Biological Conservation 168 (2013) 24-30

Contents lists available at ScienceDirect

**Biological Conservation** 

journal homepage: www.elsevier.com/locate/biocon

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



BIOLOGICAL CONSERVATION

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#### ARTICLE INFO

Article history: Received 19 April 2013 Received in revised form 19 August 2013 Accepted 27 August 2013

#### Keywords: Beta diversity Decay stage Forest management Nestedness SDR simplex Similarity

### 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

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<sup>0006-3207/\$ -</sup> see front matter © 2013 Elsevier Ltd. All rights reserved. http://dx.doi.org/10.1016/j.biocon.2013.08.034

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 low-land 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 Download English Version:

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