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

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23 **Highlights**

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25 • Indicator fungi of conservation value signal large-scale habitat connectivity

26 • However, landscape-scale connectivity is beneficial only if resources are abundant

27 • Indicator species are successful competitors in deadwood-rich habitats

28 • Fungal indicators clearly depend on high forest age and abundance of resources

29 • Unexpectedly, they are not sensitive to local historical moderate selective logging

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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 (≥80 years) within 100 km, while non-indicator species
depended on connectivity of younger forest (≥40 years) at a smaller spatial scale (≤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 m^3 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.

Keywords: Habitat fragmentation, continuity, deadwood, basidiomycetes, red-listed species,
logging history.

84   **1 Introduction**

85

86   Loss of spatial connectivity in the availability of resources is an important driver behind

87   species declines globally and in most ecosystems (Wilson *et al.* 2016). A recent review of

88   long-running forest fragmentation experiments on five continents concluded that after two

89   decades, the species richness in the studied forests had declined on average by half (Haddad

90   *et al.* 2015). Temporal analogues to fragmentation have been less studied, but high species

91   richness and the occurrence of red-listed species or other species of conservation concern

92   are often considered threatened by lack of long temporal continuity of habitats, sites, or

93   landscapes (Nilsson *et al.* 2001; Dullinger *et al.* 2013; Nordén *et al.* 2014). In Fennoscandian

94   countries (Norway, Sweden and Finland), forestry has led to a 90% loss of near-natural

95   forests (i.e. forests that have structural characteristics resembling those of natural forests)

96   and associated coarse deadwood (Siitonen 2001), resulting in severe fragmentation and loss

97   of connectivity of such forest habitats. Many saproxylic species among beetles and fungi are

98   directly dependent on near-natural forest with deadwood, but the level of deadwood

99   needed and the strengths and scales of correlations are often poorly known (Lassauce *et al.*

100   2011). It is therefore often difficult to assess how well functionally connected a particular

101   habitat patch is in space and time from the viewpoint of the focal species.

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103   When addressing the effects of forest fragmentation on populations, the landscape pattern

104   must be assessed from the perspective of the species. The relevant spatial scale depends

105   strongly on traits such as rarity, trophic levels, reproductive mode, life span, habitat

106   specialization and dispersal ability of different species (Haddad *et al.* 2015). A different

107   response to changes in connectivity could be expected among e.g. generalist and specialist

108   species, even with equal dispersal abilities (Southwood 1977; Nordén *et al.* 2013).

109

110   As the remaining areas of old, near-natural forests are successively being cut, there is an

111   increasing need for simple and rapid assessment methods of forest conservation values and

112   measures at both local and landscape scales (Lindenmayer *et al.* 2002). One approach that

113   has been used is to use lists of indicator species from various organism groups to identify

114   areas of high conservation value or naturalness. For example, the presence of particular

115   wood-decaying fungal species have been used as a criterion to determine whether a site

116   should be assigned as a woodland key habitat (Timonen *et al.* 2010). Fungal indicator species

117   have also been used for assessing certain features that are difficult to survey directly such as

118   the presence of specific kinds of microhabitats, the level of temporal continuity in the

119   availability of deadwood (Nitare & Hallingbäck 2010; von Bonsdorff *et al.* 2014; Niemelä

120   2016), and the probable presence of red-listed species (Haugseth *et al.* 1996; Nitare &

121   Hallingbäck 2010). The indicator species approach relying on fungi has mainly been used in

122   Europe (Kotiranta & Niemelä 1996; Bredesen *et al.* 1997; Christensen *et al.* 2004; Walleyn &

123   Veerkamp 2005; Nitare & Hallingbäck 2010; Abrego *et al.* 2017; Runnel & Lõhmus 2017), but

124   lately also in North America (Brazee *et al.* 2014).

125

126   Among fungi, indicator species are generally among the more connectivity-dependent

127   species (Sverdrup-Thygeson & Lindenmayer 2003; Penttilä *et al.* 2006; Nordén *et al.* 2013;

128   Abrego *et al.* 2015; Abrego *et al.* 2017). However, this pattern is not fully consistent for

129   different spatial scales. The resource use of all fungal indicator species has not been

130   systematically analysed, but it is possible to extract from Nordén et al. (2013) that the

131   indicator species are typically very or relatively specialized in their resource use. This is likely

132   the main cause for their connectivity dependence – suitable resources for these species are

133   often rare in space and time.

134

135   The fungal indicator species have been assigned based on expert opinions rather than in an

136   evidence-based manner (Rolstad *et al.* 2002; Saetersdal *et al.* 2005), and few scientific

137   evaluations have been performed of what these species actually indicate (Nordén *et al.*

138   2007). Empirical studies are needed to unveil to what extent the occurrence of the indicator

139   species depends on local habitat quality, local forest continuity or landscape-scale

140   connectivity of near-natural forests (Heilmann-Clausen *et al.* 2017). Such research should

141   include the relevant spatial and temporal scales, as reviews indicate that both large-scale

142   and time-delayed effects can be expected (Junninen & Komonen 2011; Sverdrup-Thygeson

143   *et al.* 2014). Another important aspect is that lists of indicator species partly overlap with

144   lists of red-listed species, and the requirements of red-listed fungi are of interest for both

145   nature conservation and forestry. Understanding how the occurrence of the typically

146   relatively rare and often declining indicator species depends on local and landscape factors is

147   the basis for halting their declines and maintaining viable populations of indicator species

148   and other species restricted to the same microhabitat and with similar biology.

149

150   In the present paper, we evaluate whether wood-decaying fungal indicator species are more

151   closely associated with near-natural deadwood rich forests than non-indicator species, and

152   whether they can additionally be used as indicators of spatial and temporal connectivity. We

153   aim to find out the quality (age as a proxy) of the surrounding forest that influences local

154   occurrence (number of species or the frequency of occurrence per site) of fungi in forests

155   with high conservation value the most, and at what spatial scales this influence is the

156   strongest. We highlight variation in responses between indicator species and non-indicator

157   species, and explicitly analyze to what degree the different species share responses to

158   connectivity factors, through multilevel models. We hypothesize that indicator species are

159   better predictors than non-indicator species of spatial and temporal connectivity in the

160   availability of suitable resources (dead trees), as measured e.g. as landscape connectivity,

161   local forest age, and amount of deadwood.

162

163   We address these questions by studying a set of remaining near-natural Norway spruce

164   (*Picea abies*) forests across the Scandinavian Peninsula and contrast nine pre-selected

165   indicator species with nine non-indicator species. In our analyses, we include both local and

166 landscape scale (up to a distance of 100 km) variables of connectivity, and our study area
167 encompasses ca. 500 * 1200 km from boreonemoral to northern boreal Scandinavia (Ahti *et*
168 *al.* 1968). There are few previous studies on wood-decaying fungi of similar spatial extent
169 (but see Kouki *et al.* 2012; Nordén *et al.* 2013).
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172 **2 Material and methods**
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174 *2.1 Study design and selection of study sites*
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176 Using available public databases and expert information, we selected 14 sites among the
177 largest and the most deadwood rich spruce-dominated forest reserves in Sweden and
178 Norway (Fig. 1), aiming for a large geographical coverage of boreal and boreonemoral
179 Scandinavia. The minimum distance between two selected reserves was 110 km. We then
180 located small and isolated forest set-asides (n=14; typically a woodland key habitat) of
181 similar quality but smaller in area than the reserves, within 20-40 km from each reserve,
182 thereby forming 14 site pairs. In four landscapes there were no suitable forest set-asides
183 within the desired distance from the nature reserves, therefore the minimum (maximum)
184 distance between the large site and the small site was 12 km (65 km). All sites (n=28)
185 represent old conifer forests on mesic soils with a dense dwarf-shrub layer. None of the
186 forests had been subjected to industrial forestry or intensive selective loggings.
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188 *2.2 Focal species*
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190 We selected nine indicator species that were frequent enough in our data to be included in
191 the analyses, among the polyporoid and corticioid basidiomycetes that are classified as
192 indicator species in Sweden (Nitare & Hallingbäck 2010), Norway (Haugseth *et al.* 1996) and
193 Finland (Kotiranta & Niemelä 1996; Niemelä 2016) (Table 1). We considered also the Finnish
194 list to select species with widespread use as indicator species within Fennoscandia. The
195 selected indicator species typically have relatively large and/or distinctive fruit bodies that
196 are long-lived and/or possible to identify as dead, and therefore relatively easy to detect and
197 identify in the field. We did not include species with high inter-annual variation in fruiting to
198 ensure high detectability. All of the indicator species are included in at least one of the
199 Fennoscandian Red Lists (Kotiranta *et al.* 2010; ArtDatabanken 2015; Henriksen & Hilmo
200 2015). The indicator species are typically rare in managed forests but may be locally
201 common in near-natural forests, for instance *Fomitopsis rosea* that occurred on 36 out of 60
202 logs at one site, and *Phellinus ferrugineofuscus* on 26 out of 60 logs at one site (Appendix A).
203 Each indicator species was observed in ≥10 out of 28 sites and had in total ≥25 observations.
204
205 As a potential contrast, we selected nine species that are neither indicator species nor red-
206 listed (Table 1). Similar to the indicator species, also the non-indicator species decompose

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dead wood of spruce in various stages of decay. We used the same detectability criteria (see above) in the selection of both the indicator and the non-indicator species. In addition to occurrence in old forests, many of the non-indicator species also occur on dead trees in managed forests, which makes them typically rather widespread and common.

2.3 Surveys of fungi and deadwood

We established one sample plot measuring 200 m * 200 m (4 ha) at each site. At small sites the plot was placed at the center, while at large sites we placed the plot where we first encountered a 200 m * 200 m area with enough of suitable logs after entering the reserve. Within the sample plot, we recorded deadwood characteristics and surveyed the fruit bodies of all polyporoid and corticioid fungal species on 60 coarse Norway spruce logs. We performed the surveys in September-October 2010 and September-October 2011. We selected logs that were 20-40 cm in diameter at breast height (DBH) and represented different decay stages from fresh logs to well-decomposed logs (13-17 logs in each of the decay stage classes 1-4; Hottola & Siitonen 2008), including both trees that had fallen down because of stem breakage and by uprooting. The minimum length of the log was 13.5 m in the southern and 11.5 m in the northern part of the study area where trees are naturally shorter. The logs were chosen randomly while also making sure to cover the entire sample plot, thus we did not select logs of the same stage of decomposition that were close to each other.

To quantify the deadwood characteristics of the forest, all dead trees with the minimum diameter of 5 cm at the breast height or at the base (depending on breakage type) were surveyed in two 5 m * 200 m transects (altogether 5 m * 395 m) that crossed each other at the center of the plot. For the analysis, the volume of spruce logs (m^3 ha^{-1}) was calculated based on Laasasenaho's (1982) volume equations, and the density of large (DBH ≥15 cm) spruce logs in intermediate or advanced stages of decay (decay stages 3-5; Hottola & Siitonen 2008) per ha was calculated, as an indication of deadwood continuity.

2.4 Sampling and analyses of forest structure and temporal continuity

To describe the forest structure and history (temporal continuity) of the sites we measured the following variables: mean age of trees, the number of historical selective logging events and the density of cut spruce stumps as an indication of the intensity of the earlier forest land use.

The surveys were performed in 2011, 2013 and 2014 by using transects (n = 4, 20 m wide, 50 m apart) and sample points (n = 6, >50 m apart) pre-plotted randomly on maps of each site. We used transect surveys to identify cut stumps and trees with traces of historical logging operations (e.g. logging blazes and scars). We classified stumps into two categories: stumps

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248   of large-diameter pines felled by axe; and stumps of mid-sized pines and spruces felled by
249   saw. In addition, we cored trees standing within a 3 m radius from 4-6 cut stumps at their
250   base. We later analyzed these samples to detect possible growth responses that can indicate
251   the year the tree next to the cored tree was cut.

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253   Information on present forest structure was obtained from sample points placed randomly
254   along the transects. At each point, tree species, basal area of living and dead trees, and tree
255   height of the two largest trees were recorded. In order to estimate stand age, 5-8 randomly
256   chosen trees of DBH ≥10 cm were cored at their base. Total tree volume in the area
257   immediately surrounding each sample point was estimated using volume functions (based
258   on tree height and basal area) derived from Brantseg (1969) and Næsset & Tveite (1999) for
259   sites located in Norway, and Håkansson et al. (1994) for sites located in Sweden.

260

261   In the laboratory, all cored trees were age-determined by counting annual tree rings using a
262   measuring station with a resolution of 1/100 mm (LINNTAB 5, RINNTECH Technologies). To
263   identify growth responses to logging events in single trees we examined the radial growth
264   pattern of each of the cored trees. Following the procedure suggested by Groven et al.
265   (2002) we compared mean tree-ring width between two consecutive 10-year periods and
266   defined a growth response as an increase in mean tree width, between two successive
267   periods, of more than 100%. For trees with a moderate-high growth pattern before the
268   release (>1 mm a year), a 50% increase was applied (cf. Lorimer 1980). This way the number
269   and timing of past logging events were reconstructed. However, as pointed out by Josefsson
270   et al. (2005), several factors (including logging events, windthrow and insect outbreaks) may
271   give rise to growth responses. Accordingly, we related the growth responses to records of
272   past windthrow and insect outbreak events and occurrence of cut stumps and logging
273   blazes. We then calculated a logging impact index to describe the intensity of the historical
274   logging events. The index is based on the number of historical logging events (in 1700s-
275   1900s) that were certain or likely to have involved spruce, and the density of cut spruce
276   stumps that originate from the 1900s (older stumps have already decomposed) (Table 3, see
277   also Appendix B).

278

279   *2.5 Calculation of spatial connectivity*

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281   We acquired data on the amount of old forest within various scales in the surrounding
282   landscape from SAT-skog (Gjertsen 2007; Gjertsen & Nilsen 2012) for Norway and kNN
283   (Reese *et al.* 2003) for Sweden. Connectivity was calculated as the sum of living spruce
284   volume for each raster pixel (25 m * 25 m) within a given buffer distance from the focal site,
285   and where the maximum age (SAT-skog) or mean age (kNN) of the spruce stands within each
286   pixel was above a given threshold. This working definition of connectivity is reasonable given
287   the passive dispersal mode of fungal spores. The sensitivity of the analysis to using two
288   different criteria for forest age in the different countries was explored by including an

interaction effect of country and connectivity (see below). The contribution of each pixel to the connectivity value of each stand was weighted according to the distance to the focal site. We thus defined the connectivity of pixel i as

$$S_i = \sum_{j \mid d_{ij} < c} e^{-\frac{d_{ij}}{b}} V_j a_j \quad (\text{Eq. } 1)$$

where the sum ranges over all pixels j, d_{ij} is the distance (km) between pixels i and j, b is the characteristic distance (km) of the exponential scaling, c is the buffer radius (km), V_j is the volume of living spruce in pixel j, $a_j = 1$ if the pixel j exceeds the age threshold and $a_j = 0$ if this is not the case. We set b as $b = c/0.58$, so that the exponential weighting achieves the value of 0.18 at the distance of the buffer radius c. We performed the calculation for a range of age thresholds (40, 60, 80, 100, 120, and 140 years) and buffer radii (0.5, 1, 2, 3, 4, 5, 6, 7, 10, 25, 50, and 100 km).

In Sweden, there was a trend of increasing old forest (≥80 years) connectivity values (for a landscape with a radius of 100 km) from south to north apart from the four northernmost localities (Table 2). The four northern Swedish localities got as low connectivity values as the southern Swedish localities, partly because of dominance of young forests in the landscape and partly because of lower volumes of living spruce in the northern landscapes that include high altitude areas. The range in connectivity values in Sweden was 1.3×10^8 to 5.6×10^8. In Norway, the two localities that lie within the Nordmarka wilderness area north of Oslo had clearly higher connectivity values (7.5×10^8) than any other locality in the whole data. The rest of the Norwegian localities (range from 1.6×10^8 to 4×10^8) were more similar to the Swedish localities in their connectivity to old forests in the landscape.

2.6 Site characteristics

The sites were variable in age, the mean (max) age of trees ranging from 76.1 to 209.7 (101 to 414) years, and in the volume of spruce logs (min 8.7, max 143.2 m^3 ha^{-1}) as well as in the density of well-decayed large spruce logs (min 20, max 180 ha^{-1}) (Table 2).

2.7 Statistical analyses

The statistical analyses consist of two parts. First, we used linear models to explore how connectivity influenced the total abundance (the aggregate number of occurrences of all species) of the non-indicator and indicator species groups separately. Analyses were done with connectivity measures constructed with different age threshold (40, 60, 80, 100, and 120 years) and spatial scales (0.5, 1, 2, 3, 4, 5, 6, 8, 10, 25, 50 and 100 km buffer radii) to define the parameter values at which the connectivity measure best explained the total abundance of indicator and non-indicator species, respectively. The connectivity measurements using those parameter values were used in subsequent analyses.

329   To identify other relevant explanatory variables in addition to connectivity, we used GLMM

330   model averaging of a candidate set of models for total abundance and species richness, for

331   indicator and non-indicator species, separately. The details of these models are further

332   described in the Supplementary material. Table 3 lists the explanatory variables that were

333   considered in the model averaging, and the variables that were indicated as important and

334   later included in the final model (described below). We also performed a leave-one-out

335   cross-validation (leave one site out) on the candidate model set, which corroborated the

336   results from the model averaging, indicating the same variables as important, increasing

337   explanatory power without overfitting.

338

339   The models described so far disregard species-specific information by aggregating the

340   occurrences of several species. Therefore, and secondly, we analyzed the response

341   (abundance) of each species separately, but in a joint model where each species' individual

342   responses to the explanatory variables were allowed to vary around common means for the

343   non-indicator species and indicator species, respectively. We explicitly tested the hypothesis

344   that non-indicator and indicator species on average respond differently to the explanatory

345   variables, but also explored the extent to which individual species vary from these average

346   responses. This is equivalent to a mixed effects model of each species abundance in each

347   sample location (e.g. using the R-package lme4) with random effects (intercept and slopes

348   for each explanatory variable) for each species, and "fixed" interaction effects with each

349   explanatory variable and indicator species status. However, we employed a multilevel

350   Bayesian model using JAGS (Just Another Gibbs Sampler; Plummer 2016), to allow the fitting

351   of the relatively large number of parameters for the data set, and to incorporate the full

352   parameter uncertainty in the entire parameter space (Gelman & Hill 2007).

353

354   All the variables where centered and standardized as Z-scores ($z_i = \frac{x_i - \bar{x}}{sd(x)}$), and we included

355   weakly informative priors on the parameters to be estimated to improve the convergence of

356   the mcmc-chains (see appendix C for model specification). In addition, we included random

357   intercepts for survey location, to account for the multiple samples (species) within each

358   location. Dependent variables were the counts recorded for each species, modelled as a

359   Poisson distribution, with observation level (log-normal) random effect, to account for over-

360   dispersion. The model code and convergence diagnostics are available in Appendix C.

361

362

363   **3 Results**

364

365   *3.1 Indicator species*

366

367   The total abundance of indicator species was most strongly affected by the amount of old

368   forest ≥80 years within a 100 km radius (Fig. 2a). Connectivity values based on this forest age

369 threshold and this radius were subsequently used in the multiple regressions reported

370 below. The response surface for the regression parameter for connectivity in the linear

371 models had a similar pattern as the R^2-value plot (Fig. 2a), and is not shown here (Appendix

372 D). The higher the influence of connectivity on total abundance, the higher the explanatory

373 power of the models.

374

375 The model averaging also indicated that connectivity was an important factor for indicator

376 species (Table 3; see also Appendix D). Both species richness and total abundance of

377 indicator species was positively affected by increased connectivity. The species richness of

378 indicator species was additionally affected by the volume of deadwood, which interacted

379 with connectivity.

380

381 Using the connectivity measurement of ≥40 years and 25 km buffer in the models for

382 indicator species instead of ≥80 years and 100 km revealed few clear effects. Here, only local

383 forest age remained clearly positive (Table 3; see also Appendix D).

384

385 *3.2 Non-indicator species*

386

387 The regression analysis of forest age and buffer size indicated that the total abundance of

388 non-indicator species was mainly affected by the amount of young forest (≥40 years) within

389 an intermediately sized area (peak at 25 km radius, Fig. 2b), and these connectivity values

390 were used in the model averaging for this group (below). As with the indicator species, the

391 response surface for the regression parameter for connectivity in the linear models had a

392 similar pattern as the R^2-value plot and is not shown here (Appendix D).

393

394 The species richness of non-indicator fungi was not influenced by any of the studied

395 variables, with a relative importance of <0.12 for all variables in the GLMM model averaging.

396 The best model was the null model, without any predictor variables. In contrast, the total

397 abundance of the non-indicator species was clearly affected by local forest age, connectivity

398 and country. Interestingly, when using the connectivity measurement based on the 80 years

399 and 100 km thresholds, the volume of deadwood and its interaction with connectivity also

400 showed up as clearly important.

401

402 *3.3 Analysis of individual species*

403

404 The disparate effects of the explanatory variables on the indicator vs. non-indicator species

405 were confirmed in the multilevel Bayesian models, where these differences can also be

406 appropriately measured. Connectivity (using age ≥80 years, radius ≤100 km) interacted with

407 the local volume of deadwood (spruce logs), but in opposite ways for the indicator vs. non-

408 indicator species (Fig. 3). The non-indicator species on average responded positively to

409 connectivity when the volume of deadwood was relatively low (<29 m^3 ha^{-1}; in 6 out of 28

10

410 sites), but their responses were negative when the volume of deadwood was high (>53 m^3

411 ha^{-1}; in 9 sites). At average levels of local deadwood, the non-indicator species showed weak

412 and somewhat varying response to connectivity (Fig. 3). In contrast, all indicator species

413 showed clear positive responses to connectivity at average and high levels of deadwood,

414 while the response was negative at sites with lower levels of deadwood (<29 m^3 ha^{-1}).

415

416 The effect of the local forest age was also clearly different for the indicator and non-

417 indicator species (Figs 4a and 5). The non-indicator species showed a general negative

418 response, with an estimated mean 27% loss of individuals with each 33-year increase of local

419 forest age (1 sd of forest age). The indicator species instead showed positive effects, with an

420 estimated mean 105% increase in abundance every 33 year of increased local forest age. The

421 response to local forest age varied more within the indicator species than within the non-

422 indicator species.

423

424 As with the model averaging of the aggregate level models, the multilevel model consistently

425 showed little impact of the logging impact index on the species-specific abundances in both

426 species groups, (Figs 4b and 5).

427

428 Similarly, and also in line with the aggregate models, there was little overall evidence of an

429 impact of the density of continuity logs (Fig. 4c). The importance varied between individual

430 species, but most estimates had wide uncertainty bounds, and thus were not distinct from

431 each other.

432

433 Lastly, we explored the possible effect of country in the GLMM models on non-indicator

434 species. Allowing for separate effects for each species revealed that this effect varied

435 considerably between individual species, and that the effect was not generalizable to either

436 species group. Most of the non-indicator species occurred more often at the Swedish sites,

437 while the indicator species showed variable responses to this factor. The indicator species

438 *Cystostereum murrayi* was more common in Norway, while the non-indicator species

439 *Antrodia serialis* and the indicator species *Phellinus ferrugineofuscus* were markedly more

440 common in Sweden, taking into account the other explanatory factors (Fig. 4d).

441

442 There was a clear tendency of indicator species being more dependent on spatiotemporal

443 connectivity than the non-indicator species, when applying a connectivity measure that

444 describes the amount of old (≥80 years) forests in a large (radius 100 km) landscape (Fig. 5).

445 We also performed the same modelling exercise using the connectivity measure that

446 explained the most variation for the total abundance of the non-indicator species (≥40 years,

447 25 km buffer). Here, only the local forest age showed a clear importance with a positive

448 effect on the indicator species and no discernable effect on non-indicator species (see

449 Appendix D for more details on these models).

450

451

4 Discussion

453

Our hypotheses of the indicator and non-indicator species differing in which local and landscape scale factors they are influenced by, and in what way, were supported by several results. According to our results, large-scale connectivity of old forests is an important driver of the occurrence of indicator species and it masks other effects when it is not accounted for. For example, when old-forest connectivity was not accounted for, none of the spatiotemporal connectivity variables, apart from forest age, turned out as important for indicator species. The multilevel models revealed surprising uniformity within each species group in how they reacted to several of the environmental variables. All indicator species showed a positive response to old forest connectivity, modified through the interaction with the local volume of deadwood. The drivers of the occurrence of indicator species appear to be environmental variables of general importance, meaning that similar conservation and management efforts can simultaneously benefit many indicator species and many other species that are dependent on similar resources and habitats. Our results indicate that rarity in wood-decaying fungal species can share common causal mechanisms as there are hundreds of species that are both rare and restricted to habitats that usually occur as isolated patches in the contemporary forest landscapes.

470

For both indicator and non-indicator species there was no effect of the local forest area in the survey site, but species richness and total abundance were determined by connectivity at larger spatial scales. The indicator species are dependent on connectivity of older forest at a spatial scale of at least 100 km, and it is possible that even larger scales are relevant. The importance of connectivity at a large spatial scale and signs of dispersal limitation may seem counterintuitive at first. However, the effect being at a large spatial scale, and the coupled long temporal scale (see below), is likely because of a combination of the rarity of long-distance dispersal (more than a few kilometers) events (Norros *et al.* 2012; Norros *et al.* 2015) and the slow dynamics of some of the species which may need even decades from establishment to fruiting (Ovaskainen *et al.* 2013) and subsequent production of the dispersal agents (spores). More generally, it is likely that rare species need larger areas than common species to gain the critical population size needed for long-term survival. In our study area in Scandinavia, it may also be that the area of old forest in the landscape is usually so low that it is necessary to consider a large landscape to reach an area of old forest in the landscape that can have a discernible influence on local populations. Long-distance dispersal across 100 km seems unlikely (Peay et al., 2012; Norros et al., 2015; Golan & Pringle, 2017), but it is possible that long-distance dispersal events do contribute to the persistence of the local populations (Bohrer et al., 2005).

489

In contrast, the non-indicator species showed a stronger dependence of connectivity of younger forest at smaller spatial scales. The most relevant connectivity values, ≥40 years and

492   25 km for the non-indicator species and ≥80 years and 100 km for the indicator species,
493   were positively correlated (Pearson correlation = 0.64). Therefore, the negative influence of
494   old forest connectivity on the non-indicator species does not seem to be caused by
495   associated lower amounts of younger forests. The forest age thresholds likely reflect the
496   successional stages of forests that may be suitable as habitat for the indicator species or the
497   non-indicator species. The resources (deadwood) for the non-indicator species can be found,
498   albeit infrequently, also in the matrix of managed forests. The non-indicator species would
499   undoubtedly also benefit from a high amount of resources and a good connectivity between
500   the resource units, but they are likely to be suppressed by interspecific competition that gain
501   importance in species-rich communities. The presence and abundance of indicator species in
502   well-connected forests that are especially rich in deadwood likely increase competition
503   pressure which may explain the lower presence and abundance of the non-indicator species
504   in the oldest and the most deadwood-rich forests. In isolated or deadwood-poor forests,
505   however, the non-indicator species can become very abundant in the absence of the
506   indicator species that cannot reach the distant resource units. What may look like the non-
507   indicator species disfavoring the old forest locally and in the landscape, is more probably a
508   sign of the species abundance distribution shifting towards a more natural shape. The
509   pattern of opposite responses to old-forest connectivity in the local populations of common
510   and rare species of wood-decaying fungi has been observed earlier in spruce forests
511   (Berglund *et al.* 2011; Nordén *et al.* 2013). Experimental research has shown a trade-off
512   between ecological specialization and competitive ability: specialist species are often
513   stronger in interspecific competition than generalist species (Holmer *et al.* 1997; Holmer &
514   Stenlid 1997; Boddy 2000) which in turn can establish on many, and variable resource units.
515   Generalists can thereby manage to fulfil their life cycle in many resource units, while the
516   specialists have a strategy of conquering fewer units of particular kind and combating to
517   hold their possessions in them.
518

519   Spatial and temporal scales are coupled, so that changes in landscape structure in the
520   distant past influence the current population distribution at a larger scale than recent
521   changes in landscape structure (Paltto *et al.* 2006; Nordén *et al.* 2014). In our system of fungi
522   in coniferous forests, the connectivity effect being the strongest at the largest spatial scale
523   may be explained with time; the species may actually respond to a historical landscape
524   structure, the few remains of which we see today only if we consider a landscape large
525   enough. In broadleaved forests of southern Sweden, Paltto et al. (2006) found that the
526   landscape structure 120 years ago explained the occurrence of fungal indicator species
527   inhabiting oak whereas the current landscape structure did not affect their occurrence.
528   Indicator species of natural beech forests in Europe have been shown to benefit from
529   current connectivity at a spatial scale of 10 km (Abrego *et al.* 2017). As the indicator species
530   suites were chosen independently for different systems and habitat types, it is not possible
531   to generalize over sets of indicator species about what aspects of habitat quality,

532 connectivity and continuity the respective species indicate, even within ecologically
533 relatively uniform species such as wood-decaying fungi.

534

535 At the local scale, species richness of the indicator species was strongly positively affected by
536 the local forest age, which was not the case for the non-indicator species. The age matters in
537 addition to the presence of the necessary structures if the species are slow colonizers.
538 Interestingly, the result that the indicator species accumulate by about 35% each 33 years
539 could be interpreted as them being dependent on local ecological continuity due to low
540 colonization rates which the rare wood-decaying species are likely to have (Jönsson *et al.*
541 2008; Norros *et al.* 2015). An alternative explanation for the effect of local forest age may be
542 that some types of logs important for indicator fungi are only present in the oldest stands.
543 Both of these factors probably influence the occurrence patterns of indicator species in the
544 forest landscape.

545

546 Interestingly, the non-indicator species and the indicator species had strongly opposing
547 responses to connectivity of old forests, but both responses depended on the amount of
548 local deadwood. The indicator species benefit from long ecological continuity (forest age)
549 and high spatial connectivity of old forest in the landscape, but old forest connectivity
550 promotes the indicator species only in sites with large volumes of deadwood. This suggests
551 there is a threshold in the local amount of resources below which the site is not practically
552 available to the indicator species even if the site is well-connected to other old forests, i.e.
553 the presumed source populations. There are at least three possible explanations for the local
554 volume threshold: 1) many of the indicator species are ecologically specialized, and probably
555 only sites with high volumes of deadwood include several logs with qualities that are
556 suitable for the most specialized species and that can sustain a viable local population or
557 even only a single occurrence. The suitable logs for the specialist species are typically large,
558 intermediately decayed and naturally fallen spruce trees (Nordén *et al.* 2013). 2) As the
559 indicator species are typically rare outside near-natural forests, the passively dispersing
560 airborne spores of the indicator species are relatively few even in the well-connected forest
561 landscapes. The chances of the few arriving spores landing on a suitable host log are
562 probably very low if the amount of deadwood is low. Further, for most if not all of the
563 polypore indicator species, mycelia originating from different spores need to merge before
564 the formation of fruit bodies is possible. 3) Large volumes of deadwood occur typically in the
565 old forests with very low levels of management such as tree cuttings. Without selective
566 logging or thinning operations, trees grow slowly and provide, after their death, a special
567 type of resource for the wood-inhabiting fungi, some of which may be specialized in the
568 slowly grown, dense wood (Edman *et al.* 2006).

569

570 The threshold volume for the indicator species in our study, 29 m^3 ha^{-1} of spruce logs,
571 corresponding to a total deadwood volume (including all standing and downed deadwood of
572 all tree species) of 47.5 ±18.5 m^3 ha^{-1}, is higher than the threshold deadwood volume of 20-

573   40 m^3 ha^{-1} for red-listed (which our indicator species also are) polypore species reported for

574   mature spruce forest in other studies (Penttilä *et al.* 2004; Hottola *et al.* 2009) in Finland.

575   One explanation for the difference could be that the population densities of the red-listed or

576   indicator species are smaller in Norway and Sweden than in Finland in which industrial

577   forestry expanded to cover extensive areas later than in its western neighbors, and the

578   forests in Finland are closer to the source areas in Russia than the forests in Sweden and

579   Norway. It is noteworthy that even the lowest deadwood volume in our study sites, 18 m^3

580   ha^{-1}, is clearly higher than the average volume of deadwood in managed forests on

581   productive land which is 11 m^3 ha^{-1} in Norway (Framstad *et al.* 2017) and 7.6 m^3 ha^{-1} in

582   Sweden (Jonsson *et al.* 2016). This means that the great majority of managed forests cannot

583   sustain the populations of red-listed species. It also implies that the recommended minimum

584   level of deadwood in conservation management in boreal forests, 20-30 m^3 ha^{-1} (Dahlberg &

585   Stokland 2004; Müller & Bütler 2010; Lachat *et al.* 2013) may be too low to provide suitable

586   habitats for viable populations of several of the indicator species included here.

587

588   Wood-decaying fungi have been considered to be restricted mainly by resource availability

589   (Lonsdale *et al.* 2008), but the positive effects of connectivity found in our study indicate

590   that dispersal and establishment may also be important limiting factors of populations. The

591   mean dispersal distance for viable spores of the old-growth forest species *Phlebia centrifuga*

592   during a season is probably less than 500 m (Nordén & Larsson 2000; Norros *et al.* 2012).

593   Rare long-dispersal events may be possible (Brown & Hovmøller 2002) for species with thick-

594   walled spores (Norros *et al.* 2015). Thin-walled spores, like the great majority of wood-

595   inhabiting basidiomycete species have, lose their viability relatively quickly when exposed to

596   sunlight and cold temperatures during dispersal (Norros *et al.* 2015). Out of the spores that

597   manage to stay viable and land on a suitable dead tree, it is likely that only a small fraction,

598   perhaps just one of a million spores (Norros *et al.* 2012), manage to establish and invade the

599   already established community.

600

601   There was a tendency for the indicator species to benefit and the non-indicator species to be

602   negatively affected by selective logging in the past as indicated by the logging impact index.

603   The difference between the effect on indicator and non-indicator species was small, but the

604   indicator species were consistently estimated as positively affected though with widely

605   overlapping uncertainty intervals. This tendency was unexpected but may indicate that the

606   impact of low-intensity logging in the past has only a small effect on present occurrence and

607   abundance of wood-inhabiting fungi (cf. Josefsson *et al.* 2010). Consequently, local forest

608   age and associated habitat characteristics probably override the importance of these

609   (limited) logging disturbances.

610

611   The effect of country varied greatly among individual species. Most of the non-indicator

612   species did occur more often in the Swedish sites, while the indicator species showed large

613   variability and no clear pattern. As there does not seem to be such difference in the variation

of the connectivity values between Sweden and Norway that would explain the difference in the occurrences, it is possible that the influence of country represent individual differences in broad distribution patterns of the investigated species. These are caused by for instance land-use history, or climatic variables such as oceanity that make the polypore species, or the polyporous fruit body type (Heilmann-Clausen & Boddy 2008) or perenniality of the fruit body (Appelqvist 2008) slightly more common in Sweden.

5 Conclusions

Indicator species are used for identifying forests with natural forest characteristics and a high likelihood of the occurrence of red-listed species, for ordering the forests according to their conservation value, and for monitoring the effects of land use and climate change. Our study supports the conception that indicator fungi can be used to identify forests with high local forest age and a high amount of suitable deadwood, but not a high local resource continuity. It also shows that forests occupied by indicator species may have been subjected to low-intensity selective loggings to varying extents. In addition, the indicator species could be used to identify valuable sites with a high landscape scale connectivity of suitable habitats such as old spruce-dominated forests. Further, indicator species, which are often also red-listed, are restricted by resource and dispersal limitation. The disparate responses of indicator and non-indicator species suggests that modern forest practices have created a shift in community structure by favouring fast colonizing generalists or common species while disfavouring slower colonizing specialists or rare species. Increasing local habitat quality and landscape-scale connectivity by creating more deadwood rich set-asides (with at least 50 m^3 ha^{-1} of deadwood) through protection and restoration, as well as increasing the rotation times in managed forests (to increase the habitat, albeit temporarily, for the more demanding species) is critical for halting the declines of wood-inhabiting fungal species and other species with similar ecology and similar or lower dispersal abilities. The fungal indicator species can be used to assess the success of such restoration and conservation actions. Both spatial and temporal aspects of functional connectivity are important to consider for understanding the contemporary biodiversity patterns and for making informed conservation, restoration and management decisions.

Compliance with ethical standards
The authors declare that they have no conflicts of interest.

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Appendices A-D Supplementary material
Supplementary material associated with this article can be found, in the online version, at http://xxxxx.

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846　Table 1. The 18 focal species, the indicator species category applied in the present study, and the indicator and Red-List status in Norway, Sweden and

847　Finland. IUCN Red-List categories: LC=Least Concern, NT=Near Threatened, VU=Vulnerable, EN=Endangered and CR=Critically Endangered.

Species	Category	Indicator species status			Red-List status		
		Norway	Sweden	Finland	Norway	Sweden	Finland
Amylocystis lapponica (Amylap)	Indicator	Yes	Yes	Yes	EN	VU	NT
Antrodiella citrinella (Antcit)	Indicator	No	No	Yes	VU	CR	NT
Cystostereum murrayi (Cysmur)	Indicator	Yes	Yes	Yes	LC	NT	NT
Fomitopsis rosea (Fomros)	Indicator	Yes	Yes	Yes	NT	NT	NT
Phellinus chrysoloma (Phechr)	Indicator	Yes	Yes	Yes	LC	NT	LC
Phellinus ferrugineofuscus (Phefer)	Indicator	Yes	Yes	Yes	LC	NT	LC
Phellinus nigrolimitatus (Phenig)	Indicator	Yes	Yes	Yes	NT	NT	LC
Phellinus viticola (Phevit)	Indicator	No	Yes	Yes	LC	LC	LC
Phlebia centrifuga (Phlcen)	Indicator	Yes	Yes	Yes	NT	VU	NT
Antrodia serialis (Antser)	Non-indicator	No	No	No	LC	LC	LC
Antrodia sinuosa (Antsin)	Non-indicator	No	No	No	LC	LC	LC
Fomitopsis pinicola (Fompin)	Non-indicator	No	No	No	LC	LC	LC
Gloeophyllum sepiarium (Glosep)	Non-indicator	No	No	No	LC	LC	LC
Heterobasidion parviporum (Hetpar)	Non-indicator	No	No	No	LC	LC	LC
Ischnoderma benzoinum (Iscben)	Non-indicator	No	No	No	LC	LC	LC
Postia caesia (Poscae)	Non-indicator	No	No	No	LC	LC	LC
Stereum sanguinolentum (Stesan)	Non-indicator	No	No	No	LC	LC	LC

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Table 2. Site characteristics and connectivity values of the 28 study forests, arranged from south to north within the country. W in the site code indicates the smaller site (typically a woodland key habitat) within the site pair. For the explanation of variables, see Table 3.

| Country	Site	Local forest area	Local forest age	Continuity logs	Volume of deadwood	Logging impact index	Connectivity: ≥40 yrs, ≤25 km	Connectivity: ≥80 yrs, ≤100 km
Norway	MJ	468.9	84.6	180	143.2	0.5	27.0	402.9
Norway	MJW	13.1	129.2	170	52.6	6.0	27.2	371.9
Norway	TJ	267.4	140.7	20	10.8	7.3	50.0	409.4
Norway	SK	1392.1	130.9	55	43.9	4.9	86.8	756.0
Norway	SKW	8.2	155.4	120	49.7	7.1	72.5	741.7
Norway	RD	66.4	182.2	125	91.4	0.0	23.1	249.0
Norway	RDW	10.7	152.9	45	35.9	7.3	14.6	192.1
Norway	BF	725.0	169.2	135	113.1	4.6	9.8	258.6
Norway	NL	87.6	156.6	25	8.7	0.5	22.2	178.5
Norway	NLW	8.7	138.3	130	63.9	9.3	15.3	158.4
Sweden	MH	284.0	161.5	120	88.8	1.3	60.4	315.2
Sweden	MHW	6.0	140.5	90	45.3	2.2	67.9	251.9
Sweden	NK	103.0	174.0	145	119.9	1.8	39.1	256.3
Sweden	NKW	6.6	114.4	90	35.5	4.0	51.5	202.0
Sweden	UH	119.0	168.6	110	43.3	1.3	54.8	179.3
Sweden	UHW	8.0	76.1	95	41.5	6.1	59.4	143.2
Sweden	TJW	5.1	139.1	130	91.8	5.4	34.2	217.0
Sweden	FS	62.8	209.7	155	65.6	2.4	40.3	239.5
Sweden	FSW	7.2	121.2	50	17.9	10.4	59.0	392.9
Sweden	BT	103.0	207.6	65	31.8	0.6	42.8	499.1
Sweden	BTW	5.3	207.9	80	43.7	3.5	52.5	521.5
Sweden	KB	69.0	174.2	70	29.8	3.8	88.5	431.8
Sweden	KBW	4.1	135.9	110	66.6	4.4	76.1	487.0
Sweden	BFW	11.9	149.1	65	52.5	9.5	48.8	564.1
Sweden	AL	195.0	173.7	60	18.3	10.1	13.5	131.8
Sweden	ALW	8.2	186.5	55	28.9	12.0	28.6	208.7
Sweden	BL	645.0	183.9	55	23.5	3.3	13.7	144.2
Sweden	BLW	8.8	166.0	35	15.0	3.8	16.4	183.1
Standard deviation		302.2	32.9	44.2	34.5	3.4	23.2	174.5

870 Table 3. Summary of explanatory factors included in the analyses, with their relative importance

871 from the model averaging. Relative importance numbers of ≥0.5 in bold. Variables in bold were

872 included in the final individual species models due to large relative importance or a priori interest.

| Variable	Explanation	Indicator species			Non-indicator species		
		Total abundance ≥40 years ≤25 km	Total abundance ≥80 years ≤100 km	Species richness ≥80 years ≤100 km	Total abundance ≥40 years ≤25 km	Total abundance ≥80 years ≤100 km	Species richness ≥40 years ≤25 km
Local forest area	Area (ha) of productive spruce-dominated forest within the survey sites	-	0.14	0.06	0.12	0.03	0.09
Local forest age	Mean age based on cores from 5-8 randomly chosen trees.	**1**	**1**	**1**	**1**	**1**	0.11
Connectivity	Connectivity of surrounding forest stands. For details, see text	0.39	**0.91**	**0.89**	**0.83**	**0.96**	0.12
Volume of deadwood	The volume of spruce logs ($m^3\ ha^{-1}$)	0.09	0.28	**0.69**	0.38	**0.96**	0.09
Continuity logs	Number ha^{-1} of large (DBH ≥15 cm) spruce logs in intermediate or advanced stages of decay	0.10	0.08	0.06	0.11	0.22	0.10
Logging impact index	Calculated logging impact index, for details, see text. 0 logging events: number of cut spruce stumps * 0.1 1 logging event: number of cut spruce stumps * 0.125 2 logging events: number of cut spruce stumps * 0.15 3 logging events: number of cut spruce stumps * 0.175	0.09	0.05	0.06	0.15	0.38	0.09
Country	Survey site location in Norway (0) or Sweden (1)	0.24	0.35	0.08	**0.50**	**1**	0.09
Volume of deadwood : Connectivity interaction		-	0.23	**0.64**	0.02	**0.96**	-
Local forest area : Connectivity interaction		-	-	-	-	-	-
Country : Connectivity interaction		-	0.05	-	0.02	0.41	-

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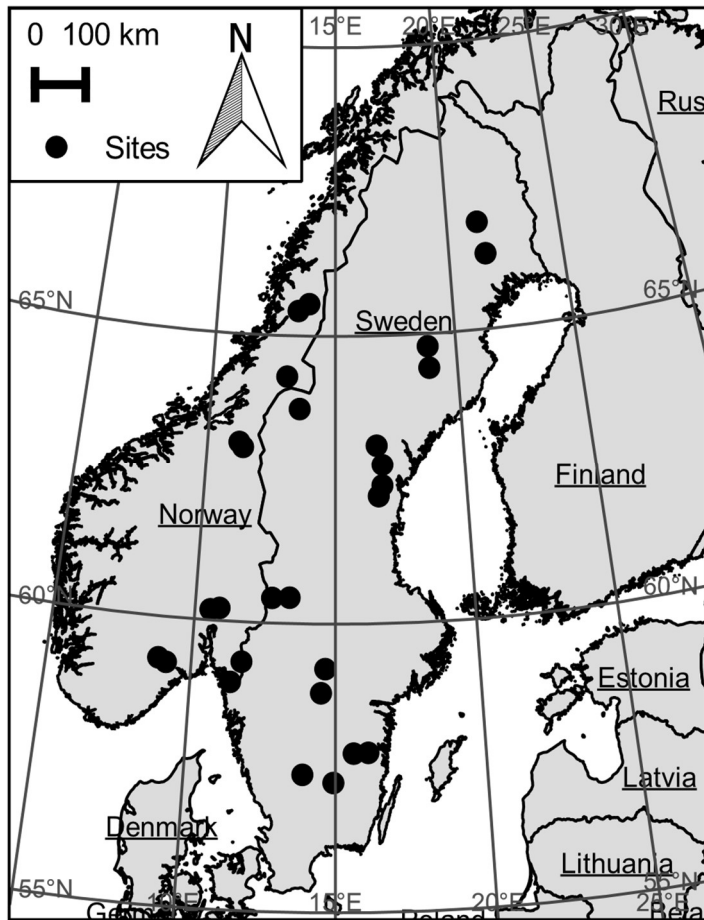
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878 Figure 1. Site locations in the Scandinavian Peninsula.

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882 a) b)
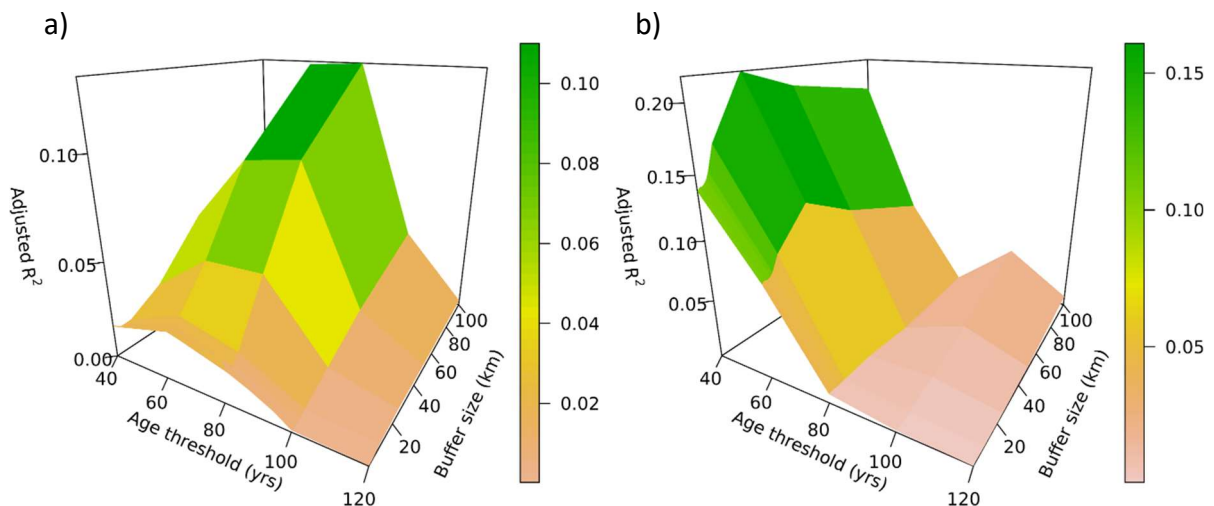
883 Figure 2. Explanatory power of connectivity for a) indicator species and b) non-indicator species,

884 given varying forest age thresholds and landscape radii. The highest explanatory power for indicator

885 species was found with a forest age threshold of 80 years and a buffer radius of 100 km, and for non-

886 indicator species with a forest age threshold of 40 years, and a buffer radius of 25 km.

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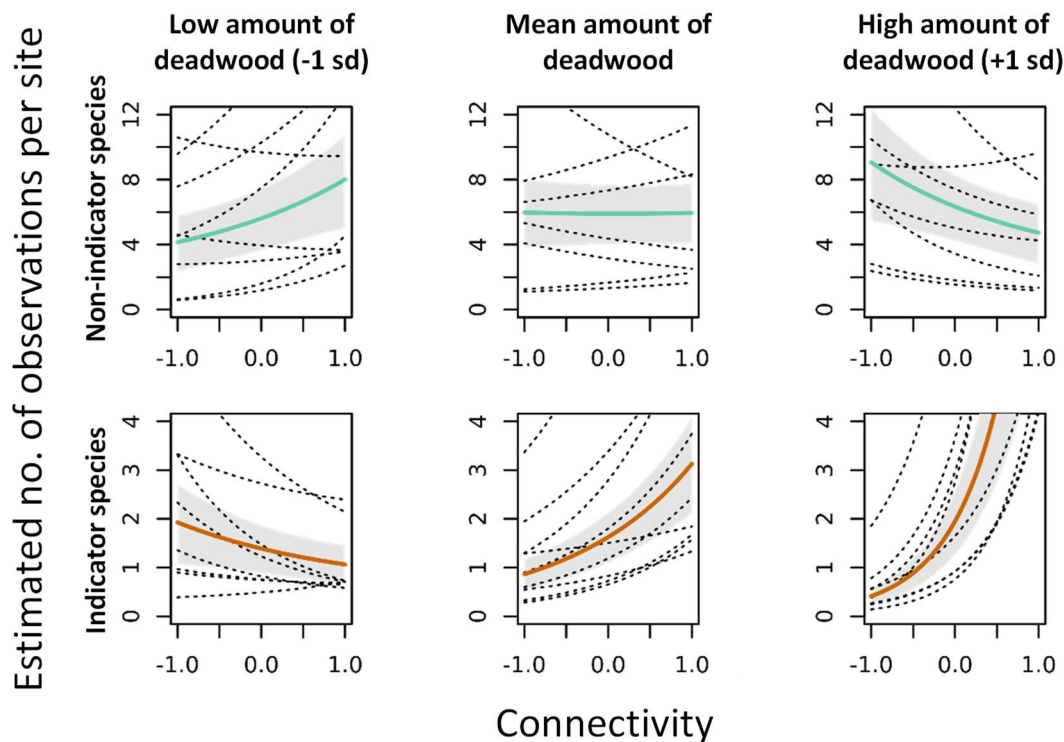
888
889 Figure 3. Connectivity (≥80 years, ≤100 km) and deadwood volume interaction for the abundance of
890 indicator and non-indicator species. Solid lines represent the estimated mean response for the
891 different groups, dashed lines show the estimated response for each individual species in the
892 separate groups. Grey areas show the ±1 standard error for the mean group effects. Low volume of
893 deadwood: 8-28 m^3 ha^{-1}; mean: 29-52 m^3 ha^{-1}; high: 53-143 m^3 ha^{-1} of spruce logs.

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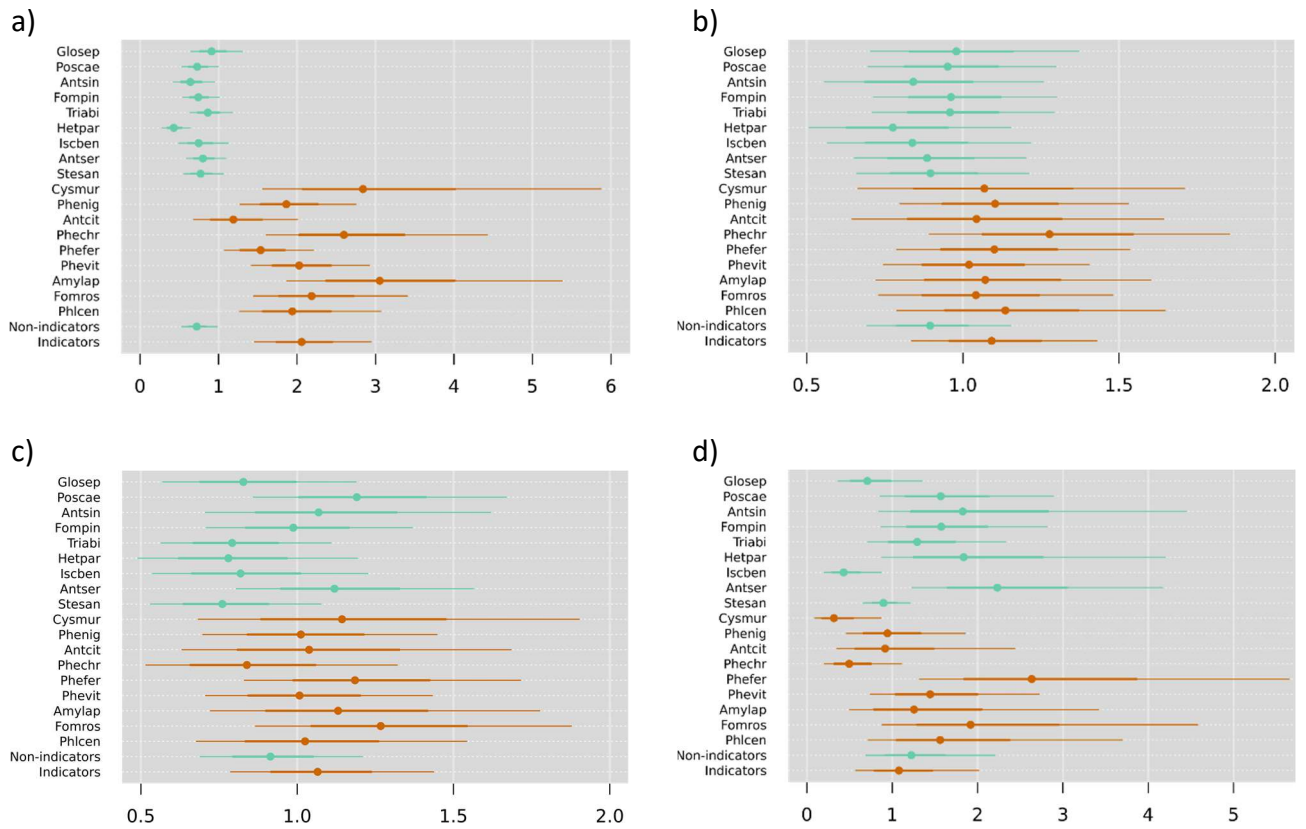
Figure 4. Estimated effect of a) local forest age, b) logging impact index, c) continuity logs, and d) country (Norway to the left, Sweden to the right) on the abundance of the non-indicator species (green), and indicator species (orange), and the mean effect for each group. Values are back-transformed to the original scale where a value of 1 indicates no effect (100%) and a value of 2 represents a doubling of the abundance per each standard deviation of the explanatory variable.
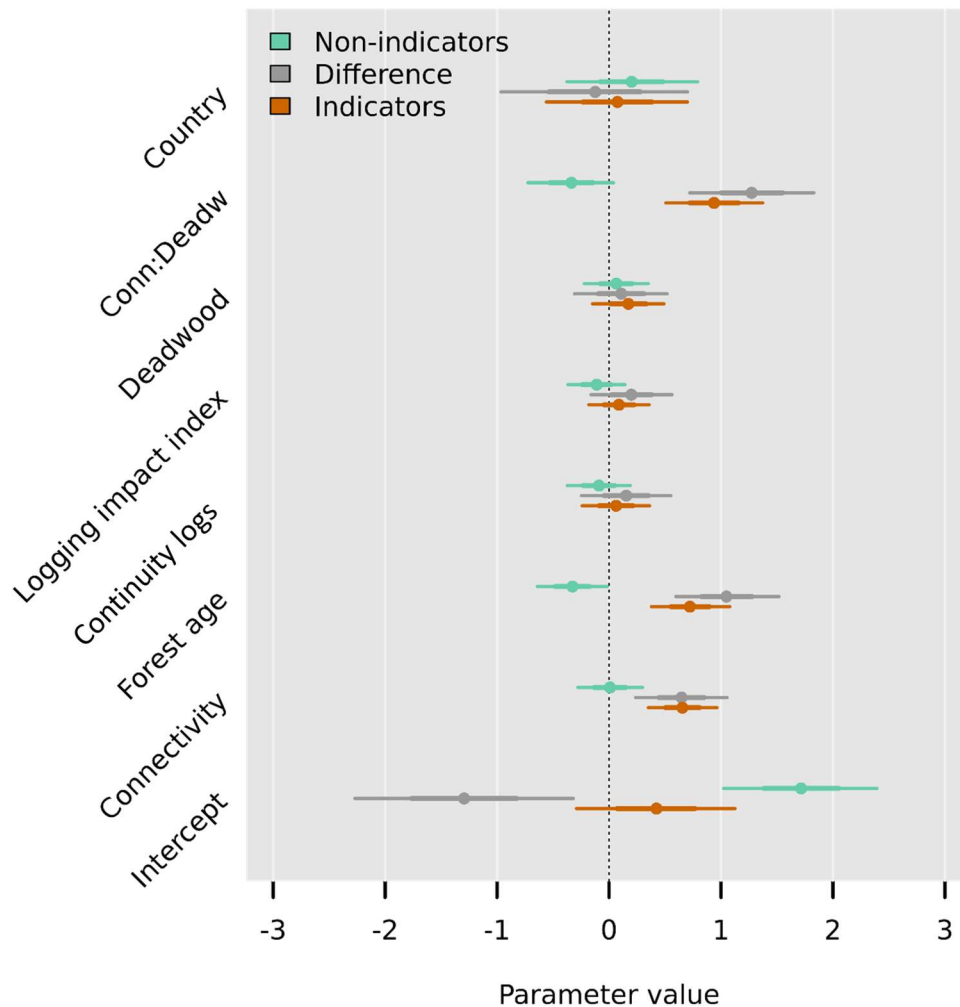
920
921 Figure 5. Group level parameter estimates for the non-indicator and indicator species and the
922 difference between these groups. The difference bar not overlapping zero indicates a statistically
923 significant difference between the two groups. Values are taken from the multilevel model using
924 connectivity values based on an age threshold of 80 years and a buffer radius of 100 km. Thin error
925 bars represent 95% credible intervals, and thick error bars represent 68% credible intervals.
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