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Short-term changes in plant functional traits and understory functional diversity after logging of different intensities: a temperate fir-beech forest experiment

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Abstract. The concept of plant functional traits has been demonstrated to be very effective in unravelling the ecological mechanisms governing plant community response to disturbance, especially when research is focused on short-term post-disturbance vegetation dynamics. In this study, we established an experiment to quantify how logging intensity affects the trait composition and functional diversity of understory communities in fir-beech forests in the Dinaric Mountains in Slovenia. Three different silvicultural treatments were implemented: control (no logging), 50% of the growing stock removed and 100% of the growing stock removed. Vegetation surveys of vascular plants were made before (in 2012) and two years after (in 2014) logging. Changes in species traits, C-S-R plant strategies (*sensu* Grime) and community-level functional diversity were analysed. The importance of traits such as small and light diaspores, short life span and anemochory increased with logging intensity. Moreover, species with the ability of both sexual and vegetative reproduction, longer flowering duration and overwintering green leaves increased in abundance after logging. C-S-R strategies mainly shifted from stress-tolerators in pre-logging conditions towards a more ruderal component in post-logging stands. Logging in the short term increased functional diversity, mainly due to newly colonized species being functionally dissimilar from persistent residents. Results suggest that logging intensity strongly influences the magnitude of change in both functional composition and diversity, which also has important implications for biodiversity conservation. At the landscape scale, increasing spatial heterogeneity by creating a mosaic of forest stands subjected to different logging intensities will likely contribute to the enhancement of plant functional diversity.

Keywords: functional composition and diversity, life-history traits, understory vegetation, canopy gap, biodiversity, beech forest.

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Introduction

How forest ecosystems respond to and recover from disturbance caused by management has been a central question in applied forest ecology (Kusumoto et al. 2015). Disturbances, including forest logging, are the major triggers of vegetation change in temperate managed forests. Gaps as empty areas within forest canopies fundamentally contribute to forest ecosystem characteristics, such as structural heterogeneity, tree species composition, variation in understory vegetation and overall species diversity (Kuulovainen 1994). Gap producing disturbances most often promote diversity, as gaps offer favourable conditions for rapid plant reproduction and growth due to greater resource availability (Muscolo et al. 2014). Furthermore, canopy gaps are essential for many plant species to be able to establish in the forest understory (Lin et al. 2014) and coexistence of ecologically different plant species (early- vs. late-successional) is facilitated in gaps compared to undisturbed overstory canopy. At the local scale, the change in forest microclimate and soil properties creates fine-scale spatial variation in aboveground (light) and belowground (water, nutrients) resources availability, which increases the diversity of microhabitats available for plants. At the broader spatial scale, gap disturbances are an important factor in regulating forest natural regeneration dynamics and in determining the landscape pattern of forest structure and species composition (Kuulovainen 1994).

Nowadays, a better understanding of the post-logging development of forest vegetation is essential for biodiversity conservation and the implementation of sustainable management practices that preserve or enhance plant community diversity and its function (Halpern & Spies 1995, Bengtsson et al. 2000). Such concerns are relevant with regard to the current situation in many forests worldwide: increasing impacts of severe large-scale natural disturbances, subsequent management activities that alter rates or patterns of succession and uncertainties associated with climate change (Degen et al. 2005). These challenges have increased the need for examining forest management outcomes from a functional trait-based perspective (Curzon et al. 2017), as plant functional traits act as link factors of biological diversity to ecosystem functioning and processess (Tilman et al. 1997, Díaz & Cabido 2001).

Despite being introduced long ago (e.g. Grime 1977, Noble & Slatyer 1980), plant functional traits have recently received new attention for evaluating plant community response to various types of disturbances (Bachand et al. 2015). Moreover, a growing list of studies have demonstrated that functional traits constitute a highly useful concept for unravelling the ecological mechanisms governing understory community response to management disturbance in forests (Canullo et al. 2017). Plant functional traits are morphological, life-history, physiological and phenological attributes with significant influence on the establishment, survival and fitness of species in the ecosystem (Díaz & Cabido 2001, Violle et al. 2007). They decisively determine how plants respond to environmental factors and disturbances (i.e. functional response traits), affect other trophic levels and have strong impacts on ecosystem processes (i.e. functional effect traits) (Lavorel & Garnier 2002, McGill et al. 2006). Vegetation ecologists have used functional traits as a universal language to overcome the problems of comparing results across regions and countries with different species pools and to maximize the utility of the data (Weiher et al. 1999, Graae & Sunde 2000).

In addition, the model of C-S-R plant strategies (Grime 1977, 2001) has become established in studies of disturbance impacts, similar to environmental and successional gradient analyses (e.g. Paušič & Čarni 2012, Rozman et al. 2013). C-S-R theory assumes that plants invest their resources in the ability to compete, tolerate stress or survive biomass destruction (disturbance) as an adaptive response to the environment (Grime 1977). Accordingly, plant species can be grouped into three main strategies (competitors, stress tolerators, ruderals) and several sub-types (CS, CR, SR, CSR) based on their preference for environmental factors associated with stress and/or disturbance; for example, disturbance favours the presence of ruderal species while adversely affecting competitors (Grime 2001).

In the context of plant community response to disturbance, the following functional traits are expected to be ecologically important: regeneration/reproductive traits (e.g. dispersal mode, phenological characteristics), plant morphology (e.g. life forms *sensu* Raunkiaer 1934) and vegetative traits (e.g. life cycle, vegetative propagation) (Weiher et al. 1999, Ramovs & Roberts 2005). Undisturbed, mature forest functional conditions (e.g. slow growth, stress-tolerant strategy, early and short flowering, vegetative spread) are expected to be different from functional conditions in disturbed forest areas, which are characterized by species traits such as ruderal strategy, long seed dispersal and generalized flowering period (Scolastri et al. 2017). For example, Patry et al. (2017) found that along a forest management intensity gradient, the prevalence of traits related to colonization increased while those related to persistence decreased. This "colonization syndrome" is defined as a suite of traits (e.g. small dispersal units, dispersed by wind or animals, tall plants) that make a species more capable to colonize a disturbed area from the surrounding forest matrix. To persist in a stable environment under intact forest canopy, plant species possess a different set of traits (e.g. perennial, larger diaspores).

Logging of overstory trees in a forest is expected to not only affect functional trait composition but also functional trait diversity, i.e. the diversity of functional trait states or values (Mayfield et al. 2010, Kusumoto et al. 2015). Greater functional trait diversity (i.e. larger extent of functional differences among the species in a community) translates to a higher degree of stability and resilience of the entire ecosystem and its capacity to respond to changes caused by disturbance (Díaz & Cabido 2001, Petchey & Gaston 2002). Managing forests for an array of functional attributes is beneficial for the development of adaptive management practices for temperate forests that address global environmental change (Curzon et al. 2017). Consequently, a great deal of work has been dedicated to exploring the effects of forest management disturbance on functional trait diversity (e.g. Kern et al. 2014, Kusumoto et al. 2015, Curzon et al. 2017).

Regarding the relationship between richness/diversity and disturbance, the intermediate disturbance hypothesis (IDH) predicts that species (taxonomic) diversity is maximized at an intermediate intensity of disturbance (Roberts & Gilliam 1995, Burton et al. 2014). This is based on a coexistence between competitively superior species and species which can rapidly colonize following disturbance (Shea et al. 2004). IDH is most commonly applied to species richness (diversity), but it can also be tested for functional diversity patterns (Catford et al. 2012). However, little attention has been given directly to this topic for forest plant communities (Biswas & Mallik 2010). Given this background, in this study our expectation was that understory communities in forest stands subjected to an intermediate level of canopy cover removal (i.e. partial logging) would exhibit the highest functional trait diversity among all treatments. Intermediate disturbance is potentially capable of supporting more species with contrasting life-history attributes, such as shade tolerance (Kern et al. 2014).

While the ecological impacts of forest management should ideally be evaluated based on long-term studies (Kusumoto et al. 2015), investigating short-term post-logging vegetation dynamics is also important and has been widely examined (e.g. de Graaf & Roberts 2009, Fornwalt et al. 2018). However, well-controlled experimental approaches with a gradient in management disturbance intensity (low-medium-high) are relatively scarce (Heinrichs & Schmidt 2009). The initial phase following overstory removal represents a period of dramatic changes when local environmental alterations and shifts in species composition (e.g. species turnover) are usually most pronounced (Canullo et al. 2017). In the context of short-term responses, it is interesting to focus on understory vegetation (due to its remarkable sensitivity to environmental and biotic changes) and to investigate the role of plant functional traits (Scolastri et al. 2017, Canullo et al. 2017). Life-history attributes may be more important than abiotic factors for determining the response of the understory community to disturbance (Gondard & Deconchat 2003). For example, Canullo et al. (2017) illustrated that species compositional changes were reflected by functional changes only in the early stage of beech forest regeneration after silvicultural management.

In this study we used a logging manipulation experiment to quantify how forest management intensity affects the plant functional trait composition and functional diversity of understory plant communities in Dinaric fir-beech forests in Slovenia. Specific aims were to analyse (1) the short-term effects of different logging intensities on functional trait composition, (2) the response of C-S-R strategies to different logging intensities and (3) differences in functional diversity of vegetation community across treatments. Additionally, our aim was (4) to identify structural changes in the forest stands (cover of tree, shrub, herb and moss layer and bare soil cover) induced by the management disturbance.

Material and methods

Experimental sites and study area

This study encompasses three experimental sites covered with temperate fir-beech forests and located in the Dinaric Mountains of Slovenia: Trnovo (T; 45.989°N, 13.759°E; 801-869 m a.s.l.), Snežnik (S; 45.672°N, 14.460°E; 753-815 m a.s.l) and Kočevski Rog (KR; 45.668°N, 15.033°E; 831-902 m a.s.l) (Figure 1). Dinaric fir-beech forests described as *Omphalodo-Fagetum* s. lat. association cover

Figure 1
Selected study sites, Trnovo (T), Snežnik (S) and Kočevski Rog (KR), within Dinaric fir-beech forests (hatched) in Slovenia. Forest area is indicated in grey.

more than 10% of the Slovenian forest area. These beech forests belong to European habitat type (Natura 2000), 91K0 Illyrian *Fagus sylvatica* forests (*Aremonio-Fagion*) (Kutnar et al. 2015). In these forests, overall plant species diversity is higher compared to that of Central European beech forests mainly due to the presence of Illyrian floristic elements (Willner et al. 2009).

Characterized by a diverse land configuration, Dinaric fir-beech forests thrive in high altitude karst areas (from 700 to 1200 m a.s.l.) with diverse terrain with numerous sinkholes, ridges and slopes. High (micro)topographic variation enables the formation of heterogeneous forest soils on limestone and dolomite bedrock, such as Leptosols, Cambisols and Luvisols (WRB 2015). Soil conditions may abruptly change over a short distance. Climate conditions are highly favourable for the growth of forests due to high rainfall and air humidity (Kutnar et al. 2015). Environmental characteristics (temperature, precipitation, parent material) and pre-treatment features (mature forest structure and tree species composition) of the three experimental sites were similar (de Groot et al. 2016). Before logging, the mean density of trees (N/ha) was 409 (varied between 203 and 598), the basal area was between 24.4 and 58.0 m^2/ha (mean: 39.6 m^2/ha) and the mean growing stock accounted for 541.4 ± 117.6 m^3/ha (Di Salvatore et al. 2016). Estimated height of mature trees adjacent to the treatment plots was on average 30.2 ± 2.0 m. Site conditions (topography, soil characteristics) in the study area within each experimental site were homogeneous.

Forest stands in experimental sites were subjected to rather conservative (i.e. less intensive, small-scale silviculture) selection management system for many decades, without any clearcuts. In general, in the Dinaric region of Slovenia, sustainable and close-to-nature forest management is traditionally favoured over intensive, even-aged management principles. The historical extent and intensity of Dinaric fir-beech forest exploitation is reflected in their complex uneven-aged structure and high degree of naturalness (de Groot et al. 2016). These are mainly non-fragmented forest ecosystems with dense canopy cover and high proportion of forest core area (mean for experimental sites in this study: 47%). At the landscape level, forests cover more than 86% of land in our study area. The primary natural disturbance agents (windthrows, ice storms, insect outbreaks) mostly cause intermediate damage, whereas stand-replacing disturbances are infrequent. Before the experimental logging, there was no evidence of significant canopy disturbances (natural or anthropogenic) with profound influence on forest vegetation dynamics in the study area. Nearest non-forested open areas, which could serve as a potential seed source for the colonization of early-successional/ruderal species, are existing small canopy gaps resulting from treefall disturbances in surroundings, forest roads and power lines. At each experimental site, there are also some other types of land use (e.g. grassland patches within the forest matrix, arable land close to the villages), but these are usually more or less distant (at least ~ 1 km of air distance) from our treatment plots.

Experimental design and vegetation assessment

A uniform area of typical karst topographic conditions was chosen at each experimental site. As karst (micro)topography is very diverse and quickly changes over small distances, the research objects were all located within comparably sized karst dolines to minimize the topographic and soil effects on species composition and to better discern different forest management effects. Dolines acted as a "common denominator", i.e. conditions were comparable between research objects (sampling plots). For example, if one sampling plot was established in a doline and another plot on a hillslope or ridge, this would result in differences in site conditions, forest vegetation composition and the response of the understory to logging treatments. Dolines, also known as sinkholes, are bowl-shaped depressions in terrain that represent a unique feature of karst landscapes (Kobal et al. 2015). These are the dominant landform, as they cover significant areas in the Dinaric Mountains in Slovenia. For instance, Kobal et al. (2015) reported that in a study area very similar to our sites, only 0.3% of the study area did not contain sinkholes. Based on lidar data, the estimated depth (i.e. difference between the bottom and the edge of the doline) of the selected sinkholes in our study was on average 8.3 ± 2.7 m.

Nine sinkholes were randomly selected at each experimental site. Within each sinkhole, a circular plot of 4000 m^2 was established with the centre at the bottom of the sinkhole, comprising 27 plots in total. To test the effects of forest logging intensities, forest stands in the sinkholes were subjected to three different logging treatments in 2012. Each applied treatment was allocated randomly to three sinkholes/dolines, which acted as per-site and per-treatment replicates. Management treatments were implemented in the entire plot area of 4000 m^2. In one third of all plots (three plots per site, nine altogether), 100% of the stand growing stock was logged (fully logged – FL). In another third of all plots, 50% of the stand growing stock was logged (partially logged – PL) using single-tree selection where residual trees were distributed homogeneously in the plot area. No logging (control – C) was implemented in one third of all plots, which served as unlogged reference stands (Kutnar et al. 2015).

Vegetation sampling was performed in two separate sampling periods: in 2012 (shortly before logging) and in 2014, i.e. two years after logging. Within each plot, all vascular plant species were recorded in a circular sampling plot of 400 m^2 during peak vegetation (June – July). The concentric sampling plot (400 m^2) was positioned in the centre of the larger 4000 m^2 plot. A separate record was compiled for each species when the species occurred in different vertical layers (herb, shrub, lower and upper tree layer) according to the modified ICP-Forests protocol (Canullo et al. 2011). The estimation of plant species cover was conducted using a modified Barkman's method (Barkman et al. 1964). Nomenclature of species names followed Mala Flora Slovenije (Martinčič et al. 2007) and Flora Europaea (Tutin et al. 1964-1980, Tutin et al. 1993). Moss species were not determined. Instead, total moss cover was estimated in each sampling plot as the sum of moss cover on rocks, coarse woody debris and the forest floor (according to Canullo et al. 2011). In addition, the percentage of bare soil cover was visually estimated in each sampling plot.

Selection of plant functional traits

We selected a set of plant functional traits related to plant growth and reproduction patterns. This selection of leaf, reproductive and whole plant traits was done based on some theoretical background (e.g. Cornellisen et al. 2003) and previous empirical studies (e.g. Scolastri et al. 2017), which highlighted the relevance of these specific traits in the context of the vegetation response to disturbance. Information on functional traits was obtained from the BiolFlor (Klotz et al. 2002) and D^3 (Hintze et al. 2013) databases. The selected plant functional trait was only included in the analysis if its state/value was known for at least 50% of all recorded species. Compiled information on selected plant traits (qualitative, quantitative, and semi-quantitative) is shown in Table 1. Growing form (distinguishing between grasses/sedges, ferns, low herbs, tall herbs, woody plants and legumes) as a trait was also considered based on our expert knowledge. In addition to these functional traits, plant strategy (according to Grime's (1977) C-S-R classification) as an overall plant strategy (i.e. functional type) was included in the analysis.

Table 1 General information on selected plant functional traits

Trait	n	%	Variable type	Number of categories (trait states)	Main source
Growing form	257	100	categorical	6	/
Life form	257	100	categorical	5	BiolFlor
Life span	241	94	categorical	3	BiolFlor
Vegetative propagation	155	60	categorical	5	BiolFlor
Leaf persistence	220	86	categorical	4	BiolFlor
Leaf anatomy	222	86	categorical	3	BiolFlor
Reproduction type	228	89	categorical	3	BiolFlor
Pollen vector	203	79	categorical	3	BiolFlor
Diaspore type	216	84	categorical	4	BiolFlor
Strategy type	222	86	categorical	7	BiolFlor
Duration of flowering [months]	226	88	quantitative	/	BiolFlor
Diaspore weight [mg]	168	65	quantitative	/	BiolFlor
Diaspore length [mm]	174	68	quantitative	/	BiolFlor
Anemochory rank	216	84	ordinal	/	D^3

Note. Abbreviations: *n* - number of species with trait data available (max. = 257), % - percentage of species with trait data available.

Statistical analyses

Vegetation and trait matrices were subjected to different univariate and multivariate statistical analyses. Categorical and numerical traits were treated differently. Abundance data for all determined vascular species (including tree and shrub seedlings) in the herbaceous layer were used. For each categorical trait, the cumulative cover of each trait state was calculated and regarded as compositional data *sensu* Aitchinson (1986). According to Egozcue et al. (2003), isometric transformation was used to project percentage data into real space to overcome the problems of closed data summing to 100%. The compositional coordinates (ilr) of each trait were then jointly used in a multivariate linear mixed model as response variables to test the effects of forest management, sampling period and their interaction. For graphical representation, a biplot based on principal component analysis (PCA) was drawn to show the correspondence between trait states and management/temporal effects. Numerical traits were analysed using a univariate linear mixed model. Plot and experimental site were used as random effects in all mixed models. Tukey post-hoc tests were used to compare levels of logging treatments at a 0.05 significance level.

Functional diversity was estimated by calculating a community-based measure of functional diversity (FD, Petchey & Gaston 2002) for each vegetation sample. This is a dendrogram-based index and equals the total length of the branches of the functional dendrogram constructed from information on species functional traits. The effects of treatments and sampling periods were again tested using a linear mixed model followed by post-hoc tests to compare the levels of logging treatments. The same procedure was also used to compare the cover of individual vegetation layers (tree, shrub, herb and moss layer) and bare soil cover across treatments and sampling periods; arcsine-square root transformation was used beforehand.

All statistical analyses were performed in the R environment (R Core Team 2016) using the vegan (Oksanen et al. 2017), nlme (Pinheiro et al. 2017) and compositions (van den Boogaart et al. 2014) packages.

Results

General patterns of vegetation change

Before the logging treatments were performed, the sampling plots did not significantly differ with respect to the cover of the main vegetation layers (tree, shrub, herb, moss) and bare soil cover (Figure 2). In the control plots (C) no significant changes in the cover of vegetation layers and bare soil were observed in the second sampling period. While changes in tree cover followed the logging treatments as expected (post-treatment cover of 5.7% in FL and 47.8% in PL), the shrub layer showed no significant short-term change in cover. The mean cover of the herb layer increased significantly with an increase in logging intensity. It increased on average by 18 and 44 percentage points in the PL and FL plots, respectively. Moss cover significantly decreased, but only in the FL plots. Bare soil decreased both in the FL and PL plots; this decrease was inversely related to the increase in the herb layer (Figure 2).

Changes in functional trait composition

In the short time period between the two successive surveys, significant changes occurred in the composition of most of the analysed traits. Functional traits which showed a significant response to experimental treatments are listed in Table 2. Management, sampling period and their interaction had a significant influence on trait composition, with the exception of diaspore type. Overall, the most responsive traits (ranked based on the F-values in Table 2) were diaspore length, life span and diaspore weight, followed by anemochory rank and reproduction type. Compositional biplots explained a major part of the variance for categorical traits, ranging from 87.5% to 100% (Figure 3).

Before logging, plots assigned to different logging treatments did not differ in the mean values of quantitative and semiquantitative traits. For these traits, as expected, no change was observed in the C plots (Figure 4). Moreover, regarding trait states for categorical traits

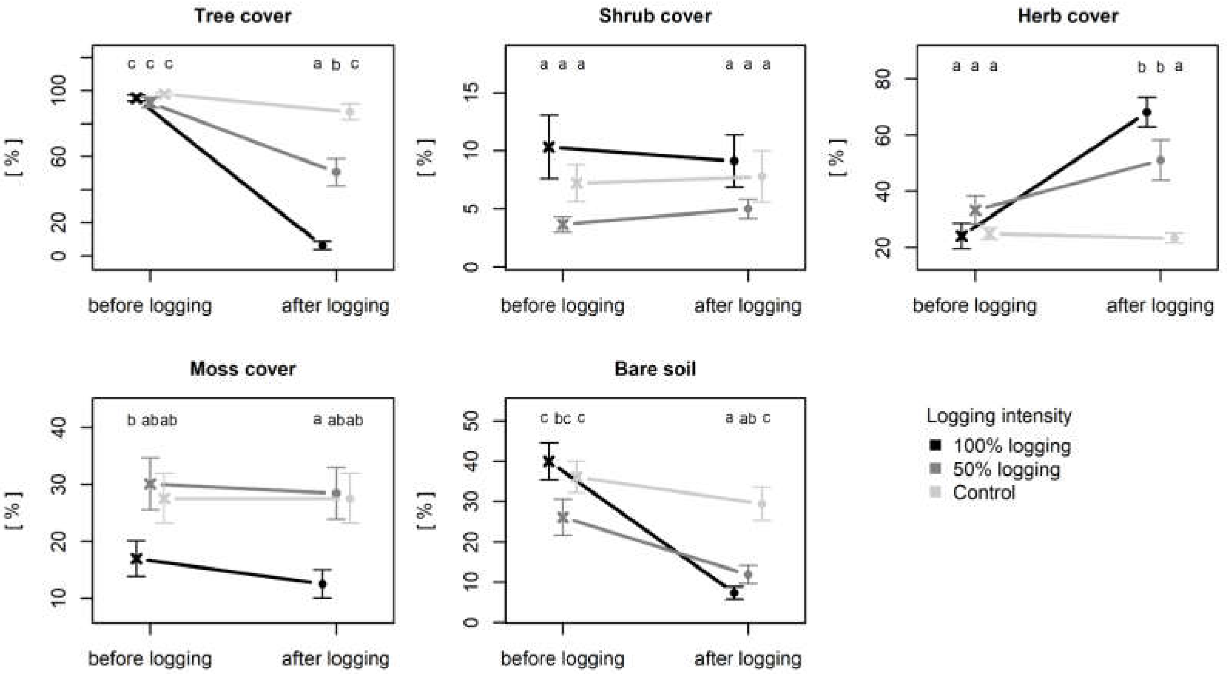

Figure 2 Mean (±SE) percentage cover of main vegetation layers (tree, shrub, herb, moss) and bare soil before and after the logging treatments. Treatments with the same letter are not statistically different at a 0.05 significance level.

Table 2 Analysis of variance (*F* values and significance) for significantly responsive plant traits separately for each of the predicting variables (management, sampling period) and their interaction.

Trait	Management		Sampling period		Interaction[a]	
	F value	Sig.	*F* value	Sig.	*F* value	Sig.
Growing form	4.82	***	12.52	***	3.39	**
Life form	3.87	***	13.93	***	2.75	**
Life span	10.10	***	62.63	***	10.76	***
Vegetative propagation	2.62	*	8.59	***	2.07	*
Leaf persistence	3.26	**	15.78	***	3.79	**
Leaf anatomy	2.99	*	1.05	n.s.	0.63	n.s.
Reproduction type	7.79	***	12.97	***	4.52	**
Pollen vector	2.70	*	6.89	**	1.26	n.s.
Duration of flowering	4.53	*	15.94	***	4.18	*
Diaspore weight	7.38	**	37.83	***	9.29	***
Diaspore length	11.42	***	38.89	***	13.81	***
Anemochory rank	5.26	**	31.63	***	6.40	**

Note. Abbreviations: [a] - interaction between management and sampling period, n.s. – no significant difference, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

(shown in Figure 3), no significant changes in the C plots occurred, and pre-treatment abundances of trait states did not differ between the logging intensities.

After logging in the FL and PL plots, species with shorter and lighter diaspores were more abundant compared to the pre-logging composition. The PL plots did not differ from the FL plots (Figure 4). Despite the prevalence of perennial species in all plots, post-treatment community composition evidently changed in favour of short-lived plants (Figure 3). Annual and biennial species increased in abundance in both FL and PL. Biennials were completely absent before logging but exhibited the largest relative increase in abundance after logging. Species with higher anemochory rank increased in frequency and abundance in the treated plots (Figure 4). Plant species with the ability to reproduce both sexually and vegetatively increased in the FL and PL treatments (Figure 3). Significant increase in the understory cover and richness was a consequence of increased abundance of resident species (e.g. forest forbs and sedges like *Omphalodes verna, Stellaria montana, Carex sylvatica*) that reproduced vegetatively in the gaps (via rhizomes or runners), release of some woody seedlings established beneath closed tree layer before canopy disturbance (i.e. advanced regeneration of shade-tolerant species) and colonization of many new distrubance-dependent species that seeded in the created gaps (from more open habitats nearby) after the logging.

The composition or mean value of other functional traits also changed significantly (Table 2). After the treatments in the FL and PL plots, species with a longer flowering period were more abundant (Figure 4). The abundance of species with overwintering green and persistent green leaves significantly increased in the FL and PL plots (Figure 3). Regarding the growing form, a significant increase in the abundance of tall herbs and grasses/sedges and a decrease in woody plants in the FL and PL plots was observed. Legume species also significantly increased in abundance in the FL plots. Changes in the spectrum of life forms (their definitions are modified from Ramovs & Roberts (2005)) involved increased abundance of chamaephytes (plants with perennating buds and shoot apices located on shoots on

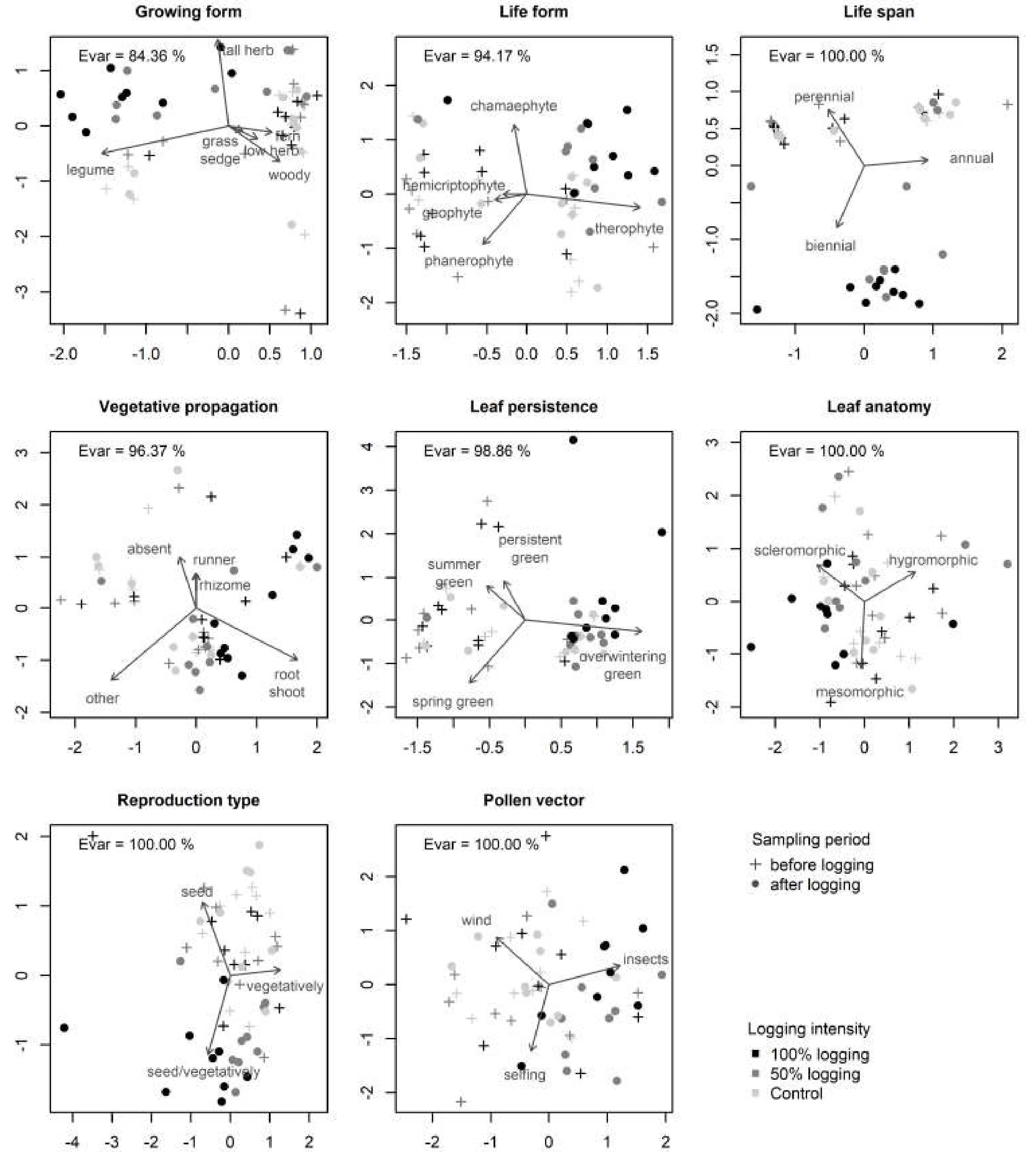

Figure 3 Compositional biplots of the first two principal component axes for functional traits which showed a significant response to experimental treatments. Points represent vegetation samples of different logging intensities and sampling periods, and arrows represent compositional parts (trait states). Evar – variance explained by the biplot.

or near the ground surface) and therophytes (annual plants, survive unfavourable season in seed form) in PL, while phaneropyhtes (species with buds and apical shoots located ± high above ground, stems survive many years) decreased in cover. In the FL plots, therophytes, hemicryptophytes (plant species with persistent buds located in immediate vicinity of the soil surface) and chamaephytes significantly increased in cover. Overall, hemicryp-

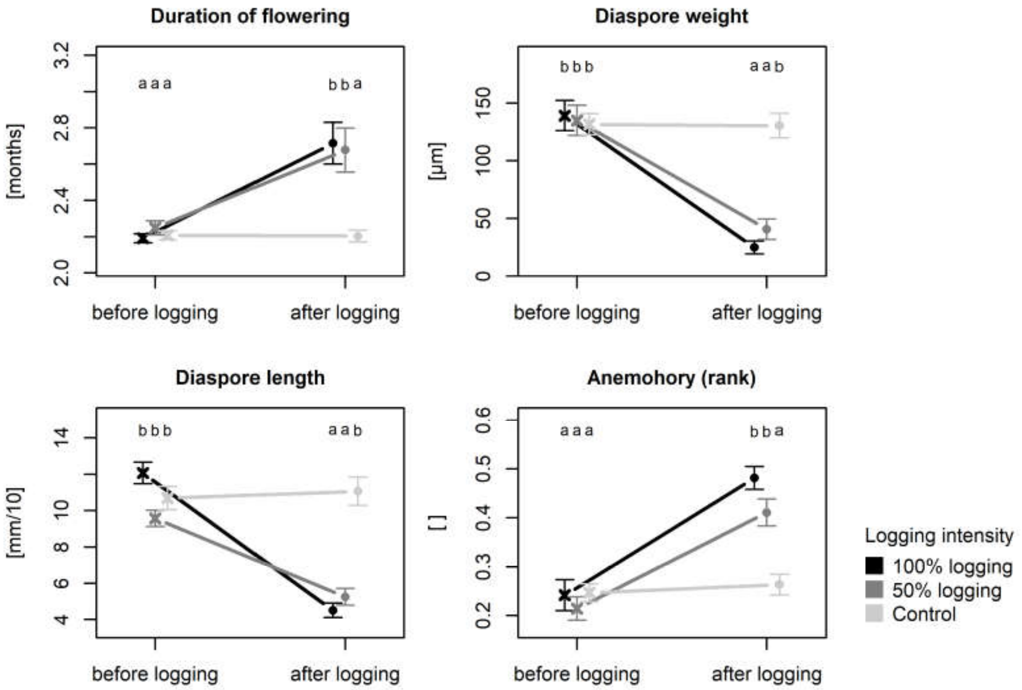

Figure 4 Mean (± SE) values of quantitative and semiquantitative traits before and after management measures of three different intensities. Treatments with the same letter are not statistically different at a 0.05 significance level.

tophytes were the predominant life form in the majority of sampled understory communities both in pre- and post-treatment vegetation. The abundance of geophytes (these species have buds and apical shoots located on subterranean shoots, deep underground) increased insignificantly in both active treatments (PL and FL).

Functional traits such as leaf anatomy, pollen vector and vegetative propagation showed less prominent changes in composition in response to the treatments. Runners and species using root shoots significantly increased in abundance in FL and PL, whereas plants unable to propagate vegetatively decreased in cover in the PL plots. In terms of pollen vector, wind-pollinated species decreased in abundance in the PL plots. Entomophilous plants dependent on insect pollinators were more abundant in the FL plots. Regarding leaf anatomy, plant species with scleromorphic leaves significantly increased in the FL plots, whereas no change for this trait was detected in the PL plots (Figure 3).

Changes in C-S-R strategies

Before logging, understory communities were dominated mostly by intermediate competitive-stress-tolerant plant species (Figure 5). There were also some species with intermediate CSR strategy, while no species with a primary ruderal strategy (R) were identified in the pre-treatment species composition. Only minor and inconsistent shifts in strategy composition were observed for the C plots. The FL and PL treatments substantially increased the importance of species with secondary plant strategies containing a ruderal component (i.e. CR and SR). An exception were the PL plots from one of the experimental sites where species with higher competitive ability increased in abundance after logging. However, pre-logging strategy composition in these plots was somewhat different from the other plots, ex-

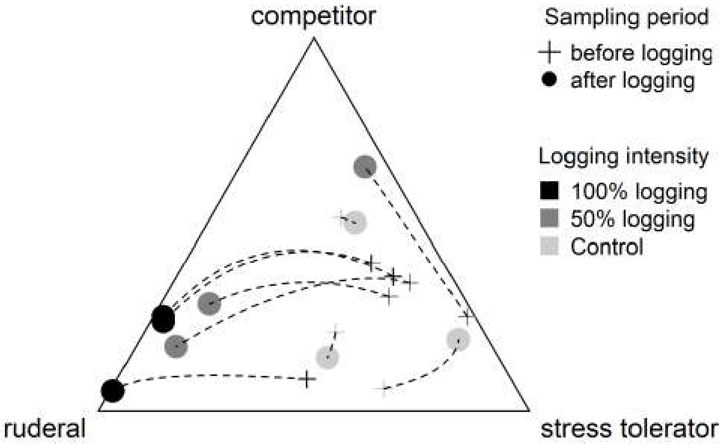

Figure 5 Ternary diagram showing the shifts in Grime's C-S-R strategies between two sampling periods (before and after logging) for three different logging intensities. Each point represents the mean composition across the three plots for each experimental site in each sampling period. Dashed lines represent compositional pathways of change. For graph legibility, compositional data were centered and scaled.

hibiting the lowest ruderal component and a relatively high share of stress-tolerant plants (Figure 5).

Change in functional diversity of the forest plant community

Based on total dendrogram branch length, the pre-treatment functional diversity of the plant community did not differ between the plots assigned to different logging intensities (Figure 6). After logging, functional diversity significantly increased, suggesting that the FL and PL treatments accommodated a greater range of species with different traits. No change in FD index was detected in the C plots. The highest post-treatment functional diversity was observed in the FL plots. PL exhibited an intermediate value of functional diversity. In addition, within the treatments, the between-plot variability in functional diversity increased with increasing logging intensity, i.e. the highest variability was observed for the FL plots (Figure 6).

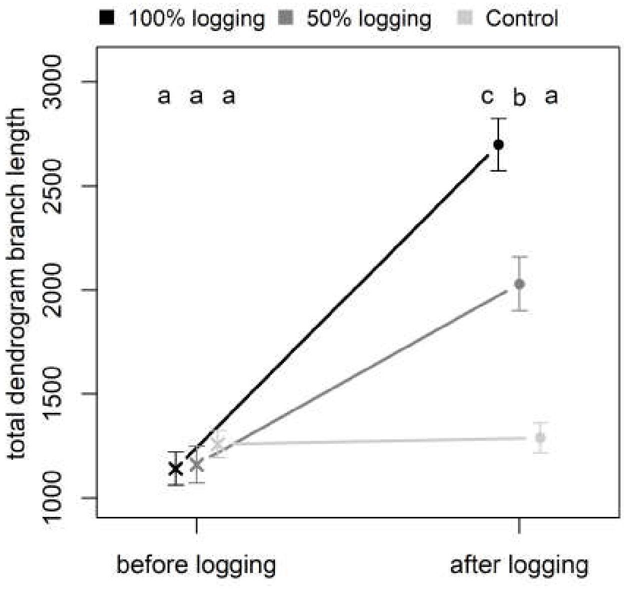

Figure 6 Mean (± SE) functional diversity expressed as the sum of dendrogram branch lengths for three different logging intensities before and after the implementation of forest management treatments. Treatments with the same letter are not statistically different at a 0.05 significance level.

Discussion

Functional traits along a logging intensity gradient

The forest manipulation experiment with different logging intensities allowed us to identify broad patterns of short-term understory vegetation response to forest management practices from a plant functional-trait perspective. Our results suggest that logging intensity is an important driver of change in the trait composition and diversity of understory communities. The most evident changes from pre- to post-treatment conditions were detected in the FL plots, both in terms of total vegetation cover of the herbaceous layer and in its composition. This forest stratum is potentially the most sensitive in its short-term response to logging-mediated disturbances (Gilliam 2007, Scolastri et al. 2017). In contrast, moss cover showed a negative trend along the logging intensity gradient. Compared to most vascular plants, mosses are known to be less tolerant to sudden environmental changes caused by forest canopy reduction (Nelson & Halpern 2005), and moss cover was additionally reduced during the logging operations (e.g. displacement of surface rocks).

The canopy gaps created in the FL and PL treatments provided suitable habitats for the growth of new individuals of pre-treatment resident species and post-treatment establishment of newly colonized species. Two environmental factors, namely light availability and soil disturbance, both induced by more intensive logging, seemed essential for the change in trait composition and appearance of new species in the FL and PL plots (Gondard & Deconchat 2003). The functional profile of many newcomers was different from the functional profile of the pre-existing plant species. Such species, especially those in canopy gaps (FL), can be mainly characterized as non-forest, early-successional ruderals with lighter (smaller) diaspores and a shorter life span. Increased anemochory rank after logging indicated that their high dispersal abilities most likely contributed to their successful post-logging colonization (Degen et al. 2005). In contrast, understory species in the pre-logging conditions were mainly stress-tolerant perennials which possessed specific traits such as larger and heavier diaspores, prevalent vegetative regeneration and a shorter flowering period.

Most of the observed changes in the abundance of functional trait states were generally substantial and in agreement with previous studies (e.g. Kern et al. 2014, Canullo et al. 2017, Patry et al. 2017; but see Graae & Sunde 2000). Similarly, Scolastri et al. (2017) found that in beech forests trait states related to an open forest environment were anemochory, therophytes, a long flowering period and scleromorphic leaf anatomy. Conversely, trait states mainly related to a shady, undisturbed environment were short flowering duration, mesomorphic and higromorphic leaf anatomy, geophytes and spring/summer leaf phenology.

Changes in some trait abundances were not consistent with those found in previous studies. For example, our results suggested higher importance of insect-pollinated plants after logging. In contrast, for beech forests in the Apennines, Scolastri et al. (2017) recognized entomophilous pollination as a common adaptation for those species that grow under canopy closure. Jafari et al. (2015) stated that pollination in a closed forest canopy is mainly carried out by insects. Nevertheless, our results regarding this trait may also have some biodiversity applications. Changes in pollen vector indicate that the higher diversity of entomophilous plant species in canopy gaps may enhance the richness of insect pollinators, supporting the idea of Kutnar et al. (2015), who suggested that increased plant diversity after logging most likely contributed to greater biodiversity in the broader sense (i.e. the diversity of other organisms). However, other trophic levels should be investigated in their response to tree logging, as demonstraded by de Groot et al. (2016).

Some authors (e.g. Patry et al. 2017, Scolastri et al. 2017) reported that in closed, less disturbed forests, more vernal geophytes and perennials can usually be found, which is presumably due to their limited capacity to quickly colonize newly disturbed areas (Ramovs & Roberts 2005). However, our results did not show a decline in the abundance of geophytes after logging. In fact, their abundances showed an increasing trend in the PL and FL plots. This suggests that in the short term, geophytes, along with other resident species, can persist after intensive logging. Despite the unfavourable environmental conditions in the created canopy gaps (i.e. increased direct solar radiation and reduced air humidity), they were able to survive and regenerate mainly due to their vegetative regeneration. This was most likely from root shoots, runners and rhizomes after these were fragmented through soil disturbance caused by skidding operations (Halpern & Spies 1995, Graae & Sunde 2000). While some evidence underlined the major importance of clonality in undisturbed conditions, a recent study by Canullo et al. (2017) in beech forests highlighted the importance of clonal spread for the expansion of typical forest species in the initial stage of forest regeneration after overstory removal. Furthermore, the initial resistance of resident forest taxa also indicates that the size of the created canopy gaps in FL (0.4 ha) may not be too extensive to be detrimental to plants already present in the understory.

The importance of plant C-S-R strategies changed significantly in the logged plots. In accordance with evidence from previous studies (e.g. Graae & Sunde 2000, Decocq et al. 2004), which demonstrated that rapid colonization by ruderal, non-forest species with high light requirements is one of the underlying successional processes in the early recovery of forest understory following logging (Halpern & Spies 1995), the ruderal component increased. Forest management stimulates the presence and abundance of species with a strong affinity for disturbed habitats (Kern et al. 2014).

Functional trait diversity in relation to logging intensity

Our field experiment showed the positive effects of logging intensity on the functional diversity of understory plant communities in the forests under study. Logging-created canopy gaps enhanced functional trait diversity. Higher functional diversity (larger FD index) in the post-logging understory communities indicated greater differences between species' trait values. Logging disturbance provided more available resources (e.g. light) and increased local availability of niches, allowing post-treatment colonization from the regional pool of functionally different plant species (compared to pre-established residents) that span a greater range of trait states and values. Similarly, evidence from the study of Kern et al. (2014) suggested that intensified silvicultural treatments (larger canopy gaps) generally result in higher trait variation, i.e. the additional species in more intensively logged stands possessed different traits than those in less intense treatments. In contrast, Kusumoto et al. (2015) reported that functional diversity decreased in clearcut forests compared to unmanaged stands despite an increase in species richness.

For the plant communities in boreal forests, Biswas & Mallik (2010) showed that functional diversity reached a peak at an intermediate disturbance intensity. However, contrary to our prediction related to IDH, our PL plots (representing a moderate disturbance intensity) did not show the highest community-level functional trait diversity. The progressive increase in functional diversity along the logging intensity gradient matched higher species richness/diversity observed in the canopy gaps (FL) compared to the PL and C plots (see Kutnar et al. 2015). This confirms theoretical expectations and empirical evidence that functional diversity is expected to scale positively to species diversity because new species added to the community will likely bring a suite of functional trait values and states not yet present in the community (Mayfield et al. 2010, Biswas & Mallik 2011, Lohbeck et al. 2012). In addition, observed relationship between logging intensity and functional diversity can be also explained by the short-term responses tracked in our research.

In our study, an increase in species richness and consequently elevated functional diversity resulted from two phenomena: the survival of pre-logging understory species through disturbance and the establishment of more pioneer, non-forest species after disturbance. Such conclusions are consistent with studies (Degen et al. 2005, Patry et al. 2017) showing that the arrival of newly colonized species made a major contribution to the higher diversity in disturbed sites compared to untreated sites. Functional dissimilarity between pre-treatment resident species and post-treatment colonizing species is the main factor for the increased functional diversity of the understory layer in the logged plots, especially in the canopy gaps in FL treatment.

Compared to FL, where plot-scale environmental conditions were presumed to be more uniform, in the PL plots there was greater heterogeneity of resources, since partial felling created a patchy distribution, i.e. a mixture of shaded and sun-exposed microsites. Such post-logged stands are characterized by fast open-to-close dynamics (Canullo et al. 2017). This may lead to the co-existence of species with functional characteristics related to disturbed conditions (early-successional) and plant species related to mature habitats (late-successional). Such a variety of functionally different species most likely increases the functional diversity of the entire plant community. However, our short-term study of the vegetation response might not sufficiently cover longer-term patterns of secondary succession. It is expected that in the following few years, diversity in the disturbed stands will gradually change, particularly when stronger competitive exclusion of newcomers acting on resident species occurs.

Forest management implications

The key findings of our research could be beneficial for forest managers to understand the potential response of vegetation to different logging intensities and may inform forest and biodiversity management aimed at increasing adaptive capacity in Dinaric fir-beech forests. Silvicultural treatments that maintain or foster spatial and temporal diversity of resources and environments will be most effective in maintaining plant species diversity (Halpern & Spies 1995) and consequently the functional diversity of the whole forest community. In terms of biodiversity-promoting silvicultural practices, it was shown that regularly creating canopy gaps in different places in a forest area is a better option than trying to maintain some open spaces over a long period of time (Degen et al. 2005). However, larger clear-cutted openings with high resource conditions and large microclimatic variability should be avoided, particularly in more sensitive forests (e.g. karst areas) such as in our case study. Dinaric fir-beech forests are in larger part characterized by small- to intermediate-scale natural disturbance patterns, whereas larger canopy openings (more than ~ 0.5 ha in size) are rare (Nagel et al. 2017). Artificially created canopy gaps in FL treatment are considered to be quite large for the studied forest type compared to the gaps that occur either naturally (individual tree dying) or due to silvicultural measurements (e.g. group selection system, shelterwood). On the other hand, our FL canopy gaps (gap radius approx. 1.2 times the average tree height of mature forest stands) are still rather small compared to gaps common in some other management systems (e.g. extensive clearcuts) in managed beech forests of Central Europe. This intermediate gap size is important at interpreting the speed and magnitude of vegetation change found in our experiment. It is expected that in large-scale, intensively logged areas, forest recovery will be prolonged, both due to longer dispersal paths of forest species and due to more intense domination of highly competitive non-forest species.

Forest management affects spatio-temporal landscape-scale heterogeneity through creating a complex mosaic of forests stands in different developmental stages, including small and medium-sized clearings (Decocq et al. 2004). At the landscape scale, managing for heterogeneous conditions will create a range of ecological niches and potentially support a greater number of species than managing for homogeneous conditions (Kern et al. 2014). The heterogeneity in a landscape and within a community is an important feature affecting species richness in understory communities. Emulating natural disturbance regimes and deliberately designing various forest management approaches at the stand-scale (e.g. no logging, methods of variable retention, single-tree or group selection, intensive logging creating canopy openings of different sizes and shapes) will most likely contribute to higher species richenss, plant functional diversity and biodiversity in the forest landscape of Dinaric fir-beech forests and beyond.

It is important to note that, apart from advocating canopy gaps for promoting species and functional diversity, maintaining undisturbed forest patches that ensure the presence of late-successional, disturbance-sensitive or rare plant species should greatly contribute to the maintenance of many elements of biodiversity (Halpern & Spies 1995, Kern et al. 2014). Although our results, at least in the short-term, suggested the relative resistence of the herbaceous layer to overstory logging, intensive logging practices may in the long term remove key plant species and consequently important functional traits, which, in turn, may considerably affect the ecological functioning of the forest ecosystem (Jafari et al. 2015). Thus, further investigations of logging effects on post-disturbance forest vegetation development are necessary.

We demonstrated that different silvicultural treatments can be used to manage the functional aspects of forest ecosystems. Based on this, we recommend creating a landscape scale (between-stand) patchy distribution of forest stands subjected to different logging intensities. By implementing various silvicultural practices to maintain and stimulate functional diversity, such heterogeneity, and thus also overall landscape-scale stability (and sustainability) and biodiversity goals, can be achieved.

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