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Does a minimal intervention approach threaten the biodiversity of protected areas? A multi-taxa short-term response to intervention in temperate oak-dominated forests



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ABSTRACT

Efficient conservation management must be applied in protected areas in order to slow the loss of biodiversity in Europe. Regarding forests, a conservation approach based on minimal intervention prevails in most protected woodlands, thus facilitating the expansion of closed-canopy forests at the expense of open forests. To identify effective conservation strategies for protected forests, the minimal intervention or "hands-off" approach must be compared with active measures to support biodiversity.

We carried out a study in the oak-dominated forests of Podyji National Park (Czech Republic), an historically managed area left for natural succession since 1950. Twelve experimental clearings were created in closed-canopy forests within the core zone of the park; six of these clearings were connected to forest edges and open meadows, the remaining six clearings were isolated from open habitats within closed forest. To assess the importance of minimal intervention and active management measures in protected forests, we compared the richness and composition of insects, reptiles, birds and vascular plants in the clearings and in four reference habitats, including closed forest, forest edge, open forest, and meadow, in the first season following the intervention.

In comparison to closed-canopy forest, the clearings had higher species richness of butterflies, saproxylic and floricolous beetles, reptiles, and vascular plants but lower richness of moths and epigeic beetles, and similar richness of birds. For most groups, the species composition of clearings differed from that of closed forest or even the forest edge, indicating that the latter habitats cannot serve as a sufficient replacements for the conservation of open woodland species. The species richness of isolated clearings was generally lower than that of clearings connected to open habitats, and their communities contained a larger proportion of species associated with closed forest. Most threatened species were associated with clearings or open forest, closed forest and meadow hosted only a few.

The creation of the clearings in closed-canopy forests had a positive effect on overall species richness and supported threatened species in most model groups. It is thus a valuable management tool in the conservation of temperate woodland biodiversity. Our results also point to the importance of connectivity of open habitats in wooded landscapes. Further surveys of the clearings are needed to

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ascertain the effect of such interventions to see how communities change throughout succession, or alternatively to what extent hindering succession by repeated cutting may alter communities.

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1. Introduction

Biodiversity conservation has long been a goal of European conservation policy (CBD, 2010; CEC, 1998). However, despite the fact that more than 25% of European land is afforded some level of protection for conservation, biodiversity continues to decline (EEA, 2009). One factor contributing to this decline may be unsuitable management practices in protected areas, or more specifically, the insufficient application of evidence-based conservation recommendations (Sutherland et al., 2004). A major concern involves the selection of efficient strategies for the conservation of biodiversity in forest ecosystems.

Today, most forests in Europe are closed, shady habitats. This contrasts with their past state, which was much more open and dynamic. The open structure was maintained by disturbances such as grazing and fires (Adámek et al., 2015; Bengtsson et al., 2000; Niklasson et al., 2010; Rackham, 1998; Szabó, 2010; Vera, 2000). These disturbances were later substituted by human silvicultural practices such as wood pasturing, controlled burning and coppicing. Wood pasturing and burning prevented full canopy closure and led to the formation of open, park-like habitats with numerous open-grown trees. In coppices, trees were usually cut down every 7–20 years (Szabó, 2010), which maintained a cyclical pattern of extreme changes in ground-level light penetration (Buckley, 1992; Joys et al., 2004). Traditionally managed woodlands were thus open, sunny, heterogeneous mosaics of forest in various stages of succession, which harboured a high richness of animals and vascular plants (Hédli et al., 2010; Benes et al., 2006; Bengtsson et al., 2000; Bugalho et al., 2011; Spitzer et al., 2008; Vodka and Cizek, 2013; Warren and Thomas, 1992).

However, the traditional management practices maintaining these disturbance regimes have largely been abandoned in most of Europe, especially over the last 200 years (Bergmeier et al., 2010; Müllerová et al., 2014, 2015; Tárrega et al., 2009). The formerly common, open woodlands have gradually been transformed into high closed-canopy forests in order to satisfy increased demand for timber or due to secondary succession. Due to the absence of regular disturbances, increases in canopy closure have also occurred in forests in protected areas. For instance, within nature reserves in the south-east of the Czech Republic, the expansion of closed-canopy forest has reduced the cover of open woodlands from 68.5% to 14.1% between 1938 and 2009 (Miklín & Čížek, 2013). Similar reductions have occurred across the European continent (Hartel and Plieninger, 2014; Rackham, 2003). As a result, species composition in forests has shifted from light-demanding and oligotrophic species towards more generalist, mesic and shade-tolerant species (Hédli et al., 2010; Kopecký et al., 2013; Van Calster et al., 2008; Van der Werf, 1991; Vild et al., 2013). Many species associated with open woodlands, including numerous plants, fungi, and animals that were common in the past have thus become rare or endangered.

In commercial forests, the maintenance of high canopy closure is economically justifiable, although even in these forests some forms of management may result in short-term canopy openings (e.g. selection cutting, thinning) (Pawson et al., 2013; Verschuyl et al., 2011). On the other hand, protected areas are mostly dedicated to biodiversity conservation. Management of protected forests therefore must consider the requirements of the species that inhabit those forests, including endangered species. Active

management measures restoring or maintaining the open structure of forests in European protected areas are surprisingly rare (but see for instance Plieninger et al. (2015) for the use of wood pasturing), despite the fact that their need is emphasized by many studies concerning biodiversity of temperate forests (Götmark, 2013). Yet while active approaches to forest conservation management are continuously recommended by the scientific community, the “strict forest reserve” concept (Schultze et al., 2014) which prevents intervention is a standard practice applied to over 3 million hectares (or about 1.7% of forested area) in Europe (COST Action E4, 2000). Although traditionally managed open woodlands require a special approach to nature conservation (Götmark, 2013; Lindbladh et al., 2007), policies often consider coppicing or wood pasturing as undesirable disturbances to the “naturalness” of forests (Miklín and Čížek, 2014). Numerous studies compared the biodiversity of unmanaged (minimal intervention approach) and commercially managed forests concluding that minimal intervention favours biodiversity (Lassauce et al., 2013; Martikainen et al., 2000; Paillet et al., 2010). In protected areas, however, the choice is often between active conservation measures and minimal intervention approach rather than between the minimal intervention and commercial management. Yet there is little information comparing the effects of active conservation measures and the minimal intervention (Franc and Götmark, 2008; Götmark, 2013). Managers of protected forests thus lack basic information needed for qualified management decisions.

In order to quantify the effects of minimal intervention and active management approaches on biodiversity of protected forests, we carried out a multi-taxa study in the oak-dominated forests of Podyji National Park (Czech Republic). Twelve experimental clearings were created in unmanaged, closed-canopy forests of the core zone of the park. In the first season after their creation, eight model groups (butterflies, moths, epigeic, floricolous and saproxylic beetles, reptiles, birds and vascular plants) were sampled in the clearings and in adjoining reference habitats (including closed-canopy forest, open forest, forest edge, and meadow). To assess the effect of the active intervention we compared the species richness and the species composition of the model groups among the newly created clearings and the reference habitats. We also assessed the importance of individual habitats for sustaining threatened species in the sampling area.

2. Material and methods

2.1. Study area and design

This study was carried out in Podyji National Park (South Moravia, Czech Republic) (48°50'56"N, 15°53'13"E), an area covering 63 km² of the Dyje River canyon (ca 300 m a.s.l.). The canyon is characterised by nutrient poor, shallow soils. Until the Second World War, a large part of the area was managed by livestock grazing and coppicing, which kept the landscape open. After the war, these practices were abandoned, and secondary succession has led to an increase in canopy closure. Today, the area is covered with closed-canopy forests (hereafter referred to as “closed forest”), or more open remnants of the formerly coppiced and pasture forests (hereafter referred to as “open forest”) on the upper slopes of the canyon.

Closed forests in the lower part of the river valley belong to Hercynian oak-hornbeam forests (*Melampyro nemorosi-Carpinetum betuli*; *Carpinion betuli*) (Chytrý et al., 2008). The average basal area of the closed forests is 35.4 m²/ha, the canopy openness is 5.7% (SD = 1.82) (openness was measured by digital hemispherical photographs at 1.3 m above the ground analysed in WinSCANOPY image processing software; Regent Instruments Inc. 2015). These forests are composed of sessile oak (41%), hornbeam (37%), small-leaved lime (18%), and other species (4%). Open forests on the upper slopes belong to open thermophilous oak forests of the association *Sorbo torminalis-Quercetum*, *Genisto pilosae-Quercetum petraeae* (alliance *Quercion petraeae*) (Chytrý et al., 2008). These forests are characterised by a lower mean basal area (25.5 m²/ha), and higher mean canopy openness (16.9%, SD = 8.25) than the closed forests. The open forests are composed predominantly of sessile oak (90%), with small-leaved lime (5%), hornbeam (4%), and other species (1%) comprising a much smaller component.

At six sites in the core zone of the park (Fig. 1), a pair of small clearings (each ~40 × 40 m) were created. A few trees were left standing in each clearing in order to replicate an open forest environment. The clearings were located near the bottom of the river canyon, close to the alluvial meadow. The clearings were created to support populations of the critically endangered butterfly, the

clouded apollo *Parnassius mnemosyne*. One clearing in each pair was always directly connected to the meadow, while the other clearing was isolated from the meadow and from the first clearing by at least 20 m of closed forest (see Fig. 1). After felling, mean canopy openness in the clearings increased to ~22%. Clearings were created at four of the sites (Lipina, Hlubocke louky, Stary Galis, Hardegg) in February 2011, while the remaining two sites (Novy Galis, Siroke pole) were cleared in February 2012. Before felling, the average basal area of the clearings was 40.6 m²/ha, with composition of sessile oak (36%), hornbeam (39%), small-leaved lime (15%), and others (10%), thus very similar to the closed forests. See also Table A1 in Supplementary material.

Furthermore, at each of the six sites, four reference plots (~40 × 40 m) were established within four types of habitats for comparisons. These reference habitats were: closed-canopy forest, open forest, forest edge, and alluvial meadow (Fig. 1). Therefore, in total there were 12 experimental clearings and 24 reference plots established across six sites.

2.2. Model groups and data collection

Sampling of clearings and reference plots at each site was carried out in the spring and summer following the creation of the clearings. Thus, the four sites cleared in February 2011 were

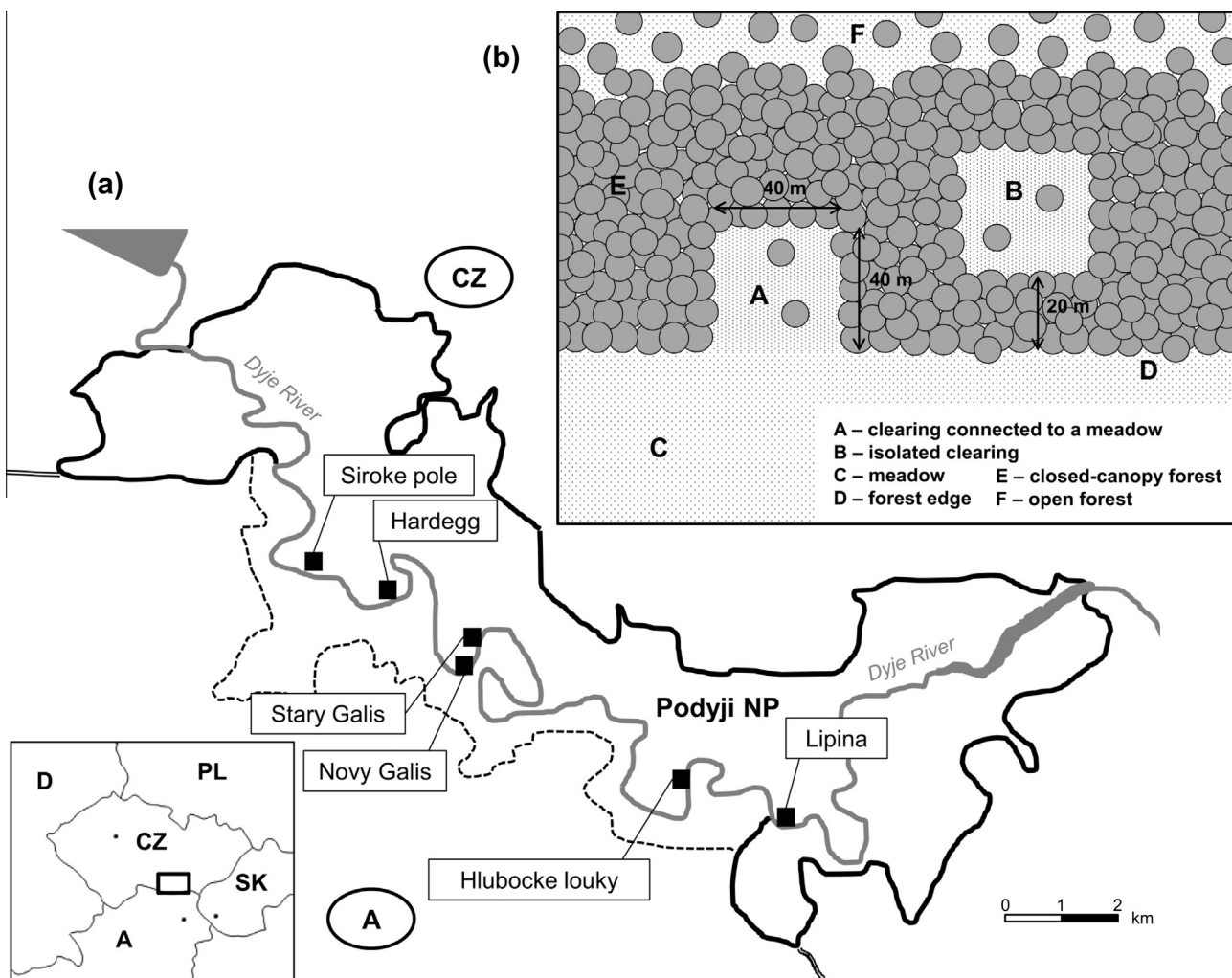


Fig. 1. Study area and design – position of the study sites in Podyji National Park (a). The sites are represented by black squares. The thin dashed line signifies a border of adjoining Thayatal National Park (Austria). A schematic arrangement of the study plots (two types of clearings and four types of reference plots) within each site is displayed in (b). Clearing A was always connected directly to the alluvial meadow C, clearing B was isolated from other open habitats: meadow (C), forest edge (D), open forest (F) and from clearing A by at least 20 m of closed forest (E).

sampled between May and September 2011, while the two sites cleared in February 2012 were sampled between May and September 2012. To cover a wide range of taxa and life strategies, the following groups were sampled: (a) butterflies, (b) moths, (c) epigeic beetles, (d) saproxylic (deadwood dependent) beetles, (e) floricolous beetles, (f) reptiles, (g) birds, and (h) vascular plants.

Day-flying butterflies were recorded by timed records (7 min per each plot), at five times throughout the season (May, June, July, August, September) during suitable weather conditions. Moths were captured using ultra-violet light traps (one trap per plot) on one night each month during the season (May, June, July, August, September). Since the meadow is often a narrow strip between the river and the forest, samples of moths from meadows were omitted to avoid false inclusion of species from neighboring habitats. Epigeic beetles were captured using pitfall traps containing ethylene glycol as a killing agent and preservative. In each plot, five traps were randomly placed and operated from the end of April to the end of July. The traps were emptied every two weeks. Saproxylic beetles were sampled using two window flight interception traps (FITs) in each plot. These traps were placed at 1.5 m above ground level (meadow plots were omitted) and operated from the end of April till the end of July. The samples were collected every two weeks. Floricolous beetles were collected by yellow pan traps filled with salt water (3 traps per each plot) exposed for one day three times in the season (May, June, July). Reptiles were sampled using artificial shelters made from toughened plastic sheets (1 × 1 m). Four such shelters were placed on the ground in each plot and the presence of the reptiles hiding beneath them were recorded each week. Visual observations and bird-song identifications of bird species in each plot were recorded. Because our plot area is smaller than the territories of most birds, all utilizations of the space (including feeding, singing, or nest-building) were recorded. Only those birds that used the plot as an “activity territory” were recorded. Observations were collected over a 30 min period three times during the season (April, June, July; 90 min in total); first 5 min of each observation were not counted to avoid disturbance/attraction effects. Finally, a census of all vascular plants was made in each study plot twice during the year (start of June, start of August). For more information on the species selected for analyses, see [Appendix A in Supplementary material](#).

2.3. Statistical analysis

We focused on the total number of species (species richness), and species composition of sampled habitats.

The differences in species richness among the habitats were analysed separately for each group by generalized linear mixed-effect models with quasi-Poisson distributions, where the habitat represented a fixed effect factor variable, and the site represented a random effect variable (to filter out the effect of site and year of sampling). The models were fitted using the Generalized Estimating Equations algorithm in the *geepack* package (Hojsgaard et al., 2006) in R 2.14.2 (R Development Core Team, 2012), the effect of habitat type being tested by Chi-squared distribution. For all groups $n = 36$ (12 clearings, 24 reference plots), except for moths and saproxylic beetles where $n = 30$ (meadows were not sampled).

Post-hoc comparisons among habitat levels were done by setting different treatment contrasts.

Species composition of the habitats was analyzed by multivariate ordination analyses. For each group of organisms, partial Canonical Correspondence Analysis (CCA) was performed based on the abundances of all species in the plots (representing samples); the response data of all groups had a gradient length greater than 1.9 SD units in preliminary DCA analysis. For vascular plants, a presence/absence matrix was used instead of abundance data. The response data were log-transformed and rare species were downweighted. To filter out the effect of site, the site affiliation was used as a covariate. The habitat type represented an explanatory factor variable, differences in species composition were tested by Monte Carlo tests with 999 permutations. The ordination analyses were performed in Canoco 5 (ter Braak and Šmilauer, 2012). We created ordination diagrams based on the analyses of the whole communities but only the preferences of threatened species are emphasized, i.e. centroids representing the highest abundance of particular species, and hence their optimum, were plotted in ordination diagrams. We considered species with a conservation status (IUCN categories RE, CR, EN, VU and NT) in the national red lists as “threatened” (but see also [Appendix A in Supplementary material](#)).

3. Results

We recorded 2003 butterflies from 66 species (15 of them threatened), 10,462 moths from 403 species (53 threatened), 6055 epigeic beetles from 89 species (13 threatened), 2927 saproxylic beetles from 293 species (58 threatened), 1039 floricolous beetles from 62 species (7 threatened), 1296 reptiles from 7 species (4 threatened), 806 birds from 49 species (9 threatened), and 449 species of vascular plants (64 threatened). Mean number of threatened species found in particular habitats is displayed in [Table 1](#).

In all the studied groups, analyses revealed significant differences among habitats in species richness ([Fig. 2](#)) and in their species compositions ([Table 2](#)).

For butterflies, the meadow was the richest habitat ($\chi^2_{(5)} = 23573439$, $P < 0.001$), and closed forest was the poorest. Clearings connected to meadow habitats supported a similar number of species as the forest edge and the open forest, while isolated clearings supported fewer species. The ordination analysis revealed that the species composition of the clearings was most similar to the one of forest edge ([Fig. 3A](#)), most threatened species preferring meadow, forest edge and the clearing connected to meadow. No threatened species was associated with the closed forest.

For moths, the highest richness was found in closed forest, then open forest ($\chi^2_{(4)} = 86.1$, $P < 0.001$), and then the clearings connected to a meadow, the forest edge, and lastly the isolated clearings. The forest edge and the clearings connected to meadows had similar species composition, whereas the composition of the isolated clearing tended to resemble the one of closed forests. The open forest harboured distinct species composition from these two groups. The majority of threatened species were, however, associated with the open habitats, mainly the open forest ([Fig. 3B](#)), although a few species were associated also with closed forest.

Table 1

Mean number of threatened species in the habitats – mean number of threatened species found in particular habitats (standard deviation, in parentheses).

Habitat	Butterflies	Moths	Epigeic beetles	Saproxylic beetles	Floricolous beetles	Reptiles	Birds	Plants
Clearing connected	2.3 (1.37)	3.8 (2.23)	0.8 (1.17)	5.8 (4.22)	12.8 (5.6)	2 (0.63)	0.3 (0.82)	4.5 (1.97)
Clearing isolated	1.2 (1.17)	2.2 (1.83)	1 (0.89)	4.3 (1.63)	6 (0.89)	1.5 (0.84)	0 (0)	5.5 (2.66)
Forest edge	2 (0.63)	3.2 (2.04)	1.8 (1.33)	4.5 (2.59)	8.2 (2.71)	1.8 (0.41)	0 (0)	2.2 (1.17)
Closed forest	0 (0)	6.3 (4.97)	1.8 (1.17)	4.8 (1.94)	2.7 (1.97)	0.2 (0.41)	0.5 (0.84)	4.8 (2.32)
Open forest	3.5 (0.84)	8.8 (1.47)	0.3 (0.52)	5.8 (3.13)	8.3 (3.08)	3 (0.89)	2.3 (0.82)	13.8 (7.36)
Meadow	3 (1.79)	–	1.5 (1.64)	–	8.7 (2.42)	2.5 (0.55)	0.8 (0.75)	3 (0.89)

For epigeic beetles, the forest edges and meadows had significantly higher species richness than the remaining habitats, with open forest being the poorest ($\chi^2_{(5)} = 118$, $P < 0.001$). The two types of clearings had a similar species composition (Fig. 3C), lying in between of open forest and closed forest with forest edge (at the axis 2). The threatened species associated with wooded habitats generally avoided open forest, but otherwise they mostly did not discriminate among the remaining habitats.

For saproxylic beetles, the greatest species richness was found in the clearings connected to meadows ($\chi^2_{(4)} = 36.74$, $P < 0.001$), followed by the isolated clearings, the open forest and the forest edge, while the closed forest was the least species-rich habitat. The ordination analysis showed three clusters representing differences in compositions, first, the clearings, second, the closed forest and forest

edge, third, the open forest. Numerous threatened species were associated with the clearings, the open forest, the closed forest and the forest edge, although many threatened species exploited several, mostly open-canopy habitats (Fig. 3D).

For floricolous beetles, the richness was greatest in the clearing connected to meadow, and lowest in the closed forest; the isolated clearing was less rich than the connected one, and also less rich than the open forest or the edge ($\chi^2_{(5)} = 140.6$, $P < 0.001$). The meadow had different species composition from the other habitats. Regarding the woody habitats, the two types of clearings had a similar species composition which was different from the edge, closed and open forest. Threatened species were approximately evenly distributed among the open habitats, avoiding the closed forest (Fig. 4E).

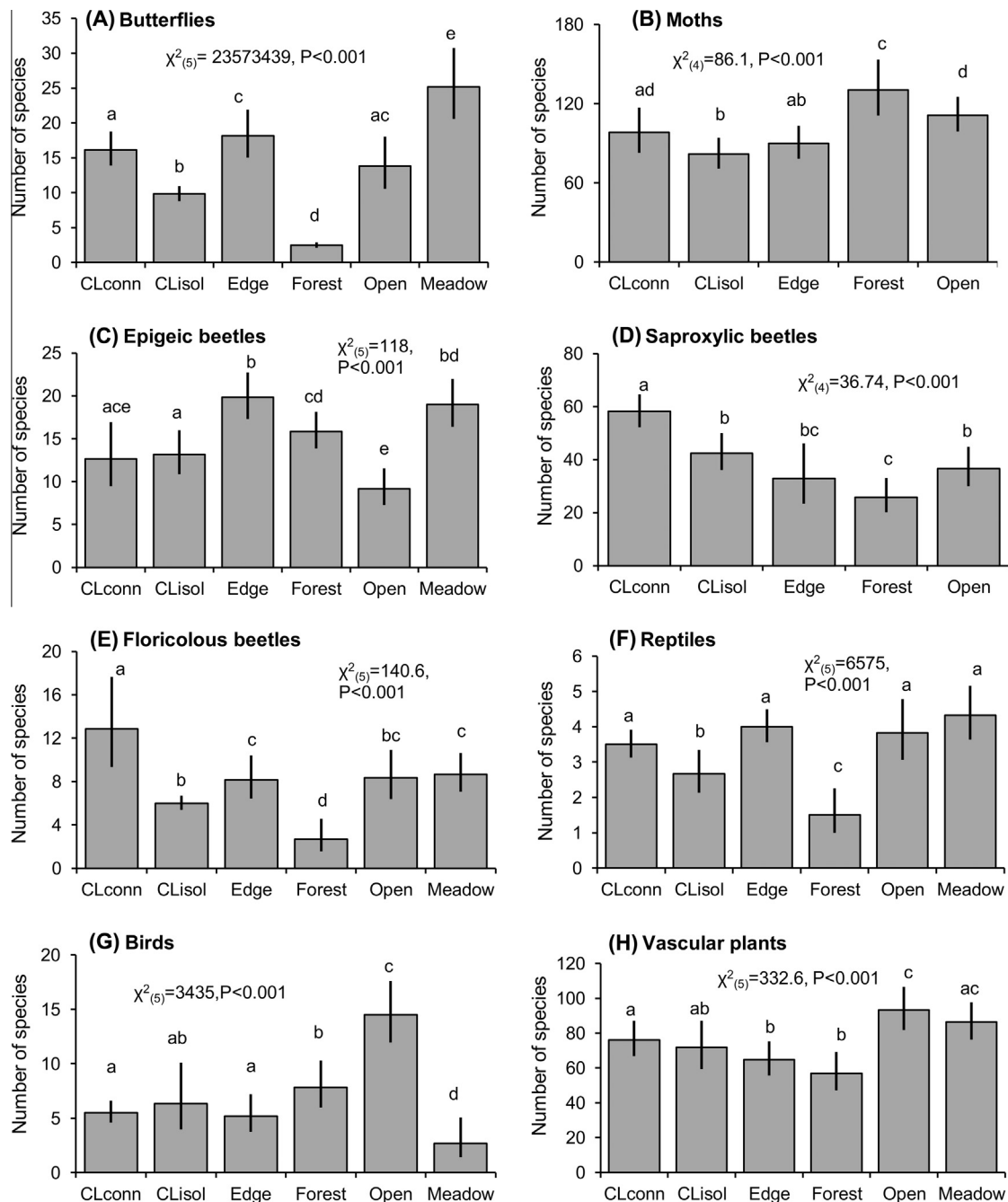


Fig. 2. Species richness – estimated mean ($\pm 95\%$ CI) number of species in each habitat type. Estimates were generated by a generalized linear mixed-effect model with a quasi-Poisson distribution, with site as a random factor. The effect of habitat was tested by χ^2 test. Differences between habitat levels are displayed by different letters above the bars. For all groups $n = 36$, except for moths and saproxylic beetles where $n = 30$.

Table 2

Variation explained by partial CCA axes – the effect of the habitats on community composition was tested by partial CCA for each group of organisms. Numbers in the table show the percentage of residual variation (after the effect of site being filtered out) explained by first and second constrained axes (displayed in Figs. 3 and 4). Pseudo-*F* statistics and *P* level were obtained by Monte Carlo tests with 999 permutations.

Group	CCA axis	Explained variation (%)	Pseudo- <i>F</i>	<i>P</i>
Butterflies	1st	15.45	4.6	0.001
	2nd	13.08	4.6	0.001
Moths	1st	12.49	2.9	0.001
	2nd	6.71	1.7	0.001
Epigeic beetles	1st	23.28	7.6	0.001
	2nd	7.57	2.7	0.002
Saproxylic beetles	1st	9.56	2.1	0.001
	2nd	7.45	1.8	0.001
Floricolous beetles	1st	8.26	2.2	0.003
	2nd	7.01	2.1	0.008
Reptiles	1st	32.29	11.9	0.001
	2nd	18.16	9.2	0.001
Birds	1st	19.49	5.8	0.001
	2nd	5.78	1.9	ns
Plants	1st	20.13	6.3	0.001
	2nd	12.48	4.6	0.001

For reptiles, the closed forest was the poorest habitat in species richness, followed by isolated clearings ($\chi^2_{(5)} = 6575$, $P < 0.001$). The closed forest, the open forest and meadows differed significantly in species composition. The open forest, the edge, and the clearings had a similar species composition, different from the meadow and the closed forest. All the threatened species were associated with open habitats, mainly clearings and open forest (Fig. 4F).

For birds, the highest species richness was found in the open forest, and the lowest number of species were recorded in the meadow ($\chi^2_{(5)} = 5330$, $P < 0.001$). There was a difference in composition between meadow and woody habitats, the woody habitats did not differ in the composition (see Table 2). The clearings and the closed forest shared a similar species composition, while the other habitats differed significantly from them and from each other. The majority of threatened species were associated with open wooded habitats, especially the open forest (Fig. 4G).

For vascular plants, the highest species richness was found in the open forest, followed by the meadow. Among the other habitats, species richness decreased from the clearings to the forest edge, and was lowest in the closed forest ($\chi^2_{(5)} = 332.6$, $P < 0.001$). Communities in the meadow and the open forest differed from each other, the closed forest shared a similar composition with clearings. The great majority of threatened species were associated with open forest (Fig. 4H).

Among the six groups for which samples from meadow habitats were included in analyses, there were two partly contrasting responses. Butterflies and reptiles responded mainly to an insolation gradient between fully shaded (closed forest) and sunlit habitats. The epigeic and floricolous beetles, birds and plants, on the other hand were most affected by the gradient between non-wooded (meadow) and wooded habitats, rather than by the insolation gradient within wooded habitats. Of the two groups sampled in the wooded habitats only, moths and saproxylic beetles, the insolation gradient was always a secondary factor, as the first axis differentiated between clearings and other habitats in saproxylic beetles and between open forest and the remaining habitats for moths (Table 2, Fig. 3).

4. Discussion

This is one of the first studies (see also Götmark, 2013; Rancka et al., 2015) to investigate the effect of active interventions in temperate closed-canopy forest that used a large number of model groups with different life histories. The design of the study also

allowed for an assessment of the importance of connectivity of open wooded habitats. Other studies show that interventions to closed-canopy forests, like partial cutting, may have positive effect on some groups of organisms (e.g. butterflies, moths, saproxylic beetles) (Bolz, 2008; Fartmann et al., 2013; Götmark, 2013) but also negative effects on another groups (e.g. fungi, molluscs) (Nordén et al., 2008; Rancka et al., 2015).

The clearings had higher richness of butterflies, saproxylic beetles, floricolous beetles, reptiles and vascular plants than the closed forest. By contrast, the richness of moths and epigeic beetles was lower, while the diversity of birds did not differ. The clearings were rarely colonized by meadow species. Instead, they were inhabited mainly by edge and/or open woodland species of butterflies, moths, and reptiles. Among birds and vascular plants, and also for some moths, most species found in clearings were also associated with closed forest habitat. For saproxylic and floricolous beetles, the clearings created new habitat inhabited by highly diverse communities distinct from the other sampled habitats. The isolated clearings were generally poorer in species richness than those connected to open habitats, although the composition of the respective communities was similar.

4.1. Diversity in closed forest

To assess the impact of intervention in the national park's core zone, it is necessary to carefully weigh the subsequent negative and positive effects on biodiversity by comparing the biota of clearings to the previous state of the habitat, i.e. closed forest. Such an assessment must consider not only overall species richness in the two habitats, but also the requirements of threatened species.

With the exception of reptiles, butterflies and floricolous beetles, all the sampled groups contained at least some threatened species with an affinity for closed forest. No genuine closed-forest specialists were detected among the threatened species of moths. Indeed, only the elm-feeding *Cosmia affinis* (Noctuidae) is able to live within closed forest, but it is not restricted to this habitat. Of the few threatened epigeic beetle species, three exhibited some affinity to the closed forest, but all were abundant also in other habitats. All five species of threatened saproxylic beetles that were at least partly associated with closed forest were xylomycetophages. They may thus prefer more humid conditions, which promote the growth of their host fungi (Hulcr et al., 2008). Of the four threatened plant species associated with closed forests, only *Cyclamen purpurascens* (Primulaceae) and *Neottia nidus-avis* (Orchidaceae) are typically found in closed-canopy habitats. The remaining species are generally considered open woodland species (Štěpánková, 2010) and might be relicts of the past state of the habitat.

Although the species richness of groups such as moths and epigeic beetles was highest in the closed forest, in comparison to more open wooded habitats, closed forest supported impoverished communities of most other studied taxa. Further, it supported very few threatened species. This indicates that the conservation value of the closed forests left for succession within our study system is rather limited at present. Since absence of disturbances leads to gradual replacement of light demanding oak by shade tolerant trees (Hédli et al., 2010; Kopecký et al., 2013), and since the diversity of organisms associated with oaks is substantially higher than that associated with its most common shade-tolerant successors (e.g. ash, maple, hornbeam) (Southwood, 1961), it is likely that conservation value of the closed forest will decrease even further in the future.

4.2. The effects of artificial canopy opening

The groups that responded positively to the intervention were generally thermophilous, and thus prefer more open, sunny habi-

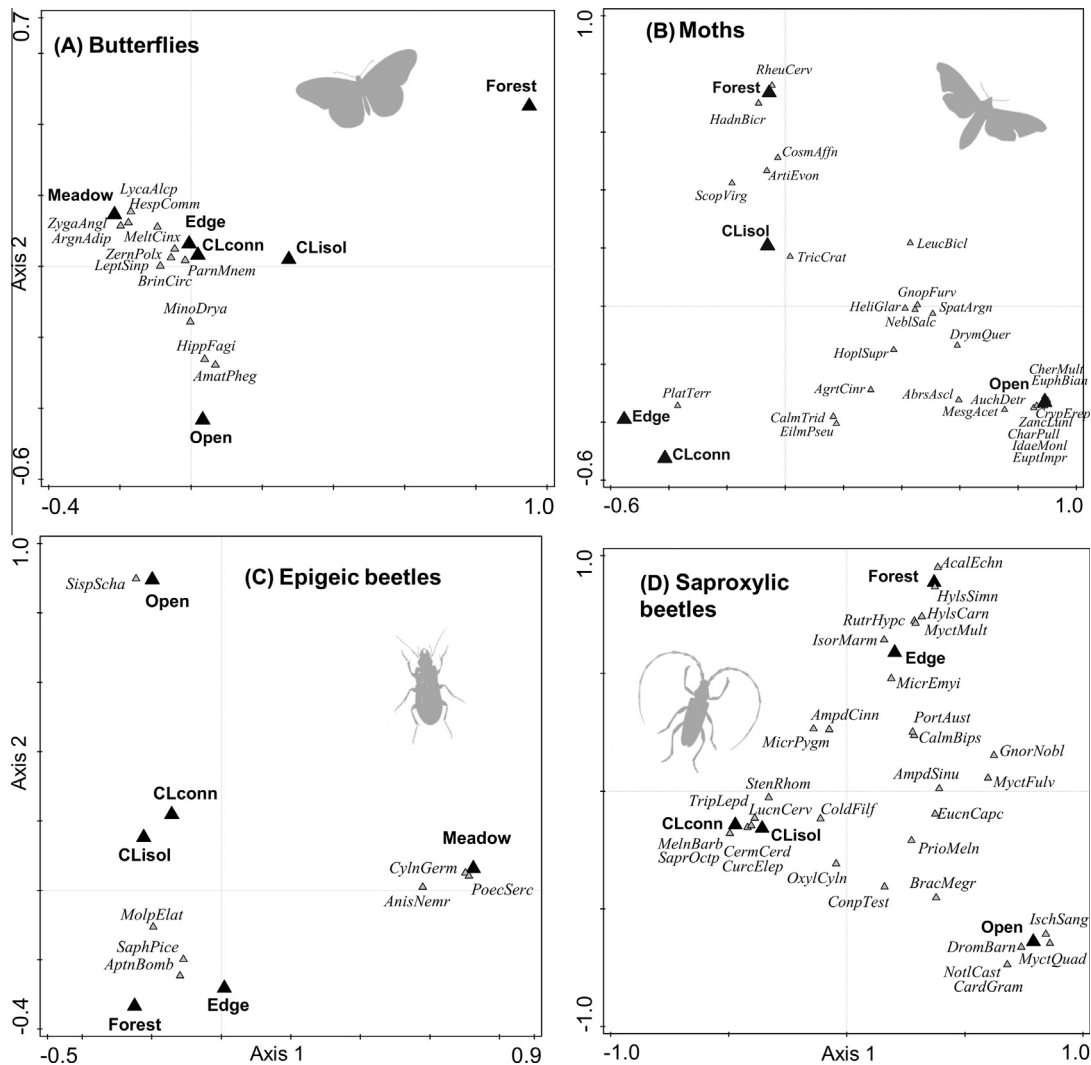


Fig. 3. Species composition and threatened species preferences. Ordination diagrams displaying differences in species composition among habitats, and preferences of threatened species for four groups of insects. The first two axes of the partial Canonical Correspondence Analysis are displayed. Habitats are depicted by full black triangles. The analyses are based on full sets of species, but only best fitting threatened species are depicted (by small grey triangles and abbreviations; for full names, see [Appendix A in Supplementary material](#)). See also [Table 2](#) for variation explained by ordination axes.

tats (Benes et al., 2006; Decocq et al., 2004; Fartmann et al., 2013; Hédl et al., 2010; Horak et al., 2014; Kopecný et al., 2013; Ramírez-Hernández et al., 2014; Vodka and Cizek, 2013).

Although bird assemblages are generally richer in gaps than in closed forest, the differences are often small and depend much on the habitat requirements of the species involved (Fuller, 2000). Our clearings were probably too small to be recognized as a distinct habitat by birds. Further, many open-woodland birds, such as the European roller *Coracias garrulus* or the hoopoe *Upupa epops*, are either locally extinct or very rare in the Czech Republic (Štastný et al., 2009).

The clearings had poorer communities of moth and epigeic beetles than the closed forest. Unlike butterflies, a number of moth species are associated with closed forests. Interestingly, Bolz (2008) found richer moth communities in four year old copices than in mature forests. The clearings therefore may have been too young for many moth species in this study. The activity of most epigeic beetles increases with humidity (Thiele, 1977). The drier conditions of the clearings and the open forest plots are thus likely to be at least partially responsible for the observed pattern of low species richness of these beetles in these habitats.

Most of our model groups contained threatened species associated with clearings. They were especially numerous among saproxylic beetles, most likely because the clearings contained insolated dead wood in the form of post-logging residues and stumps. Five endangered species that are a focus for conservation efforts in the national park, the clouded apollo *Parnassius mnemosyne*, the great capricorn beetle *Cerambyx cerdo*, the stag beetle *Lucanus cervus*, the European green lizard *Lacerta viridis*, and the Aesculapian snake *Zamenis longissimus*, exhibited clear associations with the clearings (Figs. 3 and 4). All of these species prefer open biotopes such as forest steppes (Buse et al., 2007; Luoto et al., 2001; Mikatova and Vlasin, 2012).

In comparison to the closed forest, the creation of clearings created habitats preferred or even required by numerous threatened species. This result is particularly important as the study occurred in the first season following clearing. It remains to be seen what the longer-term effects of open forest conversion will have on the diversity of native species, and threatened species in particular. Also, study of additional taxa, like molluscs (Rancka et al., 2015), fungi (Nordén et al., 2008) or cryptogams, would be beneficial to allow for wider generalization of the effect of canopy-opening in lowland forests.

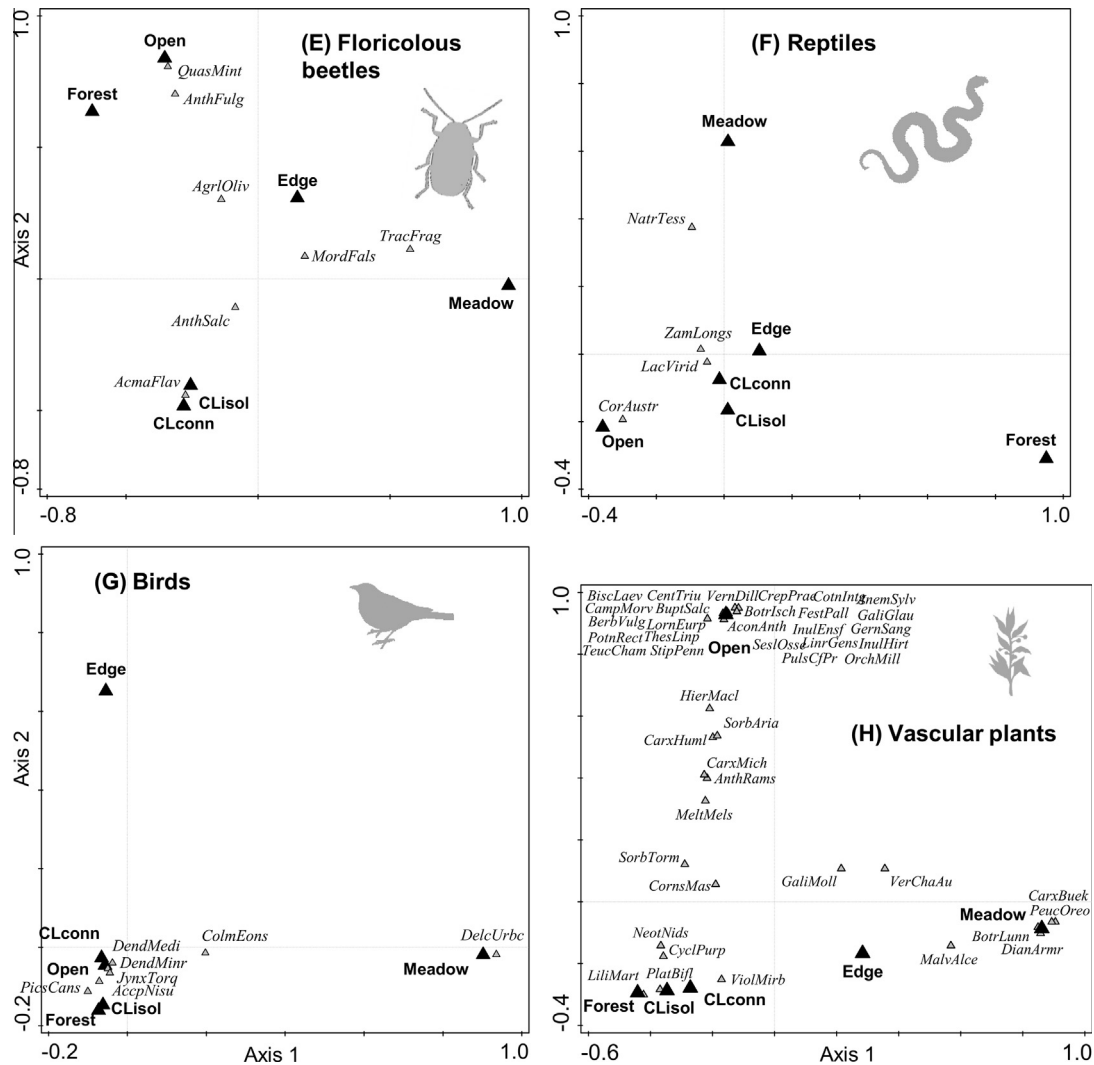


Fig. 4. Species composition and threatened species preferences (*continued*). Ordination diagrams displaying differences in species composition among habitats, and preferences of threatened species for four groups of organisms. The first two axes of the partial Canonical Correspondence Analysis are displayed. Habitats are depicted by full black triangles. The analyses are based on full sets of species, but only best fitting threatened species are depicted (by small grey triangles and abbreviations; for full names, see Appendix A in Supplementary material). See also Table 2 for variation explained by ordination axes.

4.3. The importance of open forests

The open forest hosted distinct communities (being often on extremes of first or second ordination axes) in most groups. The communities often included a large number of threatened species. Furthermore, for six out of the eight studied groups the open forest supported greater number of species than the closed forest. The open forest is thus a key habitat in the study system. It is also a crucial habitat for biodiversity conservation in Europe. It is, however, also highly threatened. The extent of open forest continues to decrease locally (Miklín and Čížek, 2014; Szabó, 2010), as well as across the continent (Kirby and Watkins, 1998). Substantial effort hence should be put into restoration of open forest habitats in Europe.

At this stage, it is difficult to assess if and when the clearing will resemble open forests. The clearings represent new habitats, and are hardly comparable with old open forest plots that have a well developed herb layer. However, although the species composition of the clearings differed from those in open forests, they were also distinct from those in closed forest, often occupying a transitional state similar to the forest edge between open and closed forest

(Figs. 3 and 4). Longer-term observations are needed to ascertain whether species composition in clearings will gradually move towards the open forest or return to the closed forest in the course of succession.

4.4. Succession and colonization processes

While our results come from the first season after clearing, the species composition of our model taxa is likely to change in the following years depending on their colonisation abilities and the changing availability of resources during succession.

Richness of slow colonizers, such as plants, is likely to increase over time. Plant species richness tends to peak in the second or third year after coppicing (Mason and MacDonald, 2002). In our study, the plant composition of the clearings was very similar to the original composition of the closed forest, but they are likely to diverge as shade-tolerant forest herbs are replaced with light-demanding taxa typical of the early stages of secondary succession (Prach et al., 2014). Vegetation succession is tightly connected with the subsequent turnover of animal assemblages, especially those directly associated with plants such as phytophagous insects

(Warren and Thomas, 1992). The diversity of butterflies and moths in coppices is known to peak 2–5 years after felling (Bolz, 2008; Fartmann et al., 2013). Similarly, for some other butterflies or birds the clearings are not suitable until the shrub-layer develops (Fuller and Henderson, 1992). Conversely, for many early successional specialists that demand open conditions with bare ground (for instance some butterflies, or reptiles), and weak competitors among plants, the clearings may become less suitable after a few years due to increased regrowth and shading. Therefore, it is important to observe the course of succession over a longer period to allow for a more precise quantification of the effect of canopy opening on biodiversity.

Since our clearings were created shortly before the sampling and were not connected to the open forests, they were prone to be colonized mainly by species from adjacent habitats. Indeed, the species composition in the clearings was most similar to the forest edge or closed forest in most groups, indicating that these might serve as the main source of colonizing species. Only for epigeic, floricolous and saproxylic beetles did the clearings have a distinct composition from the other habitats. This is particularly interesting for saproxylic beetles because some threatened species were primarily found in the clearings, perhaps owing to the presence of rare and ephemeral resources such as post-logging wood residues. This also shows that the forest edge, representing an ecotone habitat, cannot serve as a substitute for open-canopy habitats.

Finally, the design of the study allowed us to observe differences in the colonization of two types of clearings. Generally, both types were very similar in terms of species composition. The clearings connected to meadows were however, richer in five of the eight model groups. This illustrates that connectivity in open forest habitat is an important factor affecting colonization by light-demanding species. Therefore, it is important to ensure the connectivity of open habitats within forests in order to facilitate their colonization by plants and animals (Eggers et al., 2010).

5. Conclusions

The present study shows that shortly after intervention, valuable habitats for woodland biodiversity were created in closed-canopy temperate forests. Further research should investigate the importance of such habitats in the longer term. Information on how these communities change throughout secondary succession, or the best policies to maintain the suitability of the habitats for the studied groups (e.g. by repeated cutting after several years) are needed for robust conservation recommendations.

To help slow biodiversity loss, active conservation management strategies should be applied to protected temperate forests. Increasing forest canopy closure in historically open woodlands is often perceived as beneficial for the long-term observation of “natural processes”, despite that the minimal intervention approach commonly applied to reserves and national parks may have a detrimental effect on richness and diversity of most taxa. Active human intervention in protected forests should not be seen as a threat to forest ecosystems, but as an adequate substitution for traditional silvicultural practices, e.g. coppicing or wood pasturing, and natural disturbances, e.g. fires or grazing by large herbivores, that maintained biodiversity in the past (Bugalho et al., 2011; Hédl et al., 2010; Plieninger et al., 2015; Vera, 2000). The conservation management of woodlands should be aimed at the creation and maintenance of a diversified forest vegetation. As demonstrated by this and other studies, opening up the canopy of closed forests is beneficial for woodland biodiversity as it supports light-demanding biota, including numerous threatened species of insects, animals and vascular plants (Franc and Götmark, 2008; Götmark, 2013). It is also important to ensure connectivity of the

newly created open woodland structures with other open habitats to facilitate the colonization process.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version, at <http://dx.doi.org/10.1016/j.foreco.2015.09.008>.

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