may have contributed to this trend in our forests. Nonetheless, given that the degree of homogenization was higher in QP than QR plots, canopy mortality might not be the main driver of beta-diversity decline. This may suggest that the process of taxonomic homogenization acted rather independently from the observed decline in TLC. Comparing the studied QR and QP plots, homogenization was likely driven by two distinct processes. In QR forests, the colonization of canopy gaps by generalists, which occur successfully across a wide range of light and soil conditions, along with disturbance-tolerant taxa and non-native species, likely contributed to homogenization. In QP forests, however, the disappearance of infrequent taxa and group of species indicative of mesic habitats likely contributed to homogenization. In addition, the expanding species were mostly trees and shrubs in the understorey. By contrast, in sites where different degrees of disturbance occurred, we would expect beta-diversity to increase over time (floristic differentiation) because of the more heterogeneous canopy structure, creating a mosaic of ecologically contrasting microsites. Canopy gaps can promote spatiotemporal heterogeneity in resource availability, such as light, moisture and nutrients (Valerio et al., 2021; Kermavnar & Kutnar, 2024). Yet, such effects apparently did not fully manifest in our oak-dominated stands.

Eutrophication of forest soils by atmospheric nitrogen deposition has been reported to shift vegetation composition towards species with a higher indicator value for soil nutrients (EIV-N; Heinrichs et al., 2012). Excessive nitrogen loads can tip the balance in favor of nitrophilous species (which are often fast-growing competitors) and lead to the competitive exclusion of species characteristic of nutrient-poor habitats. Such trends are usually context-dependent (Verheyen et al., 2012), meaning that increase in EIV-N is not necessarily caused by N enrichment but can be caused by changes in tree species composition (increase in trees with higher litter quality) or even global warming (Kotrík et al., 2023). The observed significant increase in EIV-N in QR forests was likely related to disturbances; i.e., a decline in canopy cover facilitated the colonization of nitrophilous ruderal species. Many disturbance-tolerant species are also nutrient-demanding (Förster et al., 2017; Strubelt et al., 2019). In densely populated lowland areas, local sources from agricultural land can also be important contributors to soil eutrophication. However, without measured data for N deposition or soil nutrient status in our study plots, the potential effect of eutrophying pollutants on understorey vegetation remains unclear. Further investigation is needed to examine whether N deposition is responsible for vegetation changes in lowland oak forests.

Our results point to the conclusion that the direction of temporal changes in understorey vegetation is dependent on the forest type. The difference in the degree of canopy mortality (higher in QR) appears to cause a major difference in understorey responses between the two studied forest types. Some changes in understorey variables even showed contrasting trends between QR and QP (e.g., in species richness or community-weighted means of EIVs for soil moisture and soil nutrients). This corroborates the notion of opposing temporal trends in the different forest types (Strubelt et al., 2019; Wrońska-Pilarek et al., 2023; Kermavnar & Kutnar, 2024). We observed that different processes prevailed in QR compared with QP plots. In QR plots, species gains (colonization by disturbance-adapted species) were largely responsible for species turnover, whereas in QP plots, species losses predominated. Species with significant decreases in QP were mainly shade-tolerant species typical of mesic *Carpinus betulus* and/or *Fagus sylvatica* submontane forests and even some acidophilous herbs.

4.4 | Disturbed forests in the vegetation resurvey

There appears to be a prevalence of resurvey studies reporting an increase in tree density, growing stocks and canopy closure as a result of successional development toward a climax state and the consequent shading effect on understorey communities (Klynge et al., 2020). Several studies in temperate (Becker et al., 2017; Vojík & Boublík, 2018) and boreal biomes (Hedwall et al., 2019) have documented that vegetation shifted toward more shade-adapted and nutrient-demanding species (Vild et al., 2024). Contrary to this common trend in many European forests, we show that canopy mortality contributed to significant species turnover in the understorey layer of *Quercus*-dominated forests.

Natural and anthropogenic disturbances are an integral part of temperate forest ecosystems with pronounced impacts on stand structure and the natural regeneration of tree species (Szwagrzyk et al., 2018). Nevertheless, resurvey studies rarely include disturbed forest sites because disturbances may confound the effects of other factors under investigation. In this context, investigators involved in monitoring initiatives of forest ecosystems are faced with the dilemma of whether to abandon disturbed plots or substitute them with undisturbed ones. We advocate that disturbed sites should not be excluded from resurvey studies in order to quantify plant community responses to canopy mortality or other types of disturbance, notably in permanent plots integrated in periodic monitoring designs. An increase in forest canopy openness is becoming a new reality (De Frenne, 2024), and avoiding disturbed sites may not capture the ongoing ruderalization (synantrophization) of understorey communities. If disturbed plots are abandoned or replaced with undisturbed plots, for example, in nearby intact forest, then temporal trends may not accurately reflect the increasing effects of disturbances. This is particularly important with respect to the reduced buffering capacity of temperate forests in a disturbance-prone future because

a more open forest canopy exhibits a lower capacity to mitigate the effects of global drivers (climate warming, atmospheric depositions, invasion of non-native plants; Bhatta & Vetaas, 2016; Kermavnar & Kutnar, 2024; Verheyen et al., 2024). Including the long time series data from permanent vegetation plots allows for a more comprehensive picture of the in situ dynamics and offers the opportunity to investigate the resistance and resilience of forest understorey plant communities to a multitude of environmental pressures. Although such surveys may capture only a transient stage of forest succession, it is important to collect data on vegetation in the early stages of stand development. This information can be later used to evaluate the long-term outlook of forests threatened by global change symptoms.

5 | CONCLUSIONS

The resurvey of permanent research plots revealed that, despite some common trends, the two temperate *Quercus*-dominated forest types showed specific responses to global change symptoms. The results indicated (a) a shift in the understorey community towards disturbance-tolerant and nutrient-demanding species triggered by changes in canopy cover due to oak mortality, especially in QR forests; (b) a signal of climate change (thermophilization and increase of drought-tolerant taxa) which was more pronounced in QP forests and not related to the observed canopy changes; and (c) a floristic homogenization of the understorey communities across all sites.

Our findings contribute to a better understanding of the long-term vegetation dynamics in oak forests resulting from the combined effects of forest disturbances and climate warming. In a disturbance-prone future, resurveying disturbed forests should become common practice to gain insights into the drivers of vegetation change and to realistically evaluate the status, resilience and future trajectory of understorey plant communities.

AUTHOR CONTRIBUTIONS

JK and LK conceived the research idea; JK and LK collected the data; JK performed the statistical analyses; JK, with contributions from LK, wrote the paper; both authors discussed the results and commented on the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Plot-level vegetation data with supporting information are available in the Appendix S2 (Excel spreadsheet).

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SUPPORTING INFORMATION

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

Appendix S1. A detailed map of the spatial distribution of labelled trees from the original survey.

Appendix S2. Plot-level vegetation data with metadata (Excel spreadsheet).

Appendix S3. Deviation of monthly temperature for the study period 1993–2022 from the 30-year mean of 1961–1990.

Appendix S4. Statistical tests for 30-year time series of monthly temperature and precipitation.

Appendix S5. Deviation of monthly precipitation for the study period 1993–2022 from the 30-year mean of 1961–1990.

Appendix S6. Species accumulation curves for the 1992/93 survey and 2023 resurvey.

Appendix S7. Spearman rank correlation coefficients between ΔTLC and changes in understory response variables.

Appendix S8. NMDS ordination diagrams for compositional shifts of resurveyed plots.

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