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Effects of local forest continuity on the diversity of fungi on standing dead pines

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ABSTRACT

Human-induced fragmentation affects forest continuity, i.e. availability of a suitable habitat for the target species over a time period. The dependence of wood-inhabiting fungi on landscape level continuity has been well demonstrated, but the importance of local continuity has remained controversial. In this study, we explored the effects of local forest continuity (microhabitat and stand level) on the diversity of wood-inhabiting fungi on standing dead trunks of Scots pine (*Pinus sylvestris* L.). We studied species richness and community composition of decomposers and *Micarea* lichens on 70 trunks in 14 forests in central Finland that differed in their state of continuity. We used dendrochronological methods to assess the detailed history of each study trunk, i.e. the microhabitat continuity. The stand continuity was estimated as dead wood diversity and past management intensity (number of stumps). We recorded 107 species (91 decomposers, 16 *Micarea* lichens), with a total of 510 occurrences. Using generalized linear mixed models, we found that none of the variables explained decomposer species richness, but that *Micarea* species richness was positively dependent on the time since tree death. Dead wood diversity was the most important variable determining the composition of decomposer communities. For *Micarea* lichens, the community composition was best explained by the combined effect of years from death, site and dead wood diversity. However, these effects were rather tentative. The results are in line with those of previous studies suggesting the restricted significance of local forest continuity for wood-inhabiting fungi. However, standing dead pines that have been available continuously over long periods seem to be important for species-rich communities of *Micarea* lichens. Rare specialists (e.g. on veteran trees) may be more sensitive to local continuity, and should be at the center of future research.

1. Introduction

Intensive forestry activities have led to severe forest fragmentation throughout the globe (Riitters et al., 2000). The spatial aspects of fragmentation, such as decreased habitat amount, size, and connectivity are well known for a negative effect on biodiversity and ecosystems (Bengtsson et al., 2000; Fahrig, 2003). Temporal aspects of fragmentation, such as decreased habitat continuity, have been studied less than the spatial aspects, but have similarly been shown to have negative impacts on biodiversity (Nordén et al., 2014).

Forest continuity can be considered at local level where it relates to longevity of a single, available patch of suitable habitat for the target species or community, and where the scale of habitat patch is equivalent to one local population (Hanski, 2005; Nordén et al., 2014). With higher local continuity, higher species richness and larger variety of specialist species can occur as the colonization and/or breeding probability of species with establishment constraints, slow rates of establishment, development, or growth is enhanced (Esseen et al., 1997; Fritz et al., 2008; Nilsson and Baranowski, 1997; Nordén et al., 2014). The cause for higher species richness and larger variety of specialists may also be the emergence of special microhabitat types confined to late successional phases or larger diversity of different microhabitats. This is due to the absence of large-scale disturbances, which promotes the time-demanding development of these resources (Tibell, 1992; Sverdrup-Thygeson, 2001; Winter and Möller, 2008). Landscape level continuity, on the other hand, refers to a network of available habitat patches within a given region or landscape over time (Fritz et al., 2008; Hanski, 2005; Nordén et al., 2014). Here, the role of dispersal

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limitations increases when the landscape level continuity decreases (Nordén and Appelqvist, 2001).

Wood-inhabiting fungi are among the organism groups suffering most from the decreased landscape level forest continuity caused by fragmentation (Nordén et al., 2014; Flensted et al., 2016). The importance of this landscape level continuity for wood-inhabiting fungal diversity has been well demonstrated (Flensted et al., 2016; Gu et al., 2002; Junninen and Komonen, 2011; Paltto et al., 2006; Ranius et al., 2008; Sverdrup-Thygeson and Lindenmayer, 2003). Apparently, the biological reason for this dependence is that some species of wood-inhabiting fungi are in fact dispersal limited (e.g. Norros et al., 2012), although species dependent on ephemeral habitats have a high dispersal ability in general (Herben et al., 1991).

The role of local continuity has remained less clear, compared to landscape level continuity. Stokland and Kauserud (2004) suggested that a polypore *Phellinus nigrolimitatus* cannot effectively colonize suitable trunks when the stand level dead wood continuity decreases. With epiphytic lichens, forest age and continuity appear to have a positive effect on their species richness and affect their community composition (Fritz et al., 2008). Also here, the increased colonization probability with increasing forest age and continuity was considered as the most probable explanation. On the other hand, several studies have detected no effects of local continuity (Groven et al., 2002; Rolstad et al., 2004; Sverdrup-Thygeson and Lindenmayer, 2003), and many studies have been criticized for not demonstrating the effect of continuity *per se* (Nordén and Appelqvist, 2001; Nordén et al., 2014).

In their review, Junninen and Komonen (2011) deduced that boreal polypores are not affected by continuity on a stand scale in any way, and Nordén et al. (2014) concluded that local continuity does not have a significant effect on the diversity of fungi. Nevertheless, this generalization may be misleading; fungi encompass species with divergent ecological characteristics, with many of the species being habitat specialists, requiring dead wood in advanced stages of decay (Nordén et al., 2013). Moreover, studies have not focused on the smallest scale of local continuity, i.e. the detailed history of the microhabitats. Especially the standing dead coniferous trees may retain their qualities for decades, and therefore constitute a microhabitat with potentially high continuity. Considering ephemeral habitats in general, standing dead coniferous trees may be among the slowest constantly changing microhabitats (compared to more persistent abiotically determined microhabitats, such as those in soil).

In this study, we explored the effects of local forest continuity (microhabitat and stand level) on the communities of wood-inhabiting fungi. We studied fungal communities on standing dead wood of Scots pine (*Pinus sylvestris* L., hereafter pine) in 14 forests with varying state of continuity. We used trunk age parameters as estimates for microhabitat continuity, and estimated stand continuity as dead wood diversity and past management intensity. We focused on pine because the species is characterized by slow death and decay process (Niemelä et al., 2002; Siitonen, 2001). Specifically, we asked:

1. How does local forest continuity affect (i) species richness and (ii) community composition of wood-inhabiting fungi inhabiting standing dead pines?
2. How different scales of continuity (from microhabitat continuity to stand continuity) affect (i) species richness and (ii) community composition?
3. Are the effects of local continuity different for different fungal groups?

2. Materials and methods

2.1. Study sites and trunk selection

Our 14 study forests (Table 1) were located in central Finland (Fig. 1), 12 of them being in the southern boreal zone, and two in the middle boreal zone (Ahti et al., 1968). In each forest, the study trunks were selected on a 10-m wide transect. Each transect was established 15 m from the point of easiest access into the study stand. The direction of the transect was towards the center of the stand, except in smaller stands (< 100 m wide) where the transect followed the direction of the longest side of the stand. If the opposite side of a stand was met before trunks were surveyed, the transect was turned around and continued parallel to the first transect. The first five pine trunks within a transect that fulfilled the criteria of being (1) standing (leaning max. 45°) and dead, (2) trunks or high stumps (≥0.5 m in height), and (3) ≥7 cm in diameter, were selected for sampling.

Table 1
Site information. Dominant tree species and mean age classes are derived from Natural Resources Institute Finland (2015).

	Site	Municipality	Dominant tree species	Mean age class
1	Hallinmäki	Jämsä	spruce	96–132
2	Ilmakkamäki	Suonenjoki	pine	56–65
3	Kalaja	Rautalampi	pine	62–71
4	Kirkkokangas	Muurame	spruce	85–109
5	Kivetty	Äänekoski	spruce	72–84
6	Kotinen	Hämeenlinna	spruce	75–89
7	Kuusimäki	Muurame	spruce	45–55
8	Latokuusikko	Kuhmoinen	spruce	88–108
9	Leivonmäki	Joutsa	pine	62–78
10	Lortikka	Kuhmoinen	spruce	70–80
11	Pyhä-Häkki	Saarijärvi	pine	101–144
12	Vaarunvuoret	Jyväskylä	spruce	62–72
13	Vesijako	Padasjoki	spruce	54–63
14	Vuorilampi	Toivakka	pine	45–55

2.2. Data collection and preparations

2.2.1. Species data

All decomposer fungi and *Micarea* lichens were recorded from each study trunk based on the occurrence of fruit bodies. Sampling of *Micarea* and *Mycocaliciales* species was conducted in three parts: October 2014, May–June 2015, and September 2015. Rest of the groups (agarics, corticioids, discomycetes, jelly fungi, polypores, and pyrenomycetes) were sampled in separate surveys in August–September 2015. Agarics were sampled again during October 2015 to meet a better share of a local species community (their detectability is lower than in other groups, see Abrego et al. (2016) and Purhonen et al. (2016)). The trunks were carefully examined throughout from ground level up to a height of 1.8 m. Species of *Mycocaliciales* were recorded only from sapwood, all other fungal groups also from bark. Fungi were identified to species in the field if possible. Otherwise, specimens were taken for later microscopical identification in the laboratory. Species nomenclature followed Coppins (1983), Czarnota (2007), and Czarnota and Guzow-Krzemínska (2010) with *Micarea* species, Tibell (1999) with species of *Mycocaliciales*, and Index Fungorum (Royal Botanic Gardens Kew et al., 2016) with the rest. If possible, identifications were made to species level, otherwise to genus level.

In the analyses, we used species level identifications. We also included genus level identifications that were different from the identified species of the same genus. We have thoroughly aimed at a similar taxonomic resolution throughout the data. In the case of taxonomically very poorly known groups of *Chaenothecopsis* and *Mycocalium*, several undescribed species were separated based on spore size, type and some other anatomical and chemical characters, and considered as distinct species. Also, some pyrenomycetes remained unidentified, but when it was possible to separate them from the rest of the detected species, they were considered as species in the analyses.

2.2.2. Study trunk specific measures

Several variables were recorded for each study trunk in the field.