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Fruit body based inventories in wood-inhabiting fungi: Should we replicate in space or time?

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ABSTRACT

We assessed the effect of survey design on the results when conducting fruit body surveys of wood-inhabiting fungi. Our results demonstrate that the optimal design depends on the ecological question to be addressed, as well as the group of fungal species under research. If the aim is to record the total species richness in a dead wood unit or to estimate the population size of a species, repeating the survey over time is generally necessary. However, if the aim is to estimate the total species richness in the forest or to assess how environmental covariates influence species richness or community composition, it is generally more efficient to increase the number of dead wood units than to re-survey the same ones. Among the morphological fungal groups, the results of agarics improved the most and of polypores and corticioids the least with repeating surveys over time.

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1. Introduction

Wood-inhabiting fungi play an important role in ecosystem functioning as they create habitats and supply nutrients for many other groups of organisms (Boddy et al., 2008; Stokland et al., 2012). Due to their sensitivity to management, wood-inhabiting fungi are considered as indicators of the conservation values of forests (Christensen et al., 2004; Stokland et al., 2012). The massive decline in the amount and quality of dead wood in forests all around the world has significantly decreased the diversity (the number of species and their abundance) of wood-inhabiting fungal communities (e.g. Penttilä et al., 2004; Lindner et al., 2006; Ódor et al., 2006; Hattori et al., 2012).

The high species diversity, vulnerability, and life-cycle characteristics of wood-inhabiting fungi make them an interesting group for research in community ecology and conservation biology, but these same characteristics make them a methodologically challenging group. Thus far, fruit body surveys have remained the most popular method for recording the occurrence of wood-inhabiting fungal species (e.g. Junninen and Komonen, 2011; Halme and Kotiaho, 2012; Abrego et al., 2014; Bässler et al., 2014; Heilmann-Clausen et al., 2014). The generality of results derived from fruit body based surveys has been questioned by the fact that while wood-inhabiting fungal communities within a single dead wood unit can include tens to hundreds of species, only a fraction of them are visible as fruit bodies at any given time (Allmér et al., 2006; Ovaskainen et al., 2010, 2013), typically those that are most abundant at mycelial level (Ovaskainen et al., 2013). Some species produce microscopic fruit bodies that remain undetectable to the naked eye (Lumley et al., 2000). Furthermore, different fungal species have different fruiting times and longevities (Halme and Kotiaho, 2012).

Due to the above listed methodological challenges, there is an ongoing debate on the efficiency of fruit body based surveys as compared to DNA based surveys (Allmér et al., 2006; Ovaskainen

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et al., 2010; Halme et al., 2012; Jang et al., 2015; Runnel et al., 2015). Another related question, which we will address in this paper, is whether fruit body surveys should be repeated in general, and in particular within or between fruiting seasons (e.g. Halme and Kotiaho, 2012; Yamashita et al., 2015). Yamashita et al. (2015) showed that when aiming to record as many polypore species in a forest as possible, increasing the sampling area is more efficient than repeating surveys in the same area. This is because wood-inhabiting fungal communities are characterized by a high spatial turnover among logs within a forest (Kubartová et al., 2012; Abrego et al., 2014). In contrast, Halme and Kotiaho (2012) showed that a single survey is insufficient for acquiring proper information about species diversity at the dead wood unit level, and consequently for estimating population sizes. This is due to the high phenological variation in fruit body production, both among fungal species and among fruiting seasons (see also Berglund et al., 2005). In general, the optimal sampling design depends on the levels of temporal and spatial autocorrelation inherent in the study system (Cochran, 1977; Legendre et al., 2002). If there is a lot of turnover in time, but only little in space, repeated surveys over time to the same site are expected to provide more information than a single survey that covers several sites. Conversely, if there is a lot of turnover in space, but only little in time, surveying more sites is more critical than surveying the same site repeatedly.

As fungal surveys call for much effort, it is critical to know what kind of a survey method is optimal for different species groups and ecological questions. For addressing this issue, we used an extended version of the dataset used in Halme and Kotiaho (2012), which consists of 107 dead wood units (large decaying logs) that were surveyed six times per season for six years (2005–2010). We examined the trade-off between repeating the surveys in time versus space. In particular, we examined the effect of the survey design on the results of the following five ecologically relevant questions: (1) What is the species richness of a forest site, defined as the total number of species that ever fruit on the surveyed dead wood units during the study period? (2) What is the species richness of an individual dead wood unit, defined as the number of species that ever fruit on a single dead wood unit during the study period? (3) What are the population sizes of the species at the forest level, defined as the total number of occurrences in the surveyed 107 dead wood units? (4) What is the influence of the dead wood unit-scale habitat factors on species richness? (5) What is the influence of habitat factors on community composition, i.e. are species communities different among different kinds of dead wood units?

2. Material and methods

2.1. Data collection and species identification

In this paper, we use the same study system which was described in more detail by Halme and Kotiaho (2012). In brief, the study was conducted in Kuusimäki, a 108 ha conservation site located in the municipality of Muurame, Central Finland. Kuusimäki has a boreal climate and is located in the southern boreal vegetation zone (Ahti et al., 1968). The forest cover is dominated by Norway spruce (*Picea abies*, roughly 50% of the standing volume) and birch (*Betula* spp., 39% of the standing volume), but Scots pine (*Pinus sylvestris*) and aspen (*Populus tremula*) are also abundant (6 and 4% of the standing volume, respectively).

Altogether, 107 dead wood units were surveyed: 29 spruce, 30 birch, 30 pine and 18 aspen logs. To ensure the persistence of the dead wood units over the entire study period, we did not select decay stage 5 logs; the selected logs were initially in decay stages 1–4 (15 logs were in decay stage 1, 43 in 2, 39 in 3 and 10 in 4, stages according to Renvall, 1995). Each dead wood unit was surveyed six times a year during the snowless season (monthly from May to October) from 2005 to 2010, totaling 36 surveys. In addition to recording the fruit bodies, the dominant decay stage and maximum diameter were measured for each dead wood unit.

The target species group included all wood-inhabiting fungi that form easily observable, robust fruit bodies. Considering ascomycetes, we included only discomycetes with large fruit bodies (genera like *Gyromitra, Peziza, Helvella* etc.). Specimens were collected for further identification in the laboratory if species identification was unreliable under field conditions. Only small pieces of fruit bodies were collected to minimize the impact on the communities. The species were classified into the morphological groups of polypores, agarics, corticioids and the other fungi, the last group including gasteromycetes, ramarioids, heterobasidiomycetes and ascomycetes (see Appendix 1).

2.2. Data analysis

We simulated eight survey strategies, called Survey Designs 1–8, which varied in the number of surveyed dead wood units and survey repetition in time (Table 1). Our interest was in assessing which of the survey designs yielded most informative answers to the five study questions listed above. To do so, we considered the results from the full survey as the reference point, to which we compared the results obtained by Survey Designs 1–8. As detailed in Table 1, the total survey effort in the Survey Designs 1–4 was identical and so these are directly comparable, as was the case also for Survey Designs 5–8. The total survey effort of the Survey Designs 1–4 equaled one sixth of that of the full survey, whereas the total survey effort of the Survey Designs 5–8 was 1/36 of that of the full survey. To further increase comparability, we generated the same number of replicates for each of the Survey Designs 1–4 and for each of the Survey Designs 5–8, even if some designs would have allowed for a larger number of replicates. We conducted all analyses both for all species and for the three major morphological fungal groups, viz. polypores, corticioids and agarics.

For assessing species richness at the forest level, we computed the total number of species ever observed in all the surveyed dead wood units as well as separately in each host tree species. Although the 107 dead wood units included in our study constitute only a small fraction of the dead wood pool in the study site, we argue that it is a good enough proxy of the forest level species richness because the main point here is not to estimate the total species richness, but to show the effects of survey design on the species richness found on a set of dead wood units.

For assessing species richness at the dead wood unit level, we computed the total number of species ever observed in each dead wood unit, and then averaged that over the dead wood units. We assumed that the researcher would estimate the population sizes of the species in a forest by multiplying the total number of dead wood units by the fraction of dead wood units at which each species was ever observed to fruit. We further assumed that the researcher would estimate the total number of resource units using some other kind of data, e.g. by surveying the amount of resource units in sample plots. Thus, for estimation of population sizes, we used the data from the survey designs to estimate the fraction of dead wood units at which each species was ever observed to fruit. As this fraction, averaged over the species, is directly proportional to the average species richness at the dead wood unit level, we report here the results only for species richness.

To examine whether the data were informative about the influence of the properties of the dead wood units on species richness, we fitted Poisson regression models in which species richness was the response variable. The explanatory variables included: (1)

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