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ORIGINAL PAPER

Winners and losers in the wilderness: response of biodiversity to the abandonment of ancient forest pastures

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Abstract

Large areas of formerly oak-dominated woodlands are currently managed for timber products, and if they are used in a conservation-oriented way, they are often abandoned and left to become wilderness. We focused on the situation when an oak woodland is still partly managed as an ancient game park and partly abandoned as a nature conservation amendment. We studied this effect using a multi-taxa approach with lichens, fungi and beetles and investigated their response to the changing patterns in canopy openness, dead wood distribution and host tree conditions. The study was done in the Hradec Králové region of the Czech Republic. We found that the maintenance of canopy openness, as determined by management, was the primary driver influencing species composition. Canopy closure led to homogenization of the beetle and lichen communities and the loss of species. Fungi were mainly driven by the amount of dead wood, and abandonment favored their species richness. The creation of a new wilderness was only profitable for fungi, and the maintenance of canopy openness was an important driver for most of the studied taxa (i.e., biodiversity maintenance). Canopy openness and the presence of veteran trees could be used as an indicator of a management history that helps conserve biodiversity. Appropriate conditions for all taxa studied could be fulfilled using wood pasturing or game keeping in combination with dead tree retention.

Keywords Canopy openness · Dead wood · Veteran trees · Epiphytic lichens · Wood-inhabiting fungi · Saproxylic beetles

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Introduction

Large areas of formerly oak-dominated woodlands are currently managed as forests for timber products (Pandey et al. 2007). These areas in the northern hemisphere were, until the Industrial Revolution, highly influenced by wild and domesticated animals (Vera 2000). In particular, the creation of wooded pastures by Neolithic humans and the establishment of game parks in medieval times (Hartel and Plieninger 2014) led to the formation of woodlands with many open spaces and the presence of veteran broadleaved trees (Whitehouse and Smith 2010). Remnants of such forests are presently threatened and are vanishing (Plieninger et al. 2015). In addition to conversion to commercial forests (including coniferous plantations; Mladenović et al. 2018), abandonment is one of the possible threats posed by nature conservation agencies (Miklín and Hradecký 2016; Mazzei et al. 2018). This so-called creation of a new wilderness was predicted in the past to be one of the most important biodiversity remedies (Van den Berg and Koole 2006). Current research indicates that rather than enhancing biodiversity, this abandonment leads to the promotion of a single taxon (e.g., wood-inhabiting fungi; Horák et al. 2016). Furthermore, a large number of taxa could be threatened by this conservation-oriented approach (Hartel et al. 2013; Sebek et al. 2015), often called unmanaged, set-aside, hands-off or non-intervention forests (Vrška 2008; Bouget et al. 2014).

Saproxylic beetles and wood-inhabiting fungi are two of the most studied forest guilds. Saproxylic beetles have been mentioned as an ecological group that is favored by the early stages after large disturbances in middle and high elevations (Seibold et al. 2015), while in lowland areas they mainly prefer open canopy conditions. Solitary veteran trees are probably the richest in saproxylic diversity in the present landscape (Vodka et al. 2009; Parmain and Bouget 2017). Wood-inhabiting fungi are, in general, mainly favored by high accumulation of dead wood (Heilmann-Clausen and Christensen 2004; Seibold et al. 2015; Bässler et al. 2010). Their present hot spots are most likely at mid-elevations dominated by broadleaved trees other than oaks (e.g., beech forests in Europe; Heilmann-Clausen and Christensen 2004). Epiphytic lichens appear to be highly important taxa in terms of anthropogenic changes in management (Seibold et al. 2015). It is important for forest conservation to understand the changes and shifts in forest communities after nearly 50 years of abandonment.

This study addresses the assessment of the situation when a traditionally managed forest is abandoned for nearly half a century in comparison with the situation when traditional management is retained. This situation of forest abandonment is recently relatively common, at least in Europe (Vrška 2008; Horák et al. 2012; Hartel et al. 2013; Bouget et al. 2014), but relatively rarely studied and, to the best of our knowledge, no studies using a biodiversity approach have been published. In this multi-taxa study, we used three taxa (lichens, fungi and beetles) that have different demands regarding management possibilities in forests. We predicted that abandonment would affect beetles, and studies in other long-lived organisms enabled us to predict a relatively slow reaction of lichens. Based on some previous studies, we predicted an indifferent or positive response of fungi to the establishment of new wilderness.

Aim

The study was focused on revealing the response of biodiversity to the changing forest environment in formerly traditionally managed woodland pasture that was partly left abandoned. The main question was how lichens, fungi and beetles react to the three important drivers of forest biodiversity—namely, maintenance of canopy openness, the amount of suitable habitat in their surroundings, as reflected by the amount of dead wood, and the area of suitable habitat, as reflected by the diameter at breast height (DBH) of the host trees.

Methods

Study area

We studied forests in the Hradec Králové region of the Czech Republic. All the study sites were in the area surrounding the town Opočno (50.2707°N, 16.1149°E). Study sites were dominated by Sessile oak (*Quercus petraea*) in relatively flat terrain (*Galio-Carpinetum*). Mean altitude was 302 m a.s.l., mean temperature is 7–8 °C and annual precipitation is 618 mm.

Forests in our study area had been used preferentially for game management instead of forest management from the first known reports in the 16th century to at least the end of 18th century (Horák 1969). For example, for half of the 18th century, there were relatively common hunts with the emperor. Cattle were also often pastured within this area (Horák 1968).

Our study sites were part of formerly large woodland that started to be fragmented by cutting and stumping out (i.e., extraction of stumps after cutting) in the 14th century. The main reasons were the need to increase the area for permanent settlements and high demands for fuel wood and timber. This process was stopped at the end of the 18th century, and oak trees, in particular, started to be highly protected tree species. Wood pasture also started to be controlled and in some parts prohibited (Horák 1968, 1969).

Study variables

We used Sessile oaks as the centers of our study sites. The selected trees were at least 50 m apart.

We studied species from three taxa—lichens, fungi and beetles. We counted all species of epiphytic lichens (Lichenes) observed in a 20 m radius circle (patch) surrounding each studied oak tree during the early autumn of 2011. We only analyzed lichens that were present on oak woody material—i.e., living or dead parts of the oak trees. All fruiting bodies of wood-inhabiting macromycetes (Fungi), except resupinate corticioid species, that were observed during four visits per patch (in early spring, mid-summer, and early and late autumn) were used for our analyses. We observed them in the same manner as lichens. Saproxylic beetles (Coleoptera) were sampled using trunk tree traps. All trapped species that were obligately saproxylic were included in our analysis.

The sites were distributed in managed woodland pasture (N = 16) and abandoned woodland pasture (N = 12) using proportional stratified design—both with very long spatiotemporal continuity (for more than 400 years; Horák 1968). The managed ancient woodland had a study area of 70 ha, and its history was as a continually used game park from the 16th century, with occasional cattle grazing in the past. Present management type is game park with Mouflon, Fallow deer and Manchurian sika deer. The abandoned part (37.5 ha) was formerly pastured and then used from the 18th century until it was abandoned (y. 1970) as a pheasantry (Horák 1968).

We measured the diameter at the breast height (DBH) of each studied oak tree (hereinafter diameter) in cm (mean = 102.5; min = 34.4; max = 171.0 cm). The amount of dead wood material (hereinafter dead wood) was measured in a 20 m radius circle surrounding each studied oak tree as the optimal radius for forest-dwelling organisms (Loskotová and Horák 2016). All dead wood (1.4; 0.01–5.8 m^3) was measured, including all lying and standing pieces to 5 m above the ground and with a diameter > 0.10 m. When only thinner diameter dead wood was found, we used a value of 0.01 m^3 (Horák et al. 2014). The maintenance of canopy openness (12.4; 7.1–30.8%) was measured using a Canon EOS 600D camera with a circular fisheye, Sigma 4.5 mm 1:2.8 DC HSM. Each photograph was taken at ≈ 1.5 m above ground level, standardized with the studied oak tree with trunk in the northern part of the photograph (1 m from lens). All pictures were then evaluated in GLA 2.0 and canopy openness (hereinafter canopy) was counted as the percentage of clear sky. Lichen data from one site were lost, thus this site was not included in the analysis.

Statistical analyses

Since we studied patches in forests under two different management regimes, we first controlled the spatial independence of the studied variables using the test for spatial autocorrelation through the global Moran's I with 199 permutations using the GPS coordinates of each particular study site. We did not find any significant effect of spatial autocorrelation on any dependent variables—namely, Lichens ($I = -0.04$; $P = 0.226$), Fungi ($P = 0.307$) and Coleoptera ($P = 0.156$)—or any independent variables—namely, canopy ($P = 0.206$), dead wood ($P = 0.151$) and diameter ($P = 0.126$). This was computed in SAM v4.0.

Canonical correspondence analyses were computed due to the use of species presence/absence data. Dependent and independent variables were log-transformed. Analyses were evaluated with Monte Carlo permutation tests (9999 unrestricted permutations) under the full model. For visualization of species richness trends, we used GLM in data attribute plots. The number of species was used as a dependent variable and independent variables and samples were used for visualization. We used the contour diagram for a fitted GLM. For the degree of the GLM, we used stepwise selection using AIC statistics. The amount of variance explained by environmental variables independently and the variance shared with other variables was computed using partitioning of variance in canonical correspondence analyses. This was computed in CANOCO 4.5 and visualized in CanoDraw 4.12.

Results

We found 44 species of epiphytic lichens, 45 species of wood-inhabiting fungi and 173 species of saproxylic beetles (Tables S1, S2, S3).

The analysis of the lichen species composition was significant with regard to the environment ($R^2 = 17.29\%$; $F = 1.60$; $P < 0.001$). The species composition of fungi also revealed a significant response ($R^2 = 14.09\%$; $F = 1.31$; $P = 0.017$). The canonical correspondence analysis of the species composition of beetles indicated a significant pattern ($R^2 = 13.43\%$; $F = 1.24$; $P = 0.006$). Canopy had a significant influence on the species composition of all taxa studied. Dead wood significantly influenced only the beetle composition, while diameter was never significant. The first axis was the most significantly responsible for the discrimination between managed and abandoned sites for species composition (Fig. 1).

The species richness gradient was mainly influenced by dead wood and diameter in the case of lichens, while it was rather independent of the canopy gradient; the number of species increased with an increasing dead wood amount and tree diameter. The number of species of fungi mainly increased with increasing amounts of dead wood, while

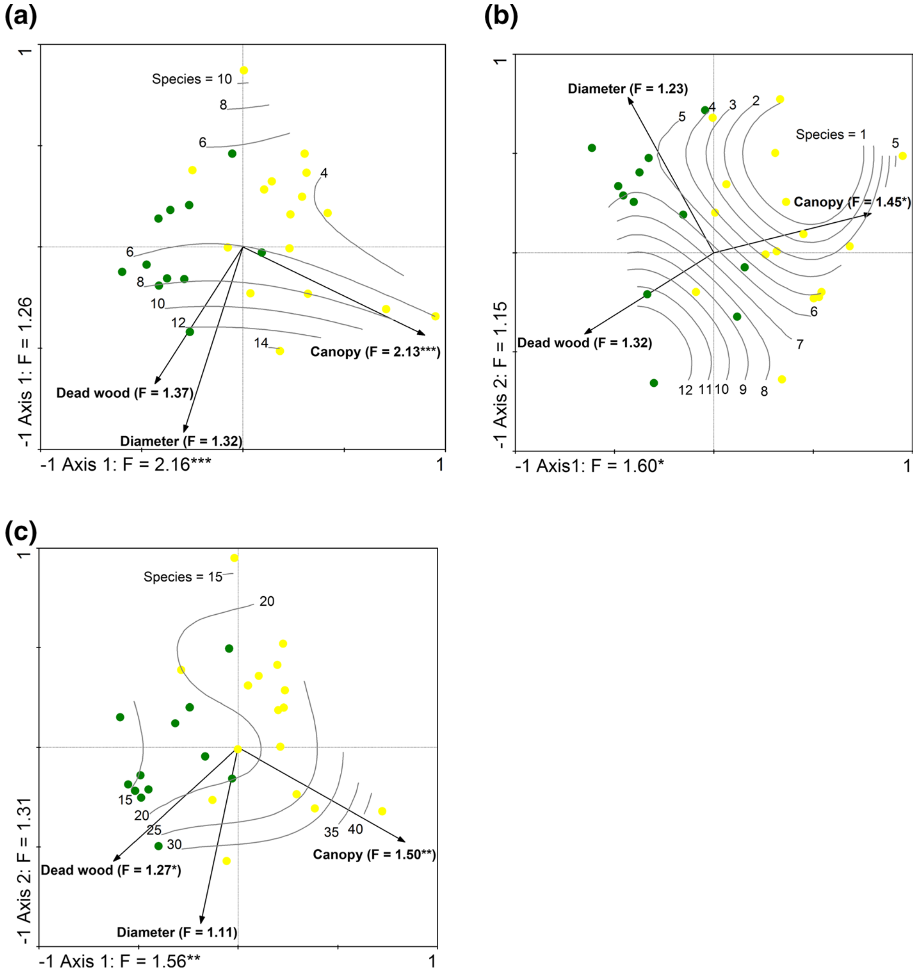

Fig. 1 Response of species composition and richness to the environment. Subfigures are for **a** lichens, **b** fungi and **c** beetles computed by canonical correspondence analyses using visualization of sample-environment plots. Gray isolines reflect the trend in species richness using GLM with **a** quadratic degree ($F = 9.95$; $P < 0.001$), **b** cubic degree ($F = 6.64$; $P < 0.001$) and **c** cubic degree ($F = 3.96$; $P = 0.008$). *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$. The yellow color is for pastured sites, and green is for abandoned sites. (Color figure online)

the influence of diameter was indifferent, and the influence of the canopy was non-linear (first decreasing and then increasing). All variables had a positive effect on species richness in the case of beetles (Fig. 1).

Patches in abandoned and pastured forests were mainly discriminated by the gradient of canopy, with pastured forests having more and abandoned forests having less. This was true in the case of lichens and beetles, where sites in the abandoned forest were more clustered and, thus, more similar in species composition than in pastured forest sites. In the case of fungi, the canopy gradient was complemented by the opposite pattern in dead wood. Patches in abandoned sites were more distributed along an increasing dead wood gradient and were as scattered as sites in the pastured forest (Fig. 1).

Canopy was the only significant variable regarding the influence of its independent contribution on the explained variance. It had significant influence in the case of lichens and beetles, while its independent contribution was not significant for fungi. The results indicated low overlaps (i.e., < 1%) of shared variance between and among environmental variables. Diameter had higher influence than dead wood in the case of lichens and fungi, while for beetles the result was the opposite (Fig. 2).

The number of species was higher for lichens and beetles in the pastured forest. In the case of beetles, this number was more than two times higher, and the number of shared species was even higher than the number of species in the abandoned forest. The opposite pattern was observed in the case of fungi (Fig. S1).

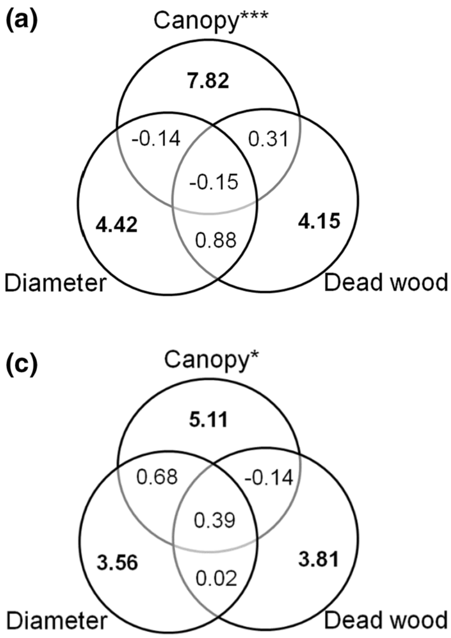

Fig. 2 Influence of environmental variables. Subfigures are for **a** lichens, **b** fungi and **c** beetles computed by variance partitioning in canonical correspondence analyses using Venn diagram visualization. Bold values are percentages of independent contributions to the total explained variance, while other values are shared variance between and among variables. * is for $P < 0.05$; *** is for $P < 0.001$

Discussion

Our results indicated that the primary driver of taxa composition was the gradient of canopy openness, which probably reflects the site management history (e.g., Miklín and Čížek 2014). While beetle species richness was significantly higher in the pastured woodland, fungi thrived in the abandoned woodland. Lichens seem to prefer maintenance management of open canopy, but their response was not as clear as that of the beetles.

Change in communities

In the case of fungi, the influence exerted by particular environmental characteristics, as reflected by the independent portion of variance accounted for by them, was highly balanced. For lichens and beetles, canopy was the most influential characteristic and the two habitat amount parameters had lower, although again balanced, influence. A low portion of shared variance indicated the independent influence of a particular environmental variable.

Canopy openness was the most influential gradient regarding the change in species composition after abandonment. Furthermore, its influence was mainly independent of other two habitat amount characteristics (see its right-angle projection to other variables in Fig. 1). However, its influence on species composition of three studied taxa was different.

The amount of dead wood played a significant role only for the change in species assemblages of beetles, which is surprising because it was expected that fungi would be the taxa that would be the most driven by this characteristic (Bässler et al. 2010; Horák et al. 2016). It is most likely that dead wood accumulation after abandonment together with canopy closure led to the significant shift of the previous communities to the new ones (e.g., Thakur et al. 2014). This shift might lead to total diversification in beetle communities. However, this could also lead to the loss of communities associated with traditionally managed forests or at least the loss of individual species that are threatened under forest management abandonment (Buse et al. 2008; Horák et al. 2012).

Surprisingly, the studied taxa composition was never significantly influenced by the habitat amount, as reflected by diameter of the host tree. This result is relatively surprising because the interconnection was previously reported (Buse et al. 2016). Nevertheless, there is a possibility that diameter might not be the only sufficient parameter for dead wood-associated taxa (e.g., Horák 2017). As diameter always had an independent relationship with canopy, this might indicate that this parameter is much more interconnected with forest history than was predicted (Miklín et al. 2017). Big trees with some signs of veteran tree conditions under the closed forest canopies are mainly left over from formerly open canopy conditions, and they are not able to sufficiently contribute to the survival of species that are connected with traditional management types in the forests that led to their open growth conditions (Horák and Rébl 2013; Johansson et al. 2013; Miklín and Cížek 2014).

One another fact is that the communities of lichens and beetles in abandoned sites have more clumped clusters, and this indicates that abandoned sites hosts more similar species than sites in managed forests.

Species richness patterns

The influence of canopy on species richness was as conspicuous as its influence on species composition. Dead wood played a more noticeable role for the species numbers of lichens and fungi. The pattern of complementarity between canopy openness (as the reflection of ambient temperatures) and dead wood amount is known for saproxylic beetles (Lachat et al. 2012; Müller et al. 2015). It can be seen in our case of fungi, while in the case of beetles and lichens, the relationship was surprisingly indifferent. Managed sites had higher species richness than abandoned sites in the case of beetles and lichens, and only fungi thrived on abandonment. Lichen species appeared to be the most resistant to the change in management with regard to the proportion of species shared between managed and abandoned sites, which coincided with our hypothesis.

Influence on taxa

The results for lichens indicated that the species composition was mainly driven by canopy openness. This gradient fairly well discriminated between abandoned and managed forests. Thus, it seems that abandonment of management led to the shift in species composition, and only a few abandoned sites retained their former species. However, the number of species was not much different between sites with different management histories. The increasing species richness was mainly driven by the two habitat amount characteristics (diameter and dead wood). Hence, forest history mainly drove the shift in lichen species composition, but their species richness was influenced by habitat amount.

The gradient in canopy openness led to the discrimination between fungal species composition in managed and abandoned sites. The number of species of wood-inhabiting fungi increased only with increasing amounts of dead wood and was unaffected by the diameter of the host tree. Nevertheless, abandoned forests hosted noticeably more species than managed ones—which could be an effect of the increased humidity of the dead wood in shaded patches.

The difference in species composition of beetles in abandoned and managed forests was also mainly driven by the gradient of canopy openness. Nevertheless, this gradient was the most responsible factor for the increase in the number of species from this specialized guild and noticeably more species preferred the managed sites.

Management possibilities

The results of our research revealed contrasting responses of the two most important dead wood-associated taxa, i.e., beetles and fungi. Both were influenced by canopy with regard to the species composition, but numbers of beetles were favored by canopy openness, while numbers of fungi were favored by canopy closure. The most important conclusion regarding the management is that biodiversity amendments are, in this case, hidden in the application of pasture in woodlands and partial abandonment. This combination can be seen in forests with more diversified topography, where the majority is pastured, and less accessible places are not affected by wild animals (Vera 2000; Hartel et al. 2013). Canopy openness can be relatively easily applied in forests that are managed for timber products by using amendments such as creaming (i.e., the cutting of carefully selected trees for special timber products; Price and Price 2006). Habitats for some wood-inhabiting fungi can be complemented by the abandonment of wood residuals (mainly fine woody debris), including stumps (Fossestol and Sverdrup-Thygeson 2009). Nevertheless, the results reported for lichens shifted the assessment of the most valuable management towards active management in the form of game keeping or cattle pasturing with the abandonment of single dead wood pieces (like dead standing and downed trees). Furthermore, the majority of fungi were common species, which relatively quickly colonized downed wood.

Conclusions

Canopy closure caused by abandonment and the creation of a new wilderness in forests led to homogenization of species composition and a decrease in species richness for lichens and beetles. The level of maintenance of the canopy is, thus, probably one of the most important drivers in forests dominated by oak on low and medium productivity soils (i.e., acidophilic and mesophilic oak woodlands). Canopy openness in combination with the presence of veteran trees could be used as an important indicator of the management history of traditionally managed woodlands.

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