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Experimental restoration of coppice-with-standards: Response of understorey vegetation from the conservation perspective

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ABSTRACT

A substantial part of European lowland woodlands was managed as coppices or wood pastures for millennia. However, traditional management forms were almost completely abandoned in Central Europe by the middle of the 20th century. Combined with the effects of nitrogen deposition and herbivore pressure, shifts in management resulted in biodiversity loss affecting particularly light-demanding oligotrophic plant species. Experimental thinning was applied in a former oak coppice-with-standards in an attempt to restore vanishing understorey plant communities. Two levels of thinning intensity and zero management as control were used on 90 plots. Ten years after the treatment, significant changes in species composition and diversity were observed in heavily thinned plots, while moderate thinning had mostly insignificant effects. Light-demanding oligotrophic species significantly increased, indicating positive consequences of restoration. However, heavy thinning also brought about the expansion of native ruderal species. Alien species remained unchanged. We conclude that the restoration of coppice-with-standards can be an efficient tool to support vanishing light-demanding woodland species. Combined with biodiversity benefits, the increasing demand for biofuel may contribute to the renaissance of traditional management forms in forestry.

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1. Introduction

A large part of European temperate lowland woodlands was historically managed as coppices or wood pastures (Bergmeier et al., 2010; Rackham, 2003). Retaining a certain density of standards (trees of generative origin) was a common feature in coppice woods, creating a structural and management type called coppice-with-standards. These woodlands were characterized by periodic harvests of coppice underwood removing substantial amounts of nutrients with the woody biomass. Frequent alternation of light and shady phases providing a patchwork of contrasting habitats was also typical for coppice woods (Ash and Barkham, 1976; Hölischer et al., 2001; Tybirk and Strandberg, 1999; Van Calster et al., 2008a). Such human impact has co-shaped European woodlands into specific ecosystems (Rackham, 2008).

In central and northwestern Europe, coppicing was almost completely abandoned by the 1940s due to changes in socio-economic

conditions (Puettmann et al., 2008; Szabó, 2010). The extension of the cutting cycle resulted in prolonged periods of canopy closure, decreased light availability in the understorey and a consequent decline in biodiversity. The composition of vascular plants changed following various species traits (Naaf and Wulf, 2011) in favour of shade-tolerant and nutrient-demanding species at the expense of light-demanding oligotrophic species (Baeten et al., 2009; Hédli et al., 2010; Naaf and Wulf, 2011; Verheyen et al., 2012). A similar composition shift was observed in animal communities including invertebrates (Grundel et al., 1998; Spitzer et al., 2008; Verschuyt et al., 2011) and birds (Fuller and Henderson, 1992). Apart from the turn in woodland management from traditional methods to modern forestry, atmospheric deposition of nitrogen (Bobbink et al., 1998) and the increase in herbivore pressure (Chytrý and Danihelka, 1993; Hopkins and Kirby, 2007) have probably played important roles in the change from open-canopy, species-diverse forests to the present shady, nitrogen-saturated and species depleted forests.

It has been suggested that the biodiversity of coppices-with-standards can be restored and maintained by the re-introduction of traditional management (Barkham, 1992; Hermy et al., 1999; Kopecký et al., 2013). Particularly light-demanding species are expected to be supported by increased light availability in the understorey (Kopecký et al., 2013). There have been several

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successful restoration-motivated attempts to sustain declining invertebrate species (Broome et al., 2011; Buckley, 1992; Warren, 1987). However, fewer studies focused on the impact of coppice restoration on understorey plant species. A similar field experiment was conducted in Białowieża forest, where selective cutting of expanding hornbeam (*Carpinus betulus*) reversed a long-term trend and helped to restore an open-canopy oak forest community (Kwiatkowska and Wyszomirski, 1990).

However, the restoration of traditional management can also have adverse effects. Canopy opening increases soil surface temperature and therefore microbial activity (Concilio et al., 2005; Howson, 1988; Ryu et al., 2009), resulting in increased nutrient availability (Binkley, 1984; Inagaki et al., 2008; Vitousek and Melillo, 1979). This may stimulate the spread of nutrient-demanding, competitively strong species, some of which have alien and invasive species status (e.g., Radtke et al., 2013). This process threatens the conservation value of woodland vegetation. Soil disturbances caused by thinning operations may also promote ruderal species further devaluating the conservation value of affected woodlands (Battles et al., 2001; Decocq et al., 2004; Thomas et al., 1999).

To improve our knowledge about the outcomes of coppice-with-standards restoration, we conducted a restoration experiment in a central European lowland oakwood. Our aim was to describe how various thinning intensities change woodland structure and species composition on a gradient from a dry acidophilous oakwood to a mesic mixed oakwood. We particularly aimed at answering the question whether coppice-with-standards restoration is a viable way to restore vanishing plant communities. To emphasize conservation implications, we focused on light-demanding oligotrophic species, i.e. the group showing perhaps the most dramatic decline in European lowland forests. These species are not confined to woodlands, some also occur in open habitats, but not in ruderal sites. To assess the potentially negative effects of coppice-with-standards restoration, we also analysed the response of native ruderal and alien species.

2. Methods

2.1. Study site

The study site is Krumlov Wood in the southeastern part of the Czech Republic (16°22'N, 49°03'E). This region comprises a high proportion of light, oak-dominated woodlands hosting a variety of species. Shortly after the abandonment of coppice management, these woodlands harboured a high number of light-demanding oligotrophic species, including many recently endangered species (Hédli et al., 2010; Kopecký et al., 2013). The restoration potential of such sites, including Krumlov Wood, appears to be high. Krumlov Wood (35 km²) is composed mainly of oak and oak-hornbeam communities. They range from acidophilous oakwoods dominated by sessile oak (*Quercus petraea* agg.) to mesic oakwoods with an admixture of lime (*Tilia cordata*), European hornbeam (*Carpinus betulus*) and pedunculate oak (*Quercus robur*). Altitude varies between 278 and 415 m a.s.l. Climatically the Wood belongs to a relatively warm and dry part of Central Europe, located near the northwestern fringe of the Pannonian Basin. The mean annual temperature and precipitation are 8–9 °C and 500–550 mm, respectively (Tolasz, 2007). The prevailing bedrock is biotitic granodiorite; calcareous sediments are locally present. The most common soil types are cambisols and luvisols. The first written record about the Krumlov Wood dates back to 1369. The Wood was mainly used as a source of firewood (Kvasová et al., 1970) partly as wood-pasture. Nowadays the Wood is composed mainly of trees of seed origin older than 110 years (former standards) and trees of

vegetative origin (former coppices), 60–90 years old (Utinek, 2004a).

2.2. Experimental design

The field experiment was established in 1999 in the abandoned coppice-with-standards converted into high forest. We examined how the restoration of the active coppice-with-standards management influences the radial increment of remaining oak individuals, i.e. “standards” in the coppice-with-standards management system (Utinek, 2004a). The experimental design includes 90 plots divided into six ecologically distinct localities. In each locality, 15 plots with two levels of thinning intensity and 15 control plots with no thinning intervention were established using the counter-balanced measures design (Fig. 1; Utinek, 2004a, 2004b). Control plots were regarded to represent the initial conditions. Each locality contains five replicates of each treatment. The experimental design is therefore a two-factorial one, with the factors “locality” and “thinning intensity”. Because of the lack of data documenting the pre-treatment vegetation, treatment effects were assessed by the differences between treatment and control plots.

The plots are circles of 10 m radius. A special type of tree thinning was applied once at the beginning of the experiment. The goal was to simulate the tree structure characteristic for coppice-with-standards (Troup, 1924). Economically viable mature trees (mainly oaks) were retained, whereas other individuals of different species were harvested (Fig. A.1); hornbeam and lime were completely eliminated from the heavily thinned plots where present. The average number of trees (DBH > 4 cm) before felling was 830 ha⁻¹ with a basal area of 28.6 m² ha⁻¹ (Utinek, 2004a). Mean tree density was reduced on average by 25% to 519 individuals ha⁻¹ during the moderate thinning treatment and by 70% to 141 individuals ha⁻¹ during the heavy thinning treatment. Similarly, basal area was reduced on average by 34% to 21.3 m² ha⁻¹ after moderate thinning and by 83% to 8.5 m² ha⁻¹ after heavy thinning.

2.3. Data collection

To capture the intensity of thinning, tree diameter at breast height (DBH > 4 cm) was measured in the circular plots using a girthing tape before thinning in 1999 and after thinning in 2001. Vegetation composition was sampled during the summer of 2009 in 10 × 10 m plots placed in the centers of the circular plots (Fig. 1). All vascular plants in the understorey layer (below 3 m of height) were recorded. Nomenclature follows Kubát et al. (2002). Percentage cover of the herb layer (0–0.5 m) and the cover-abundance of each species were visually estimated on a 9° Braun-Blanquet scale (Dengler et al., 2008). For data analyses, these values were

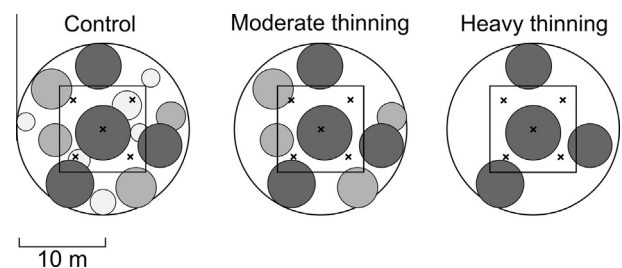


Fig. 1. Schemes of the three thinning treatments. Left: control (no intervention); center: moderate thinning (the smallest trees removed); right: heavy thinning (most trees removed, a few big trees retained). Grey circles represent individual trees. The outer circle delimits the extent of the thinned plot (10 m radius); the inset square shows the position of the vegetation sample plot (10 × 10 m). Crosses indicate locations where soil samples and hemispherical photographs were taken.

transformed into mid percentage values of each cover interval. The percentage cover of both vegetative (from stumps) and generative (from seeds) tree regeneration was visually estimated.

Hemispherical photographs were taken in 2009 to measure light availability in the understorey. Nikon FC-E8 fish-eye lens was used with fully automatic setting. Five shots were taken 1 m above ground (see Fig. 1). The photographs were processed in the Sidelook programme, where black and white pixels were distinguished using an automatic algorithm (Nobis and Hunziker, 2005). Canopy openness was calculated from the proportion of black and white pixels in the Gap Light Analyzer programme (Frazer et al., 1999). We used the average value from five individual measurements as canopy openness for each plot.

To assess the possible effect of variation in environmental conditions among localities, soil samples were collected in autumn 2009 from the topsoil on each 10 × 10 m plot. They consisted of five subsamples taken in the center and near each corner (Fig. 1). Litter was carefully removed and soil was sampled to the depth of 5 cm, regardless of soil horizons. Fresh soil was air dried at room temperature, sieved to 2 mm fraction and analysed. Total carbon and inorganic nitrogen were measured in 0.1 mm fraction of mixed samples. Available phosphorus was determined colorimetrically in mixed samples prepared with 1 M solution of sodium bicarbonate at pH 8.5. Content of cations (Ca²⁺, Mg²⁺, K⁺) was determined from mixed samples in extraction Mehlich II. Soil acidity (pH in H₂O) was measured in the five subsamples from each plot. A suspension of 20 g of dried soil and 50 ml of distilled water was shaken and measured using glass electrodes.

2.4. Data analysis

2.4.1. Structural differences

Canopy openness, cover of shrub, herb and tree regeneration were compared between differently thinned plots through permutation based Kruskal–Wallis test implemented in the *coin* package (Hothorn et al., 2006) for R, ver. 2.14 (R Development Core Team, 2012). In case of a significant ($p < 0.05$) result, Wilcoxon pair test from the *coin* package adjusted by Bonferroni correction was used to test differences between the control and individual thinning treatments. Statistical significance in both tests was evaluated by a randomization test based on 999 permutations restricted to blocks defined by localities.

2.4.2. Plant species composition

Differences in species composition between treatments were tested through Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson, 2001) on dissimilarity matrix calculated with Bray–Curtis index from square-rooted percentage cover data first standardized by species maxima and then by sample totals (i.e. Wisconsin double standardization). To account for the differences among localities, we used 999 permutations restricted to blocks defined by localities. Significant results in PERMANOVA can reflect directional changes in species composition or differences in compositional heterogeneity (Anderson, 2001). To separate these effects, we performed an analysis of multivariate homogeneity of group dispersions (PERMDISP; Anderson et al., 2006) on the same dissimilarity matrix and with the same permutation scheme as used in PERMANOVA. To assess the site specific reaction of vegetation to experimental treatments, we tested the interaction between treatment and locality through PERMANOVA with split-plot permutations – treatments were randomly shuffled within localities, while localities were randomly shuffled as blocks. These analyses were done with the *adonis* and *betadisp* functions from the *vegan* package (Oksanen et al., 2012) and the *shuffle* function from the *permut* package for R (Simpson, 2013).

To visualize variation in species composition, we performed two-dimensional Non-metric Multidimensional scaling (NMDS) on the same dissimilarity matrix as was used in PERMANOVA (function *metaMDS* from the *vegan* package). To facilitate the interpretation of the resulting ordination, we related environmental and structural variables to ordination axes through the *envfit* function from the *vegan* package.

2.4.3. Restoration success

Restoration success was analysed focusing on species richness and on the occurrence of several functional groups of species. First, the frequency of light-demanding oligotrophic species was evaluated. They were defined as species with Ellenberg indicator values for *light* ≥ 6 and *nutrients* ≤ 4 (Ellenberg et al., 1992); ruderal species, defined as species with *urbanity* value ≥ 3 in the BIOLFLOR database (Klotz et al., 2002), were excluded. Second, the plot frequency of ruderal species was used as a measure of ruderalization. Third, the number of alien species was assessed using the list of species alien to the Czech Republic (Pyšek et al., 2012). Finally, to detect whether coppice-with-standards restoration also affects shade-tolerant forest species, we defined these as species with values for *light* ≤ 4 and *urbanity* ≤ 2 . The treatments were compared using the same approach we used for testing structural differences.

To evaluate species-specific responses, species fidelity to each experimental treatment expressed as phi coefficient (Chytrý et al., 2002) was calculated using multilevel pattern analysis (De Cáceres et al., 2010) from the *indicspecies* package (De Cáceres and Legendre, 2009). Species fidelity was calculated on presence-absence data and its significance was tested through a randomization test based on 999 permutations restricted within individual localities.

3. Results

3.1. Stand structure

Ten years after the experimental treatment, moderately thinned plots still had a more open canopy than control plots (by 6.8% on average), while heavily thinned plots were substantially more open than control plots (by 17.8% on average). Increased light availability resulted in vigorous woody regeneration and heavy thinning was followed by a 12-fold increase in the shrub layer (Table 1). Herb layer cover increased less following moderate thinning, while it increased significantly (on average by 1.6-times) after heavy thinning.

3.2. Plant species composition

The restoration treatment resulted in significant changes in species composition (PERMANOVA, $F = 2.14$, $p = 0.001$). This effect was caused by directional changes in species composition rather than by the differences in compositional heterogeneity among treatments (PERMDISP, $F = 0.03$, $p = 0.97$). Differences in species composition were not significant between control plots and moderate thinning (PERMANOVA, $F = 0.94$, $p = 0.06$). However, species composition on plots subjected to heavy thinning differed significantly from that on control plots ($F = 1.99$, $p = 0.001$). The interaction between treatment and locality was insignificant (PERMANOVA, $F = 1.06$, $p = 0.38$), indicating a similar vegetation response to restoration treatments in spite of differences in environmental conditions between localities (Fig. 2, Table A.1).

The first axis of the NMDS ordination represents the environmental gradient from mesic to acidophilous habitats and clearly separates plots at different localities (Fig. 2). The second NMDS axis is correlated with changes in basal area and represents

Table 1

Comparison of characteristics of understorey structure, species diversity and restoration success indicators among three thinning treatments. Mean values and standard deviations are shown. The effect of treatments was evaluated using Kruskal–Wallis test. Pair-wise comparison (Wilcoxon test) between control plots and each thinning treatment was done only in case of a significant overall effect. *P*-values were adjusted by Bonferroni correction.

Variable	Control	Moderate thinning	Wilcoxon test, Z and <i>p</i> -value	Heavy thinning	Wilcoxon test, Z and <i>p</i> -value	<i>K</i> – <i>W</i> test, <i>p</i> -value
<i>Structural variables</i>						
Canopy openness (%)	14.6 ± 1.9	15.6 ± 1.7	–2.09; 0.074	17.2 ± 3.2	–3.79; <0.001	<0.001
Shrub layer (cover, %)	1.8 ± 2.8	5.3 ± 7.7	–2.63; 0.014	21.5 ± 22	–5.89; <0.001	<0.001
Tree regeneration (cover, %)	10.7 ± 8.2	15.0 ± 8.7	–2.59; 0.016	32.2 ± 19.5	–5.49; <0.001	<0.001
Herb layer (cover, %)	23.8 ± 12.3	29 ± 9.4	–1.97; 0.098	37.4 ± 15.3	–3.46; <0.001	<0.001
<i>Species diversity</i>						
Species richness (N plot ^{–1})	27.9 ± 9.9	29.9 ± 9.5	–1.43; 0.312	34.7 ± 11.3	–3.64; <0.001	<0.001
<i>Restoration success</i>						
Light-demanding oligotrophic species (N plot ^{–1})	2.6 ± 2.3	2.9 ± 1.8	–1.21; 0.47	3.9 ± 2.3	–2.97; 0.005	0.007
Shade tolerant species (N plot ^{–1})	5.5 ± 2.5	5.4 ± 2.5	–	6.0 ± 2.7	–	0.272
Native ruderal species (N plot ^{–1})	3.4 ± 1.6	4.2 ± 2.2	–1.45; 0.296	5.6 ± 2.4	–4.09; <0.001	<0.001
Alien species (N plot ^{–1})	1.2 ± 1.1	1.4 ± 1.2	–0.93; 1	1.5 ± 1.3	–0.63; 1	0.648

compositional differences among the treatments. The pattern of the “shift” from control plots through moderately towards heavily thinned plots is similar among the localities and shows a trend in the restoration treatment. The NMDS diagram also reflects the insignificant effect of the interaction between thinning treatment and locality on understorey species composition.

3.3. Restoration success

The total number of species (gamma diversity) differed between the experimental treatments, increasing from control to moderately and heavily thinned plots (124, 130 and 155 species, respectively). The number of species per plot (alpha diversity) showed a statistically significant difference between control and heavily thinned plots (27.9 and 34.7 species per plot on average,

respectively), but not between control and moderately thinned plots (Table 1).

An increase in the group of light-demanding oligotrophic species was observed (Table 1). The effect of heavy thinning was strong, while the effect of moderate thinning was not significant. Similarly, the number of ruderal species significantly increased in the heavily but not in the moderately thinned plots (Table 1). Several scattered alien species were recorded, four of them neophytes (*Robinia pseudacacia*, *Conyza canadensis*, *Impatiens parviflora* and *Erigeron annuus*), but their frequency did not differ among treatments. The frequency of shade-tolerant forest species did not change, either.

Eleven species were significantly associated with individual thinning treatments or their combination (Table 2). Seven species, mainly ruderals, were associated with heavy thinning, while three species were associated with both thinning treatments (Table 2). Only *Hieracium sabaudum* s.lat. was significantly associated with control plots.

4. Discussion

4.1. Species composition changes after coppice-with-standards restoration

Light is the main limiting factor in most broadleaved woodlands (Hofmeister et al., 2009) and species respond to increased light availability by increased growth and reproduction (Van Calster

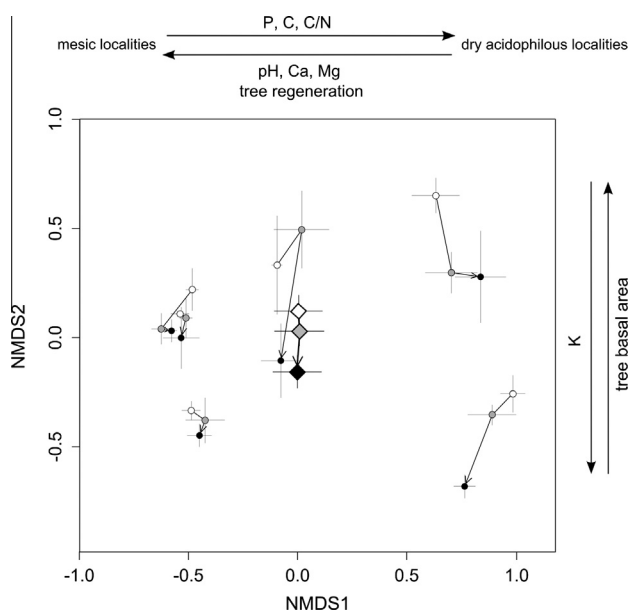


Fig. 2. NMDS diagram showing differences between localities and thinning treatments. Centroids (±SE) of all plots (diamonds) and of six studied localities (circles) are displayed. Centroids of control plots are white, centroids of moderately thinned plots are grey and centroids of heavily thinned plots are black. Variables significantly correlated with the first (NMDS1) or second (NMDS2) axes are shown. The general pattern is similar among localities reflecting an insignificant effect of interaction between thinning treatment and locality on understorey species composition.

Table 2

List of herb species most strongly related to experimental treatments. Species are sorted decreasingly according to the fidelity value (phi coefficient) and treatment. Species fidelity to each treatment is marked by bolded values. The frequency (number of occurrences) of each species in each group is given. Species characteristics are marked using upper case characters: a – light-demanding oligotrophic species, b – shade-tolerant species, c – ruderal species.

Species name	Heavy t.	Moderate t.	Control	Phi
<i>Urtica dioica</i> ^c	10	1	1	42
<i>Calamagrostis epigejos</i> ^c	10	2	1	38
<i>Scrophularia nodosa</i> ^b	16	3	9	34
<i>Hypericum perforatum</i> ^c	17	9	6	31
<i>Agrostis capillaris</i> ^c	11	5	2	29
<i>Cirsium arvense</i> ^c	5	1	0	28
<i>Veronica chamaedrys</i> agg.	15	9	5	27
<i>Fragaria vesca</i>	11	7	2	26
<i>Clinopodium vulgare</i> ^a	8	8	2	24
<i>Vicia hirsuta</i> s. lat.	4	4	0	22
<i>Hieracium sabaudum</i> s.lat.	12	9	18	24

et al., 2008b; Lindh, 2008; Lindh and Muir, 2004). The increase in tree regeneration after thinning probably partly limited the increase in herb layer cover and influenced plant species composition changes.

The increase in species richness is significant and consistent with the results of most thinning experiments (Ares et al., 2009; Thomas et al., 1999; Thysell and Carey, 2001; Verschuyt et al., 2011). The increase in light-demanding oligotrophic species indicates that restoration of coppice-with-standards may be an efficient tool to support vanishing woodland biodiversity. Higher intensities of overstorey thinning appear to be more beneficial for conservation purposes, in spite of the risk of the expansion of ruderal species discussed below. Such positive effect of thinning on light-demanding oligotrophic species was reported also from Białowieża forest in Poland (Kwiatkowska and Wyszomirski, 1990). The lack of differences in the frequency of shade-tolerant species (Table 1) and the association of a single species with control plots (Table 2) suggest that species loss caused by thinning was small and shade-tolerant species were able to sustain the environmental changes caused by experimental treatment. This is consistent with observations during a coppice cycle, when shade-tolerant species remained in the initial stage (Ash and Barkham, 1976).

The conspicuous increase in ruderal species after heavy thinning is probably the most challenging output of this restoration experiment. The “nitrogen time bomb” scenario suggests that canopy opening may release nitrogen accumulated in forest soils over decades of biomass accumulation and atmospheric deposition (Verheyen et al., 2012). An “explosion” represented by an unprecedented increase in ruderal, often nitrogen-demanding species is therefore likely to happen. This hypothesis is partly supported by our observations (e.g. the increased frequency of *Urtica dioica*).

However, there are at least three possible objections towards this pessimistic scenario. First, we do not know whether or not the process of ruderalization following coppicing was an integral part of coppice ecosystem dynamics in the past. There is no evidence from before the mid-20th century, when some central European coppices were still actively managed (e.g., Szabó, 2010). Second, the ruderal flash may not last long, because increased nitrogen availability may be typical only during the initial phase immediately after canopy opening. This knowledge gap calls for further investigation. The third possible explanation is the effect of soil disturbance. Species taking advantage from increased nutrient availability are difficult to separate from species colonizing disturbed sites. Topsoil disturbances that inevitably occur during experimental thinning provide colonization opportunities for R-strategists (Levin and Paine, 1974; Pickett and White, 1985). Such fast-colonizing anemochorous species, e.g. *Cirsium arvense*, *Epilobium ciliatum* and *Taraxacum* sect. *Ruderalia* increased on our study plots.

Disturbance caused by thinning can be further amplified by other organisms, such as smaller or larger mammals (Collins and Pickett, 1988). On our plots, wild boar (*Sus scrofa*) rooting around stumps, particularly of oaks, is a common sight. Wild boar is known to feed on invertebrates (Schley and Roper, 2003). The animals observed on our study plots were probably searching for the larvae of xylophagous beetles. The abundance of stumps was higher in the heavily thinned plots compared to moderately thinned plots. Heavily thinned plots were therefore more affected by wild boar than other plots. This could explain the increased frequency of ruderal species. Wild boar has begun spreading in Europe after World War II and it has sharply increased in the Czech Republic in the last few years (Havránek et al., 2010). This historically new biotic factor must be considered in attempts to restore previous management systems.

The last focal group of alien species is of particular interest, because its increase has been reported following coppicing (Radtke et al., 2013) or thinning (Bailey, 1998; Battles et al., 2001; Griffis

et al., 2001; Thysell and Carey, 2001). In our study, no increase in the frequency of alien species has been recorded. The prevalence of nutrient-poor soils, remote position from potential sources of alien species diaspores (e.g. river alluvia; Chytrý et al., 2008) and the large extent of Krumlov Wood and its long-term continuity probably limited the chance of invasions.

4.2. To coppice or not to coppice?

As noted in the previous part, coppice-with-standards restoration has no direct model in the study region. No woodland is presently managed as a coppice or coppice-with-standards; in particular, historical vegetation composition data from the times when the traditional management was still practised are not available. Nonetheless, we can compare our results with the conditions shortly after coppice management was abandoned. Two examples from oakwoods in Pálava Hills, ca. 20–25 km southeast from Krumlov Wood, show that in the 1950s these communities comprised a high proportion of light-demanding species (which strongly decreased later) and approximately four times more presently endangered species than today (Hédl et al., 2010; Kopecký et al., 2013). Ruderal and alien species were not analysed in detail but they were present, possibly constituting an indispensable component of the initial stages of the coppicing cycle (Ash and Barkham, 1976). It remains unsettled whether the nitrogen enrichment is reversible in the long run (Baeten et al., 2009; Van Calster et al., 2008a) and how will nitrogen deposition affect biodiversity when restoring coppice-with-standards. Our results suggest that successful restoration can be achieved if factors, such as artificially high densities of wild boar, are taken into consideration. Negative effects can be minimized by selecting sites where detrimental factors are negligible. Fencing during initial stages after coppicing can help, but it is rather problematic since it prevents other large animals from entering. Their browsing on regenerating trees can be beneficial, because it slows down succession and thus lengthens the light period (Horsley et al., 2003; Royo et al. 2010).

Coppice management is considered a promising source of biofuel production (Jansen and Kuiper, 2004; Kadavý et al., 2011; McKay, 2006) and has been also implemented in urban forestry (Nielsen and Møller, 2008). Our results show that it may be beneficial for biodiversity as well.

5. Conclusions

The restoration of a coppice-with-standards oakwood resulted in a significant response of forest understorey. In addition to increased light availability, soil disturbances occurring during and after thinning turned out to be important drivers of vegetation

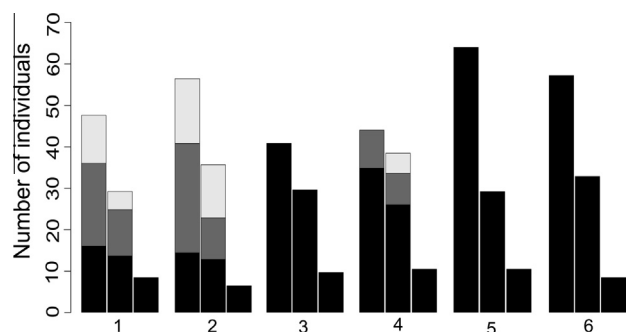


Fig. A.1. Average numbers of the three most abundant trees with DBH > 4 cm on the study plots in control (first column of the triplet), moderately thinned (middle column) and heavily thinned (third column) plots in each locality. Black filling: oak (*Quercus petraea*), dark grey filling: hornbeam (*Carpinus betulus*), light grey filling: lime (*Tilia cordata*).

Table A.1

Characteristics of localities. Mean values and standard deviation are shown; calculations are based on control plots.

Variable/stand	1	2	3	4	5	6
<i>Overstorey structure</i>						
Tree basal area (m ² ha ⁻¹)	3.46 ± 0.52	2.53 ± 0.51	2.64 ± 0.37	3.12 ± 0.48	2.65 ± 0.37	3.01 ± 0.53
Tree stem density (ha ⁻¹)	719 ± 140	847 ± 211	768 ± 221	919 ± 232	885 ± 204	840 ± 192
Canopy openness (%)	14.0 ± 1.2	13.4 ± 2.0	16.5 ± 1.1	15.0 ± 1.8	13.5 ± 2.6	15.0 ± 1.1
<i>Understorey structure</i>						
Shrub layer (cover, %)	4.2 ± 6.1	1.8 ± 0.8	1.6 ± 1.5	1 ± 1.7	1.8 ± 1.9	0.2 ± 0.5
Tree regeneration (cover, %)	16.8 ± 12.5	16.9 ± 10.5	8.7 ± 3.1	8.1 ± 3.8	8.3 ± 6.2	5.12 ± 1.47
Herb layer (cover, %)	32.0 ± 10.4	26.2 ± 14.4	35.0 ± 5.0	15.8 ± 7.0	18.0 ± 13.2	15.8 ± 9.0
<i>Soil chemistry</i>						
pH	5.5 ± 0.3	5.3 ± 0.2	4.9 ± 0.1	4.9 ± 0.1	5.2 ± 0.1	5.0 ± 0.1
Ca (mg/1000 g)	889 ± 334	844 ± 327	652 ± 56	203 ± 95	770 ± 251	267 ± 122
Mg (mg/1000 g)	177 ± 63	163 ± 69	156 ± 20	60 ± 19	174 ± 52	60 ± 32
P (mg/1000 g)	6.4 ± 1.7	6.4 ± 0.8	5.8 ± 0.8	15.0 ± 10.9	11.3 ± 6.4	24.5 ± 12.5
K (mg/1000 g)	142 ± 29	131 ± 53	114 ± 46	151 ± 45	178 ± 23	136 ± 64
N (mg/1000 g)	0.49 ± 0.11	0.54 ± 0.07	0.35 ± 0.04	0.5 ± 0.11	0.41 ± 0.05	0.51 ± 0.09
C (mg/1000 g)	8.4 ± 2.2	9.1 ± 0.7	6.0 ± 0.6	10.4 ± 3.6	8.3 ± 1.4	9.7 ± 1.9
C/N	17.1 ± 1.1	17.0 ± 1.5	16.9 ± 0.8	20.3 ± 2.9	19.9 ± 0.8	19.1 ± 0.9
<i>Species diversity</i>						
Species richness (N plot ⁻¹)	32.6 ± 2.2	27.6 ± 6.9	43.4 ± 5.0	17.0 ± 2.5	26.0 ± 8.5	20.8 ± 3.4
<i>Restoration success</i>						
Light-demanding oligotrophic species (N plot ⁻¹)	1.2 ± 1.1	1.2 ± 1.6	4.8 ± 2.2	1.6 ± 1.9	2.8 ± 3.1	4.0 ± 0.0
Shade tolerant species (N plot ⁻¹)	7.6 ± 2.5	7.8 ± 0.4	6.8 ± 1.3	2.6 ± 0.5	4.6 ± 2.5	3.4 ± 0.5
Native ruderal species (N plot ⁻¹)	3.4 ± 1.5	2.4 ± 0.6	4.6 ± 1.7	2.8 ± 1.3	2.4 ± 1.5	5.0 ± 1.2
Alien species (N plot ⁻¹)	1.2 ± 0.5	0.5 ± 0.5	1.0 ± 1.4	1.4 ± 1.1	0.4 ± 0.6	2.8 ± 0.5

change. Although variance in site conditions was high and ranged from acid to mesic habitats, the general species composition change after experimental thinning was similar. Moderate thinning changed understorey species composition only slightly. Heavy thinning significantly increased the frequency of light-demanding oligotrophic species, which have generally decreased in most European forests during the last decades. At the same time, heavy thinning led to the expansion of ruderal species, but it did not increase the frequency of alien species. A gradual decrease in species richness due to local extinctions can be expected in the long run. However, a shifting mosaic of differently aged coppice stands can facilitate the long-term survival of light-demanding species at the site level. A more widespread employment of coppice-with-standards in forestry should be considered to preserve the biodiversity of European lowland forests.

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Appendix A

See Fig. A.1 and Table A.1.

References

- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32–46.
- Anderson, M.A., Ellingsen, K.E., McArdle, B.H., 2006. Multivariate dispersion as a measure of beta diversity. *Ecol. Lett.* 9, 683–693.
- Ares, A., Berryman, S.D., Puettmann, K.J., 2009. Understorey vegetation response to thinning disturbance of varying complexity in coniferous stands. *Appl. Veg. Sci.* 12, 472–487.
- Ash, J.E., Barkham, J.P., 1976. Changes and variability in the field layer of a coppiced woodland in Norfolk, England. *J. Ecol.* 64, 697–712.
- Baeten, L., Bauwens, B., De Schrijver, A., De Keersmaecker, L., Van Calster, H., Vandekerckhove, K., Roelands, B., Beeckman, H., Verheyen, K., 2009. Herb layer changes (1954–2000) related to the conversion of coppice-with-standards forest and soil acidification. *Appl. Veg. Sci.* 1, 1–11.
- Bailey, J.D., 1998. Understorey vegetation in old and young Douglas-fir forests of western Oregon. *Forest Ecol. Manage.* 112 (3), 289–302.
- Barkham, J.P., 1992. The effects of coppicing and neglect on the performance of the perennial ground flora. In: Buckley, G.P. (Ed.), *Ecology and management of coppice woodlands*. Chapman & Hall, London, pp. 115–146.
- Battles, J.J., Shlisky, A.J., Barrett, A.J., Heald, R.C., Allen-Diaz, B.H., 2001. The effects of forest management on plant species diversity in a Sierran conifer forests. *Forest Ecol. Manage.* 146, 211–222.
- Bergmeier, E., Petermann, J., Schröder, E., 2010. Geobotanical survey of wood-pasture habitats in Europe: diversity, threats and conservation. *Biodivers. Conserv.* 19, 2995–3014.
- Binkley, D., 1984. Does forest removal increase rates of decomposition and nitrogen release? *Forest Ecol. Manage.* 8, 229–233.
- Bobbink, R., Hornung, M., Roelofs, J.G.M., 1998. The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. *J. Ecol.* 86, 717–738.
- Broome, A., Clarke, S., Peace, A., Parsons, M., 2011. The effect of coppice management on moth assemblages in an English woodland. *Biodivers. Conserv.* 20, 729–749.
- Buckley, G.P., 1992. *Ecology and Management of Coppice Woodlands*. Chapman & Hall, London.
- Chytrý, M., Danihelka, J., 1993. Long-term changes in the field layer of oak and oak-hornbeam forests under the impact of deer and mouflon. *Folia Geobot.* 245, 225–245.
- Chytrý, M., Tichý, L., Holt, J., Botta-Dukát, Z., 2002. Determination of diagnostic species with statistical fidelity measures. *J. Veg. Sci.* 13, 79–90.
- Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L., Danihelka, J., 2008. Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89, 1541–1553.
- Collins, B., Pickett, S., 1988. Demographic responses of herb layer species to experimental canopy gaps in a northern hardwoods forest. *J. Ecol.* 76, 437–450.
- Concilio, A., Ma, S., Li, Q., LeMoine, J., Chen, J., North, M., Jensen, R., Moorhead, D., 2005. Soil respiration response to burning and thinning in mixed conifer and hardwood forests. *Can. J. Forest Res.* 35 (7), 1581–1591.

- De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. *Ecology* 90 (12), 3566–3574.
- De Cáceres, M., Legendre, P., Moretti, M., 2010. Improving indicator species analysis by combining groups of sites. *Oikos* 119, 1674–1684.
- Decocq, G., Aubert, M., Dupont, F., Alard, D., Saguez, R., Wattez-Franger, A., De Foucault, B., Delelis-Dusollier, A., Bardat, J., 2004. Plant diversity in a managed temperate deciduous forest: understorey response to two silvicultural systems. *J. Appl. Ecol.* 41, 1065–1079.
- Dengler, J., Chytrý, M., Ewald, J., 2008. Phytosociology. In: Jørgensen, S.E., Fath, B.D. (Eds.), *Encyclopedia of Ecology*, vol. 4. Elsevier, Oxford, pp. 2767–2779.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, W., Werner, W., Paulißen, D., 1992. *Zeigerwerte von Pflanzen in Mitteleuropa*. second ed., Scr. Geobot. 18, 1–248.
- Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA), Version 2.0: Imaging Software to Extract Canopy Structure and Gap Light Transmission Indices from True-Colour Fisheye Photographs, Users Manual and Program Documentation. Simon Fraser University; the Institute of Ecosystem Studies, Burnaby, BC; Millbrook, NY.
- Fuller, R.J., Henderson, A.C.B., 1992. Distribution of breeding songbirds in bradefield woods, suffolk, in relation to vegetation and coppice management. *Bird Study* 39, 73–88.
- Griffis, K., Crawford, J.A., Wagner, M.R., Moir, W.H., 2001. Understorey response to management treatments in northern forest. *Forest Ecol. Manage.* 146, 239–245.
- Grundel, R., Pavlovic, N.B., Sulzman, C.L., 1998. Habitat use by the red-listed Karner blue butterfly in oak woodlands: the influence of canopy cover. *Biol. Conservation* 85, 47–53.
- Havránek, F., Ježek, M., Hučko, M., 2010. O čem hovoří myslivecká statistika. *Myslivost* 10, 47–49 (In Czech).
- Hédli, R., Kopecký, M., Komárek, J., 2010. Half a century of succession in a temperate oakwood: from species-rich community to mesic forest. *Divers. Distrib.* 16, 267–276.
- Hermý, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and the implications for forest conservation. *Biol. Conserv.* 91, 9–22.
- Hofmeister, J., Hošek, J., Modrý, M., Roleček, J., Modrý, M., 2009. The influence of light and nutrient availability on herb layer species richness in oak-dominated forests in central Bohemia. *Plant Ecol.* 205, 57–75.
- Hölscher, D., Schade, E., Leuschner, C., 2001. Effects of coppicing in temperate deciduous forests on ecosystem nutrient pools and soil fertility. *Basic Appl. Ecol.* 2, 155–164.
- Horsley, S.B., Stout, S.L., DeCalesta, D., 2003. White-tailed deer impact on the vegetation dynamics of a northern hardwood forest. *Ecol. Appl.* 13, 98–118.
- Hopkins, J., Kirby, K.J., 2007. Ecological change in British broadleaved woodland since 1947. *Ibis* 149, 29–40.
- Hothorn, T., Hornik, K., van de Wiel, M.A., Zeileis, A., 2006. A Lego system for conditional inference. *Am. Stat.* 60 (3), 257–263.
- Howson, G., 1988. Use of the cotton strip assay to detect potential differences in soil organic matter decomposition in forests subjected to thinning. In: Harrison, A.F., Latter, P.M., Walton, D.W.H. (Eds.), *Cotton strip assay: an index of decomposition in soils*. NERC/ITE, Grange-over-Sands, pp. 94–98.
- Inagaki, Y., Kuramoto, S., Torii, A., Shinomiya, Y., Fukata, H., 2008. Effects of thinning on leaf-fall and leaf-litter nitrogen concentration in hinoki cypress (*Chamaecyparis obtusa* Endlicher) plantation stands in Japan. *Forest Ecol. Manage.* 255, 1859–1867.
- Jansen, P., Kuiper, L., 2004. Double green energy from traditional coppice stands in the Netherlands. *Biomass Bioenerg.* 26, 401–402.
- Kadavý, J., Kneifl, M., Servus, M., Knott, R., Hurt, V., 2011. Nízký a střední les – plnohodnotná alternativa hospodaření malých a středních vlastníků lesa. In: *Metodika založení a popis vzorových objektů porostů v převodu na les nízký a střední v ČR*. Mendel University, Brno (in Czech).
- Klotz, S., Kühn, I., Durka, W., 2002. BIOLFLOR – Eine Datenbank zu biologisch-ökologischen Merkmalen der Gefäßpflanzen in Deutschland. *Schriftenreihe für Vegetationskunde*, vol. 38. Bundesamt für Naturschutz, Bonn.
- Kopecký, M., Hédli, R., Szabó, P., 2013. Non-random extinctions dominate plant community changes in abandoned coppices. *J. Appl. Ecol.* 50, 79–87.
- Kyasová, V., Obršlík, J., Špačková, J., Špačková, V., 1970. Velkostatek Moravský Krumlov, Inventář F 177, Státní archiv v Brně, Brno. (In Czech).
- Kubát, K., Hrouda, L., Chrtěk Jr., J., Kaplan, Z., Kirschner, J., Stěpánek, J. (Eds.), 2002. *Klíč ke květeně České republiky*. Academia, Praha, CZ. (In Czech).
- Kwiatkowska, A.J., Wyszomirski, T., 1990. Species deletion in *Potentillo albae-Quercetum* phytocoenoses reversed by the removal of *Carpinus betulus*. *Vegetatio* 87, 115–126.
- Levin, S.A., Paine, R.T., 1974. Disturbance, patch formation, and community structure. *Proc. Natl. Acad. Sci.* 71, 2744–2747.
- Lindh, B., 2008. Flowering of understorey herbs following thinning in the western cascades, Oregon. *Forest Ecol. Manage.* 256, 929–936.
- Lindh, B.C., Muir, P.S., 2004. Understorey vegetation in young Douglas-fir forests: does thinning help restore old-growth composition? *Forest Ecol. Manage.* 192, 285–296.
- McKay, H., 2006. Environmental, economic, social and political drivers for increasing use of woodfuel as a renewable resource in Britain. *Biomass Bioenerg.* 30, 308–315.
- Naaf, T., Wulf, M., 2011. Traits of winner and loser species indicate drivers of herb layer changes over two decades in forests of NW Germany. *J. Veg. Sci.* 22, 516–527.
- Nielsen, A.B., Møller, F., 2008. Is coppice a potential for urban forestry? The social perspective. *Urban For. Urban Green.* 7, 129–138.
- Nobis, M., Hunziker, U., 2005. Automatic thresholding for hemispherical canopy-photographs based on edge detection. *Agric. Forest Meteorol.* 128 (2), 243–250.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2012. *Vegan: community ecology package*. R package version 2.0-3. <http://CRAN.R-project.org/package=vegan> (7 May 2013).
- Pickett, S.T.A., White, P.S. (Eds.), 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando.
- Puettmann, K.J., Coates, K.D., Messier, C. (Eds.), 2008. *A critique of silviculture: Managing for complexity*. Island, Washington.
- Pyšek, P., Chytrý, M., Pergl, J., Sádlo, J., Wild, J., 2012. Plant invasions in the Czech Republic: current state, introduction dynamics, invasive species and invaded habitats. *Preslia* 84, 575–629.
- R Development Core Team, 2012. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/> (7 May 2013).
- Rackham, O., 2003. *Ancient woodland: its history, vegetation and use in England*. Castlepoint Press, Colvend.
- Rackham, O., 2008. *Ancient woodlands: modern threats*. *New Phytologist* 180, 571–586.
- Radtke, A., Ambraß, S., Zerbe, S., Tonon, G., Fontana, V., Ammer, C., 2013. Traditional coppice forest management drives the invasion of *Ailanthus altissima* and *Robinia pseudoacacia* into deciduous forests. *Forest Ecol. Manage.* 291, 308–317.
- Royo, A.A., Collins, R., Adams, M.B., Kirschbaum, C., Carson, W.P., 2010. Pervasive interactions between ungulate browsers and disturbance regimes promote temperate forest herbaceous diversity. *Ecology* 91, 93–105.
- Ryu, S., Concilio, A., Chen, J., North, M., Ma, S., 2009. Prescribed burning and mechanical thinning effects on belowground conditions and soil respiration in a mixed-conifer forest, California. *Forest Ecol. Manage.* 257, 1324–1332.
- Schley, L., Roper, T.J., 2003. Diet of wild boar *Sus scrofa* in Western Europe, with particular reference to consumption of agricultural crops. *Mammal Rev.* 33, 43–56.
- Simpson, G., 2013. *Permute: functions for generating restricted permutations of data*. R package version 2.0-8. <http://CRAN.R-project.org/package=permut> (12 July 2013).
- Spitzer, L., Konvička, M., Beneš, J., Tropek, R., Tuf, I.H., Tufová, J., 2008. Does closure of traditionally managed open woodlands threaten epigeic invertebrates? Effects of coppicing and high deer densities. *Biol. Conserv.* 141, 827–837.
- Szabó, P., 2010. Driving forces of stability and change in woodland structure: A case-study from the Czech lowlands. *Forest Ecol. Manage.* 259, 650–656.
- Thomas, S.C., Halpern, C.H.B., Falk, D.A., Liguori, D.A., Austin, K.A., 1999. Plant diversity in managed forests: Understorey responses to thinning and fertilization. *Ecol. Appl.* 9 (3), 864–879.
- Thyssel, D.R., Carey, A.B., 2001. Manipulation of density of *Pseudotsuga menziesii* canopies: preliminary effects on understorey vegetation. *Can. J. Forest Res.*, 31.
- Tolasz, R. (Ed.), 2007. *Climate Atlas of Czechia*, 1st ed. Czech Hydrometeorological Institute, Prague.
- Troup, R.S., 1924. *Silvicultural systems*. Clarendon Press, Oxford.
- Tyrbirk, K., Strandberg, B., 1999. Oak forest development as a result of historical land-use patterns and present nitrogen deposition. *Forest Ecol. Manage.* 114, 97–106.
- Utinek, D., 2004a. *Převody pařezin na střední les v městských lesích Moravský Krumlov (založení pokusných ploch)*. Ph.D. dissertation, Mendel University, Brno. (in Czech).
- Utinek, D., 2004b. *Conversions of coppices to a coppice-with-standards in Urban Forests of Moravský Krumlov*. *J. Forest Sci.* 50 (1), 38–46.
- Van Calster, H., Baeten, L., Verheyen, K., De Keersmaecker, L., Dekeyser, S., Rogister, J.E., Hermý, M., 2008a. Diverging effects of overstorey conversion scenarios on the understorey vegetation in a former coppice-with-standards forest. *Forest Ecol. Manage.* 256, 519–528.
- Van Calster, H., Endels, P., Antonio, K., Verheyen, K., Hermý, M., 2008b. Coppice management effects on experimentally established populations of three herbaceous layer woodland species. *Biol. Conservation* 141, 2641–2652.

- Verheyen, K., Baeten, L., De Frenne, P., Bernhardt-Römermann, M., Brunet, J., Cornelis, J., Decocq, G., Dierschke, H., Eriksson, O., Hédli, R., Heinken, T., Hermy, M., Hommel, P., Kirby, K., Naaf, T., Peterken, G., Petřík, P., Pfadenhauer, J., Van Calster, H., Walther, G.-R., Wulf, M., Verstraeten, G., 2012. Driving factors behind the eutrophication signal in understorey plant communities of deciduous temperate forests. *J. Ecol.* 100, 352–365.
- Vitousek, P.M., Melillo, J.M., 1979. Nitrate losses from disturbed forests: patterns and mechanisms. *Forest Sci.* 25, 605–619.
- Verschuyf, J., Riffell, S., Miller, D., Wigley, T.B., 2011. Biodiversity response to intensive biomass production from forest thinning in North American forests – a meta-analysis. *Forest Ecol. Manage.* 261, 221–232.
- Warren, M.S., 1987. The ecology and conservation of the heath fritillary butterfly *Mellicta athalia*, III Population dynamics and the effects of habitat management. *J. Appl. Ecol.* 24, 499–513.