Dynamics of herbaceous vegetation during four years of experimental coppice introduction

Radim Hédl[a,b,*], **Jan Šipoš**[a,c], **Markéta Chudomelová**[a,d], and **Dušan Utinek**[e]

[a]Department of Vegetation Ecology, Institute of Botany, Czech Academy of Sciences, Lidická 25/27, 602 00 Brno, Czech Republic

[b]Department of Botany, Faculty of Science, Palacký University, Šlechtitel 27, 783 71 Olomouc, Czech Republic

[c]Department of Biology and Ecology, Faculty of Science, University of Ostrava, Chittussiho 10, 710 00, Ostrava, Czech Republic

[d]Institute of Botany and Zoology, Faculty of Science, Masaryk University, Kotlá ská 2 611 37 Brno, Czech Republic

[e]Ministry of the Environment of the Czech Republic, Vršovická 1442/65, 100 10 Praha 10, Czech Republic

Abstract

Understanding the effects of coppicing on forest ecosystems is important for progress towards sustainable forest management. A newly established coppicing experiment in a secondary temperate deciduous forest in the SE Czech Republic provides a rather unique insight into succession driven by canopy thinning in a forest still lacking species typical for forests established since long time ago. Herbaceous layer vegetation was monitored for four subsequent years in 2012–2015. We focused on the influence of canopy thinning intensity in two different forest types defined by dominant tree species (oak and lime). Our results showed that the opening of the canopy had immediate effects on herbaceous vegetation. Coverage, species richness and compositional patterns followed the coppicing intensity gradient. The dominant tree species had contrasting effects. Under oak, the reaction to coppicing was weak. Under lime, strong reaction both related to coppicing intensity and temporal development was observed. Herbs with short life cycle had the greatest contribution, but perennial grasses also began to increase their coverage after coppicing. Several invasive species, mostly short-lived herbs, emerged but are supposed to retreat as the succession will proceed. We conclude that coppice introduction to a secondary forest led to contrasting patterns related to dominant tree species. The marked difference was probably due to the slow sucession towards a future forest community saturated by species. This process may be now further diversified by coppicing management.

[*]Corresponding author: Tel. 00420 541 126 219; fax 00420 541 126 234; radim.hedl@ibot.cas.cz.

Introduction

Coppicing is one of the oldest forest management systems in temperate regions worldwide (Matthews 1991). Many species and their assemblages were sustained by coppicing for long time periods. Coppicing operated on the scale of whole regions and maintained an important part of extant forest biodiversity (Buckley 1992; Fuller and Warren 1993; Rackham 2006; Savill et al. 2010). Among the main ecological features of coppicing is a specific light environment. It can be characterized as a shifting mosaic of light and dark phases. These phases last long enough to keep viable populations of light-demanding, but also shade-tolerant organisms. Rackham (2006:592) concisely defined *coppicing plants* as 'plants that appear or especially flourish every time a wood is cut down'.

The effects of coppicing are related not only to light but also to regular soil disturbance and nutrient uptake. Both were viewed negatively in older forestry literature, where soil 'degradation' was commonly considered a typical consequence of coppicing. For example, a prominent Czech forestry soil scientist J. Pelíšek (1957:106) argued that 'coppicing strongly interfered with the basics of soil production and at places it manifested itself in such a deteriorative manner that it led to soil degradation and a lowering of soil production capacity.' [translated by R.H.] Despite earlier pessimistic views, it was later shown that coppice management can help to sustain favourable levels of soil nutrients (Hölscher et al. 2001). Moreover, nutrient balance in ecosystems completely changed during the 20th century. In today's nitrogen-oversaturated temperate forest ecosystems, nitrogen removal can be one of the main benefits of coppicing for biodiversity conservation (Bobbink et al. 1998; Bernhardt-Römermann and Ewald 2006; Dirnböck et al. 2014). However, our knowledge is surprisingly limited in this field. In a recent review, Hobbie (2015) showed that species-dependent mechanisms underlying plant litter decomposition, nutrient cycling (in particular of nitrogen) and potential effects of atmospheric depositions are still not sufficiently known.

Vascular plant species characteristic for temperate forests in Europe are adapted to long-term coppicing. The persistence of many of these species depends on regeneration from the soil seed bank (Van Calster et al. 2008b) while other species groups are able to quickly colonize forest patches opened after coppicing (Ash and Barkham 1976). Even the long-persistent, shade-tolerant woodland species profit from the light phases by accumulating assimilates for vegetative growth, flowering and fruiting (Lindh 2008). Coppicing has similar effects on other groups of organisms including several invertebrate taxonomical and functional groups, such as butterflies (Warren and Thomas 1992; Benes et al. 2006) or epigeic invertebrates (Spitzer et al. 2008), and vertebrates, such as birds and small mammals (Buckley 1992; Rackham 2003; but see Burgess 2014).

One of the main reasons for currently declining biodiversity are changes in land use. This includes changes in management systems. One of the major management shifts of the past two centuries in Europe was the conversion of coppices to high forests. In many regions, coppicing historically dominated in forest management and its decline and eventual abandonment during the 19th and 20th centuries had a serious impact on forest biodiversity. Various scenarios of conversion from coppicing to other types of management can provide diverging effects on herbaceous layer diversity, cover and composition (Decocq et al. 2004a; Van Calster et al. 2008a). Studies on the effects of coppice abandonment from central and western Europe mostly reported strong changes in species diversity and composition, resulting in biotic homogenization and decreases (but also increases) in species richness (Van Calster et al. 2007; Baeten et al. 2009; Hédl et al. 2010; Kopecký et al. 2013).

The main goal of this study is to evaluate the effects of coppice introduction in a secondary forest established after the WWII on an agricultural land. The focus was on the diversity and composition of understory vegetation. It is defined as the herbaceous layer, the forest stratum composed of all vascular plant species less than 1 m in height (Gilliam 2014). The studied secondary forest has not been colonized yet by species characteristic for long-established forests (e.g. Hermy et al. 1999). Such 'ancient forest' species are typical slow-colonizers, sensitive to disturbances and substrate chemistry. One of the factors preventing colonization by these species may be high level of soil phosphorus due to the former agricultural use (Honnay et al. 1998). We aimed at the quantification of the effects of tree canopy cutting of two intensities on the herbaceous layer. In addition to the canopy thinning intensity, we analyzed two markedly different forest types defined by dominant tree species: oak and lime. It was shown that European tree species considerably differ in their effects on humus quality, nutrient content in forest floor and mineral soil (Muys 1995; Vesterdal et al. 2008). We analyzed the effects to the structural and compositional properties of the herbaceous layer with the intention to assess the success of coppice introduction from a conservation perspective (Newton 2007). In the light of the existing research (e.g. Buckley 1992; Kirby and Watkins 2015), the experimental introduction of short-rotation coppicing system in a secondary forest appears to be quite unique attempt, when compared to studies focusing mostly on ancient forests and species related to them.

We hypothesized that the interaction of canopy thinning intensity and dominant tree species would significantly affect the herbaceous layer over the four years of the experiment. Specifically, we hypothesized that thinning intensity in the initial years of coppicing introduction would be positively correlated with coverage and species richness in the herbaceous layer. This is due to lowering the competition for light by trees and because of disturbance promoting immigration of annual species (Ash and Barkham 1976; Vild et al. 2013) or possibly even alien species (Radtke et al. 2013). After the disturbance caused by canopy thinning, the herbaceous community would temporarily become more differentiated than before this impact (Grime 2006). We consider all these effects, except for the spreading of aliens, positive indicators from a nature conservation point of view. However, the assessment of long-term impacts needs longer observation and is beyond the scope of this study.

Methods

Study site

The effects of coppice restoration were studied in a deciduous forest (Utinek's Grove – Utink v háj in Czech) near Lechovice, SE Czech Republic (48.8840° N, 16.2510° E). The forest is located on the flat edge of a plateau at 230–235 m above sea level. The climate is subcontinental (Dfb) with average yearly temperature 9.3 °C and precipitation 569 mm (Lechovice; web 1). Geological substrate is Quaternary sand and gravel deposits (web 2), soil is arenic cambisol (web 3). Biogeographically the site is located in the westernmost edge of the NATURA 2000 Pannonian region (web 4). Utinek's Grove is a secondary forest about five decades old. It was planted after WWII on agricultural land, which had probably been cleared centuries before. After establishment, the forest was not felled until recently. It is composed of oak (*Quercus petraea*, *Q. robur*), lime (*Tilia cordata*) and non-native black locust (*Robinia pseudoacacia*). Black locust groves were massively planted in the region during the 20th century. Utinek's Grove was recently purchased by a private owner. His decision to transform the high forest to coppice-with-standards has led to the creation of a system of compartments. In the surrounding forests, mainly state and municipal properties, coppicing was abandoned about a century ago. Coppicing was the most common forest management type in the region until the end of the 19th century (Szabó et al. 2015), providing the present coppice restoration a meaningful historical background.

Coppicing experiment

Transformation from high forest to the coppice-with-standards took the form of a field experiment. An area of about 2 hectares was divided into four blocks. Two blocks were dominated by oak, two by lime. Each block was further divided into three compartments. In total, 12 compartments were subject to the coppicing experiment (Fig. 1). Each compartment covers an area of about 1/8 to 1/4 of a hectare. Selected trees were removed so that the closed canopy was thinned at two intensities in order to promote the resprouting of shoots from stumps. One compartment in a block was left as a control, one was lightly thinned and one was heavily thinned. Light thinning resembled selective cutting rather than a coppice system, while heavy thinning created a habitat that can be best described as coppice-with-standards (cf. Matthews 1991). Thinning was carried out in winter 2011/2012. Stumps of oak and lime resprouted immediately in the first vegetation season. In summer 2015, four years after coppicing, the young lime sprouts formed dense growths over 3 m tall (Fig. 2). Deer browsing played no visible role probably because the forest is situated next to a frequented road.

An important feature of the experiment is the division to oak- and lime-dominated parts. The respective forest blocks differed substantially in light conditions, litter quality and understory vegetation. The oak part was lighter before the thinning, litter tended to accumulate, understory vegetation was dense and dominated by three graminoids (*Poa nemoralis*, *P. angustifolia* and *Arrhenatherum elatius*). The lime part was much darker with leaf litter decomposing readily. The herbaceous understory developed only after canopy thinning. The canopy under lime or oak and subjected to two thinning intensities was sampled by using hemispheric photographs in 2013 and 2015. It was unfortunately in

different months, which however does not disrupt the main canopy openness patterns shown in Fig. 3.

Data sampling and treatment

In September 2012, twelve 30m-long transects were established in the coppicing compartments. One transect per compartment included four plots arranged 10 m from each other. Plots were circles with 1m radius, i.e. the plot size was 3.14 m^2. This relatively small plot size was chosen to balance the tradeoff between a sufficient number of (pseudo)replicates and sampling demands – the whole set can be sampled by a two-person team in one day. The twelve transects with 48 plots were sampled once a year (2012, 2013, 2014 and 2015) in the late summer. Coverage of herb and moss layers were recorded in each plot, as well as the presence and relative abundance of each herb species and woody species juvenile (i.e. not resprouts). The Braun-Blanquet scale was used to estimate the species' relative abundances, with degrees defined as r (1 or 2 individuals), + (up to 1% cover), 1 (up to 5% cover), 2 (6–25%), 3 (26–50%), 4 (51–75%) and 5 (76–100%). The nomenclature of vascular plants followed Kubát et al. (2002). Mosses were not determined.

To assess the affinity of life cycle length to coppicing treatment, each species was labelled either short-lived or long-lived. The former included species with life cycle spanning one to few years (typically annuals and biennials), the later were species with life cycle longer than a few years (perennials including woody seedlings). The life cycle category was assigned based on our own experience and following internet resources. In case of multiple life cycles, the more commonly occurring option was chosen. The resulting dataset contained 81 species entering statistical analyses. This dataset was reasonably balanced, with 40 short-lived species and 347 occurrences (species in a sample), and 41 long-lived species and 710 occurrences.

Statistical analyses

Four types of statistical analyses were used to answer the research questions. First, response of the herb layer total coverage (visual estimate per plot) and species richness (number of vascular species per plot) to thinning intensity and dominant tree species over four years of the experiment were analyzed by regression modelling. The same explanatory variables were used in ordination analyses to assess their effect on community compositional variability. In addition, rank-abundance analysis was performed to evaluate the impact of thinning intensity on species abundance distribution. Lastly, indicator analysis using species fidelity was used to define species characterizing groups of samples defined by the combination of dominant tree and thinning intensity.

Regression analyses

We used three fixed effects: sampling year, thinning intensity and dominant tree species. Four replicated plots in each treatment, in total 48 plots, were sampled on four occasions. Therefore we used a mixed model procedure to get the correct number of degrees of freedom and to estimate the correct standard errors. The relationship between the response variable 'species richness' and the explanatory variables was examined by a generalized linear mixed model (GLMM) with Laplace Approximation using glmer, part of lme4

package. Three mixed models (for total, short- and long-lived species richness) were designed as nested random intercept effect models, because 48 plots were nested at four within twelve forest compartments with various thinning intensity. As the distribution of error term, in this model we used Poisson distribution with correction for overdispersion and 'log' link function. For the response variable 'herbaceous layer cover' we constructed the same GLMM model with Gaussian error distribution and link function 'identity'. Gaussian distribution was used because the response variable was transformed by logit-transformation. We used the likelihood-ratio test based on log-likelihood ratio statistic (LRT) to test whether the deviance of the full model significantly increased after each of the explanatory variable was excluded from the model. Data were analyzed using the R software (R Developement Core Team 2014).

Ordinations

Canonical correspondence analysis (CCA) was chosen because of relatively heterogeneous data (the length of the main gradient was more than 4). Two CCA models were computed using the statistical software CANOCO, version 5 (ter Braak and Šmilauer 2012). The significance of each explanatory variable was tested by forward selection procedure. Estimated P value was adjusted for multiple testing by Bonferroni correction. Abundances of species were transformed by logarithm with base 10 and added 1 (in order to avoid zero values for abundances equal 1). In the CCA1 model we tested the effect of interaction between the year of sampling and thinning intensity, while in the CCA2 model we tested the effect of interaction between the dominant tree species and thinning intensity. In CCA1, the year of sampling and plot ID were defined as covariables. Species life cycle (short- or long-lived) was passively projected into the ordination diagrams. They were community weighted-means of the trait values calculated for samples (Roscher et al. 2012). By this model we tested the hypothesis that the development of the herbaceous community over four years of canopy thinning followed unique scenarios regarding thinning intensity and dominant tree species. In CCA2, the interaction between thinning intensity and dominant tree species were used as explanatory variables and plot ID and year of sampling were defined as covariables. Species life cycle was passively projected into the ordination diagram. By this model we tested the hypotheses that the effect of thinning intensity on herbaceous layer composition and abundance depends on the dominant tree species in the forest. The permutation test for each model was restricted by defining split-plot design. The samples from each year were (in CCA1) or the triplets of thinning intensity (in CCA2) were held together and permuted across the whole-plots. The distorting effects of temporal autocorrelation between samples from the same plot were resolved by the setting of the permutation test. The number of permutations in each model was set to 2000.

Species abundance distribution

For fitting species abundance distribution (SAD) we chose the gambin model. The gambin model is supposed to provide superior fit than the commonly used SAD models and represents a flexible model for fitting different types of species data (Matthews el al. 2014). The shape of the model is described by the single parameter *alpha*: low values of alpha demonstrate logseries-like SAD and high values demonstrate more evenly distributed abundances in the species communities. Matthews et al. (2014) showed that alpha generally

decreased from relatively native habitats to highly transformed habitats. Therefore this parameter can be used as an ecological indicator of land use on species communities. The relationship between thinning intensity and alpha parameter was tested by a Kruskal-Wallis test.

Indicator species analysis

Species characteristic for combinations of dominant tree species and thinning intensity were defined by means of fidelity. Fidelity was calculated as phi-coefficient from presence/absence data for samples belonging to each of the six groups (Chytrý et al. 2002). The groups were of equal sizes (32 plots) hence no standardization to plot size was performed. The species fidelity analysis was performed in JUICE, version 7 (Tichý 2002).

Results

Our results showed that thinning intensity in combination with dominant tree species influenced herbaceous vegetation. This effect appeared already in the first vegetation season (2012) and persisted for all four monitored years. Regarding herbaceous species composition, richness and coverage, heavy thinning had the most significant effects. However, the impact of canopy thinning was pronounced only under lime, while under oak, the change was relatively weak.

Coverage and species richness

Temporal patterns in herbaceous layer coverage and richness were examined by generalized linear mixed models. The test statistics of four types of GLMM are summarized in Table 1. Canopy thinning intensity as well as dominant tree species had a significant effect on herbaceous layer coverage (GLMM1). The increasing rate in coverage over the four years of experiment was linked with canopy thinning intensity. Whereas control plots marked moderate and light-thinned plots almost no increase, a clear trend can be observed for heavy-thinned plots (Fig. 4a). As for total species richness (GLMM2), both thinning intensity and dominant tree species showed a significant effect at $p=0.05$. After the initial increase, the species richness slowly decreased, an effect clearly apparent in light and heavy thinned plots (Fig. 4b).

Looking at the patterns in herbaceous layer regardless of the temporal development, coverage was significantly lower in the lime-dominated than in the oak-dominated compartments, and it increased along the thinning intensity gradient under lime but not under oak (Fig. 5a). Total species richness steeply increased along the thinning intensity gradient under lime, but no change could be observed under oak (Fig. 5b). Partitioning the species richness among short-lived (GLMM3) and long-lived species (GLMM4) showed that short-lived species were affected by the thinning intensity under both tree species, although relatively less under oak (Fig. 6a). Long-lived species differed only sligtly from the short-lived species in their higher richness under oak than under lime (Fig. 6b).

Compositional variability

Two ordination analyses helped to analyze the patterns in species compositional variability. The CCA1 model with temporal patterns in thinning intensity and dominant tree species significantly explained 4.2% variability in species composition (Table A1). This model reveals that the herbaceous layer composition had a unique succession for particular types of management intensity and dominant tree species (Fig. 7). Statistically significant temporal effects were observed for both dominant tree species, but only for heavy thinning intensity, not for control and light thinning (Table 2).

The second ordination analysis (CCA2) model was used to determine the combined effects of dominant tree species and managhement intensity. This model explained 7.4% of species compositional variability and five of six combinations were statistically significant (Table 2, Table A2). Therefore we can assume that the effect of thinning intensity depends on the tree species composition. This model also revealed that the changes in herbaceous plant communities were most strongly associated with heavy thinning intensity in lime, while the oak forest patches showed somewhat lower variation (Fig. 8).

Passively projected community weighted means of functional traits represented two contrasting life cycles traits in both ordination models. Short-lived species were strongly positively correlated with temporal development in lime-dominated compartments, while long-lived species adhered to oak-dominated forest (Fig. 7). This pattern was less clear but still visible when the combination of tree species and thinning intensity were considered (Fig. 8).

The reaction of species abundance distribution on canopy thinning showed a statistically not significant gradient of thinning intensity (Chi-squared=0.34, p=0.841). The alpha parameter decreased with thinning intensity, which may suggest decreasing evenness in the community.

Individual species

The affinity of individual species to combinations of thinning intensity and dominant tree species are presented in Table 3 and are also partly visible in ordination diagrams (Figs 7, 8). Three patterns can be observed: oak stands were relatively homogeneous with little variation due to thinning intensity, lime stands controls had no species strongly confined to them and the greatest number of species was associated with heavily thinned lime-dominated plots. Among them, ruderal species such as *Conyza canadensis*, *Cirsium vulgare*, *Myosotis arvensis*, *Cirsium arvense*, *Erigeron annuus* or *Stellaria media* prevailed. None reached higher frequencies or dominance. Control plots in lime had no indicator species at all, because the herbaceous layer was very little developed or even absent there. Thinned variants of oak-dominated plots were characterized by woody species juveniles, such as *Rosa canina* s. lat., *Quercus robur*, *Robinia pseudoacacia*, or *Crataegus* spp. The oak forest regardless of thinning was generally associated with graminoids of usually high coverages: *Poa nemoralis*, *Poa angustifolia*, *Arrhenatherum elatius* and *Calamagrostis epigejos*. The lime forest had no universally characteristic species, perhaps with the exception of *Taraxacum* sect. *Ruderalia*, which readily appeared even in lightly thinned plots.

Discussion

Coppicing and forest succession

Coppicing can be viewed as an anthropogenic disturbance to the forest ecosystem, along with other management-related disturbances, such as clear-cut or selective cutting, and natural disturbances, such as windbreak. All these disturbances effectively alter the competition for light and other resources, such as soil water and nutrients, between trees and the herbaceous vegetation. The diversity and structural properties of the herbaceous layer are largely controlled by this competition, and the temporary removal of trees leads to a new type of competition dynamics. In other words, coppicing periodically restarts forest ecosystem succession. The initial conditions and trajectory of this succession depend, under otherwise equal environmental conditions including tree species composition, on species pool, management history and land use history, to name but a few other factors. These factors influence patterns in the herbaceous layer shortly after tree cutting, in a mid-term perspective (several years) and on a long run (decades and longer).

The reaction of the herbaceous layer to tree removal is typically very fast and gradually dissipates as the trees regenerate. The steep increase in the number of species after coppicing in our case study is in congruence with the common observation of many studies. The positive correlation between the management / disturbance intensity and the rate of species richness increase can be supported by the observations of several studies (Griffis et al. 2001; Dodson et al. 2008). This correlation can be valid up to a certain threshold, after which the species richness decreases with further increasing disturbance intensity. Intermediate disturbance (cf. Connell 1978) may be the best way of maintaining high species diversity at local scales.

According to the 'stress-dominance theory', relative importance of physical factors of environment increases and species competition decreases along the disturbance gradient (Coyle et al. 2014). This would suggest that abiotic factors (i.e. light) rather than interspecific competition have probably structured species community. This was most apparent in the heavy-thinning compartments with the frequent establishment of new species, while light-thinning only supported the remaining trees, with no effects on the herbaceous layer. Similarly, soil disturbance related to management operations was not intense enough to cause a significant increase in species richness. In the heavy-thinning *Tilia*-dominated compartments, the increase in species richness and herbaceous layer coverage was particularly marked because these stands had almost no herbaceous layer before tree cutting. In a certain sense, this situation was similar to the conditions in non-intervention forests, which are also very species poor as compared to managed forests (Battles et al. 2001; Burton et al. 2009).

Coppicing systems are a more dynamic environment than other forest management systems, because disturbance frequency is higher. Consequences for the herbaceous layer will depend on resources of diaspores, which can be from the soil seed bank or from seed rain (Calçada et al. 2015). Too intensive management on a local scale can lead to a depletion of local plant populations and a deficient soil seed bank, while landscape-scale management may deplete whole meta-populations and destroy the diaspore resources from the seed rain. Our study

forest was established on agricultural land only about five decades ago and lacks canopy cutting history thus, populations of slowly-dispersing forest species were deficient in soil seed bank (Honnay et al. 1998; Hermy and Verheyen 2007). Even after fifty years, they did not disperse to the site, therefore no new species characteristic of forest habitats were recorded during four years of observation. Such strikingly slow colonization by forest species implies a strong appeal on conservation of ancient forest habitats in agricultural landscapes.

Still, the relative role of dispersal versus seed bank for many newly occurring species is difficult to assess without an analysis of soil seed bank and surrounding habitats – potential resources of diaspores. The newly emerged species share an important functional trait: they produce large amounts of small seeds enabling long-distance dispersal. Most of these species are commonly present in the surrounding agricultural landscape. It would suggest that they have colonized the forest following the coppicing disturbance. At the same time, most of these species typical of frequently disturbed arable habitats build a permanent soil seed bank (Thompson et al. 1998). Populations of many newly emerging species could have originated from the local soil seed bank, surviving several decades of the forest cover.

In our case, the establishment of nitrogen-demanding weedy species was probably further enhanced by the land use history of the study site (former agricultural land) and the close vicinity of a frequented road, supplying airborne nitrogen depositions to the forest soil. Some authors consider the increase of weedy species following canopy disturbance a danger for 'native' communities (Decocq et al. 2004b). Other studies (Ash and Barkham 1976) nonetheless showed that this increase is only short-term, lasts only a few years after canopy disturbance and declines after the canopy closes up. After ten years, very few weedy species will persist (Vild et al. 2013, a coppicing experiment with similar experimental design as the present one).

Several studies argued that disturbances linked with canopy thinning, especially intensive ones, often led to invasion by neophytes (Griffis et al. 2001; Radtke et al. 2013). This is of particular concern for nature conservation, however unimportant these invasions might be in the overall dynamics of the herbaceous layer (Dodson et al. 2008). Our plots were invaded by several weedy neophytes (*Amaranthus* spp., *Erigeron annuus*, *Conyza canadensis*) including C4-grasses (*Echinochloa crus-galli*, *Setaria pumila*, *Digitaria ischaemum*). Nonetheless, these weakly competitive short-lived species can hardly impose a major threat to the forest herbaceous layer in a long-term perspective and most of them will disappear in the course of forest succession (Thysell and Carey 2001). The only threatened species newly occurring after tree cutting was *Polycnemum arvense*, ranked 'critically threatened' on the Czech Red list (Grulich 2012). Interestingly, *P. arvense* is also a weedy species, although it strongly decreased in the last decades due to management intensification.

The role of dominant tree species

One of the main results of this study is that the dominant tree species controlled the development of structural and compositional properties of the herbaceous layer after coppicing. The temperate European species of *Quercus* and *Tilia* differ in shading intensity, leaf litter quality and decomposability, and content of soil nutrients. The litter of *Tilia*

decomposes fast, results in a high-quality mull type of humus and supports higher biomass of earthworms than the litter of *Quercus* (Muys 1995; Neirynck et al. 2000). At the same time, *Quercus* stands have a higher content of C and N in forest floor and mineral soil than *Tilia* (Vesterdal et al. 2008). Despite favourable topsoil conditions, there were very few herbaceous layer species in our control plots under *Tilia*.

The rapid development after coppicing indicates that the cause of suppression was deficient light. Pure *Tilia* stands are characterized by extremely shady conditions, while *Quercus* allows enough light to the forest understory. Similar effects as *Tilia* can have *Acer* spp. or *Carpinus betulus*, commonly occurring in European forests. An experiment by Elemans (2004) supports our field observation. Elemans studied the mechanisms governing the trade-off between light and nitrogen availability. The combined effects of the two factors were quantified using the biomass of forest understory species. Under low light, no differences between nutrient-poor and nutrient-rich soils were observed. Enough light resulted in rapid biomass increase even without increased nitrogen content (except for high-nitrogen environments). From a more theoretical perspective, coppicing results in a pulse release of resources (light, nutrients and water). It is a characteristic feature not only of coppices but almost any regularly managed forest habitats.

The contrasting stories of oak and lime stands could also be viewed from the perspective of available living space. The virtually empty understory under *Tilia* enabled, once the limitation by low light was over, an immediate establishment of a number of short-lived species. The understory of *Quercus* stands was already occupied by dense populations of grasses hence the space for potential newcomers was blocked. Unlike *Tilia* stands, the *Quercus* understory was not much changed even by increased light availability, which resulted mainly in the consolidation of existing populations of species with long life cycle rather than the arrival of new species. Episodic occurrences of a few species with short life cycle can be explained as an effect of soil disturbance resulting from tree harvesting operations.

Variation in dominant tree species composition involves also variation in the dynamics of ecological conditions. The fast change after tree removal, mostly so in heavy-thinning *Tilia* stands, will probably decline in the following few years (Metzger and Schultz 1984; Kirby 1990). In our newly established coppicing system, it can be predicted that the slow resprouting of *Quercus*, after four years only about 1–1.5 m tall, will provide enough space for the further development of grass coverage for the next several years. *Tilia* resprouted much faster and reached over 3 m in height four years after cutting. After just one or two vegetation seasons of full-light environment, the coppiced *Tilia* stands started to get crowded with numerous resprouts. In summer 2015, it was very difficult to walk through the heavy-thinned *Tilia* compartments, which contrasted with their *Quercus* counterparts. In about five years after cutting, the *Tilia* stands will probably provide no space for light-demanding species anymore.

Conclusion

Patterns in forest herbaceous layer dynamics connected to introduction of coppicing in a secondary forest can be, at least in the present study, explained by three types of factors or processes related to forest succession (Shugart 1984; West et al. 2012).

(i) Short-term processes

The immediate reaction of the herbaceous layer following canopy thinning was a consequence of pulse-increased light availability. Herbaceous vegetation reacted by increased cover and the occurrence of short-lived, light-demanding species. Increased solar energy input may also have enhanced soil microbial activity, leading to more nitrogen availability through increased litter decomposition and nitrogen mineralization. Regarding species richness, this development slowly declined and probably will further decline in the coming years, while the herbaceous layer cover continuously increased.

(ii) Long-term processes

Land cover history is overriding the short-term succession within the forest ecosystem. While the latter operates at a decadal scale, land cover dynamics is usually a much longer story. In our case, land cover history had no spatial variation. It had nevertheless a major influence on the patterns in vegetation since forest establishment. As afforestation happened only about five decades ago, the studied vegetation was far from the species-saturated temperate forest vegetation of the study region. Only relatively few herbaceous species managed to establish viable populations. There were no slow-colonizing species characteristic for forests with long continuity, which means that no 'ancient forest' species yet colonized the forest after five decades of its existence.

(iii) Tree species

Environmental conditions determined by dominant tree species left a strong trace on both short- and long-term processes. They influenced light availability and succession in the herbaceous layer, and the subsequent reaction to the coppice introduction. The dominant tree effect was as strong as the effect of thinning intensity and markedly modified its impact on the herbaceous layer community.

Supplementary Material

Refer to Web version on PubMed Central for supplementary material.

Acknowledgements

References

Ash JE, Barkham JP. Changes and variability in the field layer of a coppiced woodland in Norfolk, England. J Ecol. 1976; 64:697–712.

Baeten L, Bauwens B, De Schrijver A, De Keersmaeker L, Van Calster H, Vandekerkhove K, Roelandt B, Beeckman H, Verheyen K. Herb layer changes (1954–2000) related to the conversion of coppice-with-standards forest and soil acidification. Appl Veg Sci. 2009; 12:187–197.

Battles JJ, Shlisky AJ, Barrett RH, Heald RC, Allen-Diaz BH. The effects of forest management on plant species diversity in a Sierran conifer forest. For Ecol Manage. 2001; 146:211–222.

Benes J, Cizek O, Dovala J, Konvicka M. Intensive game keeping, coppicing and butterflies: the story of Milovicky Wood, Czech Republic. For Ecol Manage. 2006; 237:353–365.

Bernhardt-Römermann M, Ewald J. Einst zu wenig, heute zu viel: Stickstoff in Waldlebensgemeinschaften. Gefahrstoffe Reinhaltung der Luft. 2006; 66:261–266.

Bobbink R, Hornung M, Roelofs JGM. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. J Ecol. 1998; 86:717–738.

Buckley GP, editorEcology and management of coppice woodlands. Chapman & Hall; London, UK: 1992.

Burgess M. Restoring abandoned coppice for birds: Few effects of conservation management on occupancy, fecundity and productivity of hole nesting birds. For Ecol Manage. 2014; 330:205–217.

Burton JI, Zenner EK, Frelich LE, Cornett MW. Patterns of plant community structure within and among primary and second-growth northern hardwood forest stands. For Ecol Manage. 2009; 258:2556–2568.

Calçada EA, Lenoir J, Plue J, Broeckx LS, Closset-Kopp D, Hermy M, Decocq G. Spatial patterns of water-deposited seeds control plant species richness and composition in riparian forest landscapes. Landsc Ecol. 2015; 30:2133–2146.

Chytrý M, Tichý L, Holt J, Botta-Dukát Z. Determination of diagnostic species with statistical fidelity measures. J Veg Sci. 2002; 13:79–90.

Coleman BD, Mares MA, Willig MR, Hsieh YH. Randomness, area, and species richness. Ecology. 1982; 63:1121–1133.

Connell JH. Diversity in tropical rain forests and coral reefs. Science. 1978; 199:1302–1310. [PubMed: 17840770]

Coyle JR, Halliday FW, Lopez BE, Palmquist KA, Wilfahrt PA, Hurlert AH. Using trait and phylogenetic diversity to evaluate the generality of the stress-dominance hypothesis in eastern North American tree communities. Ecography. 2014; 37:814–826.

Decocq G, Aubert M, Dupont F, Alard D, Saguez R, Wattez-Franger A, De Foucault B, Delelis-Dusollier A, Bardat J. Plant diversity in a managed temperate deciduous forest: understorey response to two silvicultural systems. J Appl Ecol. 2004a; 41:1065–1079.

Decocq G, Valentin B, Toussaint B, Hendoux F, Saguez R, Bardat J. Soil seed bank composition and diversity in a managed temperate deciduous forest. Biodivers Conserv. 2004b; 13:2485–2509.

Dirnböck T, Grandin U, Bernhardt-Römermann M, Beudert B, Canullo R, Forsius M, Grabner M-T, Holmberg M, Kleemola S, Lundin L, Mirtl M, et al. Forest floor vegetation response to nitrogen deposition in Europe. Glob Change Biol. 2014; 20:429–440.

Dodson EK, Peterson DW, Harrod RJ. Understory vegetation response to thinning and burning restoration treatments in dry conifer forests of the eastern Cascades, USA. For Ecol Manage. 2008; 255:3130–3140.

Elemans M. Light, nutrients and the growth of herbaceous forest species. Acta Oecol. 2004; 26:197–202.

Fuller RJ, Warren MS. Coppiced woodlands: their management for wildlife. Joint Nature Conservation Committee; Peterborough, UK: 1993.

Gilliam F. Introduction: The herbaceous layer – the forest between the treesThe herbaceous layer in forests of eastern North America. Gilliam F, editorOxford University Press; Oxford, UK: 2014. 1–9.

Griffis KL, Crawford JA, Wagner MR, Moir WH. Understory response to management treatments in northern Arizona ponderosa pine forests. For Ecol Manage. 2001; 146:239–245.

Grime JP. Plant strategies, vegetation processes, and ecosystem properties. John Wiley & Sons; New York, USA: 2006.

Grulich V. Red List of vascular plants of the Czech Republic. Preslia. 2012; 84:631–645.

Hédl R, Kopecký M, Komárek J. Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. Divers Distrib. 2010; 16:267–276.

Hermy M, Honnay O, Firbank L, Grashof-Bokdam C, Lawesson JE. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. Biol Conserv. 1999; 91:9–22.

Hermy M, Verheyen K. Legacies of the past in the present-day forest biodiversity: a review of past land-use effects on forest plant species composition and diversitySustainability and Diversity of Forest Ecosystems. Nakashizuka T, editorSpringer; Japan: 2007. 361–371.

Hobbie SE. Plant species effects on nutrient cycling: revisiting litter feedbacks. Trends Ecol Evol. 2015; 30:357–363. [PubMed: 25900044]

Hölscher D, Schade E, Leuschner C. Effects of coppicing in temperate deciduous forests on ecosystem nutrient pools and soil fertility. Basic Appl Ecol. 2001; 2:155–164.

Honnay O, Degroote B, Hermy M. Ancient-forest plant species in Western Belgium: a species list and possible ecological mechanisms. Belg J Bot. 1998; 130:139–154.

Kirby KJ. Changes in the ground flora of a broadleaved wood within a clear fell, group fells and a coppiced block. Forestry. 1990; 63:241–249.

Kirby KJ, Watkins C, editorsEurope's changing woods and forests: from wildwood to managed landscapes. CABI; Wallingford, UK: 2015.

Kopecký M, Hédl R, Szabó P. Non-random extinctions dominate plant community changes in abandoned coppices. J Appl Ecol. 2013; 50:79–87.

Kubát K, Hrouda L, Chrtek jun J, Kaplan Z, Kirschner J, Št pánek J, editorsKlí ke kv ten eské republiky [Key to the flora of the Czech Republic]. Academia; Praha, Czech Republic: 2002.

Lindh BC. Flowering of understory herbs following thinning in the western Cascades, Oregon. For Ecol Manage. 2008; 256:929–936.

Matthews JD. Silvicultural systems. Oxford University Press; Oxford, UK: 1991.

Matthews TJ, Borregaard MK, Ugland KI, Borges PAV, Rigal F, Cardoso P, Whittaker RJ. The gambin model provides a superior fit to species abundance distributions with a single free parameter: evidence, implementation and interpretation. Ecography. 2014; 37:1002–1011.

Metzger F, Schultz J. Understory response to 50 years of management of a northern hardwood forest in Upper Michigan. Am Midl Nat. 1984; 112:209–223.

Muys B. The influence of tree species on humus quality and nutrient availability on a regional scale (Flanders, Belgium)Nutrient Uptake and Cycling in Forest Ecosystems. Nilsson LO, Hüttl RF, Johansson UT, editorsSpringer; Netherlands: 1995. 649–660.

Newton AC. Forest ecology and conservation: a handbook of techniques. Oxford University Press; Oxford, UK: 2007.

Neirynck J, Mirtcheva S, Sioen G, Lust N. Impact of *Tilia platyphyllos* Scop., *Fraxinus excelsior* L., *Acer pseudoplatanus* L., *Quercus robur* L. and *Fagus sylvatica* L. on earthworm biomass and physico-chemical properties of a loamy topsoil. For Ecol Manage. 2000; 133:275–286.

Pelíšek J. Stanovištní pom ry pa ezin v oblasti SR [Stand conditions in the coppices of the Czech Socialistic Republic]. Lesnictví. 1957; 3:85–108.

R Developement Core Team. R: A language and environment for statistical computing. Vienna, Austria: 2014.

Rackham O. Ancient woodland, its history, vegetation and uses in England. Castlepoint Press; Colvend, Dalbeattie, UK: 2003.

Rackham O. Woodlands. Collins; London, UK: 2006.

Radtke A, Ambraß S, Zerbe S, Tonon G, Fontana V, Ammer C. Traditional coppice forest management drives the invasion of *Ailanthus altissima* and *Robinia pseudoacacia* into deciduous forests. For Ecol Manage. 2013; 291:308–317.

Roscher C, Schumacher J, Gubsch M, Lipowsky A, Weigelt A, Buchmann A, Schmid B, Schulze E. Using Plant Functional Traits to Explain Diversity–Productivity Relationships. PLoS ONE. 2012; 7:1–11.

Savill P, Perrins C, Kirby K, Fisher N, editorsWytham Woods: Oxford's ecological laboratory. Oxford University Press; Oxford, UK: 2010.

Shugart HH. A theory of forest dynamics: the ecological implications of forest succession models. Springer; New York, NY USA: 1984.

Spitzer L, Konvicka M, Benes J, Tropek R, Tuf IH, Tufova J. Does closure of traditionally managed open woodlands threaten epigeic invertebrates? Effects of coppicing and high deer densities. Biol Conserv. 2008; 141:827–837.

Szabó P, Müllerová J, Suchánková S, Kota ka M. Intensive woodland management in the Middle Ages: spatial modelling based on archival data. J Hist Geogr. 2015; 48:1–10. [PubMed: 28503018]

Ter Braak CJF, Šmilauer P. Canoco reference manual and user's guide: software for ordination, version 5.0. Microcomputer Power; Ithaca, USA: 2012.

Thysell DR, Carey AB. Manipulation of density of *Pseudotsuga menziesii* canopies: preliminary effects on understory vegetation. Can J Forest Res. 2001; 31:1513–1525.

Thompson K, Bakker JP, Bekker RM, Hodgson JG. Ecological correlates of seed persistence in soil in the north-west European flora. J Ecol. 1998; 86:163–169.

Tichý L. JUICE, software for vegetation classification. J Veg Sci. 2002; 13:451–453.

Tilman D. Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecol Monogr. 1987; 57:189–214.

Van Calster H, Baeten L, De Schrijver A, De Keersmaeker L, Rogister JE, Verheyen K, Hermy M. Management driven changes (1967–2005) in soil acidity and the understorey plant community following conversion of a coppice-with-standards forest. For Ecol Manage. 2007; 241:258–271.

Van Calster H, Baeten L, Verheyen K, De Keersmaeker L, Dekeyser S, Rogister JE, Hermy M. Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. For Ecol Manage. 2008a; 256:519–528.

Van Calster H, Chevalier R, Wyngene B, Archaux F, Verheyen K, Hermy M. Long-term seed bank dynamics in a temperate forest under conversion from coppice-with-standards to high forest management. Appl Veg Sci. 2008b; 11:251–260.

Vesterdal L, Schmidt IK, Callesen I, Nilsson LO, Gundersen P. Carbon and nitrogen in forest floor and mineral soil under six common European tree species. For Ecol Manage. 2008; 255:35–48.

Vild O, Role ek J, Hédl R, Kopecký M, Utinek D. Experimental restoration of coppice-with-standards: Response of understorey vegetation from the conservation perspective. For Ecol Manage. 2013; 310:234–241. [PubMed: 29367802]

Warren MS, Thomas JA. Butterfly responses to coppicingEcology and management of coppice woodlands. Buckley GP, editorChapman & Hall; London, UK: 1992. 249–270.

West DC, Shugart HH, Botkin DF. Forest succession: concepts and application. Springer-Verlag; New York, USA: 2012.

Web resources

web 1: http://de.climate-data.org/location/702451/

web 2: http://mapy.geology.cz/geocr_50

web 3: http://mapy.geology.cz/pudy

web 4: http://www.eea.europa.eu/data-and-maps/figures/natura-2000-sites-biogeographical-regions-4
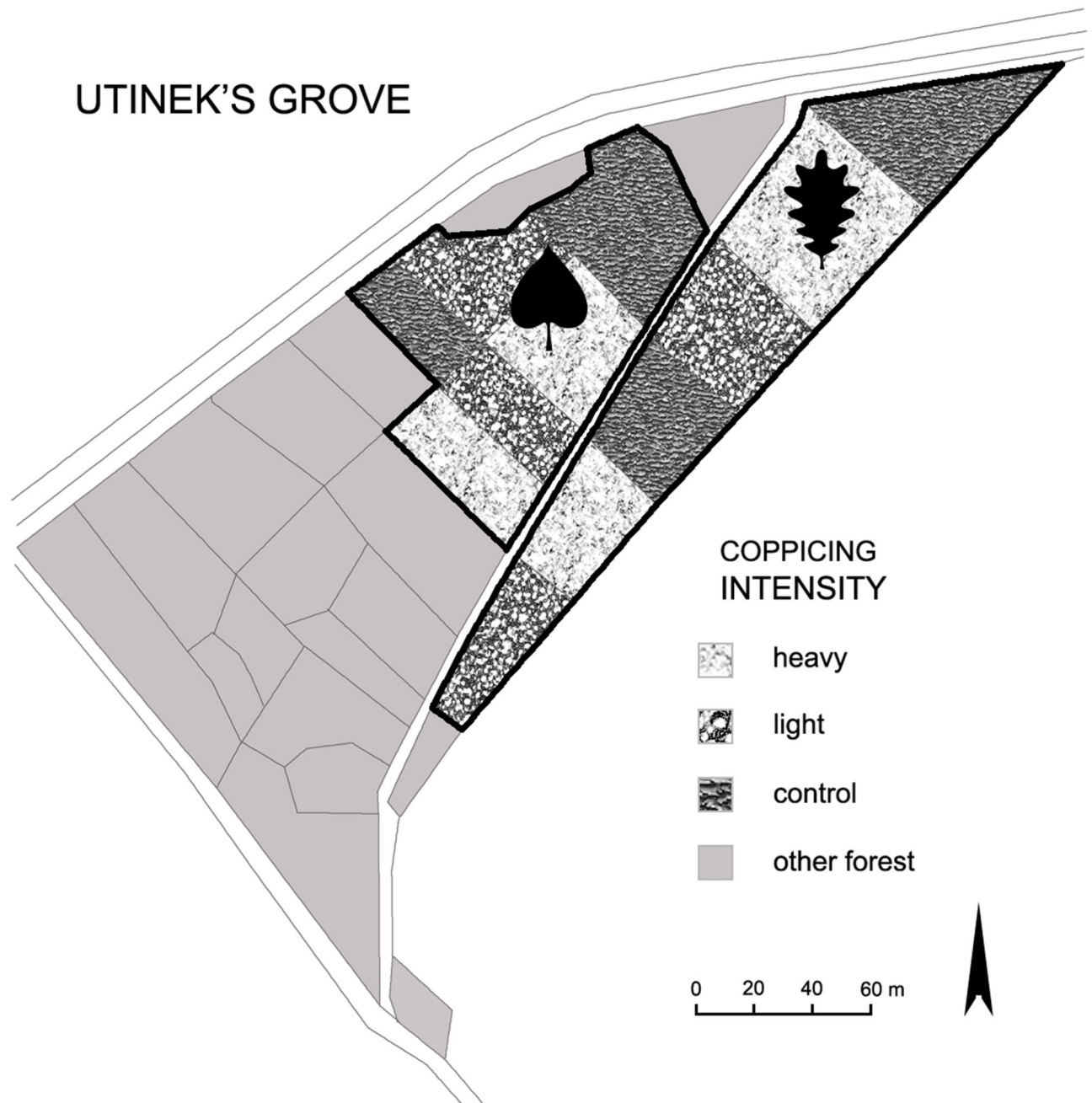
Fig. 1.
Schematic map of the Utinek's Grove with the coppice introduction experiment.
Compartments with different tree canopy thinning intensities (visualized by filling pattern)
in parts dominated by oak and lime (leaf symbols) are depicted. Each compartment contains
a 30m-long transect with four annually sampled plots.
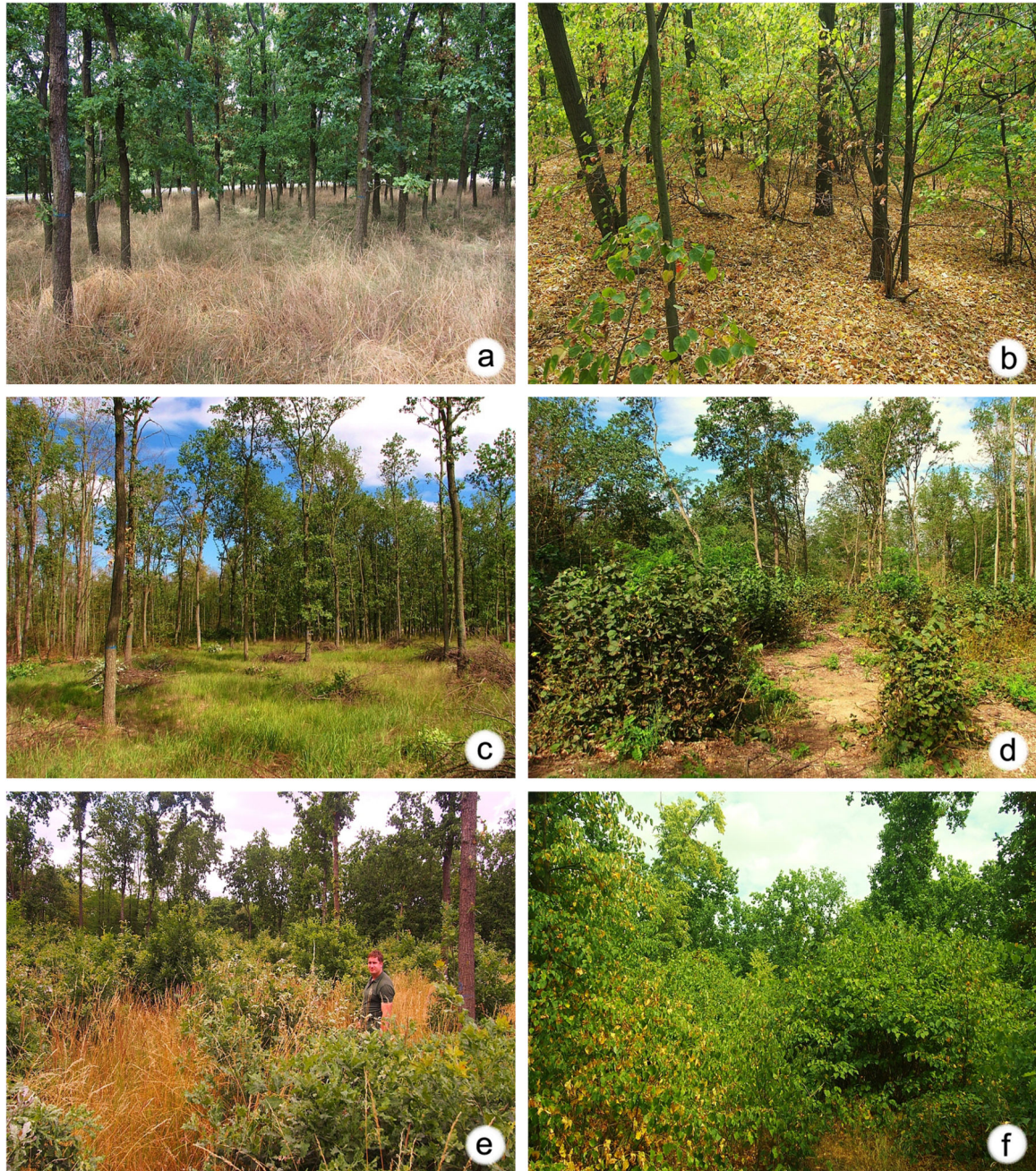
Fig. 2.
Pictures showing examples of forest compartments with increasing canopy thinning intensity: a) and b) controls, c) and d) light-thinned, e) and f) heavy-thinned forest. Left-side column (a, c and e) is from oak-dominated stands, while right-side column (b, d and f) shows lime-dominated stands. Note the differences in herbaceous layer cover and resprouting of coppiced trees.
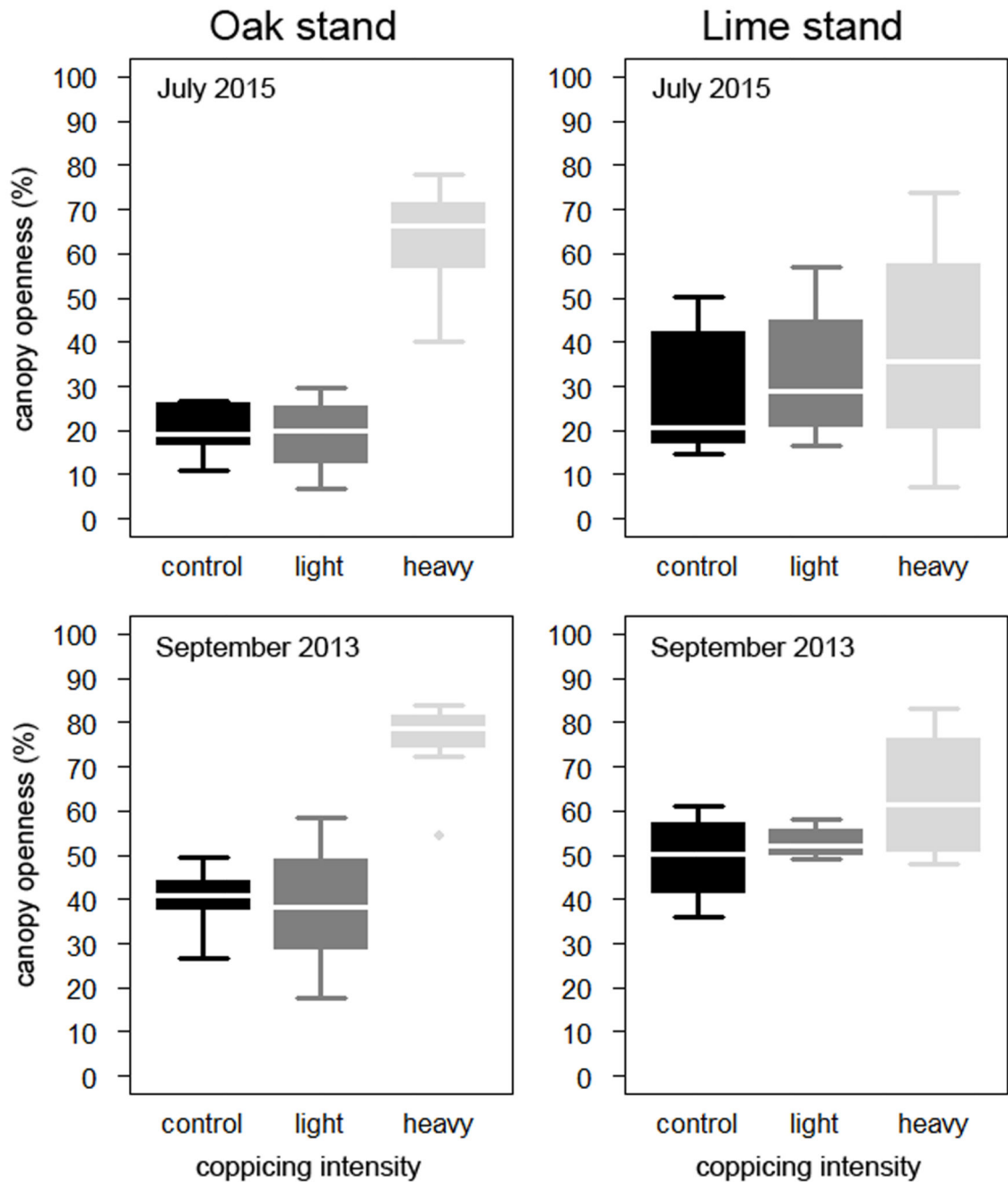
Fig. 3.
Canopy openness patterns in oak- and lime-dominated stands and under different canopy thinning intensities. Closure has gradually increased between 2013 (2nd year) and 2015 (4th year of the thinning experiment) reflecting the process of tree regeneration from resprouting, but possibly also an effect of sampling season.
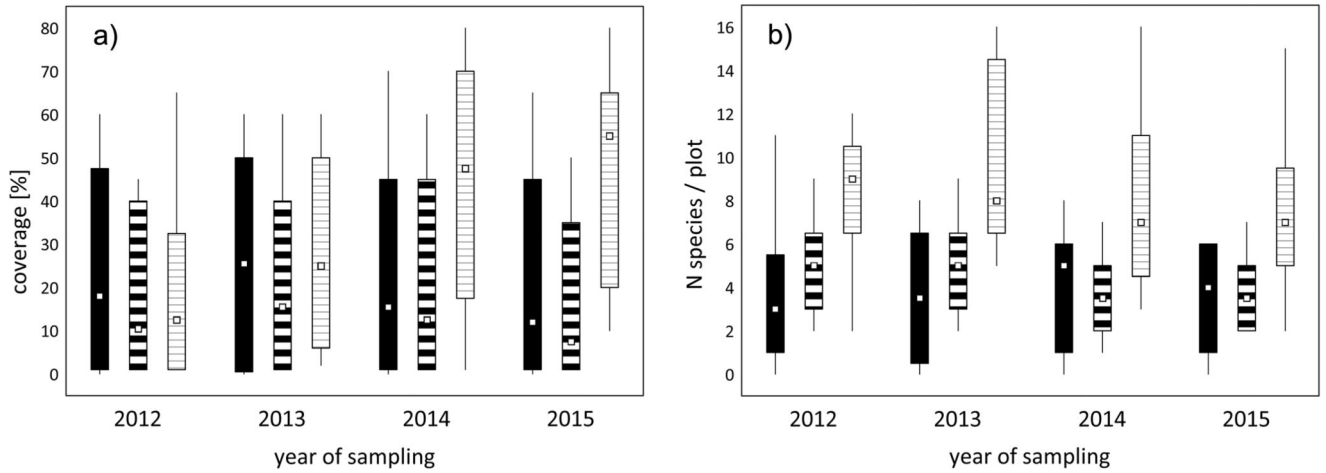
Fig. 4.
Temporal development in 2012 to 2015 of the herbaceous layer coverage (a) and total species richness (b) relative to canopy thinning intensity. Coverage significantly increased mainly due to heavily thinned plots, while species richness showed a slowly decreasing trend.
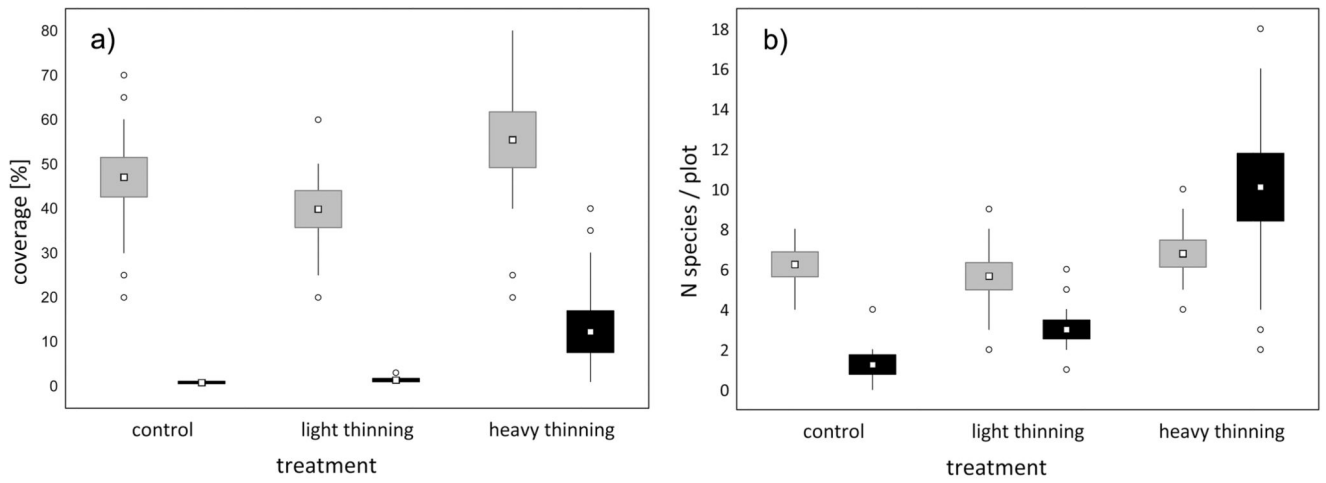
Fig. 5.
Effects of canopy thinning on herbaceous layer coverage (a) and total species richness (b). Strong increase following thinning can be observed for both parameters in lime-dominated forest compartments, while oak-dominated stands were not influenced.
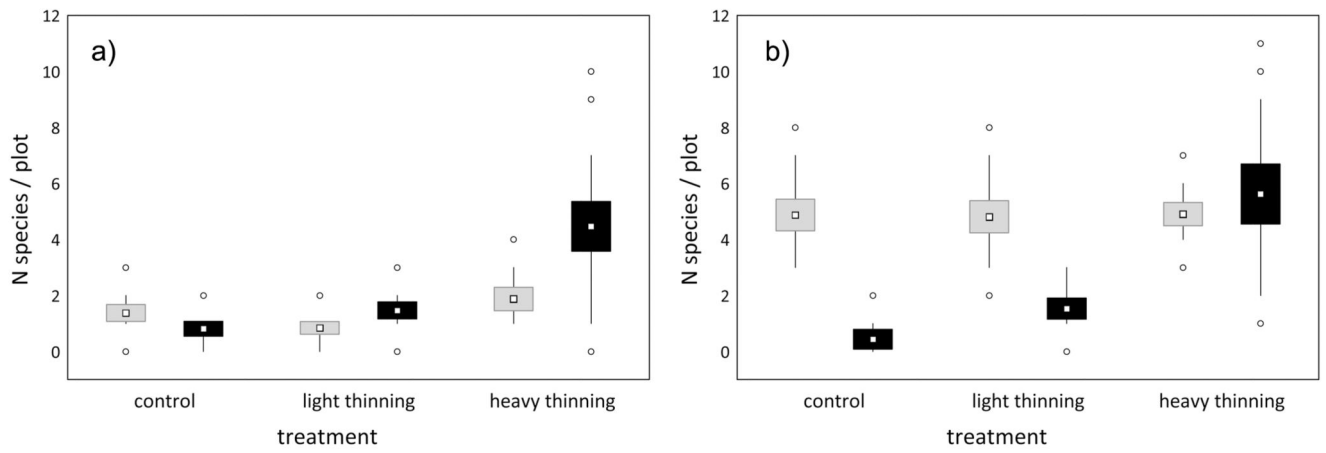
Fig. 6.
Partitioning patterns in species richness for short-lived (a) and long-lived (b) species. While the patterns did not differ much under lime, the two groups showed unequal richness in oak-dominated forest compartments.
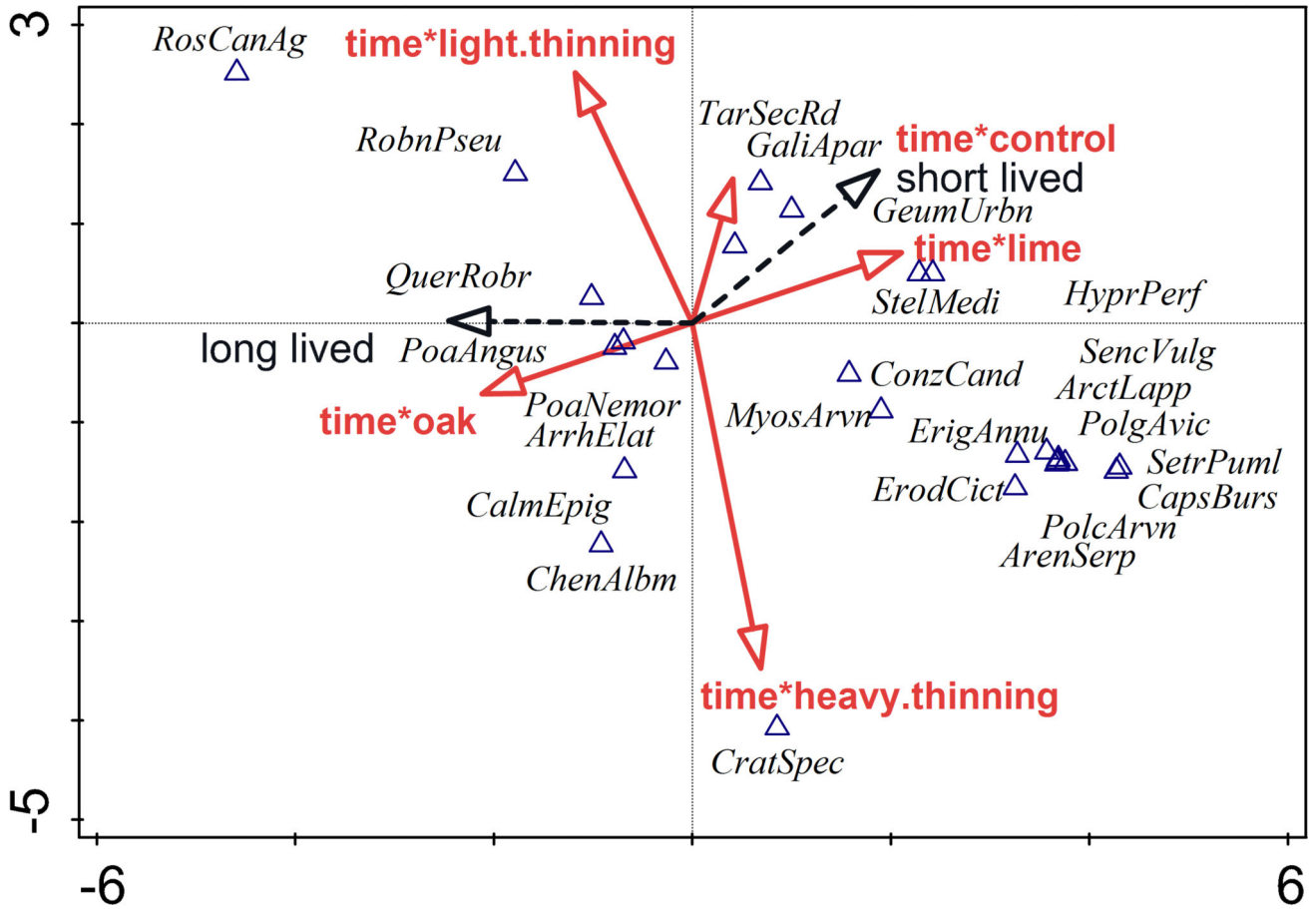
Fig. 7.
Temporal effects of tree thinning and dominant species on herbaceous vegetation composition with passively projected species life cycle traits. The two factors were relatively independent from each other. Heavy thinning led to different species composition than control and light thinning. Most of the twenty best fitting species were associated with lime overstory (for full species names see Table 3).

Fig. 8.
Combined effects of dominant tree species and thinning intensity on herbaceous layer composition with passively projected life cycle traits. Oak stands were similar regardless of thinning intensity, while lime stands differed among each other. Most species were associated with heavily thinned lime-dominated plots (for full species names see Table 3).

Table 1

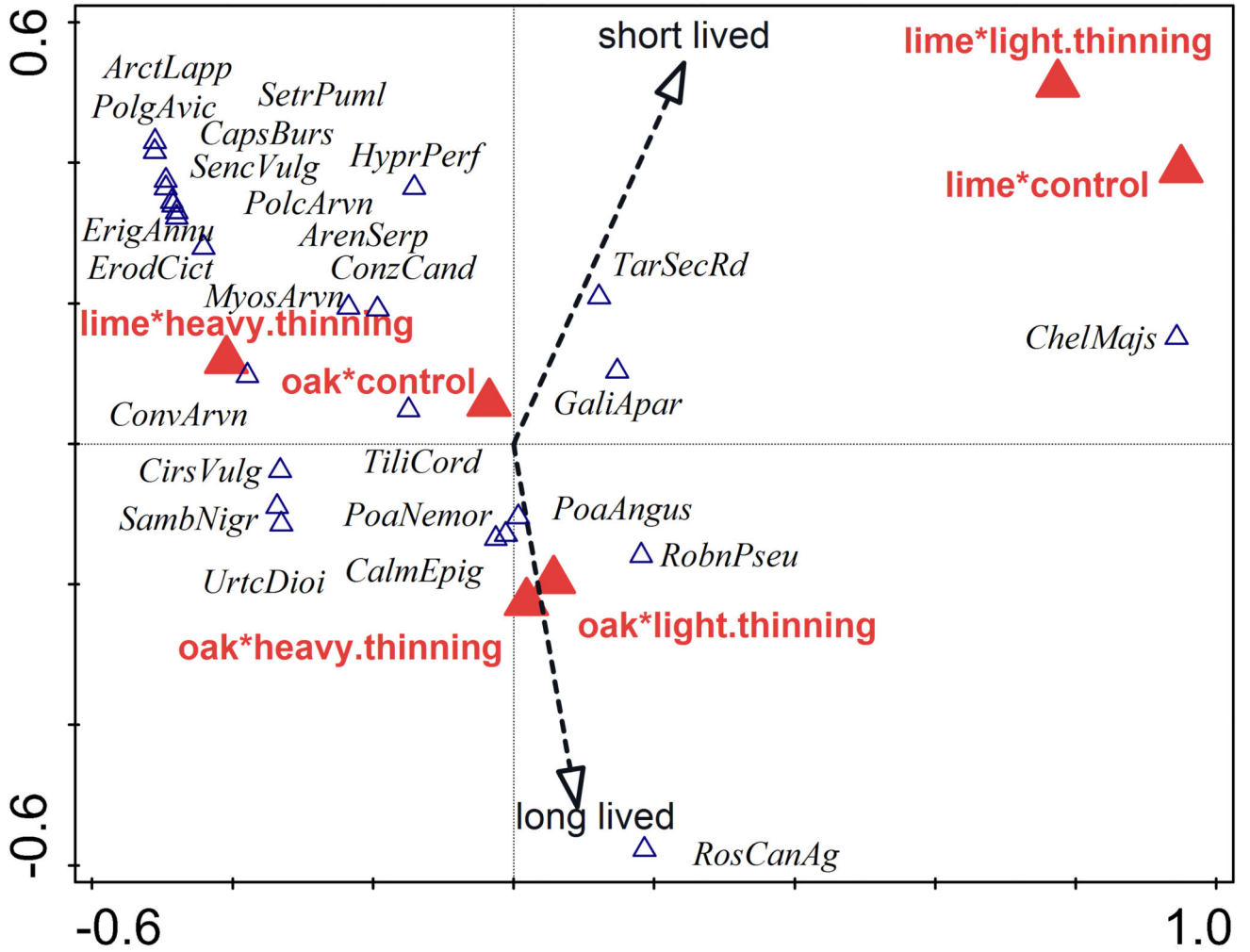Results of likelihood-ratio test generalized linear mixed models (GLMM) which compared the full models to the reduced ones by the particular factors. Sampling plots nested within compartment were used as random variable. Response variable of: GLMM1 was herb cover, GLMM2 total species richness, GLMM3 species richness of short-lived species and GLMM4 species richness of long-lived species.

model	combination	Df	AIC	LRT	Pr(Chi)
GLMM 1	full model		121.8		
	year	3	152.4	36.6	<0.001
	treatment	2	130.8	12.9	0.002
	tree species	1	157.9	38.0	<0.001
	full model		18.6		
	year : treatment : tree species	6	23.7	17.1	0.009
GLMM 2	full model		832.8		
	year	3	835.4	8.6	0.035
	treatment	2	837.5	8.6	0.013
	tree	1	835.7	4.9	0.028
	full model		810.2		
	year	3	812.7	8.6	0.035
	treatment : tree species	2	832.8	26.7	<0.001
GLMM 3	full model		718.6		
	year	3	726.6	14.0	0.003
	treatment	2	722.0	7.4	0.025
	tree species	1	725.2	8.5	0.003
	full model		573.7		
	year	3	568.1	0.4	0.939
	treatment : tree species	2	582.8	13.0	0.001
GLMM 4	full model		743.9		
	year	3	751.9	14.0	0.003
	treatment	2	749.4	9.4	0.009
	tree species	1	770.6	28.6	<0.001
	full model		692.3		
	year	3	700.22	14.0	0.003
	treatment : tree species	2	718.63	30.4	<0.001

Table 2

Significance of individual explanatory variables in the CCA models. Interactions between factors are in descending order following explained variability. Each variable was tested separately to estimate its independent effect. Adjusted p-values were calculated by Holm correction.

variable	variability explained	pseudo-F	p	p (adj.)
CCA1				
year × lime	2.0	3.9	0.045	0.076
year × oak	2.0	3.9	0.045	0.076
year × heavy thinning	1.6	3.0	0.142	0.178
year × light thinning	1.0	2.0	0.460	0.460
year × control	0.7	1.3	0.012	0.060
CCA2				
lime × heavy thinning	2.9	5.6	0.024	0.048
oak × heavy thinning	0.9	1.8	0.002	0.009
lime × light thinning	2.0	3.8	0.811	0.811
oak × light thinning	0.8	1.4	0.002	0.009
lime × control	1.6	3.1	0.005	0.015
oak × control	0.5	1.0	0.002	0.009

Table 3

Indicator species for six variants by combinations of dominant tree species (oak, lime) and thinning intensity (C: control, L: light thinning, H: heavy thinning). Values of phi-coefficient, a measure of fidelity, are displayed. Only species with phi-coefficient >20 in at least one group are included. Species with values ≥ 25 are highlighted in grey.

	oak			lime		
	C	**L**	**H**	**C**	**L**	**H**
Vicia hirsuta+tetrasperma	47	.	.	.	.	.
Portulaca oleracea	23	.	.	.	.	.
Carex praecox	23	.	.	.	.	.
Rosa canina agg.	.	33	.	.	.	.
Crataegus species	.	.	23	.	.	.
Galium aparine	1	.	20	.	4	.
Alliaria petiolata	.	.	.	.	28	.
Conyza canadensis	.	.	.	.	1	57
Convolvulus arvensis	.	.	.	.	.	55
Urtica dioica	.	.	.	.	.	47
Anagallis arvensis	.	.	.	.	.	43
Arenaria serpyllifolia	.	.	.	.	.	43
Cirsium vulgare	.	.	.	.	.	40
Epilobium tetragonum	.	.	.	.	.	40
Capsella bursa-pastoris	.	.	.	.	.	37
Sambucus nigra	.	.	.	.	.	37
Euphorbia esula	.	.	.	.	.	37
Cirsium arvense	.	.	.	.	.	36
Erigeron annuus	.	.	.	.	.	33
Senecio vulgaris	.	.	.	.	.	33
Ballota nigra	.	.	.	.	.	32
Chenopodium hybridum	.	.	.	.	.	28
Polycnemum arvense	.	.	.	.	.	28
Elymus caninus	.	.	.	.	.	28
Potentilla reptans	.	.	.	.	.	28
Stellaria media	.	.	.	5	.	27
Medicago lupulina	.	.	3	.	3	23
Arctium lappa	.	.	.	.	.	23
Erodium cicutarium	.	.	.	.	.	23
Setaria pumila	.	.	.	.	.	23
Stachys annua	.	.	.	.	.	23
Lapsana communis	.	.	.	.	.	23
Tilia cordata	.	19	.	.	.	40
Chenopodium album	.	.	23	.	.	17
Trifolium arvense	.	.	10	.	.	23

	oak			lime		
	C	L	H	C	L	H
Myosotis arvensis	.	.	9	.	.	41
Taraxacum sect. *Ruderalia*	.	.	.	.	28	45
Geum urbanum	.	.	.	.	17	30
Hypericum perforatum	.	.	.	.	8	39
Arrhenatherum elatius	36	42	36	.	.	.
Poa angustifolia	36	24	44	.	.	.
Poa nemoralis	35	29	35	.	.	.
Dactylis glomerata	29	13	16	.	.	.
Calamagrostis epigejos	23	12	51	.	.	.
Quercus robur	8	28	12	.	.	.