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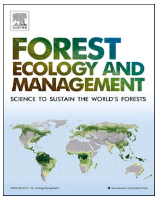

Post-harvest forest herb layer demography: General patterns are driven by pre-disturbance conditions

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ABSTRACT

Timber harvesting constitutes extensive anthropogenic disturbance in temperate forests, producing a broad range of ecological impacts that most often enhance the demographic processes of vegetation. This study monitored post-harvest herb layer demography over a 6-year period in mesic Dinaric fir-beech forests (Slovenia), a vascular plant diversity hotspot among European forests. Three experimental harvesting intensities, i.e. full harvest (FH), partial harvest (PH) and a control treatment (NH), were each applied over a circular area of 4000 m^2 and replicated three times at each of three study sites. Vegetation sampling was conducted before harvesting (in 2012), and two (2014) and six (2018) years following it, in a 400 m^2 circular plot positioned in the centre of each treatment area. We focused on identifying general demographic patterns and evaluating the effects of various pre-disturbance abiotic and biotic predictors on compositional responses to disturbance. Two years after harvest (2012–2014), compositional shifts were larger than those in the next 4-year period (2014–2018), confirming the general theoretical prediction that species turnover rate decreases along a successional gradient. The degree of compositional shifts in gaps (FH) and thinned stands (PH) was affected by local abiotic factors (geomorphology of karst sinkholes) and community attributes, such as pre-harvest species richness. Our results indicate that compositional stability is positively associated with pre-disturbance species richness. Over the whole study period, increases in plot-level species richness (alpha diversity) and overall enrichment of the species pool (gamma diversity) were accompanied by compositional convergence, i.e. a decline in floristic dissimilarity (beta diversity) between and within study sites. However, the observed tendency towards homogenization was rather weak and would have been even more pronounced if the demographic type of persistent resident species had not shown a high degree of resistance, thus leaving a strong imprint on post-harvest vegetation development by preserving the forest characteristics of the herb layer community.

1. Introduction

The Anthropocene is an age of rapid environmental change in which altered disturbance regimes and enhanced biotic invasions cause significant structural, compositional and biodiversity changes of natural ecosystems and plant communities (Vellend et al., 2017). Forest ecosystems cover 31% of the global land area and are home to most of Earth's terrestrial biodiversity (FAO and UNEP, 2020). However, the conservation status of these ecosystems is under pressure. Official reports around the globe (e.g. FOREST EUROPE, 2020) indicate that deforestation and forest degradation continue at alarming rates. In the last few decades, many temperate European forests have witnessed pronounced changes in the frequency, intensity and spatial extent of disturbances (Seidl et al., 2017; Thorn et al., 2017). Catastrophic natural disturbances, such as windthrows, wildfires, ice storms and insect outbreaks, have shifted forest management from regular management-plan-oriented harvest interventions to a prevalence of sanitary (salvage) logging (Grecs and Kolšek, 2017) in many parts of the Europe, particularly in Central and South-eastern Europe (Thom et al., 2013; Nagel et al., 2016; Nagel et al., 2017). All these effects underscore the need to improve our knowledge on the response of forest plant communities to disturbance, including overstory canopy removal through harvesting.

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On the other hand, some regions have experienced a cessation of forest management, leading to quite opposite effects on forest vegetation, e.g. the decline of rare light-demanding species and the prevalence of shade-tolerant or nitrophilous plants (Staude et al., 2020).

Variation in the composition of plant communities through time arises from a combination of the colonization of new species from dispersed or dormant propagules and the local extirpation of extant species (Shurin, 2007; Norden et al., 2012). These processes are usually most pronounced for post-disturbance plant community assembly (Halpern, 1988). Changes in species composition also integrate other demographic processes, such as increases or decreases in species abundance. Thus, species-level responses should scale-up to community-level responses. However, the relative contribution of individual vegetation processes remains elusive, partly because of a paucity of repeated temporal measurements of plant communities. Although many of the disturbance-driven responses can be linked to the general principles of succession theory, site-specific factors also need to be considered (Christensen and Peet, 1984; Small and McCarthy, 2002).

Ecological theory posits that post-disturbance forest vegetation development follows a certain trajectory, which is associated with the directional replacement of species (Platt and Connell, 2003). In most temperate mesic forests worldwide, the diversity and abundance of herbaceous plant species increase and reach a peak shortly after a disturbance. The composition of pioneer communities is largely influenced by demographic stochasticity, i.e. the chance of arrival during the very immediate phase when resources released by a disturbance facilitate species colonization and when competition is low (Halpern, 1989; Belote et al., 2012). The rapid exploitation of previously unoccupied space leads to declining levels of available resources (e.g. light, soil moisture and soil nutrients) and intensified biotic relationships. Initial herb-dominated communities, which favour species with an acquisitive resource-use strategy, usually transit towards communities composed of competitively superior woody plants and shade-tolerant herbaceous species. However, such transitions could be inhibited by numerous abiotic and biotic factors, such as the prevalence of dense recalcitrant layers (*sensu* Royo and Carson, 2006), with detrimental impacts on natural tree species regeneration (Aikens et al., 2007). In terms of the magnitude of compositional change, many studies have shown that the most dramatic shifts in the composition, diversity and abundance of the forest herb layer occur in the first few years after a disturbance. As succession unfolds, rates of compositional change tend to decrease (Anderson, 2007).

Plant ecologists have long been intrigued by the dependence of the successional trajectory of vegetation and its responses to disturbance on the “starting” characteristics. Egler (1954) emphasized that the initial floristic composition is an important factor in old-field vegetation development. This hypothesis predicts that successional pathways depend on the communities that are present at the start of succession (Gill et al., 2017). A similar assumption can be applied to the potential effects of pre-disturbance abiotic conditions and community attributes on post-disturbance community stability. For example, Urza et al. (2017) demonstrated that post-fire vegetation responses are mediated by the pre-fire community composition and site characteristics. The importance of the initial site conditions has also been addressed in the context of long-term changes in forest vegetation diversity and composition (Bunn et al., 2010; Naaf and Kolk, 2016).

Plant community assembly following disturbance, such as overstory harvesting, is primarily driven by disturbance intensity (MacDonald et al., 2014; Vanha-Majamaa et al., 2017). Moreover, post-disturbance vegetation reorganization depends on community resistance and resilience (Halpern, 1988; Belote et al., 2012; MacDonald et al., 2015). The diversity-stability hypothesis (Goodman, 1975; McCann, 2000) suggests that more diverse communities have greater temporal stability in species composition. This premise has frequently been called into question across a wide range of taxa, with contrasting results (McNaughton, 1977; Shurin, 2007). The positive effects of biodiversity on the temporal stability of plant communities have been demonstrated in theoretical and empirical studies, spanning from controlled experiments in grasslands (Roscher et al., 2011; Catford et al., 2020) to decadal records of forest herb communities (Dovčiak and Halpern, 2010).

The theory of secondary forest succession implies that plant community composition tends to converge toward a climax community. Increasing compositional similarity between different sites with similar climatic and edaphic conditions will result in successional convergence (Christensen and Peet, 1984; Kupfer and Runkle, 1996). In contrast to this overarching concept, less is known about how management disturbances, primarily causing an increase in species richness (i.e. alpha diversity), impact the floristic dissimilarity among local communities within sites or between different sites (i.e. beta diversity). Thus, even if species richness is increased or remains unaffected by forest management, it can still alter assembly patterns by imposing environmental filters that select for floristically clustered communities. A decrease in such heterogeneity can be understood as a form of biotic homogenization, which is currently one of the major threats to forest biodiversity (Naaf and Wulf, 2012; Johnson et al., 2014; Olden et al., 2018).

Here, through a manipulative *in-situ* forest experiment using pre- and post-harvest data, we ascertain how different harvesting intensities (full harvest, partial harvest, no harvest) affect demographic changes in the forest herb layer over a 6-year period (2012–2018) in Dinaric fir-beech forests. More specifically, the aims of this study were to i) evaluate herb layer compositional changes based on demographic types and demographic parameters; ii) identify pre-disturbance abiotic and biotic predictors of compositional shifts; and iii) analyse changes in the floristic dissimilarity between and within different study sites. The last approach was used for testing potential compositional convergence after disturbance and to disentangle which demographic types or processes are responsible for such patterns.

2. Materials and methods

2.1. Study area, harvesting experiment and vegetation sampling

The study was conducted in Dinaric fir-beech forests in Slovenia. Dinaric fir-beech forests (*Omphalodo-Fagetum* s. lat.) cover more than 116,000 ha or one tenth of the total Slovenian forest cover (Dakskobler, 2008). They are part of the Dinaric forest, which is the largest forest complex in Central Europe, and are characterized by pronounced spatial connectivity and temporal continuity. According to recent biogeographical vegetation studies, the forests in the north-western Dinaric Mountains have among the highest alpha diversity of vascular plants in all European forests (Večeřa et al., 2019).

Three different study sites in Dinaric fir-beech forests were selected: Trnovo (45.989° N, 13.759° E), Kočevski Rog (45.668° N, 15.033° E) and Snežnik (45.672° N, 14.460° E). The studied species-rich forest ecosystems are characterized by mixed *Fagus sylvatica-Abies alba-Picea abies* stands and rugged terrain with numerous karst sinkholes. All forest stands were composed of predominantly herbaceous and woody species characteristic of the low-light environment under closed canopy. For a detailed description of our study area and study sites, see Kutnar et al. (2015), Kermavnar et al. (2019a) and Kermavnar et al. (2020).

The study utilized a before/after - control/impact design. The experiment was designed more generally to determine how different harvesting intensities implemented in 2012 have shaped the responses of carbon stocks and forest biodiversity, with vascular plants being the most thoroughly studied so far (see Eler et al., 2018; Kermavnar et al., 2019a; Kermavnar et al., 2019b). At each site, nine karst sinkholes were randomly selected, 27 in total. In one third of the sinkholes (three per site), all overstory trees were harvested in a circular area of 4000 m^2 with the centre at the bottom of the sinkhole. This full harvest (hereafter FH) created forest gaps of 0.4 ha in size. Forest gaps or forest openings can be caused by natural or human disturbances and can be classified as small, medium or large. Our experimental gaps (with more than 30 m diameter) are according to Kern et al. (2014) and Kern et al. (2013) classified into large gaps. And will hereinafter be referred to as gaps. In one third of the sinkholes (three per site), 50% of the stand growing stock was harvested. This partial harvest (hereafter PH) created thinned stands with some retained mature trees. In one third of the sinkholes (three per site), no harvesting (hereafter NH) was performed, and these were considered as control stands. For a detailed description of our experimental scheme, see Kutnar et al. (2015) and Kermavnar et al. (2019a).

Vegetation was sampled just before (2012), two years after (2014) and six years after (2018) timber harvesting. Within each sinkhole, a survey was conducted in a circular plot of 400 m^2 during the period of peak vegetation development in the summer. This yielded 27 sampling plots in total. The centre of the sampling plot was set at the bottom of the sinkhole. We recorded all vascular plant species present in the plot. The percentage cover of each species was visually estimated using a modification of Barkman's method (Barkman et al., 1964). We differentiated between four vegetation layers: tree, shrub, herb and moss layer. The herb layer consisted of all herbaceous species. Woody plants (tree seedlings and saplings, shrubs, woody vines) with a height below 0.5 m were recorded in the herb layer, whereas those higher than 0.5 m were recorded in the shrub layer. The minimum height for the tree layer was 5 m. For additional information about our sampling campaigns, see Kermavnar et al. (2019a).

2.2. Conceptual framework for herb layer demography

First, by taking into account the species incidence (presence/absence) in three successive sampling years, each species of the herb layer was classified into one of seven demographic types (Fig. 1). As this classification was done separately for each plot, the same species could be classified into different types in different plots.

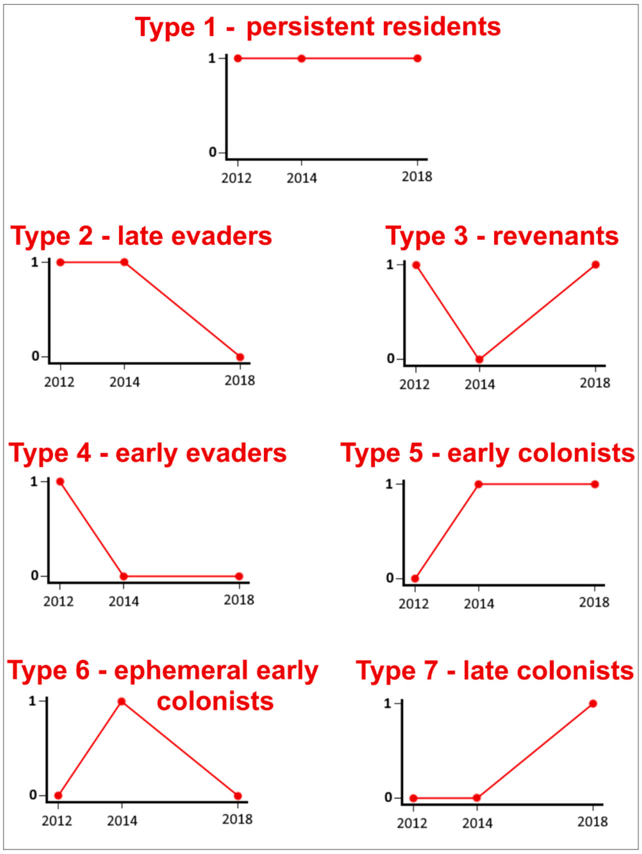

Fig. 1. Conceptual layout of seven demographic types, defined based on incidence data. 1 – present, 0 – absent.

Secondly, patterns of individual species responses to harvesting were translated into community-level demography. By combining both incidence and abundance species data, we also distinguished between several demographic parameters, such as species turnover, colonization rate and the rate of local extirpation (Table 1). Parameters were calculated for each plot and included data from two successive samplings. Consequently, three different periods were distinguished, i.e. the period 2012–2014, the period 2014–2018 and the period 2012–2018. Based on the presence or absence of species, herb layer species were classified as follows: residents are plant species recorded in plots prior to harvesting in 2012. Survivors are residents that were still present after harvesting. Evaders are residents that were not present after harvesting. Colonists are newly recorded species, not present before but present after harvesting. Based on changes in their abundance, survivors were additionally divided into groups of species with either increased, decreased or no change in cover between two successive sampling years (Table 1).

2.3. Pre-disturbance abiotic and biotic conditions

We compiled information on pre-harvest (2012) community attributes and abiotic conditions (Table 2). Various plot-level variables (40 in total) related to plant community diversity, tree species composition and diversity, stand and soil characteristics, local topography, geomorphology of karst sinkholes, woody debris (deadwood) and vegetation-derived estimates of ecological conditions were considered as potential explanatory variables for post-harvest herb layer compositional shifts.

Some of the community attributes were calculated based on herb layer data, whereas others were calculated using both herb and shrub layer data (i.e. understory layer). The proportions of the three most frequent and abundant tree species in the tree layer (i.e. *Fagus sylvatica*, *Abies alba*, *Picea abies*) and in the understory layer (i.e. *Fagus sylvatica*, *Acer pseudoplatanus*, *Abies alba*) were calculated. The cover of different vegetation layers was calculated using the sum of the mean class cover percentage of each plant species. Therefore, the total cover could exceed 100%.

Some variables were visually estimated during vegetation sampling, while others were derived from measurements, such as LiDAR data

Table 1
Definitions of different demographic parameters. N – number.

Parameter	Definition	Calculation formula
Δ species richness (%)	Relative change in plot-level species richness (SR)	$((SR_{after} - SR_{before}) / SR_{before}) \times 100$
Species turnover (%)	Relative species turnover, which includes the number of colonists, evaders, SR before and SR after; see Standovár et al. (2017)	$((N\ of\ colonists + N\ of\ evaders) / (SR_{before} + SR_{after})) \times 100$
Survival rate (%)	The ratio between the number of survivors and the number of residents (SR_{before})	(N of survivors / N of residents) × 100
Survivor increase (%)	The ratio between the number of survivors with increased abundance and the total number of survivors	(N of increasing survivors / N of survivors) × 100
Survivor decrease (%)	The ratio between the number of survivors with decreased abundance and the total number of survivors	(N of decreasing survivors / N of survivors) × 100
Survivor stable (%)	The ratio between the number of survivors with no change in abundance and the total number of survivors	(N of no change survivors / N of survivors) × 100
Extirpation rate (%)	The ratio between the number of evaders and SR before (number of residents)	$(N\ of\ evaders / SR_{before}) \times 100$
Colonization rate (%)	The ratio between the number of colonists and SR after	$(N\ of\ colonists / SR_{after}) \times 100$

Table 2
List of pre-harvest community attributes and abiotic conditions measured or estimated on the plot level.

Variable (abbreviation)	Range (min – max)	Definition/Notes
Understory composition and diversity		
Species richness (SR)	27–67	Number of plant species in the herb layer
Evenness (Even)	0.64–0.86	Pielou's (1975) formula: Shannon diversity index / log (species richness)
Understory cover (%) (Cov_U)	18.7–120.1	Cumulative cover of all vascular plant species in the understory layer (herb and shrub layer)
Moss cover (%) (Moss)	2–50	Total cover of mosses (visual estimation)
Bare soil (%) (Baresoil)	10–60	Cover of bare soil (visual estimation)
Tree species richness in the understory layer (TSrich_U)	3–10	Number of different tree species in the understory layer (herb and shrub layer)
Tree species cover (%) in the understory layer (TScov_U)	2.0–34.1	Cumulative cover of tree species in the understory layer (herb and shrub layer)
Beech cover (%) in the understory layer (Beech_U)	10.0–91.9	Proportion of *Fagus sylvatica* in the cumulative cover of tree species in the understory layer (herb and shrub layer)
Maple cover (%) in the understory layer (Maple_U)	0.0–51.9	Proportion of *Acer pseudoplatanus* in the cumulative cover of tree species in the understory layer (herb and shrub layer)
Fir cover (%) in the understory layer (Fir_U)	0.1–36.1	Proportion of *Abies alba* in the cumulative cover of tree species in the understory layer (herb and shrub layer)
Forest stand characteristics		
Tree layer richness (Rich_T)	1–5	Total number of different tree species in the tree layer
Tree layer cover (%) (Cov_T)	61.9–168.8	Cumulative cover of species in the tree layer; proxy for light availability in the understory
Beech cover (%) in the tree layer (Beech_T)	26.8–100.0	Proportion of *Fagus sylvatica* in the cumulative cover of the tree layer
Fir cover (%) in the tree layer (Fir_T)	0.0–68.4	Proportion of *Abies alba* in the cumulative cover of the tree layer
Spruce cover (%) in the tree layer (Spruce_T)	0.0–60.7	Proportion of *Picea abies* in the cumulative cover of the tree layer
Stand growing stock (m^3/ha) (StandGS)	306.7–791.1	A proxy for stand density; see Chiavetta et al. (2016) for details
Stand Shannon diversity index (StandSH)	1.99–2.79	A proxy for stand structural complexity; see Chiavetta et al. (2016) for details
Topography and geomorphology of sinkholes		
Elevation (m) (Elevat)	722.8 – 887.7	Elevation of the sinkhole centre, derived from LiDAR data
Rockiness (%) (Rock)	3–60	Cover of rocks on the surface (visual estimation)
Sinkhole depth (m) (Depth)	3.68–16.53	Estimated based on LiDAR data
Sinkhole radius (m) (Radius)	16.70–55.55	Estimated based on LiDAR data
Sinkhole slope (m) (Slope)	15.21–38.69	Estimated based on LiDAR data
Sinkhole DD ratio (DDratio)	5.79–11.86	The ratio between the diameter (radius × 2) and depth of the sinkhole; a proxy for sinkhole concavity
Sinkhole volume (m^3) (Volume)	2771–98051	Calculated as $(4/3 \times \pi \times r^3) / 2$, where $r =$ average of sinkhole depth and radius
Soil characteristics		
Organic soil thickness (cm) (Org_cm)	0.0–8.2	Thickness of organic soil layers
Mineral soil depth (cm) (Min_cm)	23.3–80.0	Depth of mineral soil layers
Organic soil pH (Org_pH)	4.69–5.91	pH of organic soil layers
Mineral soil pH (Min_pH)	4.70–5.97	pH of mineral soil layers
Woody debris (deadwood)		
Coarse woody debris (m^3/ha) (CWD)	0.26–41.31	Total volume of coarse woody debris
Fine woody debris (m^3/ha) (FWD)	1.67–13.46	Total volume of fine woody debris
Decay class 1 (m^3/ha) (Decay1)	0.1–34.7	Bark $\geq$ 90%, wood hardness $\geq$ 90%
Decay class 2 (m^3/ha) (Decay2)	0.3–10.5	Bark 90–60%, wood hardness 90–60%
Decay class 3 (m^3/ha) (Decay3)	0.6–17.3	Bark 60–30%, wood hardness 60–30%
Decay class 4 (m^3/ha) (Decay4)	0.0–8.4	Bark $\leq$ 30%, wood hardness $\leq$ 30%
Vegetation-derived estimates		
Ellenberg light (EIV_L)	2.80–3.87	Community-weighted mean for Ellenberg indicator value for light
Ellenberg temperature (EIV_T)	4.50–5.19	Community-weighted mean for Ellenberg indicator value for temperature
Ellenberg continentality (EIV_K)	2.79–4.01	Community-weighted mean for Ellenberg indicator value for continentality
Ellenberg moisture (EIV_F)	5.01–5.99	Community-weighted mean for Ellenberg indicator value for soil moisture
Ellenberg reaction (EIV_R)	4.86–6.47	Community-weighted mean for Ellenberg indicator value for soil reaction
Ellenberg nitrogen (EIV_N)	5.27–6.63	Community-weighted mean for Ellenberg indicator value for soil nutrients

(Kobler, 2016) for sinkhole geomorphological features. Soil properties were sampled in three different within-sinkhole positions (i.e. centre, north-facing and south-facing slope) and then averaged across these three positions to obtain the mean value of soil depth and soil pH for the sinkhole (plot). Details are available in D'Andrea et al. (2016). The volume of woody debris, which is a potential important substrate for plant species growth and regeneration, was measured for each plot (Lombardi and Mali, 2016). Four different stages of decay (decay classes) were distinguished according to the presence of bark and hardness of wood. Vegetation-derived environmental indices (i.e. Ellenberg indicator values; Ellenberg et al., 1992) were calculated as community-weighted means based on abundance data for species in the herb layer (Table 2).

2.4. Data analysis and statistics

2.4.1. Compositional changes

To compare multivariate patterns of herb layer community compositional changes, we performed non-metric multidimensional scaling (NMS) ordination of species cover data for all plots across all years. From NMS ordination, we further calculated successional vectors, depicting community compositional change between pre- and post-harvest years. As a measure of the amount of change, we calculated the lengths of vectors as the Euclidean distance between ordination scores in 2-dimensional NMS ordination. For each plot the distances within the ordination space were calculated between repeated observations, i.e. for three different periods: i) from pre-harvest (2012) to two years post-harvest (2014); ii) from 2014 to six years post-harvest (2018); and iii) from 2012 to 2018. Distance-based measures calculated from ordination scores can be used to quantitatively evaluate the relative stability, resistance and resilience of ecological communities (Lamothe et al., 2019). Vector length can be seen as an inverse measure of compositional stability. Larger vector lengths (Euclidean distance) signify a greater degree/magnitude of compositional change (Halpern, 1988; MacDonald et al., 2015), which is inversely related to compositional resistance (Belote et al., 2012). Differences in shifts between periods were tested with the Wilcoxon rank-sum test. Based on the NMS scores of each plot, we also analysed distances to the baseline (*sensu* Lamothe et al., 2019), i. e. the starting position in the ordination space.

2.4.2. Demographic types and parameters

The association between demographic types and harvesting intensities was analysed with Correspondence Analysis using the cumulative frequencies of demographic types in a contingency table. The association was tested with the Pearson's chi-squared test.

The plot-level relative proportion of demographic type was calculated by dividing the number of plant species in the demographic type by the total number of all species recorded in a plot. Relationships between the relative proportion of each demographic type and degree of compositional changes (vector length for shift 2012–2018) were quantified by Spearman rank correlations, separately for each harvesting intensity. The same procedure was applied to evaluate the correlation between demographic parameters and the degree of compositional changes. Differences between harvesting intensities in demographic types and parameters were tested using the Kruskal-Wallis rank-sum test with Dunn's post-hoc test and Bonferroni correction for multiple comparisons (Dunn, 1961).

2.4.3. Effects of pre-harvest factors

The gradients in abiotic conditions and general community attributes were large enough to offer an opportunity to examine whether post-harvest vegetation responses depend on pre-harvest conditions. Differences in predictors between harvesting intensities were tested using the Kruskal-Wallis rank-sum test, and no statistically significant differences were detected. The dependence of the degree of compositional changes on potential explanatory variables (predictors) was modelled using Generalized Linear Models (GLM). Since Euclidean distances (i.e. vector lengths) represented dimensions in ordination space and were left-skewed and over-dispersed, we employed GLMs using a gamma distribution with a log-link function (Dunn and Smyth, 2018). The most parsimonious model was selected with forward stepwise selection based on the Akaike Information Criterion as a measure of the goodness-of-fit. We only considered models with statistically significant explanatory variables. When necessary, values of predictors were log-transformed beforehand to reduce non-normal data distribution. Multicollinearity was recorded for the final GLMs using a Variance Inflation Factor. The relationships between response variables (compositional shift, colonization rate, extirpation rate) and the most significant predictors, such as pre-harvest species richness, were further examined with univariate linear regression analysis. The coefficient of determination (R^2) was used as an overall measure of goodness-of-fit for the general linear models.

2.4.4. Floristic dissimilarity

We were also interested whether compositional differences between plots of each harvest intensity separately increased or decreased during the study period. We thus quantified herb layer floristic dissimilarity between and within study sites. This was computed as a pairwise Bray-Curtis dissimilarity index, which is expressed as the percentage difference in species composition considering both incidence and abundance data (Bray and Curtis, 1957). We compared plots subjected to the same harvest intensity. A total of 27 between-site pairwise comparisons and nine within-site pairwise comparisons were calculated for each of the three sampling years. Decreasing floristic dissimilarity can be interpreted as floristic convergence, while increasing dissimilarity implies floristic divergence. Differences in floristic dissimilarity between sampling years were tested using the Kruskal-Wallis rank-sum test.

2.4.5. R packages for statistical analyses

Data were analysed with the R statistical software version 3.5.2 (R Core Team, 2018). The following packages were used: *vegan* (Oksanen et al., 2019) for NMS ordination and the Bray-Curtis dissimilarity index, *ca* (Nenadic and Greenacre, 2007) for the Correspondence Analysis, and *nlme* (Pinheiro et al., 2020) for fitting the GLMs. Kruskal-Wallis rank-sum tests and Spearman rank correlations were performed in the *agricolae* package (de Mandiburu, 2020), whereas other statistical tests were run with built-in statistical functions in the R programme. In all statistical tests, the significance level was set at $\alpha = 0.05$. Statistical significance was considered marginal if p-values were above 0.05 but below 0.1.

3. Results

3.1. Herb layer compositional changes

Across all plots and years, we recorded 317 different plant species in the herb layer, of which 268 were herbaceous and 49 were woody species. The NMS analysis showed that variation in species composition was best explained along the first two axes (final stress = 0.176). Changes in herb layer species composition were proportional with harvesting intensity. The most disturbed FH plots exhibited the largest compositional changes, whereas the NH plots changed the least (Fig. 2). Regarding the direction of the shifts in the NMS ordination space, all harvested plots (FH and PH) shifted in similar directions, i.e. towards higher NMS axis 1 scores and lower NMS axis 2 scores. In contrast, compositional changes in the majority of NH plots were rather small and random (non-directional). Exceptions were some control stands at the Snežnik study site (NH7 – NH9), which experienced increased natural disturbance effects (ice storm damage, windthrows, bark beetle outbreaks) in the period 2014–2018 (Fig. 2).

The magnitude of compositional changes differed significantly between the period 2012–2014 and the period 2014–2018. In the FH plots, average compositional shift, measured as a vector length (i.e. Euclidean distance) in the NMS ordination space, was significantly (Wilcoxon rank-sum test: $p < 0.001$) larger in the first two years after harvest compared to that in the next four years. The average vector length for the 2012–2014 shift was 1.13, and for the 2014–2018 shift it was 0.30. The difference between the degree of compositional shift, expressed as a percentage of the total 2012–2018 shift, was 10-fold: 42.1% per year in 2012–2014 vs. 4.0% per year in 2014–2018. Thinned stands (PH plots) also shifted to a greater degree in the first two years (average vector length: 0.50), but differences with the 2014–2018 shift (average vector length: 0.35) were not statistically significant (Wilcoxon rank-sum test: $p = 0.297$). The difference between the degree of compositional shift, expressed as a percentage of the total 2012–2018 shift, was 3-fold: 30.0% per year in 2012–2014 vs. 10.0% per year in 2014–2018. All these results indicate that the harvested plots shifted to a greater degree in the first two years (2012–2014) than that in the following four years (2014–2018). In contrast to the harvested plots, the NH plots showed minimal compositional changes in the first two years post-treatment (average vector length: 0.09). However, in the period 2014–2018, some control plots shifted to a greater degree due to the effect of natural disturbances (ice storm, windthrows), leading to a higher average vector length (0.27), but the vector lengths between the period 2012–2014 and the period 2014–2018 did not differ significantly (Wilcoxon rank-sum test: $p = 0.136$). Overall, the average shift per year was similar in both periods (18.9% in 2012–2014 and 15.6% in 2014–2018).

Analysis of distances to the baseline revealed that in the period 2014–2018, there was one plot per each treatment (i.e. FH3, PH2, NH1) that slightly decreased in distance to the baseline, while all other plots continued to shift away from the starting position (Appendix A). The FH plots exhibited more or less similar behaviour in terms of their compositional shifts. Looking at the PH plots, one plot (PH2) showed an exceptionally large compositional shift compared to the other plots.

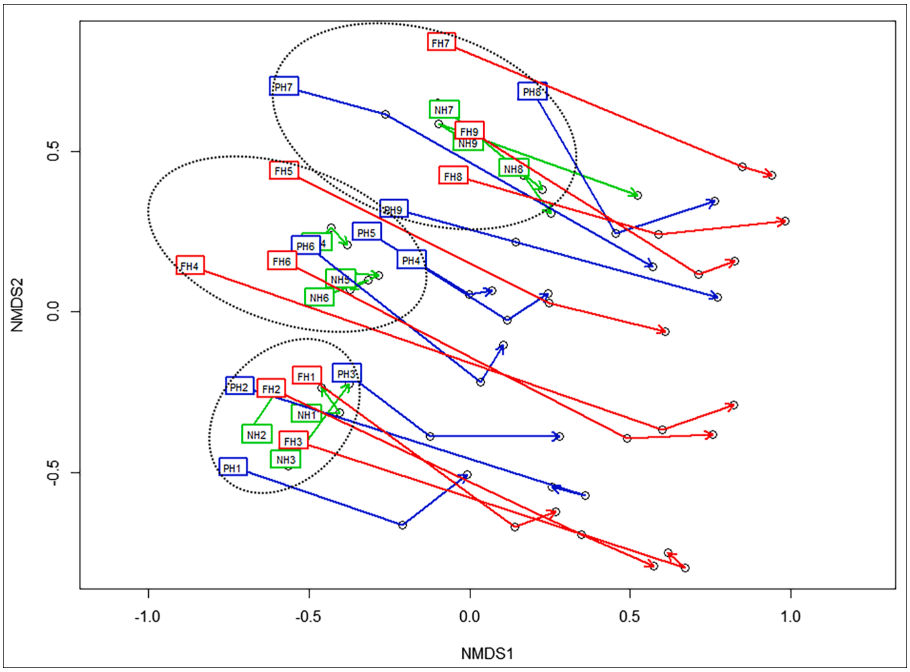

Fig. 2. Non-metric multidimensional scaling ordination of 27 plots, providing a depiction of compositional changes in the herb layer vegetation. Harvesting intensities, each represented by nine plots, are coded as follows: red – full harvest (FH), blue – partial harvest (PH) and green – no harvest (NH). Rectangles show the baseline, i.e. starting position (pre-harvest year 2012), while the arrowheads point to the 6-year post-harvest samples (year 2018). Dotted ellipses denote different study sites: numbers 1–3 belong to Trnovo, 4–6 to Kočevski Rog and 7–9 to Snežnik. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Focusing on the NH plots, between-plot differences can be recognized for the period 2014–2018, in which some plots shifted to a greater degree compared to other plots (Appendix A) due to the impact of natural disturbances.

3.2. *Demographic types and demographic parameters*

We found a significant association between harvesting intensity and demographic types (Pearson's chi-squared test: $\chi^2 = 284.81$, df = 12, p < 0.001). According to the Correspondence Analysis (Appendix B), in the FH plots the observed frequency of demographic type 1 (persistent residents) was lower than the expected frequency. In contrast, type 5 (early colonists) and type 6 (ephemeral early colonists) were more frequently found in the FH plots. In the NH plots, the observed frequency of type 1 was higher than the expected frequency, whereas the frequencies of types 5 and 6 were lower than expected. Thinned stands (PH) showed the strongest association with demographic type 7, i.e. late colonists (Appendix B).

The relative proportions of demographic types 1, 5 and 6 differed significantly between harvesting intensities (Fig. 3). The FH plots had the lowest share of type 1, whereas the NH plots had the highest. The reverse was true for demographic type 5. The share of type 6 in the NH plots was significantly lower compared to the FH and PH plots. We did not find any significant differences in the relative proportions of demographic types 2, 3, 4 and 7 between harvesting intensities (Fig. 3). The most frequent plant species for each demographic type are reported in Appendix C.

The proportion of demographic type 3 was negatively correlated with the magnitude of compositional change in the FH plots (Table 3). In the PH plots, a significant negative correlation between compositional change and type 1 was detected, meaning that a higher proportion of this type contributed to smaller compositional shifts. In the NH plots, compositional shifts were negatively correlated with the proportion of demographic types 1, 2 and 6, whereas a higher proportion of type 7 led

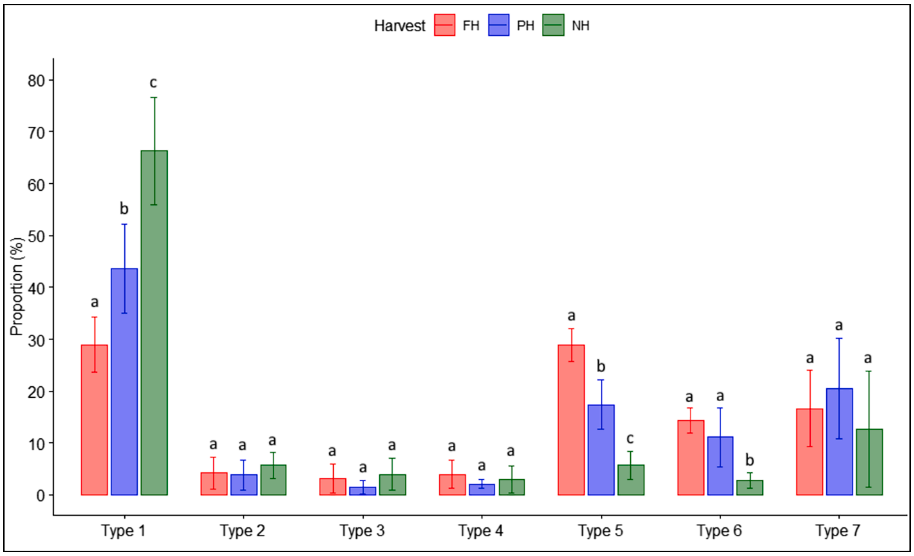

Fig. 3. Mean relative proportions of seven demographic types for each harvesting intensity: FH – full harvest, PH – partial harvest, NH – no harvest. Type 1 - persistent residents, Type 2 - late evaders, Type 3 - revenants, Type 4 - early evaders, Type 5 - early colonists, Type 6 - ephemeral early colonists, Type 7 - late colonists. Error bars represent standard deviations. Bars with different letters imply significant ($p < 0.05$) differences between harvesting intensities according to the Kruskal-Wallis rank-sum test.

Table 3
Spearman correlation coefficients between seven demographic types and degree of compositional changes (derived from NMS distances for 2012–2018 period) for each harvesting intensity (FH – full harvest, PH – partial harvest, NH – no harvest). * $p < 0.05$, ** $p < 0.01$, ns – not significant, m – marginally significant ($p < 0.1$).

	FH	PH	NH
Type 1	−0.533 ^{ns}	**−0.850** **	**−0.800** **
Type 2	−0.183 ^{ns}	0.250 ^{ns}	**−0.800** **
Type 3	**−0.800** **	−0.017 ^{ns}	0.636 ^{m}
Type 4	0.100 ^{ns}	−0.500 ^{ns}	−0.084 ^{ns}
Type 5	0.167 ^{ns}	0.561 ^{ns}	0.200 ^{ns}
Type 6	0.017 ^{ns}	0.150 ^{ns}	**−0.717** *
Type 7	0.383 ^{ns}	0.300 ^{ns}	**0.683** *

to larger compositional shifts in the control stands (Table 3).

Harvesting disturbance enhanced different demographic processes (Table 4). Two years after harvesting (period 2012–2014), the FH plots experienced significantly larger changes in all demographic parameters, except for survival rate, when compared to the NH plots. In general, harvested plots (FH and PH) showed larger changes in species richness and species turnover. Harvested plots also had a higher colonization rate and exhibited larger changes in the abundance of surviving species. Thinned and control stands had a similar extirpation rate, which was highest in gaps (FH).

In the period 2014–2018, changes in demographic parameters in harvested plots (FH in PH) were generally smaller compared to the period 2012–2014. In contrast, the NH plots exhibited larger overall changes in the period 2014–2018, especially for parameters such as the colonization rate and relative change in species richness. This pattern is congruent with the observed changes in species composition, which were detected with the NMS ordination. In the whole 6-year study period (2012–2018), plots subjected to different harvesting intensities were characterized by significantly different species turnover and colonization rates but similar extirpation rates (Table 4).

In the first two years after harvest, relative changes in species richness, species turnover and colonization rate were positively correlated with the magnitude of compositional shifts in the FH plots (Table 5). The same was true for the PH plots, where compositional shifts were additionally correlated with survival rate (negative correlation). No significant correlations were observed for the NH plots.

In the period 2014–2018, compositional shifts in the FH plots were not significantly correlated with any of the demographic parameters. In contrast, compositional shifts in the PH plots were significantly correlated with colonization rate, relative change in species richness and species turnover. Stable survivors significantly decreased compositional shifts. Compositional changes in the NH plots were positively correlated with colonization rate, relative change in species richness and increased abundance of surviving species (Table 5).

During the whole investigation period 2012–2018, compositional shifts in the FH plots were strongly correlated with colonization rate and species turnover. The latter demographic parameter was significantly positively correlated in the PH plots as well, where compositional shifts were also negatively correlated with stable survivors. The proportion of surviving species with no change in abundance was negatively correlated with shifts in the NH plots. The following demographic parameters contributed to larger shifts in the NH plots: colonization rate, species turnover, decreased abundance of survivors and relative change in species richness (Table 5).

3.3. *Significant predictors of compositional shifts*

The generalized linear models revealed that the most significant pre-harvest predictors for the larger compositional shifts in the FH plots in the period 2012–2014 were the larger proportion of beech in the understory layer, lower species richness of the herb layer community, lower volume of decay class 2 and larger concavity of karst sinkholes (Table 6). In the PH plots, four variables positively influenced the degree of the compositional shift in 2012–2014: the cover of bare soil, volume of the sinkhole, proportion of fir in the tree layer and forest stand Shannon diversity index. The last variable was also a significant predictor for the compositional shift in the NH plots (Table 6).

Significant pre-harvest predictors for the compositional shift in 2014–2018 in the FH plots were different from those for the initial shift (2012–2014). The cover of the understory layer, tree species richness in the understory layer, stand growing stock and depth of the sinkhole were negatively associated with the magnitude of compositional changes. In contrast, higher herb layer evenness and proportion of fir in the understory layer contributed to larger shifts. The magnitude of compositional shifts in 2014–2018 in the PH plots was linked to stand growing stock (positive effect) and plot elevation (negative effect). The only significant predictor for the shifts in the NH plots remained the same, i.e. the stand Shannon diversity index (Table 6).

For the whole 6-year study period, the strongest predictors for compositional shifts in the FH plots were abiotic conditions describing the geomorphology of sinkholes (DD ratio, positive effect) as well as community attributes, such as herb layer species richness (negative effect) and evenness (positive effect). Thinned stands were most impacted by the pre-disturbance total cover of tree species in the understory layer, elevation (both variables had negative effect) and bare soil cover

Table 4
Demographic parameters for each period and each harvesting intensity (FH – full harvest, PH – partial harvest, NH – no harvest). Values are means, with standard deviations in parentheses. Means with different letters signify significant ($p < 0.05$) differences between harvesting intensities within the same period.

	Period 2012–2014			Period 2014–2018			Period 2012–2018		
	FH	**PH**	**NH**	**FH**	**PH**	**NH**	**FH**	**PH**	**NH**
Δ species richness (%)	93.9 ^{a} (25.4)	51.1^{b} (20.3)	1.6^{c} (6.9)	2.3 ^{a} (15.0)	11.3 ^{a} (20.9)	13.7 ^{a} (25.8)	100.1 ^{a} (50.2)	66.9 ^{a} (30.7)	14.7^{b} (21.8)
Species turnover (%)	43.4 ^{a} (6.4)	25.6^{b} (7.0)	9.9^{c} (3.2)	25.0 ^{a} (4.2)	23.4 ^{ab} (5.7)	14.5^{b} (9.0)	46.0 ^{a} (7.1)	33.1^{b} (7.5)	16.4^{c} (6.9)
Survival rate (%)	82.9^{b} (7.5)	92.9 ^{a} (2.6)	90.9 ^{ab} (5.3)	75.8^{b} (5.4)	80.7^{b} (7.7)	89.6 ^{a} (2.8)	80.3 ^{a} (11.9)	88.4 ^{a} (6.1)	89.2 ^{a} (4.8)
Survivor increase (%)	29.6 ^{a} (8.2)	26.2 ^{a} (12.0)	11.6^{b} (5.5)	25.8 ^{a} (8.1)	21.9 ^{a} (10.1)	17.5 ^{a} (7.5)	31.9 ^{a} (7.1)	32.4 ^{a} (11.3)	22.0^{b} (5.5)
Survivor decrease (%)	21.0 ^{a} (11.1)	13.7 ^{ab} (9.1)	7.1^{b} (7.3)	19.9 ^{a} (7.3)	16.9 ^{a} (6.1)	8.1^{b} (3.8)	22.8 ^{a} (12.2)	18.1 ^{a} (10.2)	8.5^{b} (3.7)
Survivor stable (%)	49.3^{c} (7.7)	60.1^{b} (8.8)	81.4 ^{a} (8.2)	54.2^{b} (7.1)	61.3^{b} (8.8)	74.4 ^{a} (9.4)	45.3^{b} (10.9)	49.5^{b} (10.2)	69.5 ^{a} (6.7)
Extirpation rate (%)	17.3 ^{a} (7.4)	7.4^{b} (3.3)	9.1^{b} (5.3)	24.2 ^{a} (5.4)	19.3 ^{a} (7.7)	8.8^{b} (4.0)	19.7 ^{a} (11.9)	11.6 ^{a} (6.1)	10.8 ^{a} (4.8)
Colonization rate (%)	56.8 ^{a} (6.1)	37.4^{b} (9.1)	10.5^{c} (3.5)	25.0 ^{a} (8.0)	26.1 ^{a} (9.4)	18.4 ^{a} (14.0)	58.7 ^{a} (6.8)	45.5^{b} (10.1)	20.4^{c} (11.2)

Table 5

Spearman correlation coefficients between demographic parameters and the degree of compositional changes (distances derived from NMS ordination) for each period and harvesting intensity (FH – full harvest, PH – partial harvest, NH – no harvest). P-values < 0.05 are in bold; italic – marginally significant ($p < 0.1$).

	Period 2012–2014			**Period 2014–2018**			**Period 2012–2018**		
	FH	**PH**	**NH**	**FH**	**PH**	**NH**	**FH**	**PH**	**NH**
Δ species richness	**0.867**	**0.733**	0.117	0.150	**0.750**	**0.733**	0.433	0.467	**0.700**
Species turnover	**0.717**	**0.833**	0.367	0.333	**0.700**	*0.633*	**0.833**	**0.895**	**0.750**
Survival rate	−0.100	**−0.800**	−0.083	−0.217	0.300	0.433	−0.250	−0.367	−0.033
Survivor increase	0.167	−0.033	0.367	0.167	*0.617*	**0.717**	0.267	0.567	0.450
Survivor decrease	0.067	0.433	0.084	0.183	0.033	0.217	−0.200	0.083	**0.736**
Survivor stable	−0.310	−0.268	−0.383	−0.483	**−0.683**	−0.567	0.083	**−0.728**	**−0.833**
Extirpation rate	0.033	**0.800**	0.083	0.217	−0.300	−0.433	0.250	0.367	0.033
Colonization rate	**0.733**	**0.733**	0.417	0.283	**0.817**	**0.850**	**0.967**	*0.583*	**0.803**

Table 6

Significant pre-harvest predictors for post-harvest compositional shifts for each harvesting intensity and period, according to the generalized liner models. “Sense” denotes whether the predictor had a positive (+) or negative (–) effect on the magnitude of the compositional shift. The order of predictors reflects their relative importance. Sig. – statistical significance: * $p < 0.05$, ** $p < 0.01$. For the names of predictors, please see abbreviations in Table 2.

Shift 2012–2014			**Shift 2014–2018**			**Shift 2012–2018**		
Full harvest (FH)								
Predictor	**Sense**	**Sig.**	**Predictor**	**Sense**	**Sig.**	**Predictor**	**Sense**	**Sig.**
Beech_U	+	**	Cov_U	–	**	DDratio	+	*
SR	–	*	TSrich_U	–	**	SR	–	*
Decay2	–	*	Even	+	*	Even	+	*
DDratio	+	*	StandGS	–	*			
			Depth	–	*			
			Fir_U	+	*			
Partial harvest (PH)								
Predictor	**Sense**	**Sig.**	**Predictor**	**Sense**	**Sig.**	**Predictor**	**Sense**	**Sig.**
Baresoil	+	*	StandGS	+	*	TScov_U	–	**
Volume	+	*	Elevat	–	*	Elevat	–	*
Fir_T	+	*				Baresoil	+	*
StandSH	+	*						
No harvest (NH)								
Predictor	**Sense**	**Sig.**	**Predictor**	**Sense**	**Sig.**	**Predictor**	**Sense**	**Sig.**
StandSH	–	*	StandSH	–	*	TSrich_U	+	*
						EIV_K	+	*
						StandSH	–	*

(positive effect). Given that some of the NH plots exhibited prominent shifts in species composition, significant predictors were not only linked to stand characteristics (stand Shannon diversity index with a negative effect) but also to the richness of the tree species in the understory layer and Ellenberg indicator value for continentality, both showing a positive effect on the degree of compositional changes (Table 6).

Pre-harvest species richness was one of the most significant predictors for post-harvest compositional shifts. For the FH plots, linear regression models (Fig. 4) showed that this community attribute was negatively associated with the magnitude of the compositional shift in the period 2012–2014 ($p < 0.01$, $R^2 = 66.2\%$). This association was also significant ($p < 0.05$, $R^2 = 51.8\%$) for the entire period under study. In addition, the results suggested a negative correlation between pre-harvest richness and colonization rate in the FH plots. The correlation was marginally significant for the period 2012–2014 and statistically significant ($p < 0.05$, $R^2 = 55.0\%$) for the period 2012–2018. In contrast, the extirpation rate was not related to pre-harvest richness (Fig. 4). Similar to the FH plots, pre-harvest richness in the PH plots tended to be negatively associated with the degree of post-harvest compositional shift and colonization rate. Higher pre-harvest species richness induced smaller compositional changes and a lower colonization rate. However, correlations in the PH plots were weaker and in general only marginally significant. No significant correlations were detected for the NH plots (Fig. 4).

3.4. Floristic dissimilarity

During our 6-year study period, compositional dissimilarity between and within study sites tended to decrease (Fig. 5). However, the decrease was only significant in two cases. In the FH plots, pre-harvest dissimilarity (2012) between sites was significantly ($p < 0.05$) higher than dissimilarity in post-harvest years. A significant decrease in compositional dissimilarity was also observed in the NH plots, where within-site dissimilarity in 2018 was significantly ($p < 0.05$) lower compared to that in 2012 and 2014 (Fig. 5).

4. Discussion

Disturbance acts as a primary mechanism for resetting the competitive hierarchies among species (Pickett and White, 1985; Cook and Halpern, 2018; Kutnar et al., 2019). Alterations of the physical environment following forest overstory harvest initiate succession, promote the reorganization of the surviving vegetation and provide an opportunity for the establishment of new species (Halpern, 1988; Halpern, 1989; Aikens et al., 2007). Thus, disturbance generally has a net positive effect on vascular plant diversity (Small and McCarthy, 2002) but reduces community stability (Dovčiak and Halpern, 2010).

The main strength of our study lies in its complex approach in which we incorporated various aspects of post-disturbance plant community assembly. Close inspection of demography enabled us to disentangle the different mechanisms driving species- and community-level responses

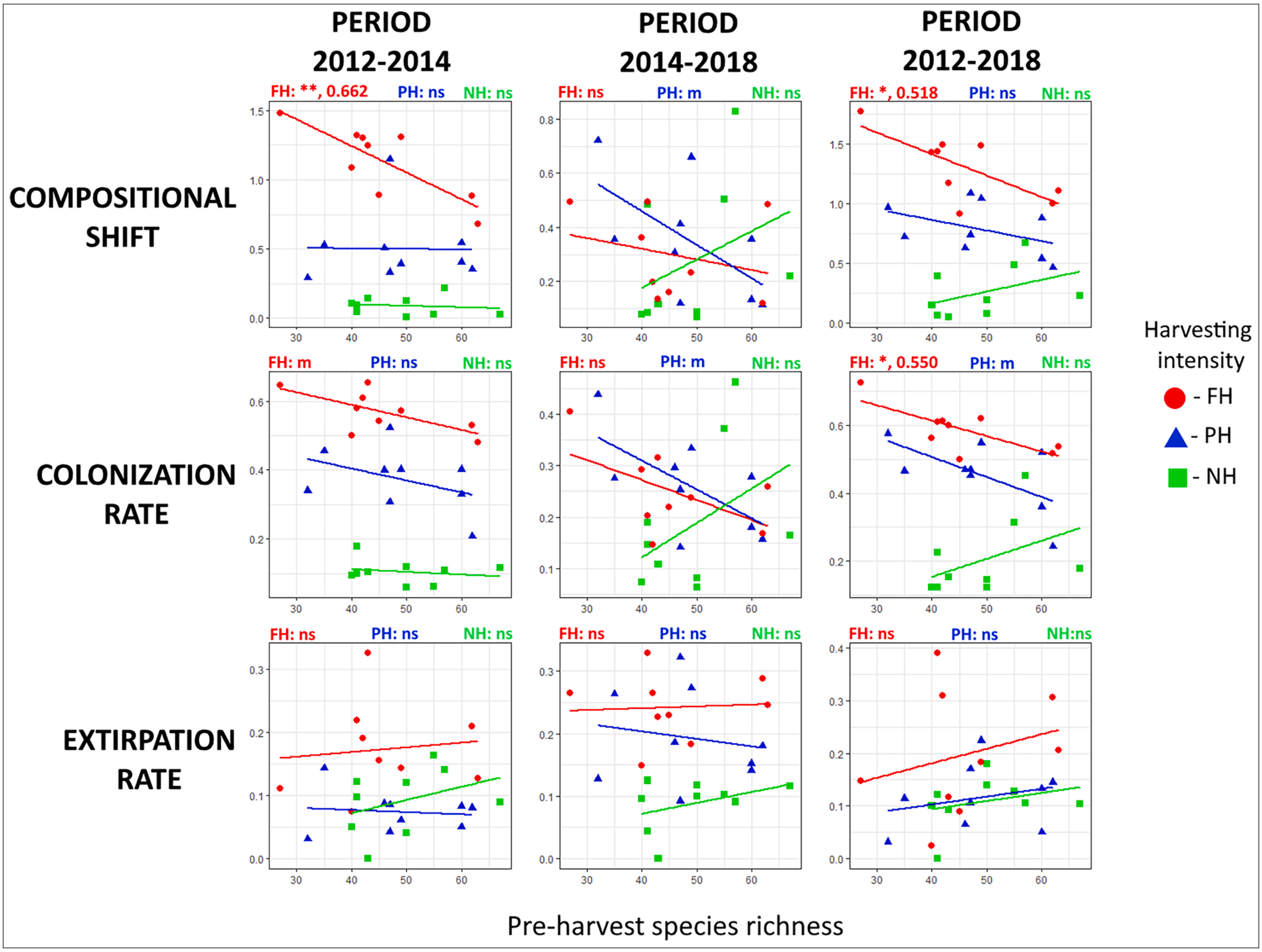

Fig. 4. Linear regressions between pre-harvest species richness and compositional shifts, colonization rates and extirpation rates. Relationships are shown separately for three different periods. Statistics from linear models are reported for each harvesting intensity. ** $p < 0.01$, * $p < 0.05$, m – $p < 0.1$, ns – non-significant. For significant results, values of R^2 (coefficient of determination) are also given.

after forest harvesting. We made use of monitoring efforts shortly after the management disturbance, which may later be beneficial for understanding long-term forest successional direction with respect to composition and the important drivers of those changes (Gill et al., 2017; Day et al., 2017).

The main findings of this study in Dinaric fir-beech forests are congruent with successional patterns that have been observed in other forest types (e.g. Halpern, 1988) but additionally point to the significance of site-specific factors for post-harvest herb layer responses. Namely, even over a relatively short-term time scale, we confirmed that the rate of compositional change in the post-harvest herb layer in harvested plots slows down as the effect of the disturbance diminishes. In the early stage of succession, shifts in harvested plots were generally directional and more rapid, whereas control stands experienced random and gradual changes in herb layer species composition. Persistent residents, one of the main demographic types, contributed to compositional stability. The magnitude of compositional shifts in gaps and thinned stands was affected by local abiotic factors (e.g. geomorphology of karst sinkholes) and community attributes, such as pre-harvest species richness. The floristic dissimilarity between and within study sites tended to decrease over the 6-year period, but the decrease was significant only in two cases. The prevalence of insignificant results suggests that strong conclusions regarding these patterns are rather difficult to make.

Harvesting intensity significantly influenced the frequency of demographic types. While the proportion of persistent residents (type 1) decreased along a harvesting intensity gradient, the opposite was observed for newly colonized species (type 5 and type 6). Scaling-up from species responses to community-level changes, we observed that early compositional shifts were positively related to harvesting intensity, which agrees with the studies of Vanha-Majamaa et al. (2017), MacDonald et al. (2014) and De Grandpré et al. (2011). Similar vegetation responses were documented for natural disturbances, such as wildfires (e.g. Urza et al., 2017). Many former studies have shown that higher disturbance intensity resulted in both reduced resistance and resilience compared to moderate- or low-intensity disturbance (e.g. Belote et al., 2012; Abella and Fornwalt, 2015). Abella and Fornwalt (2015) showed that both resistance (early post-fire deviance from pre-fire condition) and resilience (return to pre-fire condition) declined with increasing fire severity. With the progressing post-harvest natural succession, our harvested plots experienced a declining rate of deviation from pre-disturbance status.

The forest herb layer response to disturbance appears strongly linked to site and vegetation characteristics. However, most studies of understory dynamics fail to account for variations in these ecosystem properties (Small and McCarthy, 2002). In terms of pre-established vegetation at the moment of gap formation, the initial conditions are very important for future vegetation dynamics (Royo and Carson, 2006). We found that post-harvest herb layer demography depends on factors that are directly altered by management but also on several management-independent factors. Some pre-harvest community

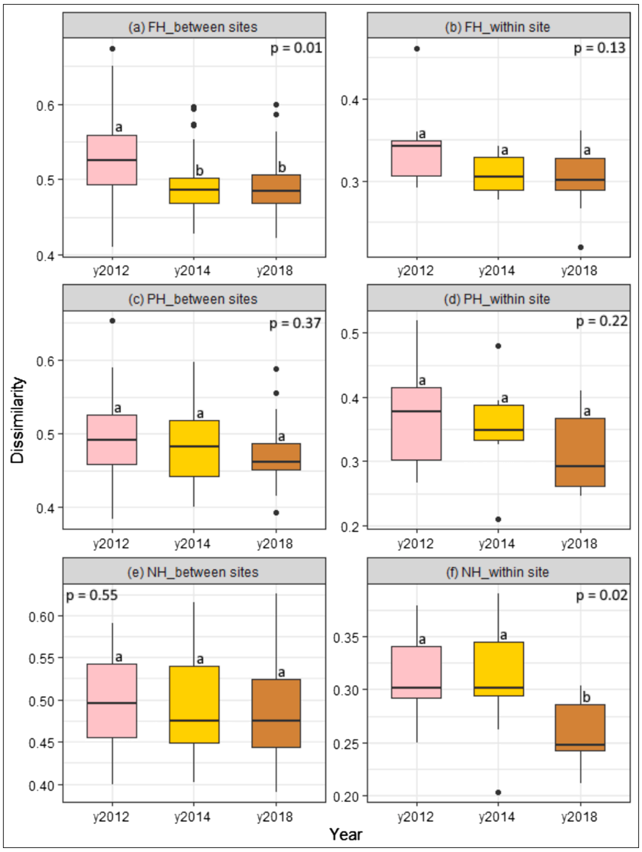

Fig. 5. Compositional dissimilarity, determined by the Bray-Curtis dissimilarity index, between (left colon) and within (right colon) the three study sites for full harvest (FH; panels a and b), partial harvest (PH; c and d) and no harvest (NH; e and f). Different letters signify significant differences according to the Kruskal-Wallis rank-sum test.

attributes were proven to have a significant effect on the extent of post-harvest compositional changes in gaps (FH plots).

The most interesting pattern that we observed was the positive relationship between community diversity (species richness and cover) and resistance to harvesting disturbance and related compositional stability (similarly reported in MacDonald et al., 2015). Direct effects of diversity on turnover manifested through negative feedback between pre-harvest species richness and post-harvest colonization rate (as in Catford et al., 2020). Declining turnover with increasing richness occurred when higher diversity reduced colonization by new species. Species richness was not significantly correlated with extinction rates of extant species. These patterns can be interpreted in the sense that higher diversity impedes or prevents the establishment of non-resident colonizing species, and diverse communities are able to resist temporal change to a higher degree compared to species-poor communities. Higher cover of resident communities suggests less empty space for potential colonists. Community evenness tended to be positively related to compositional shifts. In plant communities where evenness is lower, dominance by one or a few competitive species may increase community stability.

Furthermore, the abundance of European beech (*Fagus sylvatica*) natural regeneration layer prior to harvesting was associated with larger demographic changes. This can be explained by the response of beech to increased light and consequent ingrowth of seedlings from the herb into the shrub layer. Advance regeneration of shade-tolerant tree species, such as *Fagus sylvatica* and *Abies alba* in Dinaric fir-beech forests, may play a prominent role in post-harvest vegetation development, as tree saplings with a competitive advantage can prevent colonization of herbaceous or woody plants and speed-up the recovery towards pre-disturbance status. In temperate forests dominated by tree species with resprouting ability, Matula et al. (2020) emphasized that stump and root sprouts drive the early post-disturbance dynamics of the herb layer by offsetting vegetation shifts.

In addition to community attributes, previous studies have recognized the importance of site factors and forest stand characteristics (Small and McCarthy, 2002). For instance, Day et al. (2017) illustrated that pre-fire forest type, which was defined based on tree layer composition, was an important predictor of post-fire species richness and composition in the boreal forests of western North America. Initial species composition determined directional changes in composition. In our case, specific features of rugged karst terrain played an important role. Karst sinkholes, which are the dominant landform in the studied forests, have been shown to influence both tree layer and understory composition in mesic mixed forests in the Dinaric region (Kobal et al., 2015). We found that the geomorphology of sinkholes affected the extent of compositional shifts in gaps. Changes in herb layer composition were larger in more open and shallower sinkholes. In contrast, more closed and deeper sinkholes were less prone to community alteration, suggesting their buffering effect.

However, intensive harvesting might compromise the capacity of karst sinkholes to preserve late-successional species adapted to specific environmental conditions, as emphasized in the study of Kiss et al. (2020). In contrast, our results indicate that (in the short-term) forest management does not pose a threat to the capacity of karst sinkholes to preserve late-successional forest species, as mainly evidenced by the fact that there were no significant differences in extirpation rate between FH, PH and NH plots in the period 2012–2018. Two facilitative mechanisms are likely responsible for the preservation of typical forest plant species in harvested areas. First, within sinkholes they were more abundant on shadier north-facing slopes with lower temperatures and higher relative humidity (Kermavnar et al., 2020). Second, small-statured typical forest species likely benefited from the shade cast by taller woody and herbaceous plants (Kermavnar et al., 2019a).

The results indicate that some degree of compositional convergence occurred during the 6-year period. Although average plot-level species richness in the period 2012–2018 increased by 100.1% (FH), 66.9% (PH) and 14.7% (NH), the floristic dissimilarity between and within sites in the study period decreased by 8.4% (FH), 6.6% (PH) and 5.8% (NH). Such patterns are most likely driven by a similar suite of successful native and non-native colonists (Halpern, 1988; Royo et al., 2011). Gap closure, whether from lateral ingrowth of the surrounding trees or from recruitment from the understory, subsequently reduces the overall amount of heterogeneity among different gaps (Kupfer and Runkle, 1996). However, the decreasing trend of dissimilarity was rather weak and hardly significant. Compared to the other more prominent demographic changes observed here, the analysis of floristic dissimilarity simply cannot serve as a reliable showcase. In fact, the consideration of this facet led us to the conclusion pointing to the importance of pre-disturbance plant community persistence after tree harvest.

Despite a decrease in floristic dissimilarity, differences in species composition between and within our study sites were maintained following harvesting disturbance. A similar observation was pointed out by De Grandpré et al. (2011) . Persistent residents (demographic type 1) maintained site-specific compositional differences and can thus represent an important biological legacy in post-disturbance community assembly, contributing to its temporal stability and perhaps enhanced long-term resilience. Abella and Fornwalt (2015) also emphasized the importance of “legacy” species for increasing overall compositional stability in severely burned areas.

Post-disturbance vegetation is often characterized by a high abundance of surviving resident species (Abella and Fornwalt, 2015). Persistent herbaceous residents and responsive advance tree species regeneration can be considered as biological legacies of the herb layer composition. The presence of such legacies contributes to compositional resistance, and stability brings a steadiness to the trajectory of post-disturbance ecosystem development (Urza et al., 2017).

Maintaining the legacies of the herb layer composition and preserving the forest characteristics of vegetation has proven to be more successful with less intense silvicultural treatments (Tinya et al., 2019). Silvicultural interventions in forests primarily aim at promoting the regeneration of tree species. At the same time, changes in the species composition of the whole plant community should be minimized. Desired outcomes include higher richness and abundance of key tree species which will become dominant in the overstory vegetation. An increase in dense herbaceous vegetation is seen as an undesired response, as this can delay forest recovery. Even if tree regeneration is successful, local extirpation of less common plant species can lead to the slow, potentially hidden impoverishment of local and regional species pools (Johnson et al., 2014). Instead, our results generally indicate that harvest-created gaps are effective in conserving herb layer plant diversity by preserving resistant residents and promoting conditions necessary for disturbance-dependent plant species. However, gaps and thinned stands also contain non-native invasive plant species (e.g. annual forb *Erigeron annuus* in our case). The establishment of invasive species in post-harvest plant communities has been reported for various forest types (e.g. Belote et al., 2012; Bolton and D'Amato, 2019; Tinya et al., 2019).

5. Conclusions

The results of our study are mainly congruent with succession theory, which states that the degree of compositional changes is largest immediately after disturbance and then slows down. By analysing demographic types and demographic parameters, we identified the ecological mechanisms responsible for vegetation trajectories induced by different harvesting intensities. Recognized patterns can largely be attributed to harvesting intensity and also to the disturbance-independent dynamics of herb layer communities or even the impacts of natural disturbances (control plots). The dependence of post-disturbance vegetation responses on pre-harvest abiotic and biotic factors can have an important applied value for forest management and planning. We encourage researchers to implement different levels (species vs. community) and aspects of diversity (alpha vs. beta diversity) in order to make more reliable conclusions regarding the effects of harvesting disturbance on herb layer demography.

CRediT authorship contribution statement

Janez Kermavnar: Conceptualization, Methodology, Software, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization. **Klemen Eler:** Formal analysis, Investigation, Writing - original draft, Writing - review & editing, Visualization. **Aleksander Marinšek:** Formal analysis, Investigation, Resources, Writing - original draft, Writing - review & editing. **Lado Kutnar:** Conceptualization, Investigation, Data curation, Writing - original draft, Writing - review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

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

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Appendices A–C. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2021.119121.

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