



Mixed signals of environmental change and a trend towards ecological homogenization in ground vegetation across different forest types

Janez Kermavnar · Lado Kutnar

Received: 14 June 2023 / Revised: 29 February 2024 / Accepted: 29 February 2024
© The Author(s) 2024

Abstract Forest ground vegetation may serve as an early warning system for monitoring anthropogenic global-change impacts on temperate forests. Climate warming may induce a decline of cool-adapted species to the benefit of more thermophilous plants. Nitrogen deposition has been documented to potentially result in soil eutrophication or acidification, which can increase the proportion of species with higher nutrient requirements and species impoverishment caused by competitive exclusion. Abiotic forest disturbances are changing the light conditions in the forest understorey environment. In this resurvey study, we tested the magnitude and direction of change in alpha (species richness) and beta (within-site dissimilarity) diversity and composition of forest ground vegetation in forests of different types in Slovenia over fifteen years. Using plant-derived characteristics (Ellenberg-type indicator values) and by testing *a priori* predictions concerning expected effects of environmental drivers, we show that the magnitude and direction of forest ground vegetation diversity

and floristic changes varies greatly between forest sites. Divergent responses at different sites resulted in low net change of alpha and beta diversity and a weak overall environmental signal. The largest decrease in species number was observed in lowland oak-hornbeam forests, which were also among the sites with the greatest compositional shifts. Changes in beta diversity did not show any consistent trend, and anticipated floristic convergence was not confirmed when all sites were considered. Thermophilization was mainly detected in montane beech sites and alpine spruce forests whereas eutrophication signal was most significant on nutrient-poor sites. Vegetation responses were strongly dependent on initial site conditions. Shrinkage of ecological gradients (process of ecological homogenization) suggests that sites positioned at the ends of the gradients are losing their original ecological character and are becoming more similar to mid-gradient sites that generally exhibit smaller changes. Our results point to the importance of local stand dynamics and overstorey disturbances in explaining the temporal trends in forest ground vegetation. Ground vegetation in Slovenian forests is changing in directions also dictated by multiple regional and global change drivers.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12224-024-09445-w>.

J. Kermavnar (✉) · L. Kutnar
Department of Forest Ecology, Slovenian Forestry
Institute, Večna pot 2, 1000 Ljubljana, Slovenia
e-mail: janez.kermavnar@gozdis.si

L. Kutnar
e-mail: lado.kutnar@gozdis.si

Keywords Vegetation resurvey · Thermophilization · Eutrophication · Forest disturbances · Alpha and beta diversity · Initial site conditions · ICP-Forests network

Introduction

In the era of rapid global change, resurveys of plant communities on permanent or semi-permanent plots have become common practice and a valuable tool in evaluating the impacts of environmental changes on forest biodiversity (Kapfer et al. 2017; Knollová et al. 2024). Analyses stemming from semi-permanent plots might offer a longer time span (resurvey of historical locations where phytosociological relevés were made some decades ago), but a disadvantage of this approach is the potential risk of relocation, observer and timing (date of sampling) biases (Verheyen et al. 2018). Therefore, vegetation science needs permanent plots (de Bello et al. 2020), which are, compared to semi-permanent plots, based on much more reliable repetitions of surveys and often supported by measured environmental data taken at the exact same place as vegetation inventories. On the other hand, long-term assessments generally use global / regional data to explain various processes in vegetation. However, these can be heavily modified by many specific factors operating at local scales. Long-term studies are beneficial for the understanding of temporal dynamics in forest ground vegetation (hereafter abbreviated as GV) in response to global, regional and local environmental change. However, short- to medium-term measurements are particularly important for the timely detection of changes in biotic communities and early response with appropriate planning and forest management (Kutnar et al. 2019). This is a crucial step towards the development of effective strategies for the restoration and conservation of forest biodiversity, especially in protected areas (e.g. Natura 2000 sites).

Because of climate change, vegetation is shifting towards a higher representation of warm-adapted plant species and lower relative abundance of cold-adapted taxa (De Frenne et al. 2013; Zellweger et al. 2020). Global warming is considered the main driver of vegetation thermophilization (Stevens et al. 2015; Brice et al. 2019; Govaert et al. 2021a). Another response to increasing temperature is evidenced in the migration of plant species towards higher latitudes and / or elevations because the climate in their current distribution area is becoming increasingly unsuitable for growth and survival (Harrison et al. 2010; Savage and Vellend 2015; Kermavnar et al. 2023). Specific microclimatic conditions in forest stands due to the

buffering effect of canopy closure (shading and cooling) are causing delays in the biotic response to the progressing climate warming (De Frenne et al. 2013; Zellweger et al. 2020; Richard et al. 2021). However, intense and large-scale forest disturbances resulting in reduced tree layer cover will likely diminish such buffering effects and consequently facilitate the thermophilization of forest vegetation (Stevens et al. 2015; Dietz et al. 2020). The effects of disturbances on forest plant composition should therefore not be overlooked, since the extreme weather events and devastating large-scale disturbances tend to intensify with climate change (Seidl et al. 2017; Dietz et al. 2020; Kutnar et al. 2021; Patacca et al. 2022).

Local disturbances rapidly alter plant communities that may otherwise respond rather slowly to environmental changes (Closset-Kopp et al. 2019). Kutnar et al. (2019) demonstrated that changes in understorey vegetation across Slovenian forests are primarily driven by disturbances. Light and microclimate are significantly altered in more open forest areas with less tree cover (Kermavnar et al. 2020) and GV is especially responsive to alterations in light regime (De Pauw et al. 2022). Increased light availability in canopy gaps favours the occurrence of non-forest, ruderal species (Eler et al. 2018; Kermavnar et al. 2019). This can be referred to as ‘ruderalization’ of forest vegetation and could result in increased plant diversity. In conjunction with increasing forest disturbances, the vitality of key tree species is showing a downward trend (e.g. Čater 2015; Ogris and Skudnik 2021), partly induced by an increasing frequency of abiotic (summer drought) and biotic (pathogens) agents causing widespread canopy mortality (Senf et al. 2021).

Atmospheric nitrogen (N) deposition has been recognized as one of the major threats to forest biodiversity (Dirnböck et al. 2014). The consequences of N deposition include fertilization / eutrophication, soil acidification, nutrient imbalances and nitrate (NO_3^-) leaching (Bobbink et al. 2010). It has been concluded that the majority of ecosystem processes, relevant in determining understorey communities in forests, respond sensitively to increased N deposition and that this response generally leads to drastic shifts in species composition and a decrease in biodiversity of forest plant communities (van Dobben and de Vries 2017). This includes alterations in the composition with nutrient-demanding species profiting at

the expense of more oligotrophic species that prefer nutrient-poor soils, a pattern consistently observed at the European scale (Dirnböck et al. 2014). Changes in soil conditions caused by elevated N deposition can lead to a prevalence of nitrophilous plant species, which are usually superior competitors with an acquisitive resource-use strategy (Bobbink et al. 2010; Walter et al. 2017). Atmospheric nitrogen deposition in Europe has been declining since the late 1980s, but it has remained 2–4 times higher than in 1900 and with significant differences between European geographic regions (Schmitz et al. 2019).

Climate change, deposition of air pollutants, changes in forest management and the natural disturbance regime can lead to a decline in alpha and beta diversity of species assemblages, meaning taxonomic homogenization or floristic convergence (Rooney 2009). This process indicates that local or regional communities are becoming more similar in composition over time (Rolls et al. 2023). In the past few decades, compositional heterogeneity within sites has been decreasing at a rapid pace because of losses of rare habitat specialists and the expansion of common, competitive species (Naaf and Wulf 2010). However, there is a lack of knowledge concerning this issue, especially about the temporal trend in the spatial beta diversity of various temperate forest understoreys (Prach and Kopecký 2018). Therefore, resurvey studies should address a broad spectrum of forest types with differential ecological backgrounds because changes in GV are expected to depend on inherent site characteristics, for example the climate, parent material, forest stand and soil properties (Verstraeten et al. 2013; Naaf and Kolk 2016). Plant communities growing in sites of different types can respond differently to the same external driving factor of change (Wrońska-Pilarek et al. 2023).

To what extent GV in Slovenia is influenced by these factors remains unclear. Based on available data from the periodic monitoring of forest vegetation at sites belonging to European ICP-Forests Level II network (Intensive monitoring – IM), we quantified the magnitude and direction of temporal changes in species composition. In this study, we focused on testing the potential signal of climate change, N deposition and disturbances as drivers of community-level diversity and ecological indicator values (EIVs). Specifically, we tested the following hypotheses: (i) In general, we assumed that the magnitude and direction

of changes in GV would differ between forest types (i.e. site-specific responses). Alpha diversity (species richness) and beta diversity (spatial variation in composition) of GV are expected to decrease over time, resulting in species impoverishment and taxonomic homogenization (floristic convergence), respectively; (ii) Climate change is causing climatic warming (an increase in air temperature) and climatic drying (a decrease in precipitation amount). In this context, we expected a shift towards higher EIV-temperature and lower EIV-moisture values; (iii) Atmospheric nitrogen deposition induces soil eutrophication and acidification, and consequently higher representation of nitrophilous species (an increase in EIV-nitrogen values) and acidophilous plants (a decrease in EIV-reaction); and (iv) An increase in forest disturbances opened the overstorey canopy layer and caused more light to reach the forest floor. At IM sites with intensified natural or management disturbance events, we expected a shift towards higher EIV-light values.

Material and Methods

ICP-Forests Level II Sites in Slovenia

The International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP-Forests; <http://icp-forests.net>) was launched in 1985 under the Convention on Long-range Transboundary Air Pollution (Air Convention, formerly CLRTAP) of the United Nations Economic Commission for Europe (de Vries et al. 2003). This international monitoring network collects information on forest condition at two monitoring intensity levels, namely Level I and Level II. Monitoring of Level II plots is designed as an Intensive Monitoring Programme (hereafter abbreviated as IM) in systematically selected forest ecosystems with the aim to clarify cause–effect relationships. In Slovenia, the IM started in 2004 when ten different forest types across Slovenia were selected. In 2009, one additional beech-dominated forest site on acidic (dystric) brown soil was selected in the Pohorje mountains. As part of the ICP-Forests monitoring network, Slovenian IM sites were systematically established in all phytogeographic regions to represent the mayor forest ecosystems and forest vegetation communities across the country in homogeneous closed canopy stands

lacking evidence of recent disturbances (Urbančič et al. 2016; Kutnar et al. 2019). *Fagus sylvatica* L. is the dominant tree species at five sites, *Picea abies* (L.) H. Karst. at two sites, *Quercus robur* L. and *Carpinus betulus* L. at two sites, and *Pinus sylvestris* L. and *Pinus nigra* J. F. Arnold at one site each (Fig. 1). The selected IM forest sites cover a broad elevational gradient (160–1,397 m a.s.l.), and all sites are located in late-successional managed forests following close-to-nature, sustainability and multifunctionality principles (Kutnar et al. 2023). The disturbance regime and biotic pressure (herbivory) were comparable between the sites. However, forest disturbances intensified in the last decade across Slovenia (Kutnar et al. 2021). Detailed information on IM sites can be found in Kutnar et al. (2019) and Kermavnar and Kutnar (2020).

Vegetation Sampling

At each IM site, a relatively homogeneous monitoring area ranging from one to three hectares was selected. Vegetation plots of two sizes were installed and permanently marked with corner poles. The number of

large plots (10 × 10 m) depended on whether part of the monitoring area was fenced or not (Table 1, Fig. 2). Large plots were placed systematically across the monitoring area whereas ten small plots (2 × 2 m) were distributed across the area to capture fine-scale

Table 1 Number of vegetation plots of different sizes per each site of intensive monitoring (IM)

IM site	Fenced	10 × 10 m plots	2 × 2 m plots
1-KK	No	4	10
2-FO	Yes	8	10
3-GB	No	4	10
4-BR	Yes	8	10
5-BO	Yes	8	10
6-KL	No	4	10
8-LO	Yes	8	10
9-GO	No	4	10
10-KG	No	4	10
11-MŠ	Yes	8	10
12-TR	No	4	10
Total	5 fenced, 6 unfenced	64	110

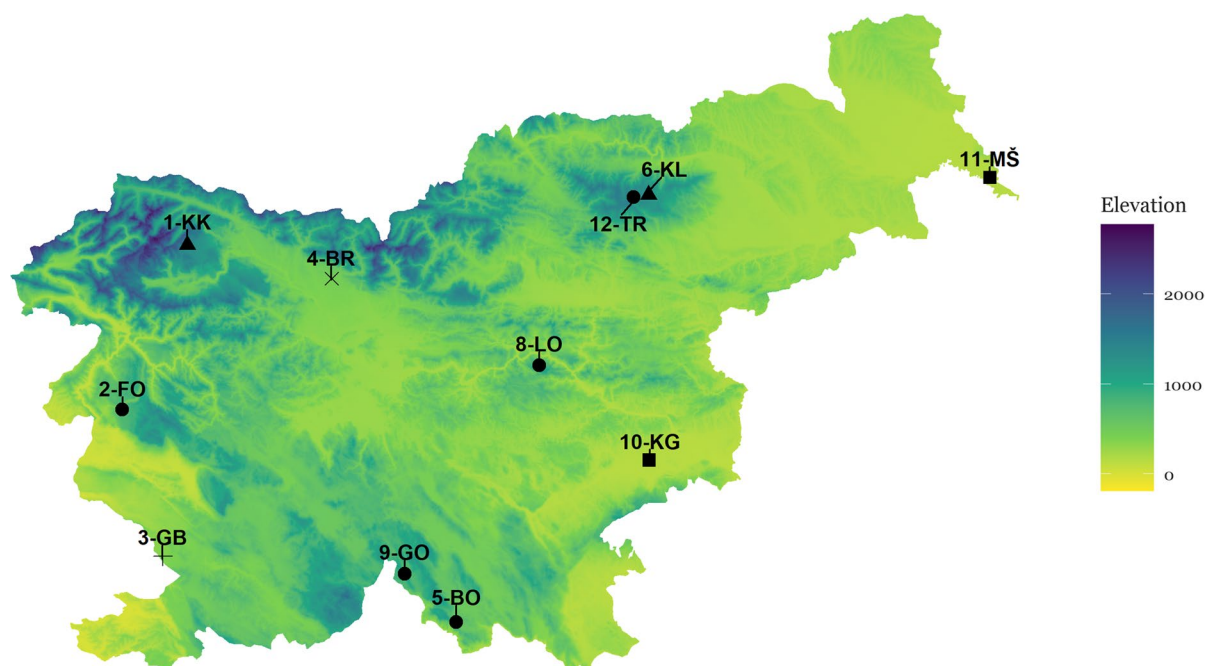


Fig. 1 Geographical distribution of eleven sites of intensive monitoring across Slovenia with an elevation raster layer. Symbols represent the dominant tree species: ● – *Fagus sylvatica*,

▲ – *Picea abies*, ■ – *Quercus robur* & *Carpinus betulus*, × – *Pinus sylvestris*, + – *Pinus nigra*

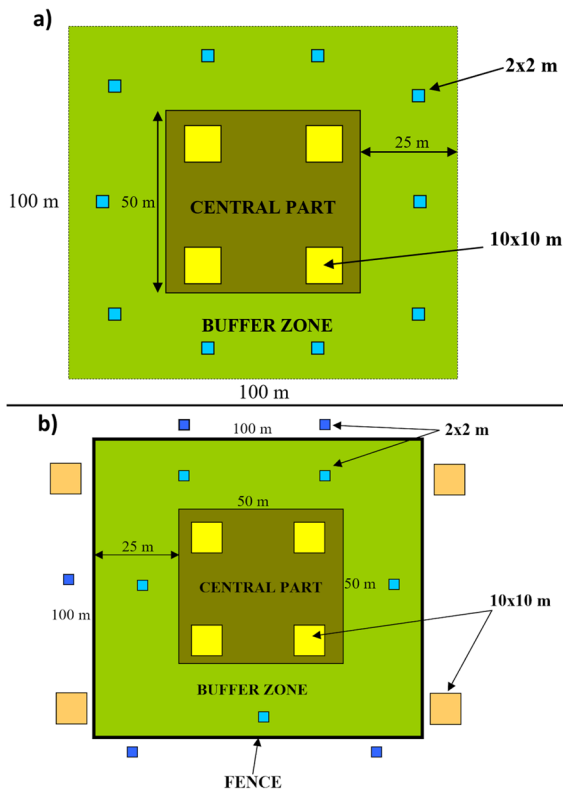


Fig. 2 Schemes of sampling design and vegetation plots for a – non-fenced and b – fenced study sites

variation in microsite conditions. A summary of field methods is given by Kutnar et al. (2019).

Slovenian IM sites with permanent vegetation plots were sampled every five years, resulting in 668 relevés in total. In this study, we used vegetation data for the first sampling period (2004 / 05) and the last period (2019 / 20) for 174 vegetation plots, that is, 348 relevés in total. The sampling followed the same harmonized protocol according to the ICP-Forests manual (Canullo et al. 2013) in all sampling campaigns. Surveys were carried out during the summer, when GV reached peak development. Sites in lowlands were sampled earlier than sites at higher elevations. The percentage of plant cover was visually estimated for all vascular plant species recorded. Cover estimation was done as the vertical projection of the canopy per species using the Barkman scale (Barkman et al. 1964) with nine abundance classes for large (10 × 10 m) plots and the Londo scale (Londo 1976) with thirteen abundance classes for small (2 × 2 m) plots. Beside recording of all vascular plants

present, we estimated the cover of each vertical layer on a plot. The height threshold for the shrub layer was 0.5 m and for the tree layer it was 5 m. The herb layer that was included in the analyses of this paper comprises all herbaceous plants and woody species (trees, shrubs and climbers) with a height below 0.5 m. In both survey periods, the vegetation sampling was conducted by the same observers, specifically LK in all surveys with JK as an assistant in the last resurvey. The nomenclature of vascular plants followed the national flora of Slovenia (Martinčič et al. 2007).

Environmental Changes

This section includes the description of data collection protocols, analysis and sources of main environmental factors (climate, N deposition, forest disturbances) potentially affecting GV at selected IM sites across Slovenia. The results of these analyses with main interpretations are reported in Supplementary materials.

Climate Change

For each IM site, we used data from SLOCLIM, a high-resolution daily gridded precipitation and temperature dataset for Slovenia (Škrk et al. 2021). We calculated mean annual temperature (MAT) and mean annual precipitation (MAP) based on daily values for the long-term period of 1950–2018 and for the fifteen-years period of 2004–2018 (data in SLOCLIM are not available for the years 2019 and 2020), which coincides with the study period of vegetation monitoring. This split was done to demonstrate that the rate of climate warming has drastically increased in the last decades. We analysed MAT and MAP with respect to their linear trends (slope coefficient derived from a regression line equation), expressed as changes in °C (MAT) and % (MAP) per decade, respectively. The results are reported in Table S1.

Atmospheric Nitrogen Depositions

We used atmospheric nitrogen deposition data at four IM sites: 2-FO, 4-BR and 5-BO, and an additional site GIS Rožnik located in an urban forest in Ljubljana, where vegetation is not regularly sampled. Other IM sites are not monitored with respect to nitrogen deposition. The data are stored in the IMGE

database, curated by Slovenian Forestry Institute (for internal use only). Based on regular field measurements, we calculated the total N deposition amount (in $\text{kg} \cdot \text{ha}^{-1}$) for each year in the period 2005–2020, using data from nearby open areas in the close vicinity to the forest stands. We calculated linear trends (regression analysis) and overall mean value across all IM sites. The results are reported in Fig. S1.

In addition, for each IM site we analysed soil data first sampled in 2007 and resampled in 2022. The sampling protocol was the same in both years and the samples were analysed in the Laboratory for Forest Ecology (Slovenian Forestry Institute). Total nitrogen (in $\text{g} \cdot \text{kg}^{-1}$) in the topsoil (organic) and subsoil (mineral) was calculated using values from different soil layers. The purpose of this analysis was to evaluate temporal change in soil nitrogen status over the fifteen-year period and whether soils are becoming enriched with nitrogen due to atmospheric deposition or local point sources. The results are reported in Fig. S2.

Changes in Tree Layer Cover

We analysed changes in tree layer cover, used as a proxy for the extent of forest disturbances at IM sites. We estimated the tree layer cover of each sampling plot during the field sampling of forest vegetation. To depict temporal trends in canopy closure, we calculated mean ($\pm SD$) values across all sites and vegetation plots for each sampling period (2004 / 05, 2009 / 10, 2014 / 15 and 2019 / 20). We tested for differences in the tree layer cover by non-parametric Kruskal–Wallis one-way analysis of variance using site-level averages for four periods and additionally with a Wilcoxon test for paired data using site-level averages for the first (2004 / 05) and the last sampling period (2019 / 20). The results are reported in Fig. S3.

Data Analysis

The analyses were composed of three major parts aimed at describing shifts of the vegetation between the first survey (2004 / 05) and the last resurvey period (2019 / 20). First, we describe temporal changes in alpha (species richness) and beta diversity and community-weighted means of ecological indicator values (EIVs). Second, we correlated EIVs changes to initial site conditions (including measured

environmental variables) to infer site-specific differences. Finally, we examined shifts in individual herb-layer species and compared increasing and decreasing plants with respect to their functional traits.

Because of the small sample size and non-normality of some response variables, a non-parametric Wilcoxon rank-sum test for paired data (Legendre and Legendre 1998) was used to test the differences between 2004 / 05 and 2019 / 20. The vegetation plots did not represent independent observations because of spatial autocorrelation (stemming from the nested sampling design) and were therefore regarded as pseudo-replicates. Valid statistical inference was thus possible only for site-level averages (i.e. mean value across all plots at a site; $N = 11$). A Wilcoxon rank-sum test for paired data was used for testing the changes in vegetation variables within each site separately (comparing original and resampled plots).

Species richness was defined as the total number of vascular plant species in the herb layer (alpha diversity). We calculated richness for each plot size and survey period and then averaged the values to obtain site-level means. These were then subjected to a Wilcoxon test for paired data ($N = 11$), separately for each plot size. The magnitude of temporal shifts was quantified with the Bray–Curtis dissimilarity index (function ‘vegdist’ in the ‘vegan’ package; Oksanen et al. 2022), which expresses the distance between first survey and last resurvey for each plot. These values were then averaged to obtain site-level means. Bray–Curtis dissimilarity was used also for the calculation of within-site variation in composition (beta diversity). All possible pairwise comparisons between plots were calculated for each site. Dissimilarity indices for within-site variation were compared between the periods of 2004 / 05 and 2019 / 20 using a Wilcoxon test for paired data. With this test we also tested for changes of the Bray–Curtis index separately for each IM site. A decrease in dissimilarity over time may be indicative of lowered beta diversity (taxonomic homogenization, floristic convergence) whereas the opposite would suggest taxonomic differentiation.

Ellenberg-type ecological indicator values of plant species (Ellenberg et al. 1992) are a tool frequently used to infer environmental changes and to measure the magnitude and direction of changes in plant community composition in resurvey studies, as they correspond fairly well with environmental factors

measured in the field (Diekmann 2003; Zolotova et al. 2023). The whole concept is based on the premise that changes in species presences / absences and abundances translate to community-level increases or decreases in EIVs and that this likely indicates changes in environmental conditions. We calculated mean EIVs per plot for light (L), temperature (T), soil moisture (F), soil reaction (R) and soil nitrogen / nutrients (N). Plot-level weighted means were calculated from species abundance data and updated data on EIVs reported by Tichý et al. (2022). We used the herb layer data, and the cover percentages of species were $\log(x + 1)$ -transformed prior to the calculation of community-weighted means. Changes in EIVs over the 15-year study period were expressed as relative change using the following equation:

$$\text{relative change}[\%] = \left((EIV_{\text{last resurvey}} / EIV_{\text{first survey}}) / EIV_{\text{first survey}} \right) \times 100. \quad (1)$$

To test how initial site conditions impacted the relative change in EIVs, we performed a linear regression analysis between variables defining average site conditions in the first survey period and the relative change in the corresponding EIVs. For all ecological gradients, the explanatory variable was the community-weighted mean of the respective EIV. Then, for each gradient, we considered one additional measured variable. In the variable selection procedure, the variable with higher explanatory power was retained in the final regression model. We opted for the following variables: tree layer shade-casting ability (an analogy to EIV-L), mean annual temperature (in °C; EIV-T), soil moisture (in %; EIV-F), soil pH (measured in CaCl_2 ; EIV-R) and total nitrogen content in the soil (in g kg^{-1} ; EIV-N). Shade-casting ability (SCA) of the tree layer is defined as a unitless proxy for light availability in the forest understorey. We used shade production values (evaluated based on the leaf area index) provided by Leuschner and Meier (2018). Low SCA values indicate a relatively sparse canopy (e.g. *Pinus sylvestris*-dominated stands), whilst high SCA values denote a dense canopy casting a deep shade (e.g. *Fagus sylvatica*-dominated stands). Mean annual temperature values were sourced from the SLO-CLIM database (Škrk et al. 2021). Soils were sampled according to the ICP methodology (Cools and De Vos 2016). Soil samples were taken for different layers, distinguishing between organic soil layers (OI,

Of and Oh) and mineral soil layers (0–5 cm, 5–10 cm, 10–20 cm, 20–40 cm and 40–80 cm), and analysed in the Laboratory for Forest Ecology (Slovenian Forestry Institute). The values were then averaged across layers and sampling points to obtain single site-level values (Kermavnar et al. 2022).

We examined species-specific changes in the herb layer by means of indicator species analysis (Dufrêne and Legendre 1997) to identify ‘winners’ and ‘losers’, meaning species that increased (showing a significant association with the last resurvey period) or decreased (showing a significant association with the first survey period). Indicator species analysis combines the relative frequency and the relative abundance of species. The resulting indicator value is a product of specificity and fidelity (de Cáceres and Legendre 2009).

Functional approaches can be indicative because global and local change drivers filter species with certain traits (Naaf and Wulf 2011; Closset-Kopp et al. 2019). For example, community-level plant height is expected to respond positively to warming and increased light availability (Govaert et al. 2021a). Therefore, ‘losers’ and ‘winners’ were compared for three plant traits: specific leaf area (SLA; $\text{mm}^2 \text{mg}^{-1}$), plant height (m) and seed (diaspore) mass (mg). We selected these plant traits because they are central to the leaf-height-seed framework of plant ecological strategies (Westoby 1998). The data on functional traits was extracted from the FloraVeg.EU database (<https://floraveg.eu>). Seed mass was log-transformed to meet the assumption of normal residuals.

We performed the statistical analyses in R software version 4.1.1 (R Core Team 2021) and assessed significance at $\alpha = 0.05$ for all tests.

Results

Changes in Species Richness and Composition

Across all vegetation plots sampled, a total of 342 different herb-layer vascular plants were recorded in both survey periods. According to the Wilcoxon test using site-level averages, mean species richness did not change significantly (Table 2). However,

Table 2 Plot-level number of plant species in the herb layer for eleven sites of intensive monitoring (IM) and each plot size (10×10 m and 2×2 m). Values are means $\pm$ SD, averaged across all plots within a site and are reported for two study periods (2004 / 05 and 2019 / 20). Significance (Sig.) is coded as: *** – $P < 0.001$, ** – $P < 0.01$, * – $P < 0.05$, n.s. – non-significant

IM site	Plot size	Species richness in 2004 / 05	Species richness in 2019 / 20	Sig.
1-KK	10×10 m	41.5 ± 10.2	43.5 ± 10.1	n.s.
	2×2 m	20.5 ± 4.7	19.8 ± 4.1	n.s.
2-FO	10×10 m	25.5 ± 5.9	24.4 ± 5.3	n.s.
	2×2 m	10.6 ± 2.8	10.2 ± 3.0	n.s.
3-GB	10×10 m	21.3 ± 3.6	17.3 ± 1.5	n.s.
	2×2 m	7.7 ± 2.9	7.6 ± 2.2	n.s.
4-BR	10×10 m	11.6 ± 1.8	10.9 ± 1.6	n.s.
	2×2 m	7.3 ± 1.2	6.1 ± 1.4	n.s.
5-BO	10×10 m	43.8 ± 3.8	39.0 ± 3.5	n.s.
	2×2 m	17.4 ± 3.2	12.8 ± 4.0	*
6-KL	10×10 m	10.5 ± 3.0	8.8 ± 2.1	n.s.
	2×2 m	6.9 ± 1.7	6.1 ± 1.4	n.s.
8-LO	10×10 m	49.9 ± 3.9	52.9 ± 5.1	n.s.
	2×2 m	26.0 ± 2.3	26.1 ± 2.7	n.s.
9-GO	10×10 m	54.5 ± 3.0	59.0 ± 4.2	n.s.
	2×2 m	26.0 ± 3.4	33.1 ± 6.3	**
10-KG	10×10 m	42.3 ± 2.9	26.3 ± 5.6	*
	2×2 m	23.3 ± 4.5	11.3 ± 3.4	***
11-MŠ	10×10 m	29.6 ± 5.9	22.0 ± 5.6	*
	2×2 m	17.0 ± 2.3	8.4 ± 2.4	***
12-TR	10×10 m	10.3 ± 3.8	12.3 ± 3.2	n.s.
	2×2 m	4.6 ± 2.3	6.5 ± 1.1	*
Mean $\pm$ SD across all sites	10×10 m	31.0 ± 16.3	28.8 ± 17.3	n.s.
	2×2 m	15.2 ± 8.1	13.5 ± 9.0	n.s.

between 2004 / 05 and 2019 / 20, species richness in large plots (10×10 m) decreased significantly at two IM sites in lowland oak forests (10-KG and 11-MŠ), which experienced a species decline also in small plots (2×2 m). Species richness in small plots decreased significantly at site 5-BO (beech forest) and increased at two sites dominated by beech (9-GO and 12-TR; Table 2).

The magnitude of temporal change in community composition varied greatly among the IM sites. Temporal shifts in small (2×2 m) plots were greater than shifts in large plots (10×10 m), a pattern consistent

across all sites (Table 3). In general, the Bray–Curtis index increased from 2004 / 05 to 2019 / 20 for both plot sizes. However, according to the Wilcoxon test using site-level averages, mean dissimilarity across all sites did not change significantly. In detail, within-site spatial variation in GV composition (dissimilarity) for large plots increased significantly at 11-MŠ and decreased at 12-TR. In small plots, compositional beta diversity increased significantly at four sites (5-BO, 8-LO, 9-GO and 11-MŠ) and decreased at site 3-GB (pine forest).

Shifts in EIVs

Using site-level averages, no statistically significant changes in EIVs were detected according to the Wilcoxon paired sample test. Relative changes in EIVs were highly site-dependent and also showed some differences between the plot sizes under study (Fig. 3). The congruence between 10×10 m and 2×2 m plots was generally decent, but there were cases where changes in EIVs differed markedly. Two IM sites (9-GO, 11-MŠ) exhibited an increase in EIV-L, while sites 2-FO and 4-BR showed significant decrease in EIV-L. Three beech-dominated sites (2-FO, 8-LO and 9-GO) increased in their EIV-T, but at two oak-hornbeam sites (10-KG, 11-MŠ), the temperature index decreased significantly (Fig. 3). In the case of EIV-F, many sites showed rather minor relative changes. Site 4-BR increased in the soil moisture index at both plot sizes whereas site 11-MŠ exhibited a significant decrease. Acidifying signal (decrease in EIV-R) was detected for four different sites (1-KK, 2-FO, 8-LO and 11-MŠ). By contrast, site 4-BR exhibited an increase in EIV-R. This site also showed the most significant increase in indicator values for nutrients (EIV-N), followed by site 5-BO. The IM sites which changed the most in the opposite direction (decrease in EIV-N) were 8-LO and 11-MŠ (Fig. 3).

The changes in the distribution of EIV values across all vegetation plots (Fig. 4) suggested that in the last resurvey period, values shifted towards the middle of the ecological gradients. It means that plots with lower EIVs tend to increase their values whereas plots with higher EIVs tend to show a decreasing trend. This resulted in a prominently reduced range for most of the EIVs in 2019 / 20 compared to 2004 / 05 (Table 4). The shrinkage effect varied among the ecological gradients (e.g. for soil reaction, the

Table 3 Average Bray–Curtis dissimilarities for each site of intensive monitoring (IM site) and plot size (10 × 10 m and 2 × 2 m). Temporal shift denotes the magnitude of change in species composition (comparison of initial and resampled rel-

evés). Dissimilarity indices in 2004 / 05 and 2019 / 20 show spatial variability of species composition (i.e. beta diversity). Statistically significant changes are in bold

IM site	Large plots (10 × 10 m)			Small plots (2 × 2 m)		
	Temporal shift	Dissimilarity 2004 / 05	Dissimilarity 2019 / 20	Temporal shift	Dissimilarity 2004 / 05	Dissimilarity 2019 / 20
1-KK	0.308	0.398	0.322	0.428	0.487	0.517
2-FO	0.239	0.325	0.306	0.305	0.505	0.490
3-GB	0.207	0.306	0.356	0.247	0.434	0.321
4-BR	0.138	0.226	0.212	0.334	0.277	0.336
5-BO	0.344	0.329	0.362	0.463	0.590	0.685
6-KL	0.079	0.114	0.146	0.185	0.381	0.382
8-LO	0.374	0.392	0.409	0.439	0.575	0.606
9-GO	0.506	0.323	0.402	0.569	0.479	0.533
10-KG	0.742	0.373	0.403	0.791	0.572	0.621
11-MŠ	0.648	0.268	0.385	0.713	0.363	0.599
12-TR	0.272	0.790	0.697	0.360	0.836	0.779
Mean across all sites	0.351	0.349	0.364	0.439	0.500	0.509

interquartile range even increased) and was the strongest for EIV-N (32.5% decrease).

Effect of Initial Site Conditions

We found negative correlations between relative changes in EIVs and initial site conditions. Significant relationships were detected for EIV-T, EIV-R and EIV-N (Fig. 5). Colder IM sites at higher elevations generally increased their EIV-T (thermophilization signal) whereas warmer sites in lowlands tend to decrease in EIV-T. More acidic sites exhibited increase in EIV-R whereas the opposite was true for sites with initially higher EIV-R (although the relative change at these basiphilous sites was rather small). Eutrophication signal (increase in EIV-N) was the strongest in more nutrient-poor sites, but more nutrient-rich sites experienced the opposite trend (Fig. 5).

Trends in Individual Plant Species

Indicator species analysis resulted in 43 plant species in the herb layer that were significantly associated with the first survey ('loser species') and 28 species that were significantly associated with the resurvey period ('winner species'). *Anemone nemorosa* was identified as a loser species at six different sites,

followed by *Cardamine enneaphyllos* (four sites) and *Cyclamen purpurascens* (three sites; Table 5). Seven plant species were losers at two IM sites and 33 species at one site. Among species with an increasing trend, *Fagus sylvatica* was identified as a winner at four different sites, followed by seven woody and herbaceous species as winners at two sites and the rest (20 species) at one site (Table 5; Table S2).

Losers and winners differed in terms of plant functional traits. Loser species were on average smaller in plant height (herbaceous species only; mean height for losers: 0.28 m, mean height for winners: 0.60 m, Wilcoxon test: $P < 0.001$) and they tended to have higher SLA values and heavier seeds compared to winner species. However, the differences for SLA and seed mass were not significant. A substantial fraction of species with a declining trend (losers) was represented by early-spring flowering species (geophytes).

Discussion

Site-Specific Trends in Ground Vegetation

By testing *a priori* hypotheses concerning the direction of forest vegetation change, this study aimed at detecting the signal of climate change, nitrogen



Fig. 3 Relative changes (%; mean $\pm$ SD) between the first survey (2004 / 05) and the resurvey period (2019 / 20) in ecological indicator values for light (L), temperature (T), soil moisture (F), soil reaction (R) and soil nutrients (N), separately for

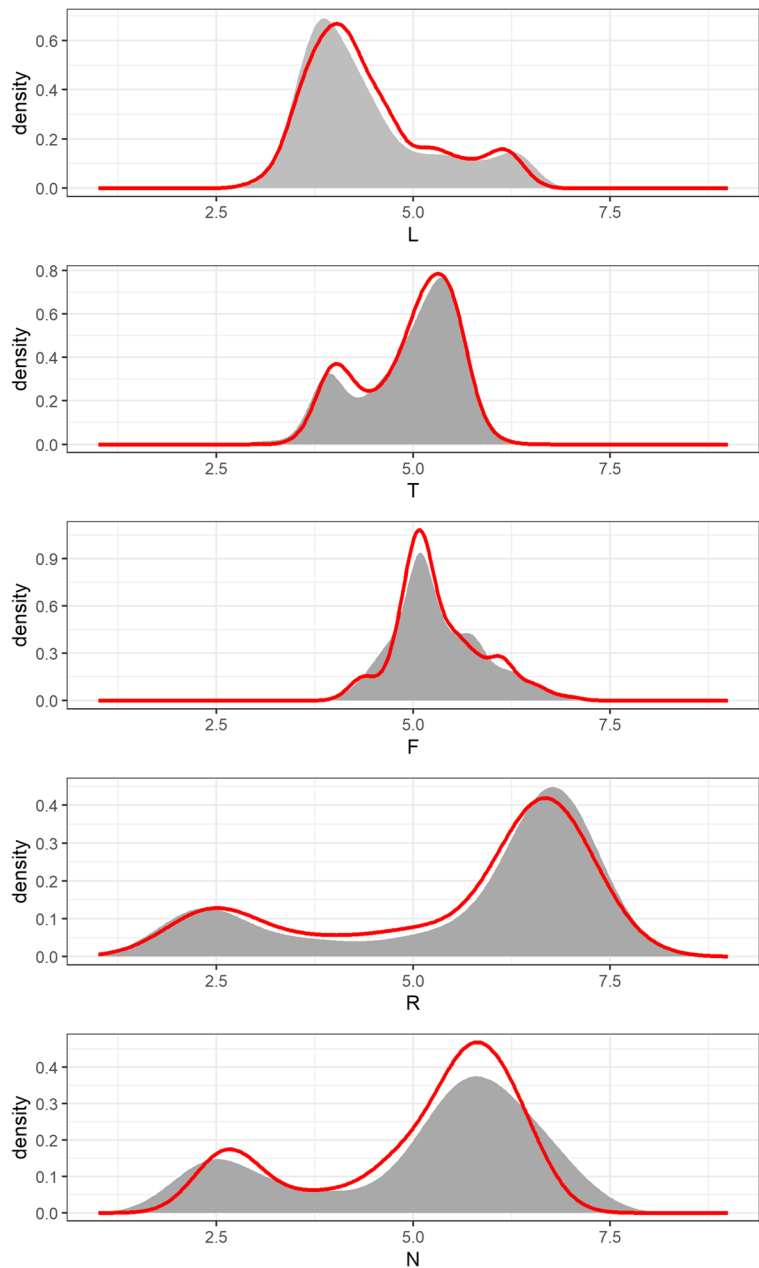
each study site (11 in total). Colours denote different plot sizes (10 $\times$ 10 m vs 2 $\times$ 2 m). Statistically significant changes are labelled with asterisks: ** – $P < 0.01$, * – $P < 0.05$

deposition and forest disturbances in ground vegetation (GV) of different forest types across Slovenia in the period from 2004 / 05 to 2019 / 20. Rather than observing a strong, uniform signal of environmental drivers, we found high variability in the magnitude and direction of GV changes at different sites, which agrees with our first hypothesis and the results from Wrońska-Pilarek et al. (2023). Site-specific factors (e.g. soil type, stand structure, tree composition) may cause a differential temporal response in GV under comparable external pressure (Verstraeten et al. 2013). Temporal trends in ecological indicator values (EIVs) were highly site-specific. This is further supported by the fact that even the same forest types (e.g. beech-dominated forests or lowland oak-hornbeam forests) exhibited divergent temporal responses in species diversity, composition and community ecological signature. Such trends point to the importance

of local stand dynamics in explaining the temporal trends in GV (Helm et al. 2017; Closset-Kopp et al. 2019; Staubli et al. 2021).

Different forest sites with contrasting ecological backgrounds are expected to respond differently to individual environmental drivers. Besides differences in site characteristics, site history (former land use or silvicultural system applied) and initial site conditions like soil nutrients status may also play an important role in shaping responses of temperate forest plant communities to environmental changes (Naaf and Kolk 2016). The presented results are in line with the assumption that signals of environmental drivers are likely to be more pronounced at sites which are at the opposite end of the ecological gradients. For example, climate warming is expected to cause vegetation thermophilization in more cold-adapted communities (higher elevations)

Fig. 4 Density plots of ecological indicator values for light (L), temperature (T), moisture (F), soil reaction (R) and soil nutrients/nitrogen (N) across all IM sites and vegetation plots ($N = 174$ for each survey period). The grey area is for the first survey period (2004 / 05) and the red line denotes the resurvey period (2019 / 20)



compared to thermophilous forests. Similarly, atmospheric deposition of nitrogen is presumed to cause colonization by nitrophilous plants in N-limited ecosystems rather than in forests on nutrient well-supplied soils (Hedwall et al. 2021). Contrasting directions of shifts, site-specific changes and an overall weak signal of environmental drivers imply a relatively high degree of stochasticity rather than deterministic (directional) changes in GV.

Our results suggest that among the forest types studied, lowland oak-hornbeam forest communities (sites 10-KG and 11-MŠ) experienced the largest decline in herb-layer species richness and also showed the largest shifts in composition and in EIVs. On the other hand, beech-dominated sites changed to a lesser degree but were recognized to also have some common response patterns (e.g. generally increase in EIV-T). Changes in beta diversity

Table 4 Main parameters of descriptive statistics for ecological indicator values (EIV), calculated for the initial survey 2004 / 05 and the last resurvey 2019 / 20: 10th percentile, median (50th percentile), interquartile range (IQR, the differ-

ence between the 75th and 25th percentiles) and 90th percentile. The analysis included all vegetation plots studied ($N = 174$)

Ecological indicator	10th percentile		Median		IQR		90th percentile	
	2004 / 05	2019 / 20	2004 / 05	2019 / 20	2004 / 05	2019 / 20	2004 / 05	2019 / 20
EIV-light	3.59	3.58	4.13	4.20	1.00	0.86	5.88	5.72
EIV-temperature	3.91	3.96	5.09	5.11	0.91	0.91	5.57	5.57
EIV-moisture	4.65	4.78	5.15	5.16	0.69	0.62	6.17	6.11
EIV-soil reaction	2.35	2.44	6.57	6.46	2.13	2.29	7.07	6.95
EIV-nutrients	2.45	2.71	5.57	5.55	2.23	1.51	6.70	6.29

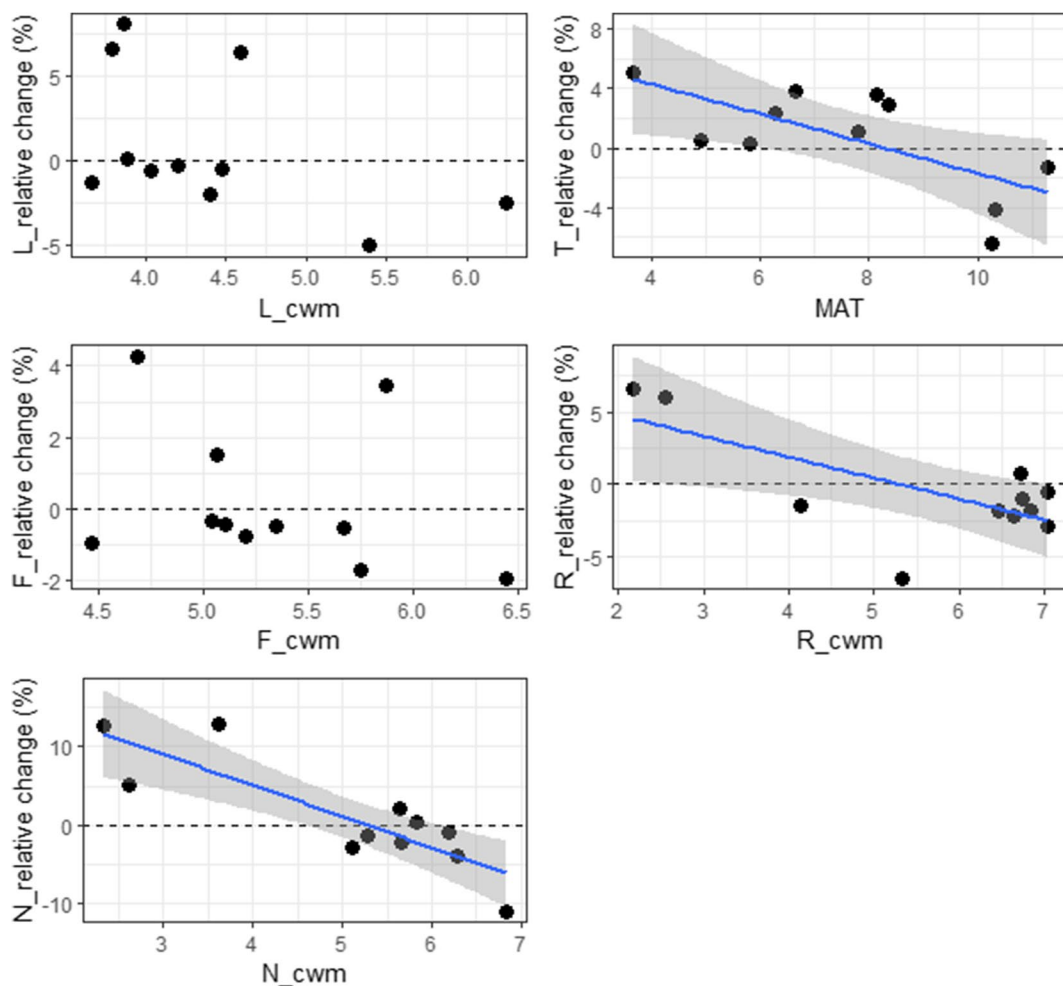


Fig. 5 Relationship between the relative change (%) in ecological indicator values and initial conditions. For light (L), soil moisture (F), soil reaction (R) and soil nutrients (N), the best predictor was the community-weighted mean (cwm) of the respective ecological gradient whereas for temperature (T),

mean annual temperature (MAT) proved more significant than the vegetation-derived index. Data points represent different sites of intensive monitoring. Statistically significant relationships ($P < 0.05$) are marked with a regression line

Table 5 List of ten plant species exhibiting significant association with the first survey 2004 / 05 (losers) and seven species with significant association with the resurvey period 2019 / 20 (winners). The results were derived from indicator species analysis (Dufrêne and Legendre 1997). Species are ranked based on the number of IM sites at which they were identified as losers and winners, respectively. A complete list of losers and winners for each IM site is provided in Table S2.

Species	No. of sites
Losers	
<i>Anemone nemorosa</i>	6
<i>Cardamine enneaphyllos</i>	4
<i>Cyclamen purpurascens</i>	3
<i>Arum maculatum</i>	2
<i>Cardamine bulbifera</i>	2
<i>Euphorbia amygdaloides</i>	2
<i>Gagea lutea</i>	2
<i>Galium aparine</i>	2
<i>Ranunculus ficaria</i>	2
<i>Veronica sublobata</i>	2
Winners	
<i>Fagus sylvatica</i>	4
<i>Acer pseudoplatanus</i>	2
<i>Brachypodium sylvaticum</i>	2
<i>Carpinus betulus</i>	2
<i>Corylus avellana</i>	2
<i>Oxalis acetosella</i>	2
<i>Salvia glutinosa</i>	2
<i>Stachys sylvatica</i>	2

(within-site compositional dissimilarity) were again highly variable and no clear trend was detected (both taxonomic differentiation and homogenization occurred). In contradiction with our hypothesis, the overall beta diversity increased slightly between 2004 / 05 and 2019 / 20, and more sites exhibited significant increase in the Bray–Curtis dissimilarity index. We hypothesized that beta diversity would have decreased on average as a result of a spread of habitat generalists and a decline in habitat specialists (Naaf and Wulf 2010; Kutnar et al. 2019). In addition, we found that patterns in alpha and beta diversity changes can be incongruent, suggesting that it is important to study multiple dimensions of plant diversity when evaluating temporal GV changes.

The Process of Ecological Homogenization

Considering the whole spectrum of IM sites in Slovenia, temporal trends in GV were not completely random. This resulted in an interesting pattern of ecological (functional) homogenization, which can be described as a decrease in the range of EIVs and a tendency towards intermediate conditions when the first survey and resurvey periods were compared. This process of shrinkage effect can be perceived as some form of homogenization and was induced by a divergent response of GV at different sites: Colder sites became warmer and warmer sites became colder; sites with acidic and nutrient-poor soils experienced increases in the EIV for soil reaction and soil nutrients whereas more basophilic and nutrient-rich sites tended to change in the opposite direction (i.e. decrease in EIV-R and EIV-N, respectively). This kind of opposing changes resulted in range shrinkage of ecological gradients across the entire spectrum of forest types studied. Hübler et al. (2008) reported a homogenization of species composition from acid, wet sites and base-rich, dry sites toward more intermediate conditions. We showed that the level of impact of these environmental changes may strongly depend on initial site conditions.

In the absolute terms, compositional and ecological changes in GV between the first survey and the last resurvey were of small to moderate magnitude. The lack of directional change over time in GV species composition can be explained by several factors. First, our resurvey spanned a relatively short time period and compared only two snapshots in time. Second, the response of GV to anticipated environmental changes may be buffered by the tree layer canopy (Helm et al. 2017; Perring et al. 2018). Because environmental drivers act over longer time periods, the response of vegetation could be delayed in time. Such effects seem to be particularly important in the case of global warming (microclimate buffering) and atmospheric nitrogen deposition (canopy interception; however, canopies can accumulate high amounts of dry deposit, which is then flushed by rainfall). Third, majority of GV communities studied are composed of perennial forest plant species, which are known for their relatively high local persistence owing to clonal reproduction. All these factors contribute to time lags in the response of forest plants to environmental change (De Pauw et al. 2022). Lastly,

the fact that multiple environmental drivers are likely operating simultaneously might induce interactions between multiple drivers (Naaf and Kolk 2016; Hedwall et al. 2021). For example, forest disturbances creating canopy gaps have been proposed to amplify the thermophilization of tree communities (Brice et al. 2019) and understorey plant communities (Stevens et al. 2015; Dietz et al. 2020).

Averaged across all sites, our analysis provided only weak evidence of an effect of environmental changes on GV. A shrinking effect was evident for all ecological gradients. Shifts towards the middle of the gradients (process of ecological homogenization) was likely driven by the decline of ecological specialists and their gradual replacement by species with broader ecological niches (generalists) and intermediate requirements for resources. This corroborates with our previous study (Kutnar et al. 2019). More extreme forest sites (positioned at both ends of the ecological gradient) are thus losing their unique character and are becoming more similar to communities positioned in the middle of the ecological gradient (Kopecký et al. 2013). The loss of rare species can lower compositional variation within a site (Vanhellemont et al. 2014) and may lead to floristic homogenization (Naaf and Wulf 2010; Durak and Holeksa 2015).

Signals of Thermophilization and Eutrophication

Slovenian IM sites are getting warmer with an average warming rate of 0.25°C per decade in the last ~ 70 years, and this rate has drastically increased during the study period (0.88°C per decade). Annual amount of precipitation has decreased in the period 1950–2018 by 2.4% per decade, but it tended to increase during the study period (Table S1). Therefore, we anticipated GV to show an increase in EIV-T and a decrease in EIV-F. Across all vegetation plots at each site, the significant increase in EIV-T was confirmed for three sites in montane beech forests (2-FO, 8-LO and 9-GO). A relatively large increase was also detected for high-elevation spruce site (1-KK). It has been previously observed that GV is shifting towards more thermophilic composition at higher altitudes compared to lowlands (Küchler et al. 2015). By contrast, two lowland oak-hornbeam forest sites (11-MŠ and 10-KG) experienced significant decrease in EIV-T. Detected trends of decreasing EIV-T values may be explained by confounding influence of local

stand dynamics. More open tree canopies in the upper tree layer due to the dieback of *Quercus robur* trees (mainly caused by lowered groundwater levels) benefited juvenile tree growth (especially of *Carpinus betulus* with high lateral spread and shade-casting ability of the canopy) and thus increased the shading and cooling effects on understorey plants. Similar effects likely occurred at site 3-GB where abundant ingrowth of deciduous tree species (*Fraxinus ornus*, *Ostrya carpinifolia*) induced microclimate buffering and consequently a decrease in the EIV for temperature in the herb layer. The discrepancy between the changes in abiotic environment and observed shifts in plant-derived indicators can be therefore explained by a confounding influence of forest stand dynamics, which were recognized as key drivers of long-term changes in understorey diversity in old-growth forests (Nagel et al. 2019).

The shifts in EIV for soil moisture were on average the least pronounced (in terms of magnitude) among all ecological gradients studied. The values decreased at eight sites, with only one site (11-MŠ) exhibiting a significant decline. Lower EIV-F values can be interpreted as an influence of spring and summer droughts and the declining trend in EIV-F was likely a consequence of changes in relative abundance of resident plant species or a substantial list of declining spring ephemerals with higher soil moisture demands, which could explain the observed trends. Site 4-BR was exceptional in the other direction, as it showed a prominent increase in moisture values. This site is a *Pinus sylvestris* forest with a packed understorey dominated by dwarf shrubs, tall grasses and ferns adapted to acidic, infertile soil. The composition shifted towards a higher dominance of graminoids and ferns, while ericaceous dwarf shrubs evidently declined.

Nitrogen deposition can induce both eutrophication and acidification of GV. The most significant increase in EIV-N was observed for one acidophilous pine forest on dystric soil (4-BR) and one montane beech forest (5-BO). A profound but non-significant increase in the nitrogen index was detected for 12-TR (an acidophilous beech forest) and 6-KL (an acidophilous spruce forest). This observation is in line with the hypothesis that forest sites on nutrient-poor soil are more susceptible to nitrogen deposition (Reinecke et al. 2014; Roth et al. 2022) compared to more nutrient-rich sites where nitrogen is not a limiting factor.

The site 4-BR, naturally N-limited forest dominated by *Pinus sylvestris* with a relatively open canopy and acidic, low-nutrient soils, is located in densely populated landscape where agricultural inputs (arable fields with high amounts of nitrogen fertilization) are a potential reason for strongest eutrophication signal at this site. Previous studies also stressed that eutrophication of GV can be context-dependent (Perring et al. 2018). The nitrogen deposition may not be the primary cause for shifts towards higher EIV-N values. Changes in tree species composition and canopy closure can contribute to GV being composed of more nitrophilous species. Tree species with higher litter quality (e.g. noble broadleaves) facilitate faster decomposition of the litter and thus greater nutrients availability for herb-layer plants (Verheyen et al. 2012). By contrast, the accumulation of slowly decomposing litter in a forest floor will lead to soil acidification (Vanhellemont et al. 2014; Durak and Holeksa 2015). Such effects could be relevant in case of site 5-BO, where different *Acer* species (with more nutritious litter compared to beech) are admixed in the tree layer. At the other side of the productivity gradient, two lowland oak-hornbeam sites (11-MŠ and 10-KG) experienced decrease in EIV for nutrients. According to the results of indicator species analysis, both sites showed the highest degree of species loss, with early-flowering species (geophytes) being the most frequent among losers (Table S2). Geophytes are considered important indicators of overall naturalness of forest stands (Šipek et al. 2023), and these taxa mostly occur on fertile soils (i.e. have higher EIV-N values).

Plants with early-spring phenology were frequently observed among losers. Geophytes have been recognized as important indicator of conservation status of forest habitats and as a functionally distinct species group in understorey communities of temperate deciduous forests (Durak and Durak 2021). They mostly occur on nutrient-rich soils and prefer higher soil moisture and relative humidity. The highest representativeness of geophytes at our sites was found in lowland oak-hornbeam forests and in beech-dominated communities. One possible reason for the observed decline of geophytes in our study might reside in climate warming. It is feasible to assume that geophytes are now starting to develop earlier in the late winter / early spring compared to 15 years ago, due to milder winters and higher temperatures.

Negative effects of winter and spring warming on the seedling emergence and overall regeneration of forest geophytes has been experimentally tested by Vangansbeke et al. (2022). A lack of precipitation in this period may also contribute to their decrease. Further evidence of why geophytes may be particularly vulnerable to climate change comes from studies in North America. A mismatch between understorey and overstorey phenology may lead to a reduction of understorey light levels in the early spring, which is a critical period when many spring-flowering forest herbs achieve the highest photosynthetic rates (Miller et al. 2023). Such effects reduce the carbon budgets of geophytes under climate change (Heberling et al. 2019). Climate warming and summer droughts are predicted to negatively impact the future distribution of spring geophytes in Europe (Puchałka et al. 2023). In contrast to our results, Nagel et al. (2019) reported a long-term increase in geophytes in fir-beech forest reserves, which was likely driven by a decline of silver fir and subsequent increase in the cover of beech in the lower tree and shrub layer, enabling higher light levels at the forest floor during early spring.

Because EIV-N and EIV-R values in the European flora tend to be positively correlated, sites that showed eutrophication signal also tended to exhibit increased EIV-R values. Acidification of GV mainly happened at more nutrient-rich (oak-hornbeam forests) and on calcareous IM sites. A decrease in EIV-R was observed for spruce forest on moraine bedrock (1-KK), where the topsoil acidification due to thick litter layer (needles) over otherwise more limestone bedrock is likely responsible for creating favourable conditions for acidic-tolerant species (e.g. *Oxalis acetosella* and *Melampyrum sylvaticum* were winners). In addition, the Pokljuka plateau in the Julian Alps receives high rainfall and is continuously exposed to wind-induced remote transport of pollutants coming from industrial and agricultural areas in northern Italy (Bragazza et al. 2005). The drop in EIV-R values was also recorded for two beech-dominated forests on limestone (2-FO) and dolomite (8-LO) parent material. Both sites had two common loser species, namely *Cardamine enneaphyllos* and *Cyclamen purpurascens*, which are known to prefer basophilic substrates. The decline of these species likely contributed to lower EIV-R values. In addition, the increase of acidophilous and/or decrease of basophilous plant species may have resulted from the long-term

deposition of airborne sulfur (Hübler et al. 2008). It is known that atmospheric N deposition can also contribute to soil acidification (Huang et al. 2014).

Differences in traits between winners and losers reflect impacts of environmental change (Naaf and Wulf 2011). According to our results, loser plant species were significantly lower in plant height and had (insignificantly) higher specific leaf area (SLA) values compared to winners. This suggests that vegetation is shifting toward taller and more conservative communities. Such trends can be interpreted as effects of disturbances and / or thermophilization (Stevens et al. 2015; Govaert et al. 2021b). Drought-tolerant species have lower SLA (Stevens et al. 2015).

Disturbances and Stand Dynamics as Local Drivers

Forest disturbances can open the overstorey layer, weakening the shading and cooling effects, and thus act as triggers for more rapid changes of forest GV (Helm et al. 2017). Increasing forest disturbances were earlier identified as the dominant factor shaping the changes in GV across Slovenian IM sites (Kutnar et al. 2019). Sites experiencing a higher intensity of disturbances also shifted more in overall GV composition. By modifying the cover of the tree layer and thus light availability at the forest floor, anthropogenic and natural disturbances play an important role in the context of global environmental changes, as they can modulate the response of GV (Hedwall et al. 2021). Two sites experienced significant increase in EIV-L, namely 11-MŠ and 9-GO. Interestingly, the first site showed a decrease in EIV-T, contradicting the assumption that more light should result in warmer microclimate in the understorey. On the contrary, microclimatic extremes and diurnal temperature ranges are much higher in canopy gaps compared to closed stands (Kermavnar et al. 2020). Both sites decreased in overall overstorey canopy cover but not in all plots. Disturbances were mainly limited to smaller spatial scales due to the mortality of individual trees or local management interventions. In this sense, disturbances can increase environmental heterogeneity where closed stands are mixed with small-scale canopy gaps. However, there was no clear direction of changes in within-site compositional variation, as some sites increased and some sites decreased with regard to the dissimilarity index (Table 3). Nevertheless, at the majority of sites, the canopy cover still

remained high enough to buffer GV against macroclimate warming and nitrogen deposition. In the absence of disturbance events, natural succession towards late-successional stages causes the tree layer canopy to become denser and light availability at the forest floor to decrease (see e.g. studies dealing with abandonment of traditional management practices such as coppicing; Kopecký et al. 2013).

Overall, the observed changes in GV can be attributed mainly to local changes in ecological conditions. This is why the overall impacts of global and regional drivers has not yet come to full expression. Local changes (e.g. in canopy cover and composition) may mimic or counterbalance the effects of regional or global drivers (Naaf and Kolk 2016). Many studies have concluded that local factors (forest stand dynamics) are responsible for temporal trends whereas the signal of global change drivers was less evident, possibly due to time lags in the response of GV. Ascribing changes in GV to environmental drivers in a reliable manner is a challenging task (Staubli et al. 2021). Moreover, the causality of changes is not uniform and multiple drivers simultaneously act on plant communities in a synergistic or antagonistic way. Caution should be taken when relating observed changes in GV to presumed environmental drivers. The inclusion of a broad spectrum of forest types in our study permitted us to improve the understanding of context dependency, as has been emphasized for the response of forest plant communities to global change (Hedwall et al. 2021), especially for potential nitrogen deposition effects (Verheyen et al. 2012; Perring et al. 2018).

Conclusion

Contrasting trends and mixed responses contributed to non-significant changes in EIVs. These outcomes prevented the formation of a general conclusion which would apply to all forest sites investigated. Whether the process of range shrinkage (ecological homogenization) is only temporary or tends to intensify in expression can only be clarified through further resurveys. We therefore recommend the continuation of regular GV monitoring at IM sites and expanding the evaluation of potential effects of environmental changes using data for other plant groups (e.g. bryophytes; Kutnar et al. 2023). Given the

relatively high variation in response of local communities (individual plots within a site), it is feasible to perform surveys using different plot sizes to capture full environmental heterogeneity within a forest stand. Specific microsites might be occupied by habitat specialists that are apparently showing a decline in occurrence.

Acknowledgements This study was performed as a part of the Intensive Monitoring Programme in Slovenia (part of EU Programme ICP-Forests). We thank many colleagues from the Slovenian Forestry Institute for contributing to the maintenance of monitoring Level II sites and plots. The authors are grateful to the anonymous reviewers for their comments on our submission. We also thank Fred Rooks for language editing.

Funding The study was funded by the Slovenian Ministry of Agriculture, Forestry and Food (JGS task 1/3) and by the Slovenian Research and Innovation Agency (ARIS/ARRS): Post-doctoral research project Z4-4543 and core Research program P4-0107.

Data Availability Datasets including vascular plant species and their ecological indicators values used in this study are available from the corresponding author upon reasonable request. More detailed information on plant species composition can also be found in Kutnar et al. (2019) and Kermavnar and Kutnar (2020).

Declarations

Conflict of Interests The authors declare that they have no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Barkman JJ, Doing H, Segal S (1964) Kritische Bemerkungen und Vorschläge zur quantitativen Vegetationsanalyse. *Acta Bot Neerl* 13:394–419
- Bobbink R, Hicks K, Galloway J, Spranger T, Alkemade R, Ashmore M, Bustamante M, Cinderby S, Davidson E, Dentener F, Emmett B, Erisman J-W, Fenn M, Gilliam F, Nordin A, Pardo L, de Vries W (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol Applic* 20:30–59
- Brice MH, Cazelles K, Legendre P, Fortin MJ (2019) Disturbances amplify tree community responses to climate change in the temperate-boreal ecotone. *Global Ecol Biogeogr* 28:1668–1681
- Bragazza L, Limpens J, Gerdol R, Grosvernier P, Hájek T, Hájková P, Hansen I, Iacumin P, Kutnar L, Rydin H, Tahvanainen T (2005) Nitrogen concentration and $\delta^{15}\text{N}$ signature of ombrotrophic *Sphagnum* mosses at different N deposition levels in Europe. *Global Change Biol* 11:106–114
- Canullo R, Starlinger F, Granke O, Fischer R, Aamlid D, Neville P (2013) ICP Forests manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests; part VII.1: Assessment of ground vegetation; UNECE ICP Forests Programme Coordinating Centre: Hamburg, Germany, 19 pp. Available at https://www.icp-forests.org/pdf/manual/2016/ICP_Manual_2016_01_part07-1.pdf
- Closset-Kopp D, Hattab T, Decocq G (2019) Do drivers of forestry vehicles also drive herb layer changes (1970–2015) in a temperate forest with contrasting habitat and management conditions? *J Ecol* 107:1439–1456
- Cools N, De Vos B (2016) Part X: Sampling and analysis of soil. In UNECE ICP Forests Programme Coordinating Centre (ed) *Manual on methods and criteria for harmonized sampling, assessment, monitoring and analysis of the effects of air pollution on forests*. Thünen Institute of Forest Ecosystems, Eberswalde, Germany, 29 pp + Annex. Available at https://www.icp-forests.org/pdf/manual/2016/ICP_Manual_2016_01_part10.pdf
- Čater M (2015) A 20-year overview of *Quercus robur* L. mortality and crown conditions in Slovenia. *Forests* 6:581–593
- de Bello F, Valencia E, Ward D, Hallett L (2020) Why we still need permanent plots for vegetation science. *J Veg Sci* 31:679–685
- de Cáceres M, Legendre P (2009) Associations between species and groups of sites: indices and statistical inference. *Ecology* 90:3566–3574
- De Frenne P, Rodríguez-Sánchez F, Coomes DA, Baeten L, Verstraeten G, Vellend M, Bernhardt-Römermann M, Brown CD, Brunet J, Cornelis J, Decocq GM, Dierschke H, Eriksson O, Gilliam FS, Hédli R, Heinken T, Hermy M, Hommel P, Jenkins MA, Kelly DL, Kirby KJ, Mitchell FJG, Naaf T, Newman N, Peterken G, Petřík P, Schultze J, Sonnier G, Van Calster H, Waller DM, Walther G-R, White PS, Woods KD, Wulf M, Jessen Graae B, Verheyen K (2013) Microclimate moderates plant responses to macroclimate warming. *Proc Natl Acad Sci USA* 110:18561–18565
- De Pauw K, Sanczuk P, Meeussen C, Depauw L, De Lombaerde E, Govaert S, Vanneste T, Brunet J, Cousins SAO, Gasperini C, Hedwall P-O, Iacopetti G, Lenoir J, Plue J, Selvi F, Spicher F, Uria-Diez J, Verheyen K, Vangansbeke P, De Frenne P (2022) Forest understorey communities respond strongly to light in interaction with forest

- structure, but not to microclimate warming. *New Phytol* 233:219–235
- de Vries W, Vel EM, Reinds GJ, Deelstra H, Klap JM, Leeters EEJM, Hendriks CMA, Kerkvoorden M, Landmann G, Herkendell J, Haussmann T, Erisman JW (2003) Intensive monitoring of forest ecosystems in Europe. 1. Objectives, set-up and evaluation strategy. *Forest Ecol Managem* 174:77–95
- Diekmann M (2003) Species indicator values as an important tool in applied plant ecology – a review. *Basic Appl Ecol* 4:493–506
- Dietz L, Collet C, Dupouey JL, Lacombe E, Laurent L, Gégout JC (2020) Windstorm-induced canopy openings accelerate temperate forest adaptation to global warming. *Global Ecol Biogeogr* 29:2067–2077
- Dirnböck T, Grandin U, Bernhardt-Römermann M, Beudert B, Canullo R, Forsius M, Grabner MT, Holmber M, Kleemola S, Lundin L, Mirtl M, Neumann M, Pompei E, Salemaa M, Starlinger F, Staszewski T, Uziębło AK (2014) Forest floor vegetation response to nitrogen deposition in Europe. *Global Change Biol* 20:429–440
- Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67:345–366
- Durak T, Holeska J (2015) Biotic homogenisation and differentiation along a habitat gradient resulting from the aging of managed beech stands. *Forest Ecol Managem* 351:47–56
- Durak T, Durak R (2021) Utilisation of traditional ecological plant classification systems to explain major dimensions of trait variation in herb layer of East Carpathians forests. *Environm Exp Bot* 185:104415
- Eler K, Kermavnar J, Marinšek A, Kutnar L (2018) Short-term changes in plant functional traits and understory functional diversity after logging of different intensities: a temperate fir-beech forest experiment. *Ann Forest Res* 61:223–241
- Ellenberg H, Weber HE, Düll R, Wirth V, Werner W, Paulißen D (1992) Zeigerwerte von Pflanzen in Mitteleuropa. 2. verbesserte und erweiterte Auflage. *Scr Geobot* 18:1–258
- Govaert S, Vangansbeke P, Blondeel H, Steppe K, Verheyen K, De Frenne P (2021a) Rapid thermophilization of understory plant communities in a 9 year-long temperate forest experiment. *J Ecol* 109:2434–2447
- Govaert S, Vangansbeke P, Blondeel H, De Lombaerde E, Verheyen K, De Frenne P (2021b) Forest understory plant responses to long-term experimental warming, light and nitrogen addition. *Pl Biol* 23:1051–1062
- Harrison S, Damschen EI, Grace JB (2010) Ecological contingency in the effects of climatic warming on forest herb communities. *Proc Natl Acad Sci USA* 107:19362–19367
- Heberling JM, McDonough MacKenzie C, Fridley JD, Kalisz S, Primack RB (2019) Phenological mismatch with trees reduces wildflower carbon budgets. *Ecol Letters* 22:616–623
- Hedwall PO, Uria-Diez J, Brunet J, Gustafsson L, Axelson AL, Strengbom J (2021) Interactions between local and global drivers determine long-term trends in boreal forest understory vegetation. *Global Ecol Biogeogr* 30:1765–1780
- Helm N, Essl F, Mirtl M, Dirnböck T (2017) Multiple environmental changes drive forest floor vegetation in a temperate mountain forest. *Ecol & Evol* 7:2155–2168
- Huang J, Mo JM, Zhang W, Lu XK (2014) Research on acidification in forest soil driven by atmospheric nitrogen deposition. *Acta Ecol Sin* 34:302–310
- Hübler K, Dirnböck T, Kleinbauer I, Willner W, Dullinger S, Karrer G, Mirtl M (2008) Long-term impacts of nitrogen and sulphur deposition on forest floor vegetation in the Northern limestone Alps, Austria. *Appl Veg Sci* 11:395–404
- Kapfer J, Hédél R, Jurasinski G, Kopecký M, Schei FH, Grytnes JA (2017) Resurveying historical vegetation data – opportunities and challenges. *Appl Veg Sci* 20:164–171
- Kermavnar J, Eler K, Marinšek A, Kutnar L (2019) Initial understory vegetation responses following different forest management intensities in Illyrian beech forests. *Appl Veg Sci* 22:48–60
- Kermavnar J, Ferlan M, Marinšek A, Kutnar L (2020) Effects of various cutting treatments and topographic factors on microclimatic conditions in Dinaric fir-beech forests. *Agric Forest Meteorol* 295:108186
- Kermavnar J, Kutnar L (2020) Patterns of understory community assembly and plant trait-environment relationships in temperate SE European forests. *Diversity* 12:91
- Kermavnar J, Kutnar L, Marinšek A (2022) Variation in floristic and trait composition along environmental gradients in the herb layer of temperate forests in the transition zone between Central and SE Europe. *Pl Ecol* 223:229–242
- Kermavnar J, Kutnar L, Marinšek A (2023) More losses than gains? Distribution models predict species-specific shifts in climatic suitability for beech forest herbs under climate change. *Frontiers Forest Global Change* 6:1236842
- Knollová I, Chytrý M, Bruehlheide H, Dullinger S, Jandt U, Bernhardt-Römermann B, Biurrin I, de Bello F, Glaser M, Hennekens S, Janssen F, Jiménez Alfaro B, Kadaš D, Kaplan E, Klinkovská K, Kuzemko A, Lenzner B, Pauli H, Sperandii MG, Verheyen K, Winkler M, et al., Essl F (2024) ReSurveyEurope: a database of resurveyed vegetation plots in Europe. *J Veg Sci* (Accepted for publication)
- Kopecký M, Hédél R, Szabó P (2013) Non-random extinctions dominate plant community changes in abandoned coppices. *J Appl Ecol* 50:79–87
- Küchler M, Küchler H, Bedolla A, Wohlgemuth T (2015) Response of Swiss forests to management and climate change in the last 60 years. *Ann Forest Sci* 72:311–320
- Kutnar L, Nagel TA, Kermavnar J (2019) Effects of disturbance on understory vegetation across Slovenian forest ecosystems. *Forests* 10:1048
- Kutnar L, Kermavnar J, Pintar AM (2021) Climate change and disturbances will shape future temperate forests in the transition zone between Central and SE Europe. *Ann Forest Res* 64:67–86
- Kutnar L, Kermavnar J, Sabovljević MS (2023) Bryophyte diversity, composition and functional traits in relation to bedrock and tree species composition in close-to-nature managed forests. *Eur J Forest Res* 142:865–882
- Legendre P, Legendre L (1998) *Numerical ecology, 2nd ed.* Elsevier, Amsterdam

- Leuschner C, Meier IC (2018) The ecology of Central European tree species: trait spectra, functional trade-offs, and ecological classification of adult trees. *Perspect Pl Ecol* 33:89–103
- Londo G (1976) The decimal scale for relevés of permanent quadrats. *Vegetatio* 33:61–64
- Martinčič A, Wraber T, Jogan N, Podobnik A, Turk B, Vreš B, Ravnik V, Frajman B, Strgulc-Krajšek S, Trčak B, Bačič M, Fischer MA, Eler K, Surina B (2007) *Mala Flora Slovenije: Ključ za določanje praprotnic in semen*. Tehniška založba Slovenije: Ljubljana, Slovenia, 967 pp
- Miller TK, Heberling JM, Kuebbing SE, Primack RB (2023) Warmer temperatures are linked to widespread phenological mismatch among native and non-native forest plants. *J Ecol* 111:356–371
- Naaf T, Wulf M (2010) Habitat specialists and generalists drive homogenization and differentiation of temperate forest plant communities at the regional scale. *Biol Conservation* 143:848–855
- Naaf T, Wulf M (2011) Traits of winner and loser species indicates drivers of herb layer changes over two decades in forests of NW Germany. *J Veg Sci* 22:516–527
- Naaf T, Kolk J (2016) Initial site conditions and interactions between multiple drivers determine herb-layer changes over five decades in temperate forests. *Forest Ecol Managem* 366:153–165
- Nagel TA, Iacopetti G, Javornik J, Rozman A, De Frenne P, Selvi F, Verheyen K (2019) Cascading effects of canopy mortality drive long-term changes in understorey diversity in temperate old-growth forests of Europe. *J Veg Sci* 30:905–916
- Ogris N, Skudnik M (2021) Beech defoliation in Slovenia is increasing. *Gozd Vestn* 79:226–237 (in Slovenian with English summary)
- Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, Minchin PR et al. (2022) vegan: Community ecology package. Accessed on 15 November 2023. Available at <https://cran.r-project.org/web/packages/vegan/index.html>
- Patacca M, Lindner M, Lucas-Borja ME, Cordonnier T, Fidej G, Gardiner B, Hauf Y, Jasinevičius G, Labonne S, Linkevičius E, Mahnken M, Milanovic S, Nabuurs G-J, Nagel TA, Nikinmaa L, Panyatov M, Bercak R, Seidl R, Ostrogović Sever MZ, Socha J, Thom D, Vuletic D, Zudin S, Schelhaas M-J (2022) Significant increase in natural disturbance impacts on European forests since 1950. *Global Change Biol* 29:1359–1376
- Perring MP, Diekmann M, Midolo G, Schellenberger Costa D, Bernhardt-Römermann M, Otto JCJ, Gilliam FS, Hedwall PO, Nordin A, Dirnböck T, Simkin SM, Máliš F, Blondeel H, Brunet J, Chudomelová M, Durak T, De Frenne P, Hédli R, Kopecký M, Landuyt D, Li D, Manning P, Petřík P, Reczyńska K, Schmidt W, Standovár T, Świerkosz K, Vild O, Waller MD, Verheyen K (2018) Understanding context dependency in the response of forest understorey plant communities to nitrogen deposition. *Environm Pollut* 242:1787–1799
- Prach J, Kopecký M (2018) Landscape-scale vegetation homogenization in Central European sub-montane forests over the past 50 years. *Appl Veg Sci* 21:373–384
- Puchalka R, Paž-Dyderska S, Dylewski L, Czortek P, Vítkova M, Sádlo J, Klisz M, Koniakin S, Čarni A, Rašomavičius V, De Sanctis M, Dyderski MK (2023) Forest herb species with similar European geographic ranges may respond differently to climate change. *Sci Total Environm* 905:167303
- R Core Team (2021) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria
- Reinecke J, Klemm G, Heinken T (2014) Vegetation change and homogenization of species composition in temperate nutrient deficient Scots pine forests after 45 yr. *J Veg Sci* 25:113–121
- Richard B, Dupouey JL, Corcket E, Alard D, Archaux F, Aubert M, Boulanger V, Gillet F, Langlois E, Macé S, Montpied P, Beaufils T, Begeot C, Behr P, Boissier J-M, Camaret S, Chevalier R, Decocq G, Dumas Y, Eynard-Machet R, Gégout J-C, Huet S, Malécot V, Margerie P, Mouly A, Paul T, Renaux B, Ruffaldi P, Spicher F, Thirion E, Ulrich E, Nicolas M, Lenoir J (2021) The climatic debt is growing in the understorey of temperate forests: Stand characteristics matter. *Global Ecol Biogeogr* 30:1474–1487
- Rolls RJ, Deane DC, Johnson SE, Heino J, Anderson MJ, Ellingsen KE (2023) Biotic homogenisation and differentiation as directional change in beta diversity: synthesising driver–response relationships to develop conceptual models across ecosystems. *Biol Rev* 98:1388–1423
- Rooney TP (2009) High white-tailed deer densities benefit graminoids and contribute to biotic homogenization of forest ground-layer vegetation. *Plant Ecol* 202:103–111
- Roth M, Müller-Meißner A, Michiels HG, Hauck M (2022) Vegetation changes in the understory of nitrogen-sensitive temperate forests over the past 70 years. *Forest Ecol Managem* 503:119754
- Savage J, Vellend M (2015) Elevational shifts, biotic homogenization and time lags in vegetation change during 40 years of climate warming. *Ecography* 38:546–555
- Schmitz A, Sanders TGM, Bolte A, Bussotti F, Dirnböck T, Johnson J, Peñuelas J, Pollastrini M, Prescher AK, Sardans J, Verstraeten A, de Vries W (2019) Responses of forest ecosystems in Europe to decreasing nitrogen deposition. *Environm Pollut* 244:980–994
- Seidl R, Thom D, Kautz M, Martin-Benito D, Peltoniemi M, Vacchiano G, Wild J, Ascoli D, Petr M, Honkaniemi J, Lexer MJ, Trotsiuk V, Mairota P, Svoboda M, Fabrika M, Nagel TA, Reyher CPO (2017) Forest disturbances under climate change. *Nature Clim Change* 7:395–402
- Senf C, Sebald J, Seidl R (2021) Increasing canopy mortality affects the future demographic structure of Europe's forests. *One Earth* 4:1–7
- Staubli E, Dengler J, Billeter R, Wohlgemuth T (2021) Changes in biodiversity and species composition of temperate beech forests in Switzerland over 26 years. *Tuexenia* 41:87–108
- Stevens JT, Safford HD, Harrison S, Latimer AM (2015) Forest disturbance accelerates thermophilization of understory plant communities. *J Ecol* 103:1253–1263
- Šipek M, Ravnjak T, Šajna N (2023) Understorey species distinguish late successional and ancient forests after decades of minimum human intervention: a case study from Slovenia. *Forest Ecosyst* 10:100096

- Škrk N, Serrano-Notivol R, Čufar K, Merela M, Črepinšek Z, Kajfež Bogataj L, de Luis M (2021) SLOCLIM: a high-resolution daily gridded precipitation and temperature dataset for Slovenia. *Earth Syst Sci Data* 13:3577–3592
- Tichý L, Axmanová I, Dengler J, Guarino R, Jansen F, Midolo G, Nobis MP, Van Meerbeek K, Ačić S, Attore F, Bergmeier E, Biurrun I, Bonari G, Bruelheide H, Campos JA, Čarni A, Chiarucci A, Čuk M, Čušterevska R, Didukh Y, Dítě D, Dítě Z, Dziuba T, Fanelli G, Fernández-Pascual E, Garbolino E, Gavilán RG, Gégout J-C, Graf U, Güler B, Hájek M, Hennekens SM, Jandt U, Jašková A, Jiménez-Alfaro B, Julve P, Kambach S, Karger DN, Karrer G, Kavgacı A, Knollová I, Kuzemko A, Küzmič F, Landucci F, Lengyel A, Lenoir J, Marcenò C, Erenskjold Moeslund J, Novák P, Pérez-Haase A, Peterka T, Pielech R, Pignatti A, Rašomavičius V, Rüşüña S, Saatkamp A, Šilc U, Škvorc Ž, Theurillat J-P, Wohlgemuth T, Chytrý M (2022) Ellenberg-type indicator values for European vascular plant species. *J Veg Sci* 34:e13168
- Urbančič M, Kutnar L, Kobal M, Žlindra D, Marinšek A, Simončič P (2016) Soil and vegetation characteristics on intensive monitoring plots of forest ecosystems. *Gozd Vestn* 74:3–27 (in Slovenian with English summary)
- van Dobben HF, de Vries W (2017) The contribution of nitrogen deposition to the eutrophication signal in understorey plant communities of European forests. *Ecol Evol* 7:214–227
- Vangansbeke P, Sanczuk P, Govaert S, De Lombaerde E, De Frenne P (2022) Negative effects of winter and spring warming on the regeneration of forest spring geophytes. *Pl Biol* 24:950–959
- Vanhellemont M, Baeten L, Verheyen K (2014) Relating changes in understorey diversity to environmental drivers in an ancient forest in northern Belgium. *Pl Ecol Evol* 147:22–32
- Verheyen K, Baeten L, De Frenne P, Bernhardt-Römermann M, Brunet J, Cornelis J, Decocq G, Dierschke H, Eriksson O, Hédrl R (2012) Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *J Ecol* 100:352–365
- Verheyen K, Bažány M, Češko E, Chudomelová M, Closset-Kopp D, Czortek P, Decocq G, De Frenne P, De Keersmaecker L, Enríquez García C, Fabšičová M, Grytnes J-A, Hederová L, Hédrl R, Heinken T, Schei FH, Horváth S, Jaroszewicz B, Jermakowicz E, Klinerová T, Kolk J, Kopecký M, Kuras I, Lenoir J, Macek M, Máliš F, Martinussen TC, Naaf T, Papp L, Papp-Szakály Á, Pech P, Petřík P, Prach J, Reczyńska K, Sætersdal M, Spicher F, Standovář T, Świerkosz K, Szczęśniak E, Tóth Z, Ujházy K, Ujházyová M, Vangansbeke P, Vild O, Wolkowycy D, Wulf M, Baeten L (2018) Observer and relocation errors matter in resurveys of historical vegetation plots. *J Veg Sci* 29:812–823
- Verstraeten G, Baeten L, Van den Broeck T, De Frenne P, Demey A, Tack W, Muys B, Verheyen K (2013) Temporal changes in forest plant communities at different site types. *Appl Veg Sci* 16:237–247
- Walter CA, Adams MB, Gilliam FS, Peterjohn WT (2017) Non-random species loss in a forest herbaceous layer following nitrogen addition. *Ecology* 98, 2322–2332
- Westoby M (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Pl & Soil* 199:213–227
- Wronńska-Pilarek D, Rymaszewicz S, Jagodziński AM, Gawryś R, Dyderski MK (2023) Temperate forest understory vegetation shifts after 40 years of conservation. *Sci Total Environ* 895:165164
- Zellweger F, De Frenne P, Lenoir J, Vangansbeke P, Verheyen K, Bernhardt-Römermann M, Baeten L, Hédrl R, Berki I, Brunet J, Van Calster H, Chudomelová M, Decocq G, Dirnböck T, Durak T, Heinken T, Jaroszewicz B, Kopecký M, Máliš F, Macek M, Malicki M, Naaf T, Nagel TA, Ortman-Ajkai A, Petřík P, Pielech T, Reczyńska K, Schmidt W, Standovář T, Świerkosz K, Teleki B, Vild O, Wulf M, Coomes D (2020) Forest microclimate dynamics drive plant responses to warming. *Science* 368:772–775
- Zolotova E, Ivanova N, Ivanova S (2023) Global overview of modern research based on Ellenberg indicator values. *Diversity* 15:14

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.