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Variety of woody debris as the factor influencing wood-inhabiting fungal richness and assemblages: Is it a question of quantity or quality?

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ABSTRACT

Conservation of saproxylic organisms requires knowledge about the effects of forest management on their habitat. To better understand such effects, 16 beech forest sites in Navarre (Northern Spain) were examined. Woody debris volume and variety of woody debris were recorded in each sampled plot. To calculate variety of woody debris, dead wood pieces were classified into nine categories according to three size and three main decay stage classes. Results showed that forest management had a negative impact on fungal diversity and woody debris variety. Likewise, a nested mixed model design performed with PERMANOVA showed that both fungal assemblages and woody debris composition were significantly dissimilar between forests with distinct management history. When fungal richness was analyzed against variety and volume of woody debris, variety of woody debris explained much more variability than woody debris volume. Similarly, canonical correlation analysis revealed that groups formed according to the forest management factor based on fungal assemblages fitted better with the variety of woody debris variable than with the woody debris volume one. Accordingly, most fungal species showed preference for the type of woody debris on which they grow, and thus, some general growing patterns were established for them. In conclusion, taking into consideration that variety of woody debris is the main factor affecting wood-inhabiting fungal diversity and forest management is the factor which most affects the presence of wood debris variety, some recommendations for wood-inhabiting fungal conservation are provided.

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1. Introduction

Many studies have proved that wood-inhabiting organisms have declined as a result of a reduced volume of dead wood in managed forests (Bader et al., 1995; Penttilä et al., 2004; Siitonen, 2001). Indeed, dead wood is one of the most important factors contributing to the preservation of biodiversity in temperate forests (Harmon et al., 1986), both as carbon storage and as habitat for many organisms. Wood inhabiting fungi are an important group of saproxylic organisms (Stokland et al., 2012) since they chemically and structurally change dead wood and generate new habitats and food resources for other fungal species and wood inhabiting organisms (Boddy, 2001; Renvall, 1995). Various dead wood fractions, such as branches and logs in different degrees of decomposition, provide a wide range of niches for wood-inhabiting fungi (Hottola et al., 2009). Among woody debris types, logs harbour the highest fungal species richness per unit, because of their large volume of dead wood, extensive surface for colonization, and unequally decomposed sections (Heilmann-Clausen and Christensen, 2003). Thus, most studies that have investigated the influence of forestry on wood-inhabiting fungi have focused their attention on the loss of dead wood volume caused by the absence of coarser woody debris in managed forests. In general, results from most published studies indicate that there is a loss of wood-inhabiting fungal diversity in managed forests (e.g. Junninen et al., 2006; Müller et al., 2007; Penttilä et al., 2004; Sippola and Renvall, 1999; Stokland and Larsson, 2011) and that forestry activities have an influence on fungal communities composition (Küffer and Senn-Irlet, 2005; Ódor et al., 2006).

The specific adaptations of wood-inhabiting fungi to utilize different dead wood qualities (different host species, decay stages and size classes) have lately motivated researchers to investigate thinner woody debris classes and more fungal groups (e.g. Abrego and Salcedo, 2011; Heilmann-Clausen and Christensen, 2004; Juutilainen et al., 2011; Küffer and Senn-Irlet, 2005; Küffer et al., 2008; Lindner et al., 2006; Nordén et al., 2004). Despite this, few mycologists (Hottola, 2009; Lindner et al., 2006; Küffer et al., 2008) have studied the influence of forest management on thinner woody debris. There are practical and methodological difficulties, since it is necessary to check comparatively many more fine and very fine woody debris (FWD and VFWD) pieces than coarse woody debris (CWD) pieces to know and compare their diversity. In addition, this

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is compounded by the fact that wood-inhabiting fungal diversity is positively correlated with woody debris size (Junninen and Komonen, 2011), which makes the analysis difficult (Heilmann-Clausen and Christensen, 2004). Furthermore, most dead wood decomposer fungal species develop small resupinate sporocarps that must be identified by microscope. Finally, when analyzing the response of fungal richness to dead wood, the possible spatial autocorrelation effects have been taken into account only in few works (e.g. Bässler et al. (2012) and Hottola (2009)).

Research on dead wood volume and wood-inhabiting fungi has been intense in northern and central Europe. The forests of these regions differ considerably in climatic conditions and floristic composition from the southern European ones. Likewise, disturbance regimes are also different throughout European forests because forest management has been done with varying intensities and techniques, depending on the local human needs and resources. With respect to the remaining dead wood left by forest management in southern Europe, there is a lack of data, which means that European guidelines for sustainable forestry are particularly appropriate for northern and central European forest types (Hahn and Christensen, 2004).

To gain a better knowledge of the influence of forest management on all groups of wood-inhabiting fungi, all woody debris sizes across 16 beech forests in Navarre (Northern Spain) were examined. In order to assess whether such impact is significant, we modelled a nested mixed experimental design applying permutational multivariate analysis of variance (PERMANOVA). The effects of forest management on two response variables, namely wood-inhabiting fungal diversity and variety of woody debris, were investigated. The specific objectives of our study were: (1) To measure the effect of forest management on wood-inhabiting fungal richness and variety of woody debris; (2) To compare the wood-inhabiting fungal assemblages between managed and unmanaged forests; (3) To determine the main factor affecting wood-inhabiting fungal richness and assemblages.

2. Materials and methods

2.1. Study area

The study area is located in northern Navarre, in the northern part of the Iberian Peninsula. It has a temperate climate, and covers two biogeographical regions: the Atlantic region in the Northwest, and the Alpine region in the Northeast. In this territory beech forest is the predominant forest (with 60,735 ha), and it represents the most productive forest type for exploitation of wood.

There are seven beech forest types in Navarre (Loidi and Báscones, 1995), which can be classified on the basis of soil acidity, rainfall conditions and biogeographical area. For the location of sampled sites the three major beech forest types were considered: (1) basophilous and ombrophilous beechwoods in the Cantabrian–Atlantic Province with calcareous soil; (2) acidophilous and ombrophilous ones in the Cantabrian–Atlantic Province with acidic soil; (3) Pyrenean basophilous and ombrophilous beech forests in the Pyrenean Province with calcareous soil. Climatic conditions and vegetation vary considerably among these forest stands (Appendix A). On the one hand, Pyrenean beech forests have a more mountainous character than the others, growing at higher altitude and with lower temperatures. On the other hand, Cantabrian–Atlantic beech forests have a more oceanic climate, and can be classified according to the substratum into beech forests with basophilic soil and beech forests with acidic soil. Although stands are dominated by beech, in some cases other tree species can also occur (Appendix A).

It was not until the early 20th century that commercial wood extractions started in Navarre. Hitherto beech forests were managed according to the local population needs, eliminating beech trees to create pastures, pollarding beech trees to obtain wood and forage for cattle and cutting trees to get firewood or to produce coal for selling. The first silvicultural practices started applying techniques such as forest thinning or the selective cutting of the largest trees. Although this management did not lead to a decrease of beech forest area, often a simplification of biological and structural complexity in managed beech forests occurred. Nevertheless, not all forests in this area have been managed with the same intensity, as there is a Network of Natural Protected Areas which has guaranteed the preservation of some old-growth beech forest areas. For this study, protected areas where forest management has allowed the conservation of old-growth-forests have been considered as unmanaged forest sites, and forest areas which are under forestry exploitation have been considered as managed forest sites (Appendix A).

2.2. Experimental design

Taking into account beech forests with different management histories, nested mixed model experimental design was used for data collection. The fixed factor was forest management and two levels were taken into account: unmanaged forest sites, and managed forest sites. Within each management type, 8 forest sites were randomly chosen, and within each forest site, 5 replicate $100\ m^2$ plots were randomly located.

In each plot all woody debris was checked and all saproxylic macromycetes (fungi with sporocarps larger than 1 mm) were identified, registering their presence for each woody debris piece. At the same time, diameter, length, decay stage and host species of all woody debris pieces present in the plot were registered, regardless of the presence of sporocarps. When microscopic identification was necessary the material was removed for further identification in the laboratory.

Woody debris was classified according to its diameter into the following categories: (1) Very Fine Woody Debris (VFWD): branches and twigs with $\leqslant$5 cm diameter; (2) Fine Woody Debris (FWD): logs with diameter between 5 and 10 cm; (3) Coarse Woody Debris (CWD): logs or snags with diameter $\geqslant$10 cm. These size ranges were chosen from the work of Küffer and Senn-Irlet (2005), although there are also different ranges in the literature (Juutilainen et al., 2011). Likewise, the decay stages of dead wood pieces were measured for each woody debris piece, following a modified classification of Renvall (1995): (I) wood hard, trunk or branch is a solid piece, pushed knife penetrates only a few mm into the wood; (II) wood fairly hard, bark usually present but not firmly attached, pushed knife penetrates 1–2 cm into the wood; (III) wood fairly soft, small areas of sapwood already decomposed and without bark where knife penetrates easily; (IV) wood soft, wood pieces extensively decayed and usually large sections of the wood completely decomposed, the knife penetrates through the wood easily; (V) wood very soft, almost completely decomposed and disintegrates easily between fingers. To enter the decay stage data in the data matrix, Renvall's five classes were condensed into three, based on a previous pilot study (Abrego and Salcedo, 2011): (a) the earliest stages (DSI) (Renvalls I and II decay stages); (b) the intermediate decomposition stage (DS2) (Renvalls III decay stage); and (c) the last stages of the decomposition process (DS3) (Renvalls IV and V decay stages). To evaluate variety of woody debris, nine woody debris classes were defined, according to both woody debris size and woody debris decay stages, i.e.: VFWD DSI, VFWD DS2, VFWD DS3, FWD DS1, FWD DS2, FWD DS3, CWD DS1, CWD DS2 and CWD DS3.

The fieldwork was carried out in 2011 during the two main periods of sporocarp production (spring and autumn) with one visit to each plot in each period. Each species found on each piece of

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