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Patterns of functional diversity of two trophic groups after canopy thinning in an abandoned coppice

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Abstract

Coppice abandonment had negative consequences for biodiversity of forest vegetation and several groups of invertebrates. Most coppicing restoration studies have focused only on a single trophic level despite the fact that ecosystems are characterized by interactions between trophic levels represented by various groups of organisms. To address the patterns of functional diversity in the perspective of coppicing restoration, we studied the short-term effects of conservation-motivated tree canopy thinning in an abandoned coppice-with-standards in Central Europe, a region where such attempts have been rare so far. The functional diversity of vascular plants and spiders, chosen as two model trophic groups within a forest ecosystem, was compared between thinned and control forest patches. To characterize functional patterns, we examined several functional traits. These traits were assigned into two contrasting categories: response traits reflecting a change of environment (for both vascular plants and spiders) and effect traits influencing the ecosystem properties (only for vascular plants). Functional diversity was analysed by CCA using two measures: community-weighted means (CWM) and Rao's quadratic diversity (RaoQ). CCA models revealed that the canopy thinning had a positive effect on diversity of the response traits of both trophic groups and negatively influenced the diversity of effect traits. In addition, we found distinct seasonal dynamics in functional diversity of the spider communities, which was probably

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linked to leaf phenology of deciduous trees and therefore an effect trait not directly examined in this study. We conclude that canopy thinning affected functional diversity across trophic groups during the initial phase of coppicing restoration. With necessary precautions, careful canopy thinning can be effectively applied in the restoration of functional diversity in abandoned coppices.

Keywords

coppice restoration; effect traits; functional diversity; response traits; spiders; trophic groups; vascular plants

Introduction

Coppicing, an ancient forest management system, was for centuries a prevailing method of forest use in Europe (Buckley & Mills 2015a, Szabó et al. 2015). It can be assumed that a whole range of species and functional groups, as well as types of temperate forest ecosystems, have developed and persisted via traditional management (Kirby and Watkins 2015). Coppice abandonment, a common feature in the 20th century forestry, has led to a decline in the biodiversity of vascular plants and several groups of invertebrates (Benes et al. 2006, Van Calster et al. 2007, Baeten et al. 2009, Hédli et al. 2010, Kopecký et al. 2013). Therefore, coppice restoration has been thoroughly debated especially in the United Kingdom (e.g. Buckley 1992, Buckley and Mills 2015b; for critical considerations see Hambler and Speight 1995a, 1995b). Elsewhere, however, the potential consequences of restoring coppicing practices in long-abandoned coppices are largely unknown. Coppicing includes a wide range of tree cutting intensities and in practice can vary from selective cutting to extensive clear-cuts. Careful tree canopy thinning can be a starting point through which the effects of coppicing renewal on biodiversity can be assessed.

Effect of tree canopy thinning on the diversity, composition, and functional properties of forest ecosystems has been richly documented (Aubert et al. 2003, Adrian et al. 2009, Verschuyt et al. 2011, Vild et al. 2013). However, the majority of works studying the effects of forest management on biodiversity focused on species diversity (Battles et al. 2001, Dodson et al. 2008, Adrian et al. 2009), while impacts on functional diversity have remained practically unexamined. Understanding functional diversity patterns is important because species diversity is not always the best predictor of ecosystem quality (Tscharntke et al. 2012). Changes in species composition and functional characteristics can have a larger effect on ecosystem functioning than on species richness or diversity (Wilsey and Potvin 2000). Despite the fact that most studies confirm the positive effect of thinning management on understory species richness, the effect of various intensities of thinning on multiple trophic groups within a given forest ecosystem is still not well understood (Collins et al. 2007, Knapp et al. 2007, Dodson et al. 2008, Atkinson et al. 2015). This lack of knowledge can pose serious limitations because species communities form ecosystems via direct and indirect trophic interactions (Schmitz and Suttle 2001, Ohgushi 2008). Understanding a species' impact on ecosystem processes (i.e., resistance, resilience, and stability) requires a complex approach, hence the inclusion of various trophic groups is of great importance.

Forest canopy thinning is a disturbance process, which directly affects many trophic and functional groups by releasing or reducing resources such as light, moisture, living space, and nutrients (Kaye and Hart 1998, Gundale et al. 2005). Thus, thinning-induced plant response will influence the diversity, composition, and functional properties of other trophic levels, e.g., of the herbivorous insects and their predators they comprise (Southwood 1977, Price et al. 1980, Pearson and Dyer 2006). Species which will occur in post logged sites should be filtered from the pool of potential colonist species with an effective competitive ability under specific habitat conditions (Townsend and Hildrev 1994). We assume that species composition will be determined by the physical complexity of the habitat in the sense of the “habitat template theory” (Southwood 1977, 1988, Aarssen and Schamp 2002). Structural and trophic complexity does not increase linearly with succession in temperate regions (Southwood 1977). Vegetation often shows greatest diversity in relatively early stages of secondary succession, before strong competitors start to dominate. Diminishing the overwhelming influence of forest succession by canopy thinning can therefore have a positive effect on the species and functional diversity of certain groups of organisms. We also expect the “stress-dominance hypothesis” will help explain the effects of canopy thinning. According to this hypothesis, the relative importance of environmental filtering increases and competition decreases along the disturbance gradient (Tilman 2004, Coyle et al. 2014). Early stages of succession should be dominated by species with generalist-feeding strategies and broad niches resistant to environmental filtering, as well as pioneer species with the ability to easily disperse and quickly utilize resources but with a weak ability to compete (Pianka 1970, Southwood 1977). In the later phases of ecosystem succession following canopy thinning, the functional properties of a species will mainly reflect competition for resources (Coyle et al. 2014).

The functional traits of species comprising communities are effective measures of various patterns, including properties of successional dynamics. The relative proportions of functional traits can be used to calculate functional diversity (Mason et al. 2005). The concept of functional diversity is a valuable tool for understanding what determines community structure (Gerisch et al. 2012, Kašák et al. 2015). Functional traits can be divided into the two main categories – species effect traits and species response traits (Lavorel and Garnier 2002, Lavorel et al. 2007). Functional effect traits are considered to *influence* ecosystem properties, whereas functional response traits are considered to *reflect* them (Lavorel and Garnier 2002). For concrete purpose, the trait groups can be associated with the strategies adopted by individual species to cope with environmental changes such as periodical coppicing. Moreover, the two groups of traits are not completely separable and assignment to one or another trait group is relative, i.e. regarding the context of studied ecosystem. Next to that, traits can be considered according to their effect on ecosystem function, hence traits with strong (assumed effect traits) and weak (assumed response traits) effects (Pakeman 2011). Two main approaches to calculating functional trait diversity exist. The community-weighted mean is the mean trait value weighted by relative species abundance. It gives a dominant trait value in a community. Rao’s quadratic entropy index (RaoQ) quantifies the distribution of trait values among species (Mouchet et al. 2010, Roscher et al. 2012). Communities simultaneously indicating high trait differentiation and high species abundances have high RaoQ values.

The purpose of this study is to evaluate the effect of conservation-motivated tree thinning by comparing functional diversity two different trophic groups: vascular plants and spiders. Our aim is to examine the response patterns and assess appropriateness of thinning intervention for biodiversity conservation. The main hypothesis is that (1) vascular plants and spiders respond similarly to canopy thinning. We assume a pulse release of resources such as light and nitrogen, and increased spatial heterogeneity of these resources because of tree canopy differentiation by selective cutting (see the description of the thinning intervention in Methods). In connection to the resource differentiation, we hypothesize that (2) canopy thinning has a positive effect on functional diversity of *response* traits and negative influence on functional diversity of *effect* traits. This prediction reflects the assumption that canopy thinning is associated with traits linked to early successional stages. Corresponding strategies are rapid colonization of suitable patches. Negative influence of canopy thinning corresponds with adaptations to late successional stages with closed canopy. Appropriate traits directly influence environmental conditions. As an additional insight into the short-term functional patterns, we examined spider communities during a vegetation season. We hypothesize that (3) tree leaf shading has a seasonally variable effect on the diversity of functional characteristics of spider communities.

Methods

Study site

The study site was Dvín Hill, southern Moravia, Czech Republic (48.8748 N; 16.6533 E) and has an area of about 380 ha, of which 3/4 is covered with temperate deciduous forest. The site has a temperate climate of subcontinental character with dry periods occurring from late spring to autumn. Average yearly temperatures are 9 to 10°C; precipitation is on average 550 mm/yr. Soils here have developed on limestone and loess substrate and are very rich in nutrients; litter decomposes rapidly into a mull-type humus. Our study plots were situated on a slope with a northwesterly aspect and were located 270 to 400 m above sea level. They are covered with a deciduous forest dominated by broad-leaved lime (*Tilia platyphyllos*), among other species such as ash (*Fraxinus excelsior*), three species of maples (*Acer plananoides*, *A. pseudoplanatus*, *A. campestre*), hornbeam (*Carpinus betulus*), elm (*Ulmus glabra*), and oak (*Quercus petraea*). Vegetation is species-rich; about 630 vascular plant species occur on the whole site, and the forest communities can contain up to 70 species per 200 m² (Nature Conservation Agency of the Czech Republic 2015 and own unpublished results).

The present-day forests in Dvín are among the best examples of abandoned coppices in Central Europe. Most compartments still retain characteristic coppicing features such as coppice stools, some of them apparently centuries old. Historical archival research has demonstrated that nearly the entire forest area of Dvín Hill was managed under a coppicing regime for centuries. The abundance of standard trees largely varied through the site's history. Currently, mainly oak standards are left in the abandoned coppices. The coppicing management system was exceptionally stable from at least from the 14th century until the early 20th century; for details see Szabó (2010) and Müllerová et al. (2014, 2015). In 1946 the site became a nature reserve with the aim to preserve valuable plant and animal species and communities. Following the then-prevailing conservation paradigm that viewed

coppicing as harmful to forest ecosystems, over the past six decades forest management has been based on the principle of least intervention. As a consequence the forests of D vín have undergone succession from short-rotation coppices less than 40 years old to old-growth forests often over 100 years old (Müllerová et al. 2015). This transformation has resulted in a considerable decline of vegetation biodiversity (Kopecký et al. 2013). The current nature conservation strategy envisages coppicing restoration. Intervention commenced in 2009 with canopy thinning in selected compartments are an attempt to support the vanishing biodiversity.

Sampling design

Four forest compartments were chosen on the NW slope of D vín. Their size varied between 10 to 20 hectares; forest age ranged from 60 to 90 years. Habitat configuration was rather homogeneous throughout the sampled stands. The tree layer in two compartments was thinned with selective cutting in 2009 and 2010; two compartments remained unthinned (Fig. 1). These treatments created a more heterogeneous light habitat as shown by analysis of hemispheric photographs taken at 1 m above the ground (Fig. 2). It should be noted that the thinned forest stands were not classic coppices but rather selectively thinned stands because the management authority, the state-owned Forests of the Czech Republic, was not in favour of more intense tree cutting.

In all four compartments, the composition of vascular plant and spider communities was sampled using plots and traps, respectively. Sampling followed canopy thinning with a one- to two-year lag and thus reflected the reaction of biotic communities to the relatively immediate effect of thinning. Vascular plants were sampled using circular plots with a radius of 1 m; thus the plot size was 3.14 m². Five such plots were regularly clumped within squares of 15 by 15 m. Six such clumps and 30 plots were symmetrically placed in the intact forest compartments; six clumps were in thinned compartments comprising another 30 sampling plots. The presence of all vascular plant species in the forest understory (up to 1.3 m height) was recorded in August 2011. No additional properties of the plant species were recorded during the sampling.

Spiders were sampled using pitfall traps. We used 500 ml plastic cups containing 4% formaldehyde solution as a fixative medium. A row of three pitfall traps spaced five meters apart was placed in each compartment. The traps were emptied five times during the vegetation season: on 6 June, 2 July, 4 August, 4 September, and 2 October 2010. The species and sexes of the collected specimens were determined. The number of individuals per species and sex were recorded. Pitfall traps were used as a standard method to evaluate epigeal spider fauna. Traps were placed on sites during the main vegetation season, between May and October. Using this method we collected nearly the entire spectrum of ground-dwelling spiders, even species that mature during autumn and live during winter time (these usually start to hatch in September). Although only pitfall traps aimed at epigeal species were used, tree species were also caught. In each compartment the same trap spacing and timing was used. Pitfall traps are able to produce a representative spider sample, also with the most ecologically important species (e.g., Niedobová and Fric 2014).

Functional traits

Based on the available literature, we chose several functional traits to describe changes in functional diversity after tree thinning (Table 1). We selected traits corresponding with adaptations of spider and vascular plant communities to early or late stages of forest succession. We differentiated between *response* and *effect* traits following the concept introduced in Lavorel and Garnier (2002) and Lavorel et al. (2007). Our aim was to interpret how the functional diversity of spider and vascular plant communities reacts to changes in the physical environment, i.e., tree thinning.

Vascular plant traits were obtained from three resources: Ellenberg indicator values (Ellenberg et al. 1992), LEDA (Kleyer et al. 2008), and BioFlor (Klotz et al. 2002). Plant traits classified as effect traits were specific leaf area, plant height, and leaf phenophase, while traits considered as response traits were light affinity, moisture affinity, and persistent soil seed bank. For an explanation and quantification of the particular traits, see the cited database resources. The selected effect traits reflect plant strategies to cope with increasing competition during the forest succession, while constituting the properties of environment at the same time. Taller plant species will tend to dominate in succession, and species with greater leaf area would become more abundant in increasingly shadier conditions. Both traits will have an effect on environmental properties experienced by organisms including vascular plants and spiders. The latter group would respond to variation in leaf phenophase, because foliage development causes changes in shading during the vegetation season. The selected response traits help to quantify the reaction of plant species on changing amount and heterogeneity of important resources, which is obvious for light and moisture affinity. Soil seed bank in periodically thinned forests would change to more persistent, because shifting environment would require persistent seeds to survive of unfavorable conditions.

For spiders, only response traits were considered plausible. These traits included light affinity, humidity affinity, and stratum affinity. They are based on species environmental requirements described by Buchar and Růžička (2002), who established them using catalogue data from the Czech Republic (more than 150,000 records). Similar categories were also established by Kasal and Kaláb (2015). We used species affinity to humidity (very dry, dry, semi-humid, humid and very humid), light (open, semi-open, partly shaded, shaded and dark habitats), and forest vertical stratum (underground, ground layer, vertical surfaces, herb layer, shrub layer, tree trunks and canopies). The affinities of species to trait values, ranging from 1 to 5, were determined subjectively. For the expected changes in individual plant and spider traits following the canopy thinning see Table 1.

Statistical analyses

A total of 36 species of spiders (302 specimens) and 86 species of vascular plants were statistically analysed. We used canonical correspondence analysis (CCA) in the statistical software Canoco 5 (Braak and Šmilauer 2012) to test the effect of canopy thinning on species composition and abundances. Vascular plant species data were obtained by determining the presence of individual species in plots; spider species data were acquired from pooled abundances across sexes. We chose presence or absence of canopy thinning as explanatory variable. Species abundance of spiders was transformed by decimal logarithm.

Calculated p-values were adjusted for multiple testing using Bonferroni correction. The significance of the canonical axis was tested with the Monte-Carlo permutation test (5000 permutations). To achieve correct Type I error estimates, the permutation test was restricted by using a hierarchical design. The effect of canopy thinning on vascular plants was analysed with a permutation test defined by 15 split-plots in each of the 4 whole plots, e.g., forest stands with thinning treatment. Statistical testing was by permutation of plots independently across the whole plots while split-plots were held together without permutation. For the analysis of spiders, we had to arrange a different statistical design following the sampling design. The permutation test used 10 split-plots (using data from two sampling years) within each of 4 whole plots—forest stands with thinning treatment. In addition, for analysing spiders we restricted the permutation to a time series because of autocorrelation between individual observations. The cases were arranged along a time scale, and therefore during permutations we had to respect the autocorrelation structure that binds the explanatory and response data. Therefore whole plots were freely exchangeable and split-plots were restricted for time series.

Functional diversity was calculated as RaoQ separately for spider and for herbaceous functional and effect traits. RaoQ is defined as the sum of pairwise distances between species divided by relative abundance and is largest when species with large trait differences reach similar high abundances (Mouchet et al. 2010). In addition, we calculated community-weighted means (CWM) of trait values to show how the particular species traits are related to canopy thinning. CWMs were then passively projected as functional traits in the ordination diagrams. The CWM is calculated by dividing mean trait values by species relative abundance indicating the dominant trait value in the community (Roscher et al. 2012). We used CWMs of functional traits as explanatory variables to find out which of them explain significant variability in species data. A CCA model with the same restricted-permutation design was used to analyse the CWMs of functional traits. Forward selection was then applied to select significant CWM traits. These traits and the functional diversity were then passively projected to the ordination space.

The relationship between the functional diversity of spiders and seasonality was fitted by generalized additive model (GAM) with Gaussian error distribution. We used an F-test to determine the significance of the relationship. To reveal if the species composition of the five subsequent samplings really differed we used analysis of similarities (ANOSIM, part of the “vegan” package in R statistical software). ANOSIM is based on computing the rank order of dissimilarity values within and between groups. A dissimilarity matrix was calculated from the species matrix using Bray-Curtis distance. To assess the significance of the ANOSIM statistic, a permutation test was used (1000 permutations). If two groups of samplings really differ in their species composition, the ANOSIM statistic R will be greater than zero. Thus, compositional dissimilarities are always greater between groups than within groups.

Results

Overall effects of canopy thinning

The functional diversity of response traits of both vascular plants and spiders increased following canopy thinning (Figs 3a and 4). The functional diversity of effect traits, considered only for plants, decreased after canopy thinning (Fig. 3b). This finding, illustrated in the ordination diagrams, is in accord with our first two hypotheses. Note the distinction between trait diversity and actual trait values. Considering the basic biodiversity and composition patterns, species richness of vascular plants varied from 1 to 22 species per plot (on average 13.3 species per plot). Plant assemblages were dominated by forest herbs, the most frequent being *Asarum europaeum* (6%) and *Galium odoratum* (6%), as well as *Fraxinus excelsior* saplings (5%). The most dominant spider species were *Trochosa terricola* (24%), a rather common epigeal forest edge species, *Amaurobius ferox* (17%), a true forest species, and *Dysdera lantosquensis* (15%), a species occurring in light forests.

Response of vascular plant functional diversity

According to the results from the CCA model, vascular plant assemblages were significantly influenced by tree thinning ($F=2.7$, $P_{adj}=0.009$). The model explained 4.4% of variability in the species data (pseudoF=2.7, $P=0.001$, for all canonical axes). The performance of functional traits included in the CCA model as explanatory variables is presented in Fig. 3 and Table 2. The first canonical axis represents a gradient of species occurring from relatively shady closed-canopy habitats to relatively open canopy. Positive correlation of functional traits with canopy thinning was observed for light affinity, plant height, leaf phenophase, and soil seed bank. Negative correlation was observed for moisture affinity, and a weakly negative correlation for specific leaf area (Fig. 5). The response of individual traits, as predicted in Table 1, conformed our expectations in five out of six traits (all except for leaf phenophase). The groups of response and effect traits explained about the same amount of compositional variability. The CCA model of the CWM of effect trait values accounted for 13.4% of variability (pseudoF=2.1, $P<0.001$, for all canonical axes) and the CWM of response traits explained 13.5% of variability (pseudoF=2.9, $P<0.001$, for all canonical axes). Passively projecting functional diversity indices (Rao's quadratic entropy index) to the CCA diagram showed the differential correlations of the response and effect traits to canopy thinning (Fig. 3 a, b).

Response of spider functional diversity

The output of the CCA model revealed that thinning had a significant effect on the structure of spider assemblages ($F=1.8$, $P_{adj}=0.015$). The model explained 4.9% of variability in the species data (pseudoF=1.8, $P=0.008$, for all canonical axes). The first ordination axis separated species that are characterized by the affinity to dry and open habitats from species characterized by the affinity to closed-canopy forest (i.e., dark and humid conditions). We also discovered that the opening of the habitat leads to an increase of species with an affinity to vertical forest stratification. The passively projected CWM of functional traits illustrate this finding (Fig. 6, Table 2). The CCA model of the CWM of trait values accounted for 19.8% of variability (pseudoF=3.0, $P<0.001$, for all canonical axes). Greater diversity of functional traits was observed in stands with thinning management applied (Fig. 4).

Passively projecting the functional diversity index (Rao's quadratic entropy index) to the CCA diagram space shows that functional diversity was positively influenced by canopy thinning (Fig. 4). This finding is congruent with the analogous pattern for vascular plants.

Seasonal variability of spider functional diversity

The functional diversity of spiders in thinned and non-thinned patches varied significantly throughout the growing season ($F_{2,37}=7.4$, $P<0.01$), thus confirming our expectation formulated in the third hypothesis. Functional diversity was the highest at the beginning of the growing season, and after a strong subsequent decline it again increased toward the end of the season (Fig. 7). This pattern was probably caused by changes in species composition, as demonstrated by the results of ANOSIM analysis ($R=0.104$, $P=0.025$). Dissimilarity of species composition between the samples was the highest at the beginning and at the end of the growing season (spring and autumn, reduced tree leaf cover). In the middle of the growing season (summer, full tree leaf cover) relatively homogeneous assemblages of spiders were observed (Fig. 8).

Discussion

Reactions of trophic groups to canopy thinning

Our results indicate that forest canopy thinning influenced compositional patterns and had positive effects on functional diversity of the two simultaneously studied trophic groups—vascular plants and spiders. The latter aspect is relatively novel and considering the coppicing restoration, our study appears to be unique. The findings are generally consistent with those of the meta-analysis by Verschuyt et al. (2011) showing that forest thinning has a mostly positive effect, or at most a neutral impact, on the biodiversity of various animal groups. Coppicing as a system using frequent canopy thinning is sometimes sharply criticised as being harmful to biodiversity and functioning of forest ecosystems (e.g., Hamblen and Speight 1995b). Our results led us to a different conclusion, but it should be considered that it is related only to an early development immediately following a coppicing of modest intensity. The positive effect of canopy thinning on biodiversity in the initial years of succession has been however documented by several studies (e.g., Collins and Pickett 1988, Wayman and North 2007, Verschuyt et al. 2011). Subsequent development can vary greatly, but in general biodiversity likely declines as the canopy closes. In order to make conclusions on the development of restored coppices that are valid for periods longer than a few years after tree cutting, greater observation periods are required (e.g., Ash and Barkham 1976, Mason and MacDonald 2002). Contrasting patterns when distinguished for response and effect traits in vascular plants may be explained by differing strategies adopted by species in relation to early versus late succession stages. The positive effects the spatial heterogeneity created by canopy thinning had on spider functional diversity was further supplemented by the similar effects of temporal heterogeneity due to tree leaf development throughout the growing season. However, vascular plants and spiders are reasonably distinct trophic groups, so their reactions to canopy thinning are further discussed separately.

Response of vascular plants

Understory vegetation showed a complex response to canopy thinning, rather than a simple one. Our results suggest that light was the critical resource influencing species composition. This factor is important for the overall performance of forest herb plants (Whigham 2004). Many studies have shown that canopy openness, regardless if it is the result of natural processes or intentional thinning like coppicing, has a significant, complex effect on understory herb species performance (e.g., Goldblum 1997, Valverde and Silvertown 1998, Mason and MacDonald 2002, Lindh 2008, Van Calster et al. 2008, Scanga 2014), demonstrating the positive effect of the increased light availability on the diversity of forest understory vegetation (e.g., Ares et al. 2009, Bailey et al. 1998, Whigham 2004). Other studies, however, determined immediate negative effects of canopy thinning on understory vegetation (e.g., Adrian et al. 2009). It was postulated that disturbance can initially homogenize vegetation structure and increase light uniformity (Beggs 2005, Bartemucci et al. 2006). We argue that the intensity and extent of canopy thinning plays a critical role. Intensive disturbance could affect the diversity at the species and functional levels by reducing the number of disturbance-sensitive taxa (e.g., Griffis et al. 2001). On the other hand, thinning not overly destructive to the physical environment can support immigration and the establishment of populations of species benefiting from the release of light and nutrient resources.

When partitioning the functional diversity for response and effect traits, we identified two complementary stories. Not surprisingly, tree thinning was positively associated with the diversity of plant adaptations responding to environmental changes, and negatively with adaptations constituting stable environment (Wellnitz and Poff 2001, Decocq et al. 2004). Coppicing restoration positively influenced occurrence of species with strategies suitable to early successional phases, which were mostly associated with response traits. Persistent soil seed bank or high light affinity are shared by species preferring frequently disturbed habitats. The occurrence of a number of typical open-habitat species supports this interpretation. These species are largely ruderals that rapidly colonize the newly open patches following canopy thinning in former or newly established coppices – e.g., *Moehringia trinervia*, *Taraxacum* sect. *Ruderalia*, *Trifolium repens*, *Ajuga reptans*, *Urtica dioica*, *Scrophularia nodosa*, and *Sambucus nigra* (Vild et al. 2013, Hédli et al., this issue). On the other hand, undisturbed forest sustains the diversity of species sensitive to disturbances, mainly competitors preferring long-term stability (Southwood 1977). They are characterized with adaptations as tall growth and high moisture affinity, which is associated with high specific leaf area. Several shade-tolerant species were associated with our control plots, e.g., *Aconitum lycoctonum*, *Asarum europaeum*, *Chaerophyllum temulum*, or *Viola mirabilis*. Most of these species prefer closed canopy, and some can significantly influence the species composition of the understory communities. In the study site, the tall herb *Aconitum lycoctonum* forms dense uniform populations in the shady parts of the forest.

Response of spiders

We expected that shifts in particular functional traits of vascular plants (namely specific leaf area, plant height, and leaf phenophase) would be reflected in changes in spider species composition and the diversity of spider response traits. Indeed, the CCA model revealed that

spider functional diversity showed the same trend as understory vegetation. In addition, we assumed that the greater variability of functional groups of spiders on the thinned sites could be caused by the increased spatial and temporal heterogeneity of physical conditions, including the vegetation structure (Southwood 1977, 1988, Schuldt et al. 2012, Mori et al. 2015). The hypothesis predicting higher spatial heterogeneity after canopy thinning can be partially supported by our results. A positive effect of thinning on vertical stratification of spider habitats was revealed. We therefore assume that the thinned patches supported spiders favouring tree canopy (*Anyphaena accentuata*, *Tegenaria ferruginea*, *Segestria senoculata*) because these spiders moved from tree canopies to shrub canopies.

Moreover, larger plant size was also positively correlated with canopy thinning. This relationship implies that after canopy thinning high light availability favoured larger-sized plant species. We can conclude that vegetation structure complexity is also an important factor positively influencing species richness (Schuldt et al. 2012, McDonald 2015). It was demonstrated that species number may be related to foliage height diversity and cover (Roth 1976). The non-linear trend between succession and spatial complexity can thus lead to a great diversity of spiders and plants after canopy thinning (Southwood 1977).

The random colonization of species with unique combinations of functional traits is a typical phenomenon for early succession stages supporting functional trait diversity (e.g., Kašák et al. 2013, Hodecek et al. 2015). The lower functional diversity of spiders in control patches can be explained by the strong shading impact of trees and therefore the relative environmental uniformity of these patches (Beggs 2005, Bartemucci et al. 2006). Our results support this prediction because none of the functional traits for spiders show a positive correlation with control patches. Similar results are also known for other groups of epigeal invertebrates as well as spiders (Spitzer et al. 2008, Purchart et al. 2013).

The development of spider functional diversity during the growing season showed a significant unimodal pattern. We explain this observation by tree leaf phenology, which influences the temperature and light heterogeneity of the forest throughout the year (Anderson 1964, Hutchison and Matt 1977). The high heterogeneity of the physical factors at the beginning and end of the growing season leads to a high level of functional diversity. Interestingly, the increases in functional diversity were not caused by species migration within the habitat but by the colonization of the habitat by new species from the surrounding areas.

Conclusions

Our study shows that careful canopy thinning in an abandoned coppice can have an immediate effect on the functional diversity of species belonging to different trophic groups. Whether functional diversity responds positively or negatively to canopy thinning depends on functional trait type (i.e., response and effect traits). The functional vascular plant diversity was largely driven by light availability, while spider diversity was positively linked to the structural parameters of vegetation and changed during the year with the development of tree leaves. Canopy thinning can be generally regarded as a way towards ecosystem-friendly coppicing restoration. Precautions need to be taken for various trophic groups,

trophic conditions, and thinning intensity. For example, canopy thinning could decrease resilience to invasive species. We therefore suggest that future research determine the habitat-differentiated intensity of canopy thinning in order to ensure optimal ecosystem stability and functioning.

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Fig. 1.
Examples of control (a) and canopy thinned (b) forest stand sampled in this study. Note the structural differences and light penetrating to forest understory.

Fig. 2.

Boxplots showing variability of canopy openness assessed by hemispheric photographs. Coefficients of variance were computed from clumps of five of plots comprising areas of about 15 by 15 m. Note the uniform light conditions before the thinning (2009) versus the increased heterogeneity after the thinning (2015). Overall difference between the 2009 and 2015 samplings is due to the use of a different camera and its operator.

Fig. 3.

Effect of canopy thinning on vascular plant species composition (CCA) with passively projected functional diversity calculated as Rao's quadratic entropy index. Separate diagrams are shown for the groups of response traits (a) and effect traits (b). Each species name is given in acronyms, as follows: *AcerPseu* – *Acer pseudoplatanus*, *AconLyco* – *Aconitum lycoctonum*, *AjugRept* – *Ajuga reptans*, *AsarEurp* – *Asarum europaeum*, *CarMurAg* – *Carex muricata* agg., *ClemVitl* – *Clematis vitalba*, *ConvMajl* – *Convallaria majalis*, *EuonVerr* – *Euonymus verrucosus*, *FallConv* – *Fallopia convolvulus*, *HeptNobl* – *Hepatica nobilis*, *HyprPerf* – *Hypericum perforatum*, *ChaeTeml* – *Chaerophyllum temulum*, *ScrpNods* – *Scrophularia nodosa*, *TarSec* – *Taraxacum* sect. *Ruderalia*, *TrifRepn* – *Trifolium repens*, *UrtcDioi* – *Urtica dioica*, *VerChmAg* – *Veronica chamaedrys* agg., *VernSerp* – *Veronica serpyllifolia*, *ViolMirb* – *Viola mirabilis*, *ViolReic* – *Viola reichenbachiana*.

Fig. 4.

Effect of canopy thinning on spider assemblage composition. CCA is with passively projected functional diversity calculated as Rao's quadratic entropy index inferred from species traits. Each species name is given in acronyms, as follows: AgroCupr – *Agroeca cuprea*, AmauFerox – *Amaurobius ferox*, ClubTerr – *Clubiona terrestris*, EpisTrun – *Episinus truncatus*, HarpRube – *Harpactea rubicunda*, MeglPSeu – *Megalyphantes pseudocollinus*, MetlMeng – *Metellina menegi*, MicrViar – *Microneta viaria*, NeriEmph – *Nerine emphana*, OzypAtom – *Ozyptila atomaria*, OzypBlac – *Ozyptila blackwalli*, PardAlac – *Pardosa*

alacris, PardLugb – *Pardosa lugubris*, TapnLong – *Tapinopa longides*, TegnFerr – *Tegenaria ferruginea*, TenuFlav – *Tenuiphantes flavipes*, TenuTend – *Tenuiphantes tenebricola*, TrocTerr – *Trochosa terricola*, ZoraNemr – *Zora nemoralis*, ZoraSpin – *Zora spinimanna*.

Fig. 5. Effect of canopy thinning on vascular plant species' composition. Canonical correspondence analysis diagram shows passively projected CWM values of species functional traits. Most of the functional traits are positively correlated with thinned forest. Each species name is given in acronyms, see caption of Figure 3.

Fig. 6. Effect of canopy thinning on spider assemblage composition. Canonical correspondence analysis with passively projected CWM values of species functional traits. Most traits are positively correlated with thinned forest. Each species name is given in acronyms, see caption of Figure 4.

Fig. 7. Scatterplot showing a U-shaped trend of spider functional diversity during the growing season. On the x-axis is number of days from the beginning of May to October.

Fig. 8.

Boxplots showing compositional dissimilarity in samples of spiders taken during 124 days of a growing season. First box shows dissimilarity within the entire dataset, the other boxplots in samples taken in consecutive days after the 1st of May. During the growing season, dissimilarity in species shows a U-pattern. R-value measures difference among samples (zero meaning no difference among sets of samples), P-value measures statistical significance of R-value. Shown are median values (black line) with quantile range (box) and total range (whiskers).

Table 1

Functional traits used in the analysis. Sources of trait values for vascular plants are Ellenberg indicator values (EIV), BiolFlor (BF) and LEDA (L). Sources of trait values for spiders are Buchar and Růžička (2002), and Kasal and Kaláb (2015). For further explanation see text. Reaction on canopy thinning indicates assumed change in each trait following thinning.

Taxonomic group	Functional trait type	Functional trait	Variable type	Expected reaction to canopy thinning
Vascular plants	response	Light affinity (EIV)	Continuous	Increase
		Moisture affinity (EIV)	Continuous	Decrease
		Soil seed bank (L)	Binomial	Increase (more persistent)
	effect	Specific leaf area (L)	Continuous	Decrease
		Plant height (L)	Continuous	Increase
		Leaf phenophase (BF)	Continuous	Decrease (earlier)
Spiders	response	Light affinity	Ordinal	Increase
		Moisture affinity	Ordinal	Decrease
		Stratum affinity	Ordinal	Increase

Table 2

Significance of spiders and herbaceous plants functional traits used as explanatory variables in the forward selection for the CCA models.

Functional trait	Functional trait type	Model variability explained %	pseudo-F	P	P(adj)
<i>Vascular plants</i>					
Light affinity	Functional response traits	5.9	3.7	<0.001	<0.001
Moisture affinity		4.7	2.8	<0.001	<0.001
Soil seed bank		3.9	2.3	<0.001	<0.001
Plant height	Functional effect traits	4.4	2.1	0.024	0.145
Leaf phenophase		4.0	2	<0.001	<0.01
Specific leaf area		3.6	1.8	0.081	0.482
<i>Spiders</i>					
Stratum affinity	Functional response traits	7.2	2.8	<0.001	0.001
Light affinity		7.0	2.7	<0.001	0.001
Humidity affinity		6.6	2.5	<0.001	<0.001