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Temporal variation of polypore diversity based on modelled dead wood dynamics in managed and natural Norway spruce forests

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ABSTRACT

Decline of dead wood in managed boreal forests has variously affected polypore species that use it as their substrate, some now being listed as threatened while some are still thriving. Management of polypore diversity requires species-specific information about their occurrence probabilities, which partially depend on stand dead wood availability and other properties.

We implemented an ensemble of polypore habitat models to simulations of stand and dead wood availability estimated with a decomposition model we fitted to data. We asked how management of a boreal Norway spruce stand influences the dead wood availability and polypore occurrence probabilities and their diversity.

Simulations of multiple polypore species with stand management scenarios provided insight to dead wood dynamics and polypore species management. In a managed stand, diversity thrived after final harvesting, but declined to low level by mid-rotation. Harvest residues and stumps, although low quality substrate for many species, were important for diversity in young managed stand due to their high quantities. High mixtures of naturalness in stand management were required to elevate diversity of managed spruce stands from the mid-rotation lows to levels in natural-like stands.

Our study suggests that dead-wood supply of managed stands could be optimised to lift lowest species expectations towards levels in natural-like forests, but it seems that reaching these levels requires dead-wood quantities much higher than provided by conventional management. Management of stand diversity can presumably be facilitated with wise landscape planning but more research is needed in order to incorporate polypores to spatio-temporal management simulation context.

1. Introduction

Timber harvesting and decreased amount of decomposing wood in managed forests is a major driver of the loss of species diversity in boreal forests (Gärdenfors, 2010; Harmon et al., 1986; Siitonen et al., 2000). As a consequence of loggings there is considerably less standing dead and down wood material in managed forests (4–10 m^3/ha) than there typically is in natural forests (70–100 m^3/ha)(Jonsson et al., 2005; Siitonen, 2001; Siitonen et al., 2000), which has led to decline in the diversity of species that are dependent on decaying wood. For instance, in polypore, which are a well-known group of wood-inhabiting basidiomycetes, over one third of the species in Finland and Sweden are recorded as red-listed (Gärdenfors, 2010; Kotiranta et al., 2010). Since the polypores are directly dependent on suitable dead wood habitats, their survival can be enhanced by altered forest management practices and by habitat conservation. Discontinuous supply of suitable habitat in space, but also in time can influence species existence in a forest stand or in larger area. One way of evaluating the importance of temporal variation of dead wood availability to polypore diversity in forests is to conduct model analyses of dead wood habitat change. Stand dynamics are typically simulated with stand management models. Traditionally, these models have focused on growth and economic return, but they are increasingly used for planning sustainable forest management, and developed further to support these goals. Sustainable forest management planning and maintaining biodiversity would greatly benefit if alternative management chains were designed with tools predicting the quality continuum of dead wood and the presence of potential species inhabiting forests.

Current knowledge of habitat requirements of dead wood dependent species, such as polypores, is sufficient for quantitative analyses of species occurrences. Polypore species have varying requirements for e.g. tree species, size, resource type (standing or down), and decay class (Bader et al., 1995; Berglund et al., 2011a; Norden et al., 2013; Renvall, 1995) and they host a rich group of associated species (Komonen et al., 2000; Stokland et al., 2012). Stand properties such as density and naturalness have also been reported to influence species presence in a stand, as well

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as factors related to spatial connectivity (Berglund et al., 2011a; Komonen et al., 2000; Norden et al., 2013; Penttilä et al., 2004; Sippola et al., 2001).

The significant role polypores play in boreal biodiversity and in wood decay calls upon including them in stand and landscape simulation models. The incorporation of polypores into these models requires accurate prediction of the temporal development of their main resource, dead wood. Recently, applicable models have been developed for representing mortality of trees in natural and semi-natural boreal Spruce forest (Peltoniemi and Mäkipää, 2011), for tree fall (Aakala, 2011; Mäkinen et al., 2006), and dead wood decomposition (Kruys et al., 2002; Ranius et al., 2003; Aakala, 2011; Mäkinen et al., 2006), which are useful for these purposes, and may be used to extend applicability of the stand simulation models from conventionally managed to more natural stands.

Acknowledging the importance of dead wood for sustainable forest management, some studies have already investigated effective ways of managing dead-wood stocks in boreal forests of Northern Europe (Ranius et al., 2003; Tikkanen et al., 2012), and in North America where focus has been on fire return interval (Brown et al., 2003; Tinker and Knight, 2001). Some of the earlier model studies have analyzed sustainable harvest scenarios by including total number of polypore species as a criteria (as explained by the total volume of dead wood)(Hynynen et al., 2005), or by making cost-effective selection of conservation areas including measured polypore diversity of stands as one of the criteria (Juutinen et al., 2004). Further development in this direction requires incorporation of a large ensemble of species-specific occurrence models, as it is unlikely that management of few species, or even species groups, is enough to maintain the whole biodiversity effectively. Applying a wide set of polypore models also allows posing life-strategy or threat-status specific questions about species vulnerability management, and replying to questions such as how much dead wood should be introduced to managed forests in order to maintain a specified group of target species.

In order to take further steps in the development of methods for integrating polypore diversity into the models of stand management, we incorporated species-level probability models of polypore occurrence into model scenarios of stand management. As the dead wood resource and its quality are crucial for these models, we first developed models of decomposition of dead wood material based on repeated measurements of dead logs. New polypore models apply widely used classification based on hardness of the log assessed with a knife (Mäkinen et al., 2006; Renvall, 1995). Earlier decomposition models of logs, which we found in the literature were not applicable for the polypore habitat models (Norden et al., 2013), because decomposition of logs was presented on continuous scale (Mäkinen et al., 2006), log decomposition was merged with dynamics of soil organic matter (Tuomi et al., 2011), or classification of decaying logs was made relying on visual features of the logs (Aakala, 2011; Kruys et al., 2002).

The objective of our study was to investigate (i) how stand management influences the continuum of dead wood habitats and the diversity of polypore species inhabiting dead wood, (ii) how model-predicted polypore diversity differ in managed and natural-like stands, and (iii) how much natural dynamics must be introduced to a typical management scenario to achieve polypore diversity leveling that of natural-like forests.

2. Materials and methods

2.1. Predicting polypore presence in forest stands

We applied recently published models of occurrence probability of polypore species in boreal forests of Finland (Norden et al., 2013). As the models have been depicted in detail earlier (Norden et al., 2013), we provide only brief summary of them here, and describe the way we applied them. The models predict the occurrence probability of individual polypore species on individual dead wood units. Models need resource-unit (i.e. dead wood) specific data about tree species, decay class, diameter, and type of the dead-wood (snag, log, stump, man-made, etc.). Besides this resource-unit specific information, the models apply also other data related to site and its spatial connectivity. Canopy cover is expressed using the basal area of the stand, naturalness as the basal area of cut stumps. Connectivity measures are provided at three scales: (i) the total amount of suitable habitat in the stand, which is estimated by applying resource-unit specific model part to the other dead wood units in the stand (dead wood having $d > 15$ cm), (ii) weighted mean age of the surrounding forests, and iii) geographical location within Finland. All stand level-variables and connectivity measures in the polypore occurrence probability models are standardized to zero and unit standard deviation. When applying the models we assumed that the original range of standardized variables was similar to our data and predictions made with the stand simulator (see Section 2.3).

In order to estimate the probabilities for the polypore presence in the whole stand, we summed up the probabilities of polypore presences on unit logs to get an expectation for probability of occurrence of species on site, $p = 1 - \prod_{k=1}^{C}(1 - p_k)$, where k runs through all log categories (1 . . . C), which were characterized by resource type, diameter and decay class. The probability of polypore species being present on a category of similar logs was $p_k = 1 - (1 - p_l)^{n_k}$, where n_k is the number of similar logs in the category k, and p_l is the probability of species being present on a single log. Probability p_l was estimated with models of Norden et al. (2013). Sum of the species-specific occurrence probabilities on site gives the expected number of species in the stand. Model predictions correspond to the presence of species in a plot of similar size as used in the original material (Norden et al., 2013). Most of the used plots were 0.2 ha (the whole range was 0.2–4 ha) (Norden et al., 2013).

2.2. Models to simulate stand and, dead wood production and decomposition

In order to predict the availability of the amount and quality of suitable dead wood for polypore species, we estimated tree mortality and quantity of harvest residues (tree tops and stumps) in a Norway spruce stand using a stand simulation model. We used a stand simulator (Motti), which simulates growth and mortality by tree diameter class. Motti stand simulator is based on a large empirical material representative to the study region (Hynynen et al., 2005). In Motti, tree growth and mortality are influenced by tree's own and competitors' sizes, and described with sets of empirical competition functions. Motti implements also a stand level self-thinning threshold,which starts to thin trees when there is no space in the canopy, but it is not usually reached in managed stands due to thinning of the stand.

In order to compare the amount of dead wood in managed stands to that in natural stands, we estimated the average mortality rate in a material collected from unmanaged Norway spruce forests in Southern Finland (Peltoniemi and Mäkipää, 2011). In this study, natural forests were assumed to be in steady-state, e.g. mortality and regeneration are balanced by small-scale gap dynamics (Janisch and Harmon, 2002), and dead wood stocks have stabilized to levels corresponding to dead wood formation.

We allocated dead trees to four size classes according to their diameter at breast height (d) in order to reduce the computational burden when applying the decomposition and polypore models. Three size classes of naturally created dead wood were the small