



## Original Articles

# At which spatial and temporal scales can fungi indicate habitat connectivity?



Jenni Nordén<sup>a,b,\*</sup>, Jens Åström<sup>a</sup>, Torbjörn Josefsson<sup>c</sup>, Stefan Blumentrath<sup>a</sup>, Otso Ovaskainen<sup>d,e</sup>, Anne Sverdrup-Thygeson<sup>f</sup>, Björn Nordén<sup>a</sup>

<sup>a</sup> Norwegian Institute for Nature Research, Gaustadalléen 21, N-0349 Oslo, Norway

<sup>b</sup> Natural History Museum, University of Oslo, P.O. Box 1172 Blindern, N-0318 Oslo, Norway

<sup>c</sup> Swedish University of Agricultural Sciences, Department of Forest Ecology & Management, SE-901 83 Umeå, Sweden

<sup>d</sup> Department of Biosciences, University of Helsinki. P.O. Box 65, FI-00014, Finland

<sup>e</sup> Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology. N-7491 Trondheim, Norway

<sup>f</sup> Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Høgskoleveien 12, N-1433 Ås, Norway

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## ABSTRACT

Isolation of habitats in space and time affects species globally and in a multitude of ecosystems. It is however often difficult to assess the level of isolation from the point of view of the focal species. Indicator species are often used to assess ‘conservation value’ of habitats. One such approach involves the use of wood-decaying fungal species as indicators of near-natural forests, continuity in old-forest characteristics over time, and/or presence of red-listed species, but not of spatial connectivity. The indicator species were commonly assigned based on expert opinions, but few scientific evaluations have been performed of what these species actually indicate. Building on previous classifications of wood-decaying fungal indicator species on Norway spruce, we hypothesized that indicator species would differ from non-indicator species in how they respond to local temporal connectivity (forest age, the intensity of historical selective logging and the presence of well-decomposed large logs), and to local and landscape-scale spatial connectivity (local forest area, local amount of deadwood and the connectivity to old forest in the surrounding landscape). Based on fungal occurrence data from a fixed number of spruce logs at 28 sites distributed across the Scandinavian Peninsula, we explored the spatiotemporal scales at which the local communities were affected by connectivity. Indicator species showed the strongest response to connectivity of old forest ( $\geq 80$  years) within 100 km, while non-indicator species depended on connectivity of younger forest ( $\geq 40$  years) at a smaller spatial scale ( $\leq 25$  km). Indicator species increased and non-indicator species decreased in total abundance with the increasing age of the local forest stand. Landscape-scale old-forest connectivity was beneficial for indicator species in all sites except those with relatively low amount of deadwood, while non-indicator species showed the opposite pattern. We identify a threshold of around  $29 \text{ m}^3 \text{ ha}^{-1}$  in the amount of spruce logs where indicator species become abundant enough to influence non-indicator species through competitive interactions. There was a pronounced uniformity within each species group in the connectivity responses. We conclude that the studied indicator species indicate high forest age, high amount of resources and, given that the resources are plentiful, also high old-forest connectivity, but they do not indicate a long history without any logging operations or local deadwood continuity. The studied non-indicator species did not indicate any of the studied spatiotemporal connectivity variables. Indicator species are usually red-listed and may continue to decline in the future without habitat restoration efforts.

## 1. Introduction

Loss of spatial connectivity in the availability of resources is an important driver behind species declines globally and in most ecosystems (Wilson et al., 2016). A recent review of long-running forest

fragmentation experiments on five continents concluded that after two decades, the species richness in the studied forests had declined on average by half (Haddad et al., 2015). Temporal analogues to fragmentation have been less studied, but high species richness and the occurrence of red-listed species or other species of conservation concern

\* Corresponding author at: Norwegian Institute for Nature Research, Gaustadalléen 21, 0349 Oslo, Norway.

E-mail addresses: [jenni.norden@nina.no](mailto:jenni.norden@nina.no) (J. Nordén), [jens.astrom@nina.no](mailto:jens.astrom@nina.no) (J. Åström), [torbjorn.josefsson@slu.se](mailto:torbjorn.josefsson@slu.se) (T. Josefsson), [stefan.blumentrath@nina.no](mailto:stefan.blumentrath@nina.no) (S. Blumentrath), [otso.ovaskainen@helsinki.fi](mailto:otso.ovaskainen@helsinki.fi) (O. Ovaskainen), [anne.sverdrup-thygeson@nmbu.no](mailto:anne.sverdrup-thygeson@nmbu.no) (A. Sverdrup-Thygeson), [bjorn.norden@nina.no](mailto:bjorn.norden@nina.no) (B. Nordén).

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are often considered threatened by lack of long temporal continuity of habitats, sites, or landscapes (Nilsson et al., 2001; Dullinger et al., 2013; Nordén et al., 2014). In Fennoscandian countries (Norway, Sweden and Finland), forestry has led to a 90% loss of near-natural forests (i.e. forests that have structural characteristics resembling those of natural forests) and associated coarse deadwood (Siitonen, 2001), resulting in severe fragmentation and loss of connectivity of such forest habitats. Many saproxylic species among beetles and fungi are directly dependent on near-natural forest with deadwood, but the level of deadwood needed and the strengths and scales of correlations are often poorly known (Lassaue et al., 2011). It is therefore often difficult to assess how well functionally connected a particular habitat patch is in space and time from the viewpoint of the focal species.

When addressing the effects of forest fragmentation on populations, the landscape pattern must be assessed from the perspective of the species. The relevant spatial scale depends strongly on traits such as rarity, trophic levels, reproductive mode, life span, habitat specialization and dispersal ability of different species (Haddad et al., 2015). A different response to changes in connectivity could be expected among e.g. generalist and specialist species, even with equal dispersal abilities (Southwood, 1977; Nordén et al., 2013).

As the remaining areas of old, near-natural forests are successively being cut, there is an increasing need for simple and rapid assessment methods of forest conservation values and measures at both local and landscape scales (Lindenmayer et al., 2002). One approach that has been used is to use lists of indicator species from various organism groups to identify areas of high conservation value or naturalness. For example, the presence of particular wood-decaying fungal species have been used as a criterion to determine whether a site should be assigned as a woodland key habitat (Timonen et al., 2010). Fungal indicator species have also been used for assessing certain features that are difficult to survey directly such as the presence of specific kinds of microhabitats, the level of temporal continuity in the availability of deadwood (Nitare & Hallingbäck, 2010; von Bonsdorff et al., 2014; Niemelä, 2016), and the probable presence of red-listed species (Haugseth et al., 1996; Nitare & Hallingbäck, 2010). The indicator species approach relying on fungi has mainly been used in Europe (Kotiranta & Niemelä, 1996; Bredesen et al., 1997; Christensen et al., 2004; Walley & Veerkamp, 2005; Nitare & Hallingbäck, 2010; Abrego et al., 2017; Runnel & Löhmus, 2017), but lately also in North America (Brazee et al., 2014).

Among fungi, indicator species are generally among the more connectivity-dependent species (Sverdrup-Thygeson & Lindenmayer, 2003; Penttilä et al., 2006; Nordén et al., 2013; Abrego et al., 2015, 2017). However, this pattern is not fully consistent for different spatial scales. The resource use of all fungal indicator species has not been systematically analysed, but it is possible to extract from Nordén et al. (2013) that the indicator species are typically very or relatively specialized in their resource use. This is likely the main cause for their connectivity dependence – suitable resources for these species are often rare in space and time.

The fungal indicator species have been assigned based on expert opinions rather than in an evidence-based manner (Rolstad et al., 2002; Saetersdal et al., 2005), and few scientific evaluations have been performed of what these species actually indicate (Nordén et al., 2007). Empirical studies are needed to unveil to what extent the occurrence of the indicator species depends on local habitat quality, local forest continuity or landscape-scale connectivity of near-natural forests (Heilmann-Clausen et al., 2017). Such research should include the relevant spatial and temporal scales, as reviews indicate that both large-scale and time-delayed effects can be expected (Junninen & Komonen, 2011; Sverdrup-Thygeson et al., 2014). Another important aspect is that lists of indicator species partly overlap with lists of red-listed species, and the requirements of red-listed fungi are of interest for both nature conservation and forestry. Understanding how the occurrence of the typically relatively rare and often declining indicator species

depends on local and landscape factors is the basis for halting their declines and maintaining viable populations of indicator species and other species restricted to the same microhabitat and with similar biology.

In the present paper, we evaluate whether wood-decaying fungal indicator species are more closely associated with near-natural deadwood rich forests than non-indicator species, and whether they can additionally be used as indicators of spatial and temporal connectivity. We aim to find out the quality (age as a proxy) of the surrounding forest that influences local occurrence (number of species or the frequency of occurrence per site) of fungi in forests with high conservation value the most, and at what spatial scales this influence is the strongest. We highlight variation in responses between indicator species and non-indicator species, and explicitly analyze to what degree the different species share responses to connectivity factors, through multilevel models. We hypothesize that indicator species are better predictors than non-indicator species of spatial and temporal connectivity in the availability of suitable resources (dead trees), as measured e.g. as landscape connectivity, local forest age, and amount of deadwood.

We address these questions by studying a set of remaining near-natural Norway spruce (*Picea abies*) forests across the Scandinavian Peninsula and contrast nine pre-selected indicator species with nine non-indicator species. In our analyses, we include both local and landscape scale (up to a distance of 100 km) variables of connectivity, and our study area encompasses ca. 500 \* 1200 km from boreonemoral to northern boreal Scandinavia (Ahti et al., 1968). There are few previous studies on wood-decaying fungi of similar spatial extent (but see Kouki et al., 2012; Nordén et al., 2013).

## 2. Material and methods

### 2.1. Study design and selection of study sites

Using available public databases and expert information, we selected 14 sites among the largest and the most deadwood rich spruce-dominated forest reserves in Sweden and Norway (Fig. 1), aiming for a large geographical coverage of boreal and boreonemoral Scandinavia. The minimum distance between two selected reserves was 110 km. We then located small and isolated forest set-asides (n = 14; typically a woodland key habitat) of similar quality but smaller in area than the reserves, within 20–40 km from each reserve, thereby forming 14 site pairs. In four landscapes there were no suitable forest set-asides within the desired distance from the nature reserves, therefore the minimum (maximum) distance between the large site and the small site was 12 km (65 km). All sites (n = 28) represent old conifer forests on mesic soils with a dense dwarf-shrub layer. None of the forests had been subjected to industrial forestry or intensive selective loggings.

### 2.2. Focal species

We selected nine indicator species that were frequent enough in our data to be included in the analyses, among the polyporoid and corticioid basidiomycetes that are classified as indicator species in Sweden (Nitare & Hallingbäck, 2010), Norway (Haugseth et al., 1996) and Finland (Kotiranta & Niemelä, 1996; Niemelä, 2016) (Table 1). We considered also the Finnish list to select species with widespread use as indicator species within Fennoscandia. The selected indicator species typically have relatively large and/or distinctive fruit bodies that are long-lived and/or possible to identify as dead, and therefore relatively easy to detect and identify in the field. We did not include species with high inter-annual variation in fruiting to ensure high detectability. All of the indicator species are included in at least one of the Fennoscandian Red Lists (Kotiranta et al., 2010; ArtDatabanken, 2015; Henriksen & Hilmo, 2015). The indicator species are typically rare in managed forests but may be locally common in near-natural forests, for instance *Fomitopsis rosea* that occurred on 36 out of 60 logs at one site, and

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