The effects of habitat degradation on metacommunity structure of wood-inhabiting fungi in European beech forests

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ABSTRACT

Intensive forest management creates habitat degradation by reducing the variation of forest stands in general, and by removing old trees and dead wood in particular. Non-intervention forest reserves are commonly believed to be the most efficient tool to counteract the negative effects on biodiversity, but actual knowledge of the conservation efficiency is limited, especially for recent reserves. The structure of ecological communities is often described with measures of nestedness, beta diversity and similarity between communities. We studied whether these measures differ among forest reserves with different management histories. For this purpose, we used a large data set of wood-inhabiting fungi collected from dead beech trees in European beech-dominated forest reserves. The structure of fungal assemblages showed high beta diversity, while nestedness and similarity was low. During the decomposition process of trees beta diversity between the communities occupying different trees increased in natural, but not in previously managed sites. Effects of management and decay process on nestedness were complex. We argue that the detected differences most likely reflect historical effects which have extirpated specialized species from the local species pools in managed sites, and resulted in more homogeneous communities in managed sites. It is alarming that community structure is affected the most in the latest decay stages where the decay process turns the dead wood into litter, and which is thus the interface between the wood decay and the litter-decaying ecosystem. The effects of simplified communities in late decay stages on soil biodiversity should be studied.

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1. Introduction

Human activities are affecting global biodiversity on different hierarchical levels ranging from genes to whole biomes. As a result we are witnessing the sixth global mass extinction (Barnosky et al., 2011) and seeing most of the biomes being severely degraded (Foley et al., 2005). Currently, an increasing number of conservation scientists are focusing on the biodiversity effects of habitat degradation to gain an understanding of the links between biodiversity and ecosystem functioning, and to find tools to counteract biodiversity loss. The focus in conservation research has often been on individual focal species or species groups, typically those considered endangered, or on species richness itself (e.g. Simberloff, 1998; Ranius and Roberge, 2011; Blaser et al., 2013). However, human activities may also affect the community assemblies in other ways than deleting some particular endangered species from the species pool, or by reducing species richness.

One possible effect of habitat degradation is the breakdown of community and metacommunity structures typical for community assemblies occupying natural biotopes. Metacommunity structures created by variation within and among local community assemblies are complex and thus challenging to study (Leibold et al., 2004). Nestedness and beta diversity are among the most often used indices for explaining (dis)similarity pattern of a set of assemblages. Nestedness describes the proportion of species in a species poor assembly that is a subset of a more species rich assembly (Almeida-Neto et al., 2008). Beta diversity on the other

hand studies the proportion of turnover between assemblies (Tuomisto, 2010). These measures are affected by several types of difference in similarity. For example, two assemblies with the same species richness may share anything between all or none of the species. On the other hand, two assemblies with high richness difference may share up to as many species as there are in the smaller assembly (Podani and Schmera, 2011).

The landscape scale effects of habitat degradation and fragmentation on community structure have attracted increasing research interest. In their review of faunal responses to habitat patchiness, Watling and Donnelly (2006) concluded that community structure is more associated with habitat patch size than the degree of geographical isolation from other patches. Later studies have provided partly controversial results. For example, a recent study on vascular plants showed that even though management reduced species richness on the landscape level, the level of nestedness between patches was not affected (Keith et al., 2011). Another recent study focusing on birds and insects showed heterogeneous response to habitat degradation between these groups (Hill et al., 2011). Despite the rather active research focusing on landscape scale community patterns, the local community structures have attracted less research interest.

One biome which has been heavily exploited already for 5000 years, are the forests of Continental Europe. The forest cover itself has been heavily reduced (Harris, 1996) and the majority of the present day forests are far from natural in their structure (Wallenius et al., 2010). Beech forests have historically covered large parts of this region, being the dominant tree species in lowland to low montane forests for at least 3000 years. Presently as less as 0.1% of the original cover remains in near primeval condition (Brunet et al., 2010).

One species group which has been shown to be heavily affected by changes in forest ecosystems is wood-inhabiting fungi. Like other organisms living on dead wood, these are habitat-tracking specialists, depending on a continuous supply of dead wood. Because of the decay process a given habitat patch is only suitable for each species in a limited time window, and all species need repeatedly to colonize new suitable habitat patches to survive in the system (reviewed in Stokland and Siitonen, 2012). In natural forests these dynamics results in ever-changing and complex mosaics of interacting metacommunities. It is expectable that broken dead wood continuity may have strong effects on metacommunity structure in this system.

It is well documented that forest management in general has a negative effect on species richness of wood-inhabiting fungi (Lonsdale et al., 2008; Junninen and Komonen, 2011; Abrego and Salcedo, 2013; Blaser et al., 2013). Furthermore, earlier studies have shown that forest management mostly affects specialized species dependent on rare substrate types (Bässler and Müller, 2010; Nordén et al., 2013), or with a poor colonization ability (Edman et al., 2004; Norros et al., 2012). The effects of habitat loss and fragmentation on metacommunity structure in wood-inhabiting fungi are generally very poorly studied. One earlier study has shown that in a natural but patchy landscape wood-inhabiting fungi show clearly nested occurrence patterns between the small and large forest patches (Berglund and Jonsson, 2003). It is unknown if the same nested community structure emerges if a landscape is fragmented more recently due to deforestation and forestry (but see Heilmann-Clausen and Christensen, 2005).

In this paper we used a diversity partitioning approach proposed by Podani and Schmera (2011) to study how different metacommunity measures change from intact to degraded beech forest communities. To explore differences in more depth, we further analyzed our data in relation to the natural succession process occurring in the community in focus. Our work is based on a continental scale dataset on wood-inhabiting fungi, collected from European beech forests and including more than 1200 sampled decaying beech trees (earlier reports utilizing part of this dataset include Ódor et al., 2006). Our main hypotheses were that: (1) Metacommunity structure is simplified and hence the degree of nestedness is higher in degraded systems; (2) There is a general trend of increasing beta diversity towards the later decay stages; (3) This community diversification trend is weaker or missing in degraded biotopes due to the absence of specialized late stage decayers.

2. Material and methods

2.1. Study sites and sampling

The study included 19 European broadleaved forests sites with different management histories. The studied forests were split in three management classes, based on Ódor et al. (2006), with natural forests incorporating pristine forest reserves never subjected to management or with only weak impacts from grazing or selective cutting. Forest reserves subject to former management were further divided into two categories: The first included all sites with continuous forest cover in their history but with more or less uniform age structure reflecting former management for timber and tree ages exceeding 200 years. The second managed class included sites with uniform age structure, tree ages up to 200 years and in some cases a broken forest continuity. The forests were located in Belgium, Denmark, Hungary, the Netherlands, Slovenia and Sweden. The names and locations of the sites are given in Table A1. The management history was geographically unbalanced with most of the natural sites located in Hungary and Slovenia. However, this reflects the true European situation, with both length and intensity of management history increasing towards west (Wallenius et al., 2010). In each site, the sampling units were the dead beech trees including their logs and snags (if present). The sampled trees were selected based on a stratified random design with the aim to secure an even distribution of size and decay stages categories (defined by Ódor and van Hees, 2004). It was attempted to survey at least five trees from each of six decay stages, but this was not always possible due to an unbalanced representation of decay stages and size classes in some former managed localities, especially in Belgium and the Netherlands. The fungal sampling was conducted to cover the fruiting season of most of the studied groups and included three sampling occasions for all the studied trees, distributed over the fungal fruiting season. See Ódor et al. (2006) for more details on the study sites and sampling.

Within each site study trees were divided into decay classes based on their median decay stage in order to analyse for changes in metacommunity structure along the succession gradient. In each forest, a particular decay stage was included only if represented by at least five sampled trees with fungal occurrences. Trees in decay stage six were omitted from all datasets, because in many study sites they were not found at all.

2.2. Analyses

To analyse the diversity patterns within different decay stages in different forests belonging to different management classes, we used the SDR simplex approach proposed recently by Podani and Schmera (2011). By partitioning the gamma diversity between two sampling units into additive components this approach enables studying simultaneously how beta diversity, nestedness and richness turnover contribute to the overall community pattern. For each sample pair, the method produces scores of similarity (shared species, S), species replacement (R) and richness difference (D), all relativized by the total number of species in

the sample pair. The scores for all possible pairs of samples in a matrix can be easily visualized using a ternary plot (Fig. 1a). The method also produces within-matrix means for each similarity measure and calculates mean beta diversity (β) and two different measures of nestedness (we use the percentage relativized nestedness PRN here, for a discussion see Podani and Schmera, 2012). In this approach, D and S are maximized in a perfectly nested pattern, whereas D and R are maximized in a set with maximum beta diversity.

The random community measures are dependent on the fill (proportion of presence records) in the species-by-sites (sites are here trees) matrix, as well as on the species richness (number of rows in the matrix). Therefore, we created a set of random assemblages within the variation range of fill and species richness in our original data to study the deviation from randomness in our results. The randomization to study the effects of fill was done by setting the matrix to the mean size in our data (13 columns and 56 species) and then reshuffling positive occurrences randomly within the whole matrix retaining the selected fill level. Similarly, the randomization to study the effects of species richness was done by setting the matrix to the mean number of columns and to mean fill (24%) in our data and then reshuffling the matrix retaining the selected species richness constant. We conducted 10 randomly assembled matrices for different fill and species richness levels within the variation in our data (fill 9–44%; species richness 12–140) and illustrated the resulting mean values to clarify the deviation from randomness in our results (Fig. 1b).

Podani and Schmera (2011) did not encourage conducting any significance testing on SDR scores, nestedness or beta diversity metrics derived from the communities, but to use them and the ternary plots for more illustrative purposes. However, the within-matrix means of the different indices are suitable for statistical testing. We used these means of different indices (within site and decay class) to test the effect of management history on meta-community structure. The data structure was problematic for conducting orthodox statistical analysis, because there were several index values produced from one site, thus potentially demanding a nested model structure. However, the averages of different indices are calculated separately for each decay stage and different decay stages are presented by trees which have grown and died in different decades and environmental conditions. Therefore the spatial context is the only issue creating pseudoreplication in our data. We decided to control the spatial context with one background variable but to conduct a normal model without nested structure. However, this should be noted while making conclusions based on our analyses.

We conducted analyses of covariance to explore the interactions of different variables in explaining the differences in the average community structure measures at different decay stages and in forests with different management history. We focused these analyses on the most interesting indices, namely beta diversity and nestedness, and used site and decay stage – specific averages of these as target variables. We added naturalness of the study site and decay stage as fixed factors, and matrix fill and the average species richness (alpha diversity) per log as covariates into the analyses. To control for the geographic variation within our data we also added one climatic variable to the analyses. We used temperature range as this climatic background variable (as a covariate), since it is a good surrogate of the oceanic-continental variation present in our data. We added first all two-way interactions between the variables into the analyses but interactions were removed in a stepwise manner if they were not statistically significant.

The SDR values were calculated with the SDR simplex program (Podani and Schmera, 2011), while ternary plots illustrating the values were drawn with Tri-plot version 1.4 (Graham and Midgley, 2000). Statistical testing was done with PASW 18 program (SPSS Inc.).

3. Results

The final data set included 15181 observations of 296 fungal species on 1098 logs (Table A2), distributed across 19 sites and five decay stages. From the 95 potential subsets 84 satisfied the defined preconditions (minimum five trees per site and decay stage).

The studied communities were characterized by high beta diversity and low similarity between the studied trees (Figs. 2 and 3). Comparing visually the random and the observed assemblages (compare Fig. 1b with Figs. 2 and 3), the position of points are closer to the D and S corners in observed assemblages, which means that the effect of richness difference (D) and similarity (S) is higher. The studied communities in general were described by clearly higher nestedness than what could be expected based on random variation.
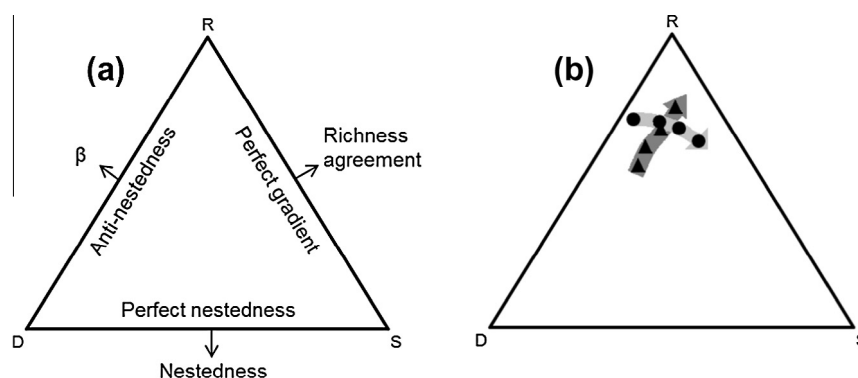

Fig. 1. Figure a (modified from Podani and Schmera, 2011) illustrates the function of the SDR simplex method and ternary plots. β = beta diversity, S = similarity, R = species replacement and D = species richness difference between the two communities. If, for example, the SDR value and thus the dot in the plot is close to the left side, the beta diversity between the communities is high. The closer the dot is to R corner, the more beta diversity is resulting from species replacement instead of richness difference between the two samples. Figure b illustrates how the variation in matrix fill (proportion of presences) and number of rows (species richness) affect the different metrics derived from the matrix. This figure shows the random variation of SDR mean scores within the variation in matrix fill (rounded symbols) and species richness (triangles) present in our data. To show the effects of variation in matrix fill (9–45% in our data), the matrix size was standardized to the mean size in our data (13 trees and 56 species in one site and decay stage) and then the matrix was randomized. To show the variation in species richness (12–140 in our data), the number of columns and matrix fill were standardized to mean values in the data (13 trees/columns and 24% fill). The four dots represent fills of 10%, 20%, 30% and 40%, with similarity (S) increasing with increasing fill (light grey arrow). The four triangles represent richnesses of 10, 20, 40 and 80 with species replacement (R) increasing with increasing species richness (dark grey arrow). Increasing species richness above 80 species did not have any notable effect on the random variation in species replacement.
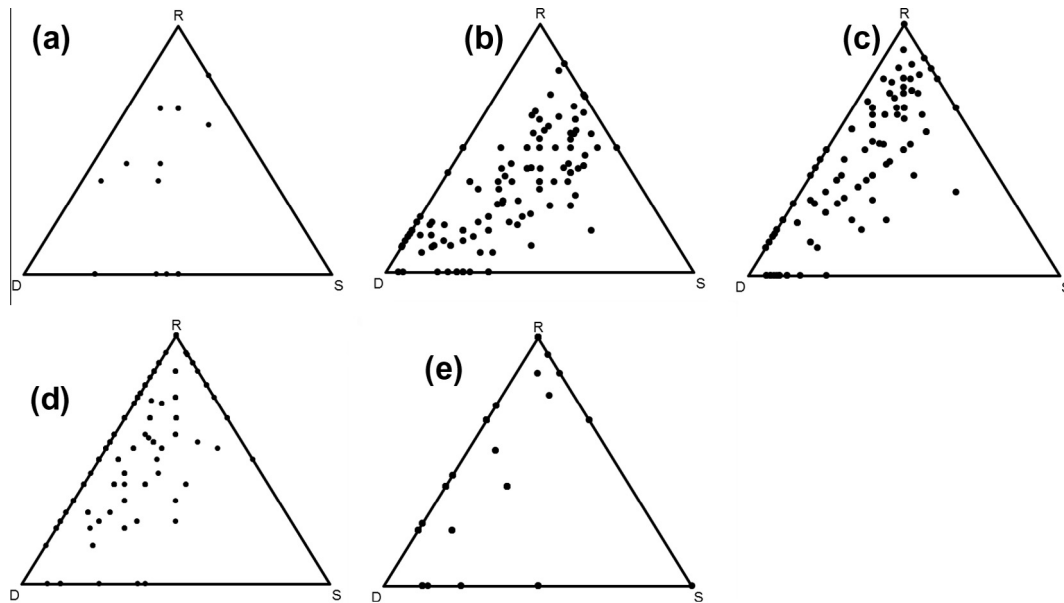
Fig. 2. Original SDR simplex scores derived from a typical natural forest (Krokar in Slovenia) in our data. Figure a shows the original SDR scores for all the possible tree pairs from decay stage 1, figures b–e show the according data points for decay stages 2–5.

Fig. 3. Original SDR simplex scores derived from a typical previously managed forest with a broken forest continuity (Zoniënwoud in Belgium) in our data. Figure a shows the original SDR scores for all the possible tree pairs from decay stage 1, figures b–e show the according data points for decay stages 2–5.
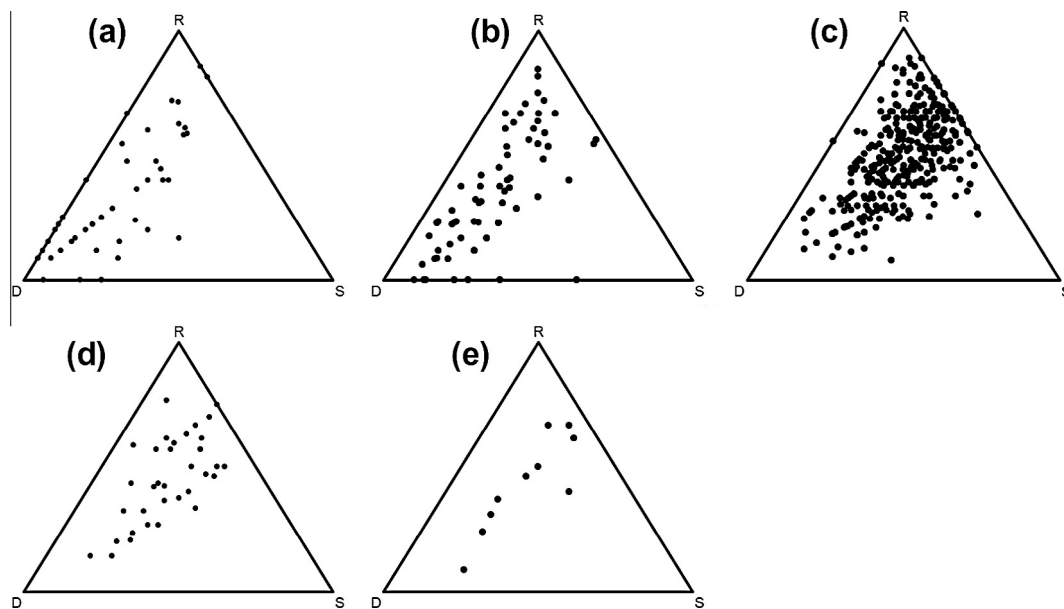
Two-way plots based on the raw data showed that matrix fill was consistently lower in natural, compared to old managed reserves, and in both cases declining with decay stage (Fig. 4a). Recent managed reserves showed a mixed pattern, with similar fill as in natural reserves in early decay stages, but shifting towards high fill in late decay stages. Beta diversity increased with decay stages in natural, but not in the two classes of formerly managed reserves (Fig. 4b). The inverse pattern was found, but less distinctly, for nestedness (Fig. 4c). Beta diversity was decreasing with increasing alpha diversity, but most strongly so in late decay stages (Fig. 5). Along with this trend, alpha diversity tended to be lower in natural compared to old managed reserves, especially in late decay stages.

Species replacement was higher in the managed sites in early decay stages (Fig. A1) but because it increased in natural sites along the decay process, it was on a similar level in later decay stages. Richness difference was higher in natural sites than in managed ones, but it did not show any trend with decay (Fig. A2). Because beta diversity is the sum of richness difference and species replacement (Podani and Schmera, 2011), the different pattern in beta diversity with decay between the management types was related to the differences of species replacement.

The analysis of covariance with average beta diversity as the dependent variable explained 74.5% of the variation in data ($F_{19,80} = 9.2$, $P < 0.001$). Alpha diversity was clearly the most powerful explanatory variable but also management history and matrix
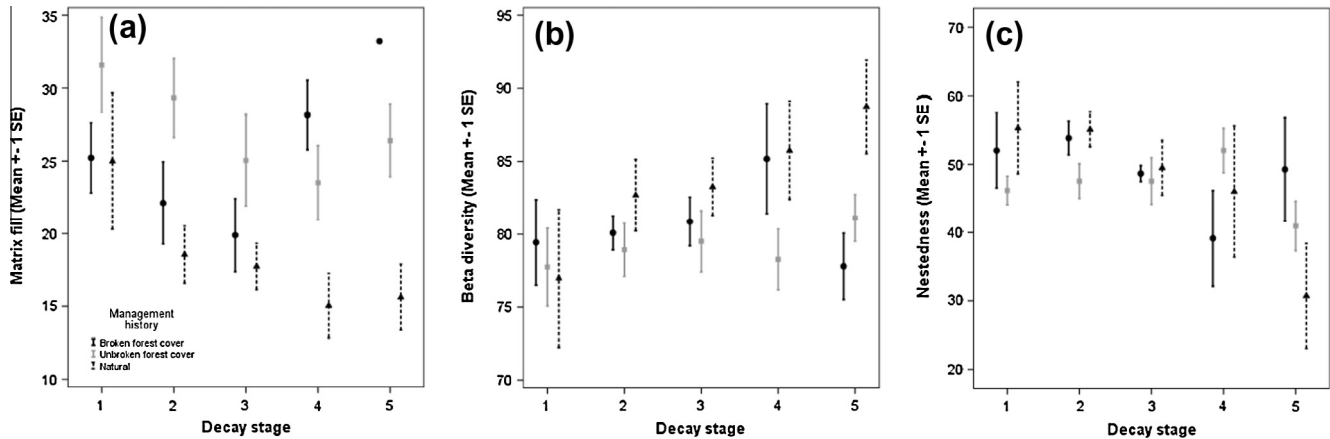
Fig. 4. The means of the within-site and within-decay class values of matrix fill (a), beta diversity (b) and nestedness (c) in relation to defined decay stages and management classes in our data.
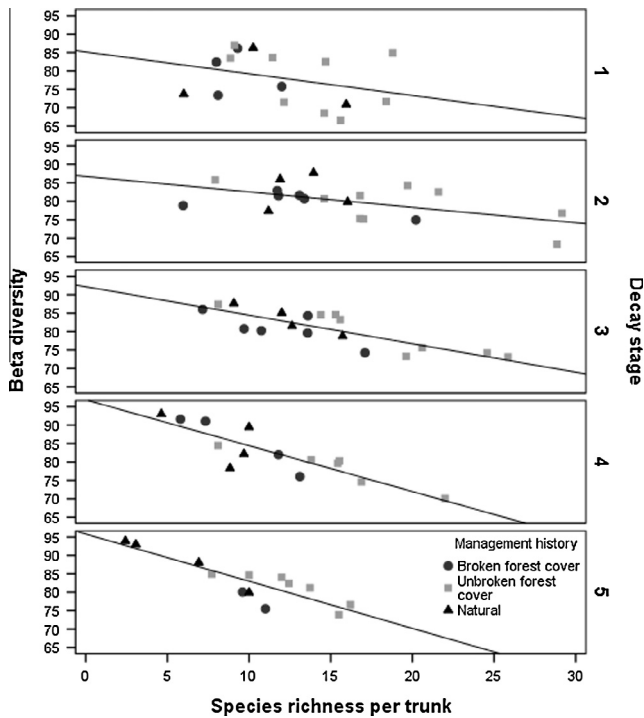

Fig. 5. The within-site and decay class averages of beta diversity in relation to management history, decay stage and the average alpha diversity per tree on that particular data set.

fill explained beta diversity as well as decay stage through two-way interactions (Table 1). Only temperature range was insignificant in this model. The significant interactions between explanatory variables confirm the more simple interactions revealed in Figs. 4a and b and 5.

The analysis of covariance with average nestedness as the dependent variable explained 63.9% of the variation in data ($F_{19,80} = 5.6$ $P < 0.001$). Alpha diversity and management history were the most powerful explanatory variables in the model, the latter as an independent variable as well as through interactions with matrix fill and decay stage. Again, the only variable with no explanatory power was temperature range. The significant interactions between explanatory variables and nestedness confirm the more simple interaction revealed in Fig. 4c, but points also to a complex interaction between matrix fill and management history (see Table 2).

Table 1
Analysis of covariance on the within site and decay stage average values of beta diversity. Partial eta squared (eta²) shows the variance explained by a given variable after excluding variance explained by other predictors.

	MS	d.f.	F	P	eta²
Decay stage	4.9	4	0.4	0.807	0.026
Alpha diversity	649.6	1	53.4	<0.001	0.471
Matrix fill	79.2	1	6.5	0.013	0.098
Temperature range	1.8	1	0.1	0.702	0.002
Management history	47.5	2	3.9	0.026	0.115
Decay stage * matrix fill	54.6	4	4.5	0.003	0.230
Decay stage * alpha diversity	53.9	4	4.4	0.003	0.228
Management history * matrix fill	42.9	2	3.5	0.036	0.105
Error	12.2	60			

4. Discussion

Based on the recent approach suggested by Podani and Schmera (2011) we found clear differences in metacommunity structure of wood inhabiting fungi in formerly managed forest reserves compared to near primeval forests with minimal human intervention. Even though we found clear effects of management history on nestedness, the effect was complex and less clear than expected, with matrix fill, alpha diversity and decay stage as important and partly interacting co-variables. Hence, it is difficult to evaluate if our results are in conflict with our first hypothesis or not. The results for beta diversity are clearer, and are in agreement with our second and third hypothesis. Thus, we found beta diversity of wood-inhabiting fungal communities to increase during the decay process, but only in natural sites. This increasing beta diversity reflected increasing species replacement between trees as decay proceeds. A community diversification along the decay process in

Table 2
Analysis of covariance on the within site and decay stage average values of nestedness. Partial eta squared (eta²) shows the variance explained by a given variable after excluding variance explained by other predictors.

	MS	d.f.	F	P	eta²
Decay stage	32.2	4	0.6	0.648	0.040
Alpha diversity	1139.9	1	22.1	0.000	0.269
Matrix fill	334.6	1	6.5	0.014	0.097
Temperature range	0.6	1	<0.0	0.913	<0.001
Management history	432.3	2	8.4	0.001	0.218
Management history * Matrix fill	631.9	2	12.2	<0.001	0.290
Decay stage * Management history	123.5	8	2.4	0.026	0.242
Error	51.7	60			

wood-inhabiting fungal communities was observed previously by Heilmann-Clausen (2001), who related the phenomenon to an increased impact of microclimatic variation in well decayed wood, with some trees being occupied by stress-tolerant species and some by combative late stage specialists. The further decay proceeds, the more the decaying wood probably reflect its physical environment such as temperature and humidity conditions and even the quality of the underlying soil. Moreover, the complex interactions between different decayer species may create successor networks along the decay process (Niemelä et al., 1995; Ovaskainen et al., 2010), promoting even further diversification of the community.

The higher diversification of communities in later decay stages is also observed in bryophyte and lichen assemblages on dead wood (McAlister, 1997; Ódor and van Hees, 2004). Combined with the variation in the primary decayer community and epixylic bryophyte community the differently sized and positioned trees may actually provide a large number of different substrate qualities and microhabitats for the wood-inhabiting fungi occupying later decay stages. However, our data suggest that these processes are compromised in managed sites where local beta diversity remains at a stable, relatively low level during the whole decay process. Thus, in the previously managed forests either the substrate in the late decay stages is more homogeneous than in the natural sites, or some of the species utilizing different substrate types are missing from the local species pool.

The latter option could be true if species occupying different decay stages differed in their colonization potential, so that specialized primary decayers would colonize a previously managed site more efficiently than late stage decayers. We argue that there is a logical reason to expect such differences. After some major natural disturbance such as fire or storm, there is suddenly a vast volume of resource available for the primary decayers to utilize. Thus, in order to have the advantage of being the first to colonize the available substrate species have to be either readily present within the living trees (Parfitt et al., 2010) or be very efficient in their dispersal and establishment on exposed substrates. Because decay proceeds at a varying speed depending on microclimatic conditions and internal community structure (Heilmann-Clausen, 2001; Kueppers and Harte, 2005; Mäkinen et al., 2006), bulky wood in late decay stages is expected to be continuously present in natural forests, even if the input is not constant. As a consequence primary decayers can be expected to be more efficient in their long-distance dispersal and thus less sensitive to extinction due to break down of metapopulation structure when suitable habitat patches disappear from managed landscape compared to late decay stage specialists (Stokland and Larsson, 2011). Another reason to expect primary decayers to be efficient in dispersal is that they are generally weakly combative (reviewed in Boddy and Heilmann-Clausen, 2008), and to be successful they should be the first to colonize open resources. The species specialized to later decay stages will always face a competitive environment (reviewed in Woodward and Boddy, 2008) and thus the need to establish in special and short-lived windows of opportunity is weakened or nonexistent, while combative traits becomes increasingly important.

The complex interactions between matrix fill, alpha- and beta diversity with decay stage and management history can be interpreted in a context of re-colonization of dead wood by fungi in previously managed forests, where such substrates have been practically absent until recent times. Thus, the low matrix fill in early decay stages in recent reserves most likely reflect random recolonization processes by effectively dispersed primary decayers, resulting in species poor communities with relatively high species turnover among trees. The much higher matrix fill and alpha diversity in early decay stages in the old managed reserves show that communities here are species rich, but uniform, with many, mainly unspecialized species competing for resources. In other words these communities can be interpreted as relatively neutral, with limited species sorting at tree level. Finally, the consistently low fill in natural reserves suggests a stronger effect of species sorting depending on priority effects (cf. Fukami et al., 2010; Ovaskainen et al., 2010) or on higher levels of niche specialization for other reasons. The increasing beta diversity and decreasing alpha diversity as decay proceeds in natural reserves, can be interpreted as a support for priority effects being important, but can also simply reflect competitive exclusion of inferior competitors as decay proceeds (Boddy, 2000).

Complementary analyses of the present dataset have shown that the natural reserves had higher frequencies of threatened fungi and more specialized trunk-rotters restricted to larger logs (Ódor et al., 2006; Heilmann-Clausen et al., unpublished results), compared to the formerly managed reserves. We believe that there is a direct link between these results and the distinct differences in meta-community structure depending on management history, and suggest that the high matrix fill and alpha diversity in recent reserves simply reflect a scarcity of competitive specialized trunk rotters, of which many are threatened, in these communities. A similar result was found in more regional analysis of fungi in beech forests in Denmark (Heilmann-Clausen and Christensen, 2005) and similar patterns have been detected on other species groups too (Summerville et al., 2009).

The succession of fungal community along the wood decay process is fundamental for ensuring proper ecosystem function in forests. Any change in the decay process could affect the vast carbon storage retained in decaying wood (Gough et al., 2008), and thus have an effect on the carbon dynamics in forests. In light of this, it is somewhat alerting that we saw clear differences in the basic metacommunity structure measures between the managed and natural sites.

Also in a conservation context our results are somewhat alerting. The fact that forest management seem to affect late decay stage specialist the most, may mean that the time lag between cessation of management actions and the detectable effects in communities is longer than expected. Recently there have been several studies focusing on the impacts of modern forest management actions (see e.g. Lõhmus, 2011; Toivanen et al., 2012) as well as restoration measures (Olsson et al., 2011) on wood-inhabiting fungi. These studies have, for practical reasons, shown mostly the results on the earliest decay stages. It may well be that the species occupying the first decay stages show weaker negative responses to for example forest fuel harvesting and on the other hand stronger positive effect on restoration measures compared to the species occupying late decay stages. This support the recommendation by many forest conservationists (Kouki et al., 2012) that conservation should first focus on protecting the existing remnants of old growth forests with intact communities, before putting a major emphasis on the protection or restoration of younger or degraded forest stands.

Our data were somewhat unbalanced in having more managed sites and most of the natural sites located in southeastern Europe. We controlled the effect of this unbalanced geographical distribution with adding temperature range as a variable in our analyses. Because this variable did not explain any differences we detected in beta diversity, it is very unlikely that our results are confounded by the unbalanced geographical distribution of the data. However, for further proof we encourage other researchers to repeat these analyses on different large data sets with forest management information collected from this same species group but from different biotopes (e.g. Halme et al., 2009) and different species groups (e.g. Sebek et al., 2012).

Acknowledgements

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.biocon.2013.08.034.

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