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Experimentally induced community assembly of polypores reveals the importance of both environmental filtering and assembly history

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3 **Title:** Experimentally induced community assembly of polypores reveals the importance of
4 both environmental filtering and assembly history
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Abstract

The community assembly of wood-inhabiting fungi follows a successional pathway, with newly emerging resource patches being colonised by pioneer species, followed by those specialised on later stages of decay. The primary coloniser species have been suggested to strongly influence the assembly of the later-arriving community. We created an artificial resource pulse and studied the assembly of polypores over an 11 yr period to ask how the identities of the colonising species depend on the environmental characteristics and the assembly history of the dead wood unit. Our results support the view that community assembly in fungi is a highly stochastic process, as even detailed description of the characteristics of dead wood (host tree species, size, decay class of the resource unit, its bark cover and how sunken it is to the ground) and the prior community structure provided only limited predictive power on the newly colonising species. Yet, we identified distinct links between primary and secondary colonising species and showed how the spatial aggregation of dead wood had a great impact on the community assembly.

Keywords

Community assembly, wood-inhabiting fungi, polypores, priority effects, time series, restoration, artificial resource pulse

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126 **Introduction**
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129 Assembly history can be a key factor affecting the dynamics of species communities (Diamond
130 1975, Drake 1991, Chase 2003, Schröder et al. 2005, Fukami et al. 2010), e.g. through so called
131 priority effects (e.g. Alford and Wilbur, 1985; Chase, 2010; Fukami et al., 2016; Hiscox et al.,
132 2015; Leopold et al., 2017; Sarneel et al., 2016; Weslien et al., 2011), which refer to the
133 influence of an occupying species on the probability of establishment of following colonisers
134 (Fukami et al. 2010). Priority effects induce historical contingency in the structure and
135 function of communities, which can lead to alternative stable states, transient states, or
136 compositional cycles (Fukami 2015). Studying when these effects take place is difficult as the
137 arrival order of species is often difficult to manipulate or to reconstruct in sufficient detail
138 (Fukami et al. 2016; but see e.g. Ejrnaes et al. , 2006, Sarneel et al., 2016).
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151
152 Extensive spatial variability in both the quantity and quality of dead wood is a characteristic
153 feature of natural boreal coniferous forests, and it influences the possibilities for colonisation
154 of dependent organisms (Jonsson and Siitonen 2012a). It has for long been recognised that
155 the community assembly (Zobel 1997, Götzenberger et al. 2012, Ovaskainen et al. 2017b) of
156 wood-inhabiting fungi does not result in a deterministic one-dimensional pathway, but may
157 follow different trajectories (Stokland and Siitonen 2012). The way the host tree has died (e.g.
158 storm, pathogens or fire) is generally considered to be the most influential filter in the very
159 beginning of community assembly, creating variability in the community structure during the
160 early stages of the decomposition process (Boddy and Heilmann-Clausen 2008, Stokland and
161 Siitonen 2012, Komonen et al. 2014). The characteristics of the forest stand affect the
162 development of the community e.g. due to differences in the microclimatic conditions (Boddy
163 and Heilmann-Clausen 2008) or contact to the forest floor allowing the colonisation through
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183 mycelia in soil (Fricker et al. 2008, Stenlid et al. 2008). The spatial distribution of dead wood
184 influences colonisation through for example distance-dependent dispersal (Norros et al. 2012)
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186 but these effects are not necessarily expected to be seen at the level of individual forest stands
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189 (Edman and Jonsson 2001).
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192 Pulsed accumulation of dead wood is a natural part of boreal forest ecology (Kuuluvainen
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194 2002, Jonsson and Siitonen 2012b). In natural boreal forests e.g. wind, insect outbreaks and
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196 forest fires are some of the main mortality factors of trees, creating resource pulses for dead-
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198 wood inhabiting species. However, in Fennoscandia more than 90% of the productive forests
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200 are under intensive forest management (Anon. 2014a, 2014b). Consequently, from the point
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202 of view of wood-inhabiting organisms, both the mean availability of resources and their
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204 spatial and temporal variability has undergone a major change (Siitonen 2001, Jonsson et al.
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206 2005, 2016). In parallel with research from other habitats suggesting that mitigating the
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208 global biodiversity crisis calls for active ecological restoration (Dobson et al. 1997, Young
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210 2000, Hobbs and Harris 2001, Brudvig 2011), halting the decline of dead-wood dependent
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212 species in boreal forests also calls for active restoration measures (Jonsson and Siitonen
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214 2012c). Artificial creation of dead wood has been a common restoration practice in
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216 Fennoscandia (Similä and Junninen 2012, Halme et al. 2013a), and several studies have
217
218 examined the potential of this method in aiding dead-wood dependent fungi. Studies have
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220 focused on surveying dead wood generated by cutting or killing trees (Olsson et al. 2011,
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222 Komonen et al. 2014, Pasanen et al. 2017), by controlled forest fires (Penttilä et al. 2013), or
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224 by a combination of these restoration methods (Vanha-Majamaa et al. 2007, Berglund et al.
225
226 2011). In addition to its relevance for the conservation context, time-series data on fungal
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228 community structure on restored sites provides opportunities for advancing the fundamental
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230 understanding of processes underlying community assembly.
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243 In addition to environmental filtering (Kraft et al. 2015), biotic interactions (Wisz et al. 2013),
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245 such as predecessor-successor associations, have been suggested to be important for fungal
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247 community assembly (Niemelä et al. 1995, Stokland and Siitonen 2012, Boddy and Hiscox
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249 2016, Hiscox et al. 2018). Interactions are likely to occur between dead-wood-inhabiting
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251 organisms, of which fungi and insects are the first ones to colonise. Insects may disperse fungi
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253 and hence facilitate their colonisation (Rayner and Boddy 1988, Boddy and Jones 2008, Strid
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255 et al. 2014). Wood-inhabiting fungi are known to be an highly interactive group of species,
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257 especially through competition, but also facilitative interactions (Woodward and Boddy 2008,
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259 Hiscox et al. 2018).

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264 Priority effects (Fukami et al. 2010, Fukami 2015) have been documented among wood-
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266 inhabiting fungi in studies based on field surveys (Renvall 1995, Rajala et al. 2011, Pouska et
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268 al. 2013, Ottosson et al. 2014), field experiments (Lindner et al. 2011, Weslien et al. 2011,
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270 Dickie et al. 2012, Hiscox et al. 2015) and laboratory experiments (Fukami et al. 2010, Hiscox
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272 et al. 2015). The influences of biotic interactions have also been detected from snapshot data,
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274 where they are considered as non-random co-occurrence patterns that cannot be attributed
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276 to environmental factors (Edman and Jonsson 2001, Ylisirniö et al. 2009, Ovaskainen et al.
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278 2010a, Kraft et al. 2015, Abrego et al. 2017). It is a plausible expectation that the succession of
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280 fungi on dead wood is interdependent and the predecessor species affect the following ones
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282 by facilitating or inhibiting their colonisation.

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286 The aim of this study is to analyse the roles of environmental filtering and biotic interactions
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288 as well as stochastic processes in the community assembly of polypores, a polyphyletic
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290 morphological group of wood-inhabiting fungi, over an 11 yr period, which starts from
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292 seemingly unoccupied resource units. This time series data set, combined with the recent
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294 progress in the field of joint species distribution modelling for studying associations between
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303 species in multispecies communities (Warton et al. 2015, Ovaskainen et al. 2017b, 2017a),
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305 provides an excellent opportunity for studying both the effects of the environment as well as
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307 potential interactions between species during the early development of the community.
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310 Specifically, we ask: (1) how well the future colonising species can be predicted based on
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312 knowledge of the environmental characteristics of the dead wood unit and the preceding
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314 community; (2) is there evidence of priority effects, either through species-to-species
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316 influences or more generally through groups of species influencing each other; and (3) is it
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318 possible to determine distinct successional pathways of community assembly initiated by
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320 specific environmental conditions and/or by the identity of the primary colonisers.
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327 **Material and Methods**

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330 *Study area and data collection*

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334 The study was conducted in Leivonmäki National Park in Central Finland (62°N, 26°E). Like
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336 many of the currently protected areas of southern Finland, it consists of forests with a long
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338 history of intensive forest management. Therefore, before the establishment of the park in
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340 2003, the study area was a low-resource environment with the amount of dead wood not
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342 different from typical managed forests of Finland, i.e. generally not exceeding 10 m³/ha while
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344 a typical amount for a natural forest in the geographic area would be 50 – 80 m³/ha (Siitonen
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346 2001).
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350 We established 40 study plots within the park's forests. The plots were of rectangular shape
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352 and of 0.25 ha (50 m × 50 m) area, and all the plots were located within a 2 × 3 km area.
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354 The dominant tree species on the plots was either Norway spruce (*Picea abies*) or Scots pine
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363 (*Pinus sylvestris*), along with some deciduous admixture, mainly birches (*Betula* spp.), grey
364 alder (*Alnus incana*) and rowan (*Sorbus aucuparia*). The age of the dominant tree layer on the
365 plots was 80 – 120 yr.
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370
371 On the study plots, we manipulated the amount of dead wood such that approximately 5 m³
372 or 10 m³ of dead wood was added by felling trees with chain saw. In each plot, we produced
373 either spruce or pine dead wood according to the dominant tree species of the plot. As
374 exception, in one plot we downed pine logs due to their large volume, even if ecosystem-wise
375 the dominant tree was spruce. The created dead wood was either evenly distributed (later
376 referred to as ‘spread’) on the plot or aggregated to form a stack at the centre of the plot (later
377 referred to as ‘piled’).
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387 We included 10 replicates of each amount × distribution combination. The plots were
388 selected in autumn 2003, the treatments were randomised among the plots, and the felling
389 was conducted during winter 2003-2004. The realised amounts of created dead wood in the 5
390 m³ and 10 m³ treatments were 5.00 ± 0.56 m³ (range 3.69 – 6.62 m³) and 10.02 ± 1.02 m³
391 (range 8.12 – 11.57 m³). We measured the following characteristics of the created dead wood
392 units: diameter, decay stage according to the five-stage classification of Renvall (1995), bark
393 cover and how sunken it is to the ground (see details of the resource unit characteristic from
394 Appendix S1). The volume of whole trees was calculated with the tree-specific equations of
395 Laasasenaho (1982).
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407 We collected polypore data yearly during 2004-2014 on the artificially produced resource
408 units (i.e. the added dead wood) as well as on all naturally formed dead wood with > 5 cm
409 diameter and > 1.3 m length. The inventories were conducted in October — early November
410 each year. All fruit bodies of a given species on one dead wood unit were regarded as one
411 occurrence. Most of the polypore species were identified in the field. In case of doubt of the
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423 correct identity of the species, we collected specimens for microscopic identification. The
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425 voucher specimens are deposited in the Natural History Museum of the University of
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427 Jyväskylä (JYV). In the classification of species, we used the Nordic concept of polypores, i.e.
428
429 all poroid Aphyllophorales (Niemelä 2005).
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432 *Statistical analyses*

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435 We calculated the yearly, cumulative (across resource units) occurrences of the species for all
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437 the resource units included in the study, as well as abundances at the plot level. We illustrate
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439 the plot level species abundances of the cumulative community resulting from the whole
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441 study period with a non-metric multidimensional scaling (NMDS), applying the ‘metaMDS’
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443 function (Oksanen et al. 2015), We used Bray-Curtis dissimilarities between the plots and
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445 global monotone regression as basis for the NMDS.
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448
449 We fitted a joint species distribution model (JSDM) called Hierarchical Modelling of Species
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451 Communities (HMSC, Ovaskainen et al., 2017a), adjusted for identifying species associations
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453 from time-series data (Ovaskainen et al. 2017a). JSDMs not only allow inference of how
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455 species respond to their environment but also capture co-occurrence patterns related to
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457 unmeasured environmental variables or biotic interactions (see Warton et al. 2015). As
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459 response variable, we used the species colonisations. We considered the species absent
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461 (absence = 0) until the first observed presence on a resource unit (colonisation = 1), after
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463 which we disregarded its occurrences (no information = NA). Hence, the response vector for
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465 a particular species on a particular resource unit was e.g. of the form [0 0 1 NA NA... NA] if the
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467 species colonised the resource unit during the third study year. Utilising species colonisations
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469 rather than their occurrences as response allows us to better address our study questions, as
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471 we are interested in the emergence patterns of the species, and not their yearly fluctuations
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481 afterwards, which, in addition to biological reasons, can be due to variation in detection
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485 (Halme and Kotiaho 2012, Abrego et al. 2016).
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488 As environmental explanatory variables at the resource unit level we included variables
489 characterising the host tree species (Scots pine or Norway spruce), log-transformed resource
490 unit size (0.04 – 2.1 m³), decay stage (1-4, see e.g. Hottola and Siitonen (2008)) and its square,
491 bark cover (0-100%), and how sunken the resource unit is to the ground (0-100%). At the
492 plot level, we included variables describing the spatial distribution of the resource units (piled
493 or spread), and the amount of dead wood produced to this study plot (5 or 10 m³). In line with
494 the study design, we included community-level random effects (Ovaskainen et al. 2017b) to
495 the model at the levels of plots and years. In addition, we included an indicator variable
496 describing whether the focal species was observed in any of the previous years in the plot
497 (including occurrences on both natural and artificially produced resource units). This variable
498 describes the effect of the surrounding occurrences of the species on its probability of
499 colonisation. For more details about the explanatory variables used, see Appendix S1.
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516 We modelled the colonisation of species j on resource unit h in year t with probit regression,
517 with
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$$519 y_{hjt} = \mathbf{1}_{L_{hjt} > 0} \tag{1}$$

$$520 L_{hjt} = L_{hjt}^K + L_{hjt}^A + L_{hjt}^R + \epsilon_{hjt}, \tag{2}$$

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527 where the linear predictor L_{hjt} is modelled as a sum of fixed (K and A) and random (R) terms
528 (Ovaskainen et al. 2017b, 2017a). The environmental term K models the effects of the
529 environmental covariates, the association term A models the effects due to occurrences of the
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543 other species in the previous years, and the random effect term R models the residual
544 variation in species colonisations at the level of plots and years, and $\epsilon_{hjt} \sim N(0,1)$.
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549 We fitted 10 model variants to the data by varying the way the components K , A and R (eq. 2)
550 were included. The environmental variables (K) and the random effects (R) were both either
551 simultaneously included or excluded. Regarding the association term (A), i.e. how the
552 influences of the species in the previous years were accounted for, we followed the modelling
553 strategies of Ovaskainen et al. (2017b) to either exclude this component completely (Model 1),
554 or to include it in four different ways (Models 2-5). This enabled us to examine how we can
555 construct the interaction network most accurately. In Model 2, we used the occurrences of the
556 most common primary colonising species (all the rest of the study species were among the
557 first colonisers on at most 17 resource units): *Trichaptum abietinum* (first coloniser on 497
558 resource units), *Trichaptum fuscoviolaceum* (133), *Skeletocutis amorpha* (128) and
559 *Fomitopsis pinicola* (72). In Model 3, we used the full interactions model and thus included
570 the whole species community of the previous year as predictors. In Model 4, we used the
571 sparse interactions model and thus assumed that only some species pairs interact with each
572 other. In Model 5, we used the community-level drivers model and thus assumed the influence
573 of species groups rather than of individuals species. This resulted in total $2 \times 5 = 10$ model
574 variants, ranging from an intercept-only null model (K , R and A all excluded) to the full model
575 (K , R and A all included, varying regarding the component A). The implementation of the
576 general structure of the model, including terms K and R are described in detail in Ovaskainen
577 et al. (2017a) and for the term A in Ovaskainen et al. (2017b). We fitted the model to the data
578 with Bayesian inference, using the posterior sampling scheme described by Ovaskainen et al.
579 (2017b). We ran all the models for 80,000 MCMC iterations and used the last quarter (thinned
580 to every 100th iteration) for inference and predictions.
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603 For comparing the predictive performances of the models, we performed a two-fold cross-
604 validation. We first split the data into two sets, of which both contain a randomly selected half
605 of the resource units for each plot. We then fitted the models to both sets of data and used the
606 fitted models to predict the colonisations in the half of the data not used in model fitting,
607 resulting in predictions for the whole data set based on independent data sets used for
608 training. We integrated the species (j), resource unit (h) and year (t) -specific colonisation
609 probabilities p_{hjt} over the n_t study years as the total probability p_{hj} that the species j will ever
610 colonise the resource unit h as
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$$621 \quad p_{hj} = 1 - \prod_{t=1}^{n_t} (1 - p_{hjt}). \quad (3)$$

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625 Separately for each species, we measured the predictive performances of the models against
626 the validation data at the levels of resource units by the Tjur R^2 coefficients of discrimination
627 (Tjur 2009), and at the plot level by the Spearman's correlation (ρ) between the predicted and
628 observed numbers of colonisations.
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634 *Scenario simulations*

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638 For examining the captured signal of different community assembly trajectories, we used the
639 model variant showing best predictive performance to simulate different colonisation
640 scenarios for hypothetical plots of 100 resource units (Table 1). In the scenario simulations,
641 the model parameters were sampled from their posterior distribution, with the random effect
642 term R being set to its year-specific effect. We conducted the simulations separately for
643 spruce and pine plots by first sampling 100 resource units randomly from the data. Next, we
644 modified the characteristics of the plot to construct eight scenarios that vary regarding the
645 plot level variables (Table 1).
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663 As a baseline (scenario **BL**), we created a plot with a small amount of artificial dead wood with
664 spread distribution. For comparing whether the differences between the scenarios were
665 greater than due to just random variation in the predictions, we produced a replicate of the
666 baseline (scenario **BL2**), i.e. another realisation of a plot with the same characteristics. To
667 investigate how an increase in the aggregation of the dead wood affects the colonisation
668 process, we created a plot with a large amount of artificial dead wood (scenario **Amount**; but
669 also in this case we simulated their dynamics only on 100 plots to keep the survey effect the
670 same among the scenarios), as well as a plot with piled distribution of the artificial dead wood
671 (scenario **Piled**). Finally, we wanted to see how the identity of the primary coloniser affects
672 the colonisation process, so we created plots with either *Trichaptum abietinum*, *T.*
673 *fuscoviolaceum*, *Fomitopsis pinicola* or *Skeletocutis amorpha*, i.e. one of the four most
674 common primary colonisers as the sole first coloniser of all the resource units (scenarios
675 **Triabi**, **Trifus**, **Fompin** and **Skeamo**). For other scenarios than the primary coloniser scenarios,
676 we assumed all resource units to be initially empty.
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694 In the course of the simulations, the values of the covariates related to the resource units were
695 assumed to change according to the data, so that e.g. the decay stage of the resource units
696 increased as a function of time. Species that had occurred in the same resource unit in
697 previous years were employed as predictors in the species-association part of the model,
698 whereas species that had occurred in any resource unit of the same plot were employed as
699 predictors for the surrounding occurrences.
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708 We calculated the yearly, cumulative (across resource units) abundances of the species for
709 each simulated plot. We illustrate the simulated community structures based on abundances
710 with a non-metric multidimensional scaling NMDS, applying the 'metaMDS' function (Oksanen
711 et al. 2015), We used Bray-Curtis dissimilarities between scenario-year-combination as basis
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723 for the NMDS, and independent monotone regressions were used for all the resulting points.
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725 We also calculated the species total abundance (sum over all abundances, across species),
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727 species richness (number of species with abundance > 0), as well as the alpha diversity
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729 (Simpson's diversity index) for all the scenario-year-combinations, for which the results are
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731 displayed in Appendix 2.
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738 Results

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741 In total 43 species fruited on the resource units during the study period. The amount of yearly
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743 new fruitings varied between species, as the primary species emerged on the resource units
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745 intensely during the first few years (descending lines in Fig. 1A), whereas secondary coloniser
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747 species gained territory towards the end of the study period (ascending lines in Fig. 1A). The
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749 total number of new species emerging on any particular substrate unit was greater during the
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751 second half than the first half of the study period (Fig. 1B), reflecting the higher species
752
753 diversity of secondary colonisers over the primary colonisers. The cumulative species
754
755 richnesses were uniform across dead wood addition treatments (Fig. 1C), and there were no
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757 striking patterns in the plot level abundances either (Fig. 1D).
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761 Of the primary colonisers, the most common one was *Trichaptum abietinum* (first coloniser in
762
763 77% of the resource units), followed by *Trichaptum fuscoviolaceum* (21%), *Skeletocutis*
764
765 *amorpha* (20%) and *Fomitopsis pinicola* (11%). The percentages sum over 100% as in some
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767 cases more than one of these species emerged on the same resource units. Of these four
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769 primary colonisers, *F. pinicola* produces brown rot and the other species white rot. All other
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771 species were among the first colonisers for less than 3% of the resource units.
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783 *Predecessor species and environmental characteristics provide explanations of community*
784 *assembly*
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788 The cross-validation exercise suggested that fungal community assembly is highly stochastic,
789 as the average predictive power of even the best model variant was only ca. 10% at the
790 resource unit level (Fig. 2A). A comparison among the model variants showed that the joint
791 influence of environmental and random effects (components K and R , eq. 2) was greater than
792 the influence of predecessor species (A). While accounting for the predecessor species clearly
793 improved the prediction of colonising species in the null model (Fig. 2A, difference between
794 Model 1 and other Models, open symbols), their added value in the full model that utilised the
795 environmental predictors was only minor (Fig. 2A, difference between Model 1 and other
796 Models, filled symbols). Models 2-5 produced essentially equally good predictions both on
797 average (Fig. 2A) and for individual fungal species (Figs. 2BC), and thus the data was not
798 informative on the structural properties of the interaction network. The overall best model
799 (though with a small margin) was Model 4, with sparse interactions. The posterior mean
800 effects of the environmental variables are shown in Appendix 1.
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817 The partitioning of explained variance among the environmental factors, plot identity and
818 study year shows that the host tree species and the measured characteristics of the resource
819 unit accounted for the largest part of the variation (Fig. 3). The spatial aggregation of the
820 artificially generated resource units (amount per plot and whether they were piled or spread)
821 also accounted for a substantial part of the variation, whereas the influence of the
822 surrounding species occurrences was negligible.
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831 *Links from the primary colonisers to the later-arriving species*
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843 As there were no major differences in predictive performance among Models 2-5, we
844 extracted species pairs that influenced each other by comparing the results for all Models.
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846 Reassuringly, the models yielded, for most cases, consistent results in which secondary
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848 colonisers were positively or negatively influenced by the primary colonisers (Fig. 4). Many of
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850 the captured associations were also supported by previous findings in the literature (asterisks
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852 in Fig. 4 and Table 2).
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855 856 857 *Succession pathways* 858

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860 The NMDS illustrates the compositional dissimilarity between all the scenario-year-
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862 combinations (Fig. 5). As the NMDS simply maps the configuration of the sites and species
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864 averages on the biplot, the axes do not have a meaning *per se*. Nevertheless, by observing the
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866 sites and species averages with respect to simulation year and scenario, we can see how the
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868 communities change as a function of these two.
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872 The first axis of variation identified by the NMDS analyses is related to the year since the dead
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874 wood was generated (Fig. 5), supporting the successional view of community development.
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876 The scenario that most deviated from the other ones was the scenario **Piled** in which dead
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878 wood was produced in a pile (Table 1), with *Antordia. serialis* and *S. carneogrisea* especially
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880 favouring this scenario. Also, scenario **Amount**, which differed from the others by having a
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882 larger amount of dead wood, differed from the other scenarios. The remaining scenarios
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884 differed from each other during the very first years of community development but showed
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886 highly convergent results during the later years. The differences between scenarios were
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888 somewhat more pronounced on pine (Fig. 5B) than spruce units of resource (Fig. 5A). The
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890 most deviating scenarios had also slightly lower species abundances in comparison to the
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892 other scenarios, but differences regarding species richness were negligible (see Fig. E2 in E-
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894 Component 2).
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903 The curved shape of the scenario lines can be explained by the short simulation time and
904 species abundance. In the beginning of the simulation, the species begin to colonise the
905 resource units. As the majority of the possible species emerge quickly, there is little room for
906 patterns of species replacement, and the abundance patterns determine the compositional
907 dissimilarities. During the midway of the simulation, the sites differ from the beginning and
908 end the most, as the species are most abundant, and the majority of all the possible species
909 have emerged (see Fig. E2 in E-Component 2). At the end of the simulation, the communities
910 start to converge, as the fruiting of the species that colonised the resource units in the
911 beginning start to decline in abundance. Hence, the second NMDS axis relates to the
912 differences between scenarios as well as the general patterns in species abundances (see Fig.
913 E3 in E-Component 2 for detrended correspondence analysis for comparison).
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931 **Discussion**

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934 Our results illustrate the difficulty of predicting the stochastic community assembly of wood-
935 inhabiting fungi, as all of our model variants had only limited power to predict which species
936 will colonise a resource unit in a given year. However, while it was difficult to make accurate
937 predictions of the colonising species at the resource unit level, the predictions were more
938 accurate at the plot level, where some of the stochasticity becomes averaged out. Beyond the
939 unexplained stochastic and potentially neutral variation, we found more evidence for
940 community assembly being structured more by environmental than biotic filtering. The
941 predecessor community, as opposed to environmental and random effects, provides an
942 alternative and only to a limited extent a complementary explanation to the observed
943 colonisation patterns.
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963 Despite of this, we identified several links between primary and secondary coloniser species
964 supported by previous experimental and observational studies, demonstrating how the
965 primary colonisers affect the probabilities of colonisations of secondary colonising species
966 (asterisks in Fig. 4 and Table 2). For example, the positive influence of *Trichaptum abietinum*
967 on *Skeletocutis carneogrisea* is in accordance with previous studies showing that *S.*
968 *carneogrisea* is a successor of *Trichaptum* species, with fruit bodies often growing on top of
969 its predecessor. As another example, the positive influence of *F. pinicola* on *Pycnoporellus*
970 *fulgens* has also been recorded before. However, we did not find that different primary
971 species to initiate distinct successional pathways, as in our scenario simulations the fungal
972 communities converged in their composition irrespective of the primary coloniser.
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986 One likely reason why we found biotic interactions to play only a relatively minor role is that
987 we characterised the species community through fruit body surveys, even if ecological
988 interactions among the species take place mainly at the mycelia stage (Fricker et al. 2008,
989 Hiscox et al. 2018). The community visible as fruit bodies presents only part of the mycelial
990 community (Ovaskainen et al. 2010b, Kubartová et al. 2012), and the production of fruit
991 bodies involves a delay following the build-up of the mycelial biomass (Allmér et al. 2006,
992 Ovaskainen et al. 2013). On the other hand, the community visible as fruit bodies has been
993 shown to reflect the dominating part of the mycelia community (Ovaskainen et al. 2013,
994 Runnel et al. 2015). The order of appearance of fruit bodies reflects the species succession
995 order, but is also affected by the ecological strategy of the species (Boddy and Hiscox 2016).
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997 Given these uncertainties, the approach taken here would be expected to pinpoint only such
998 biotic interactions that have a major structuring role in community assembly, more subtle
999 ones remaining possibly invisible in our data. A related reason for low predictive power is
1000 that we surveyed only one morphological group of wood-inhabiting fungi, namely polypores.
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1023 It would have been better to include all other groups as well, but the survey effort of such a
1024 well-replicated long-term monitoring work would have exploded. We acknowledge the need
1025 for smaller-scale studies with corticioids, ascomycetes and other groups included.
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1030 Another difficulty in identifying biotic interactions, even from a replicated field experiment, is
1031 that the characteristics of the resource unit and the fungal community structure both
1032 influence each other. For example, fungi contribute to the decay of the wood, and thus the
1033 influence of the decay class could be either seen as part of the fundamental niche (as we did
1034 here), or as the influence of biotic interactions. This makes it difficult to quantify the relative
1035 impacts of environmental filtering and priority effects, as seen from the fact that in our
1036 modelling framework the predecessor community had a substantial effect in a null model but
1037 only a minor effect in the model where the influence of environmental covariates and the
1038 random effects of plot and year were controlled for.
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1051 Even though we used the characteristics of the dead wood and the plot as a proxy for the
1052 microclimatic conditions and included these units also as random effects, we note that more
1053 detailed data on the physicochemical conditions of the studied logs would have benefitted our
1054 study. As the wood decomposes, its physical and chemical conditions change: the density of
1055 the wood decreases, its moisture and carbon dioxide levels increase and its nutrient content
1056 alters (Rayner and Boddy 1988, Stokland and Siitonen 2012). Experimental studies have
1057 shown that resource availability in the form of e.g. nitrogen availability has an effect on the
1058 priority effects taking place (Fukami et al. 2010, Dickie et al. 2012). However, we note that as
1059 these physiochemical changes result partly from the fungal decomposition process, their
1060 separation from the effects of the biotic interactions would be challenging from observational
1061 data, even if we had measured them.
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1083 In most of our scenario simulations, fungal communities diverged from each other during the
1084 very first years of community development and converged by the end of the time series. Thus,
1085 while we identified the primary colonisers to influence several secondary colonisers, these
1086 effects did not propagate through the decay process in a way that would create primary-
1087 coloniser dependent distinct successional pathways. This finding is in line with studies
1088 showing that wood-inhabiting fungal communities increase in their similarity along the
1089 succession (Stokland and Siitonen 2012), although it has also been shown that divergence
1090 may also increase along the succession in natural forests, when entering later decay stages
1091 (Halme et al. 2013b). Since our study focuses on the early steps of the succession, it remains
1092 to be seen whether it results in divergent or convergent patterns during the later stages.
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1105 We found that whether the resource units were spread individually or on a pile had a major
1106 influence in community composition, as well as the amount of dead wood produced. One of
1107 the species which benefited most of the piled scenario was *S. carneogrisea*, a known follower
1108 of the primary colonisers of genus *Trichaptum*, and *A. serialis*, which appeared to follow both
1109 *Trichaptum* sp. and *F. pinicola*. Both *Trichaptum* sp. and *F. pinicola* are ruderal pioneer
1110 species (Niemelä 2016) that might benefit from the piled resource distribution by spreading
1111 aggressively, and thus inhibiting other species from colonising. Most likely also the potentially
1112 different physical conditions of the piled dead wood may favour these species, but this
1113 influence was at least partly accounted for in the characteristics of the individual resource
1114 units (e.g. sunkenness, decay stage and bark cover).
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1128 The way the tree has died has major influence on the wood-inhabiting fungal community
1129 development (Stokland and Siitonen 2012). Intentionally cut dead wood differs from
1130 naturally formed dead wood resulting in differences in their community development
1131 (Komonen et al. 2014, Pasanen et al. 2017). The felled trees in our study were originally living
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1143 ones, and their death was thus very sudden as opposed to the slow deterioration caused by
1144 pathogens (Similä and Junninen 2011, 2012, Stokland and Siitonen 2012). Characteristics of
1145 the felled trees might give an advantage for certain pioneer polypore species (such as the
1146 primary coloniser *T. abietinum*) at the expense of others, and the dominance of one or two
1147 primary species might decrease the diversity of the following community (Similä and
1148 Junninen 2011, 2012). As the environmental conditions can strongly influence the likelihood
1149 of priority effects taking place (Fukami et al. 2016), we hope the generality of our results will
1150 be tested with future experiments, which would ideally also characterise the mycelial state
1151 and more detailed abiotic conditions.
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1182 **E-COMPONENTS**

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1185 **E1.** Details on the explanatory variables used in the models and their effects for the best
1186 performing model.
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1190 **E2.** Results regarding the associations from predecessor to successors for all species and all
1191 model variants and complementary results for the scenario simulations.
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Figure legends

Figure 1. Yearly fruiting patterns of polypores in the experimentally added units of dead wood felled in winter 2003-2014 (panels AB), and the resulting, cumulative communities (panels CD). In panel A, the lines indicate the numbers of colonisations on previously uncolonised resource units for each species. The four main primary colonisers are shown by coloured lines, and three representatives of later-arriving species by the black lines. In A, note the logarithmic scale of the vertical axis. In B, the bars indicate the total numbers of colonising species new to that particular resource unit during each year, and the line the total cumulative species richness. In C, the dots indicate mean species richness, calculated over resource units within all the plots with the treatment indicated in the axis labels. The grey bars show the standard deviations, and the black lines the complete span from minimum to maximum species richness values. In D, the non-metric multidimensional scaling (NMDS) illustrates the plot-level abundances of species. The dead wood addition treatments (for explanations, see Material and Methods) are shown: The upward pointing triangles indicate a large addition (10 m³), and downward pointing triangles small (5 m³), and the colours indicate spatial distribution of the addition, either spread (white) or piled (black). The centroid locations of the primary coloniser species, species that are strongly influenced by one of those primary colonisers (either based on our results (Fig. 4) or previous literature (Table 2)) are shown in the figure. The regression for interpoint distances between pairs of communities against the original dissimilarities resulted in R² values > 0.9 (for both linear and non-linear fits) and stress value = 0.11.

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1863 **Figure 2.** A cross-validation based comparison of predictive performance among the model
1864 variants. (A) Resource-unit level and plot-level results averaged over the species; (B and C)
1865 Species-specific resource-unit level results. In A, the filled (respectively, empty) symbols refer
1866 to model variants that include (respectively, exclude) environmental covariates and random
1867 effects. In B and C, only model variants that include environmental covariates and random
1868 effects are considered. The Models 1-5 differ in the way the current community structure is
1869 assumed to influence or not to influence future colonisations (see text). At the resource-unit
1870 level, predictive performance is measured by comparing predicted colonisation probabilities
1871 to observed ones with Tjur's (2009) coefficient of discrimination. At the plot level, predictive
1872 performance is measured by comparing predicted numbers of colonisations to observed ones
1873 among the plots with Spearman's correlation. In panels BC, the Tjur R^2 coefficients of
1874 discrimination are plotted for all species, for Models 3 (B) and 5 (C) against those of Model 4.
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1890 **Figure 3.** Partitioning of the explained variation among the environmental covariates and
1891 random effects in Model 1. Different groups of variables are indicated by different colours.
1892 Characteristics of resource units include their volume, decay stage, bark cover and sunken the
1893 unit is to the ground. The spatial aggregation of resource units includes both their amount per
1894 plot (5 or 10 m³) and whether they are piled or spread. The bars show the results for each
1895 species, and the numbers in the legend show averages over the species. The species are
1896 ordered according to their prevalence in the original data, with the most common one being
1897 on the left-hand side.
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1908 **Figure 4.** The influences of the primary colonisers on the later-arriving species. The colours
1909 indicate the level of statistical support by which each of the four primary coloniser species
1910 (*Trichaptum abietinum*, *Trichaptum fuscoviolaceum*, *Skeletocutis amorpha* and *Fomitopsis*
1911 *pinicola*) influences either positively (red) or negatively (blue) the colonisation of the later-
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1923 arriving species. The level of statistical support is measured by the number of model variants
1924 (among Models 2-5 that control for environmental covariates and random effects) for which
1925 the 95% central credible interval of the association did not intersect zero. The asterisks
1926 indicate associations that have been reported previously in the literature (Table 2). Results
1927 for all species pairs are shown separately for all model variants in Appendix 2.
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1935 **Figure 5.** Variation in community structures among the scenario simulations summarised by
1936 non-metric multidimensional scaling (NMDS). The results are shown separately for the
1937 resource units consisting of (A) Norway spruce or (B) Scots pine. Different scenarios are
1938 indicated by the different colours (for explanations of the abbreviations, see Table 1). The
1939 triangles indicate the first year of the simulated community assembly, and the lines connect
1940 the years (points) chronologically, and the squares indicate the final years. The centroid
1941 locations of species that are strongly influenced by one of the primary colonisers based on our
1942 results (Fig. 4) or previous literature (Table 2) are shown in the figure. In both NMDS analyses,
1943 the regression for interpoint distances between pairs of communities against the original
1944 dissimilarities resulted in R^2 values > 0.99 (for both linear and non-linear fits) and stress
1945 values < 0.05 . The NMDS plots are based on communities simulated with the best performing
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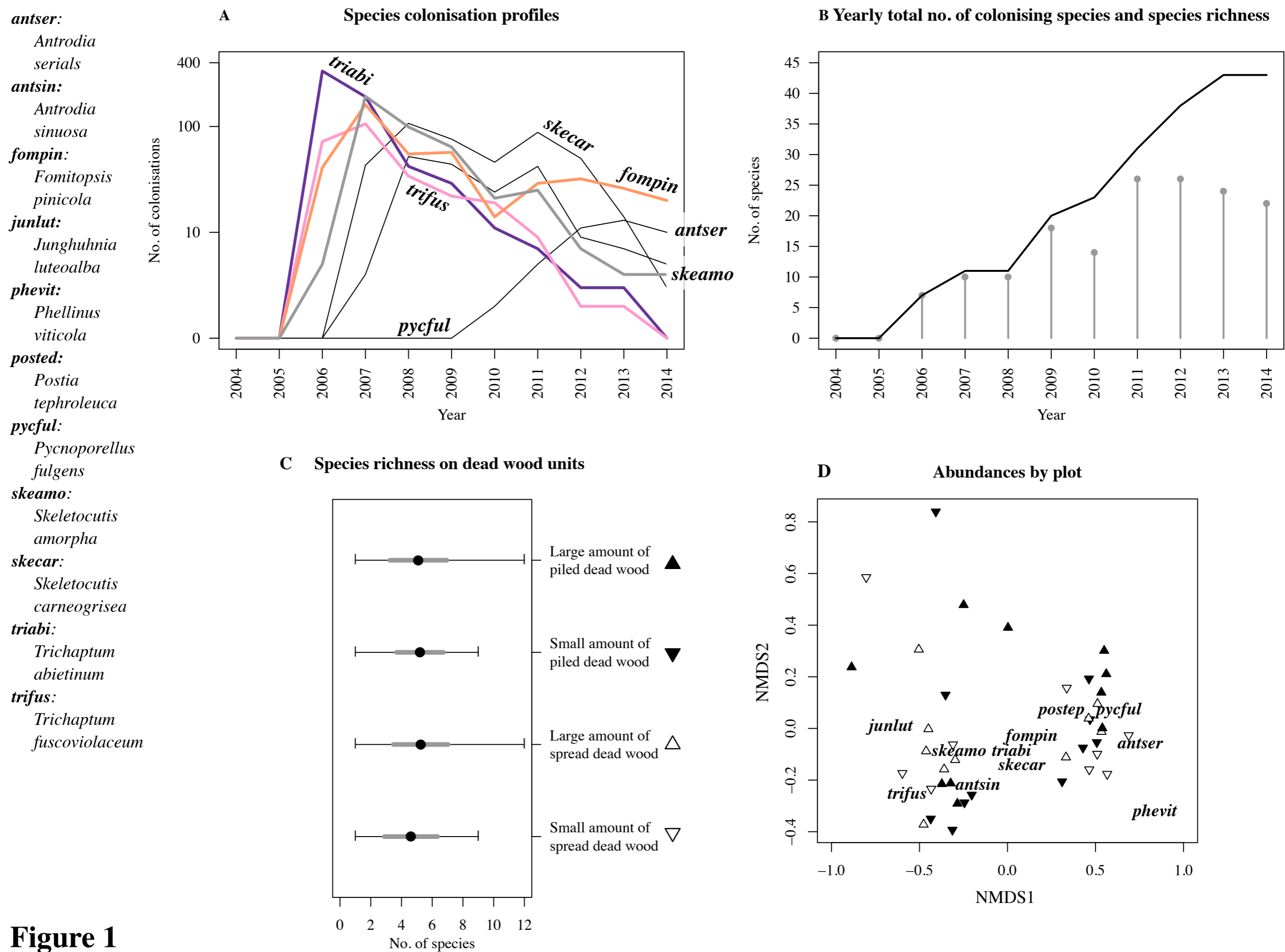
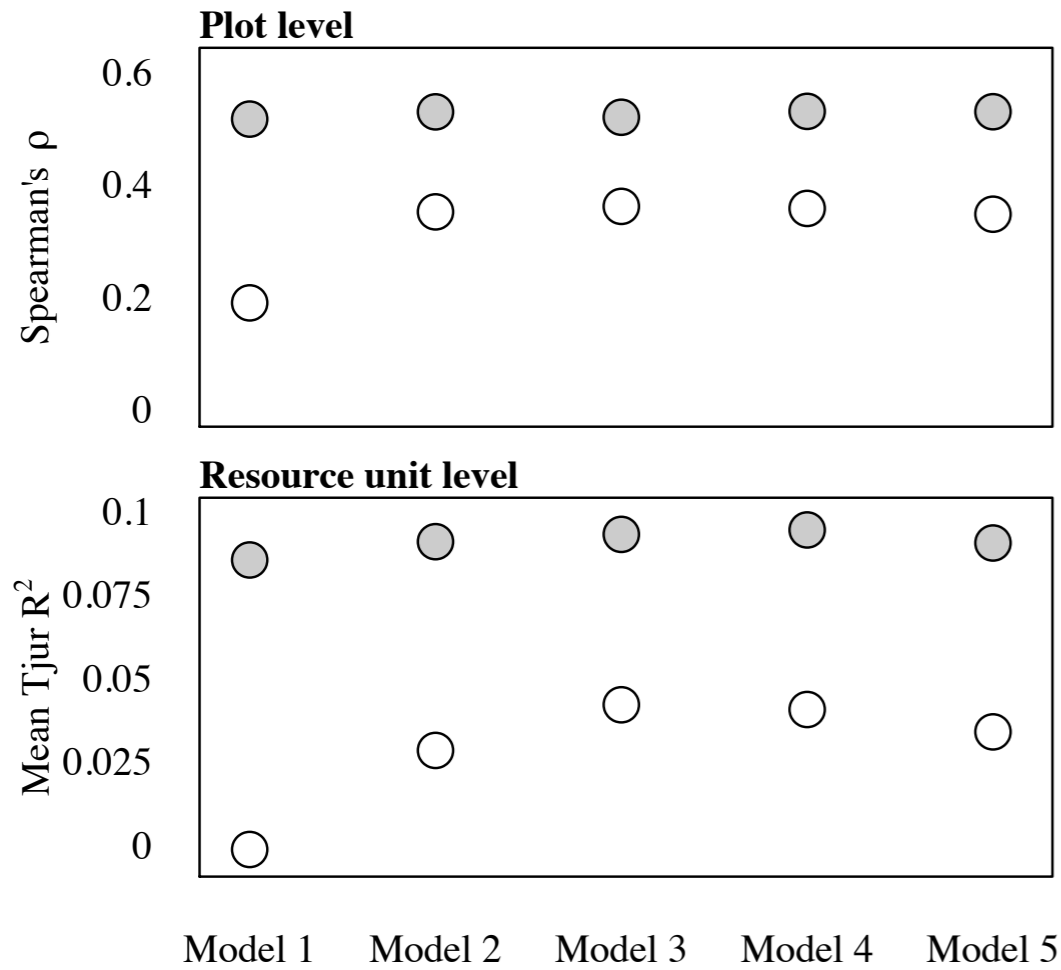


Figure 1

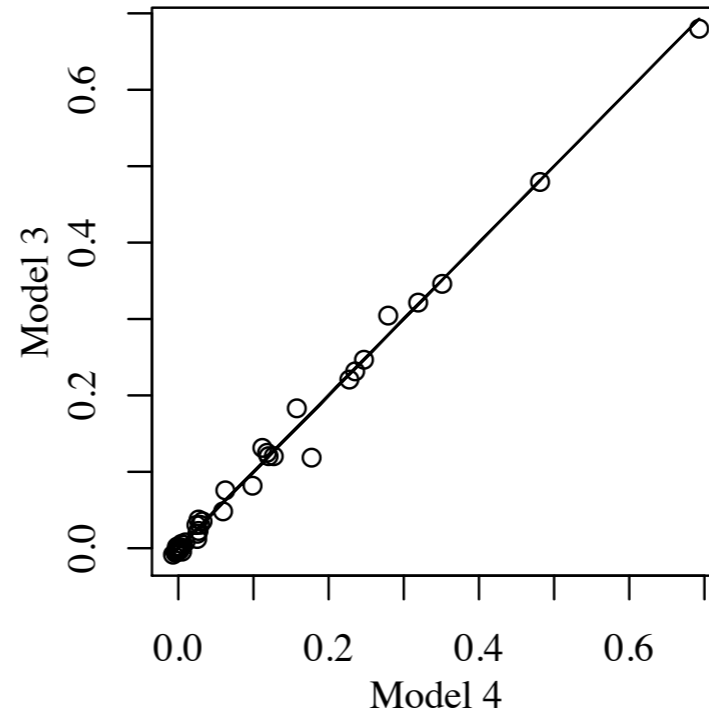
A Mean predictive performance



● Environmental and random effects included

○ Environmental and random effects excluded

B Tjur R²



C Tjur R²

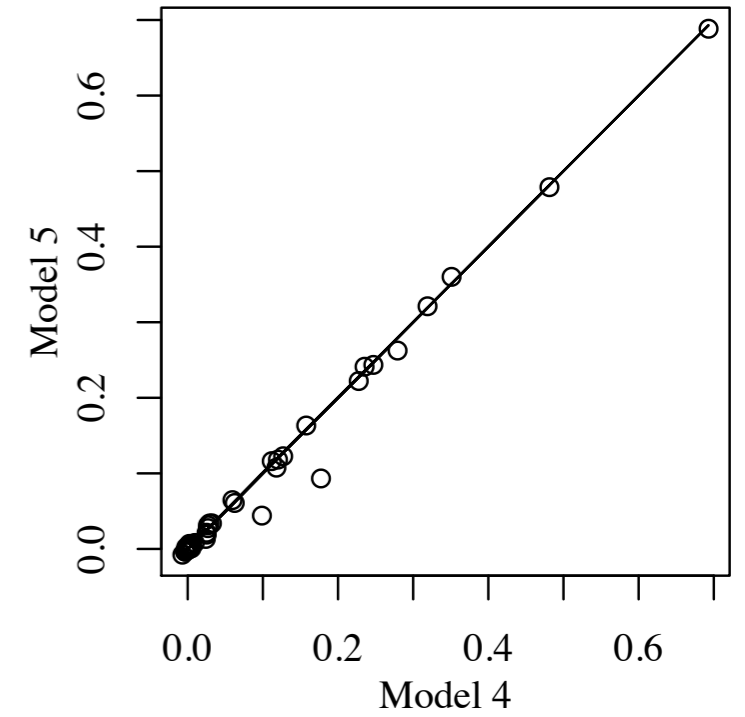


Figure 2

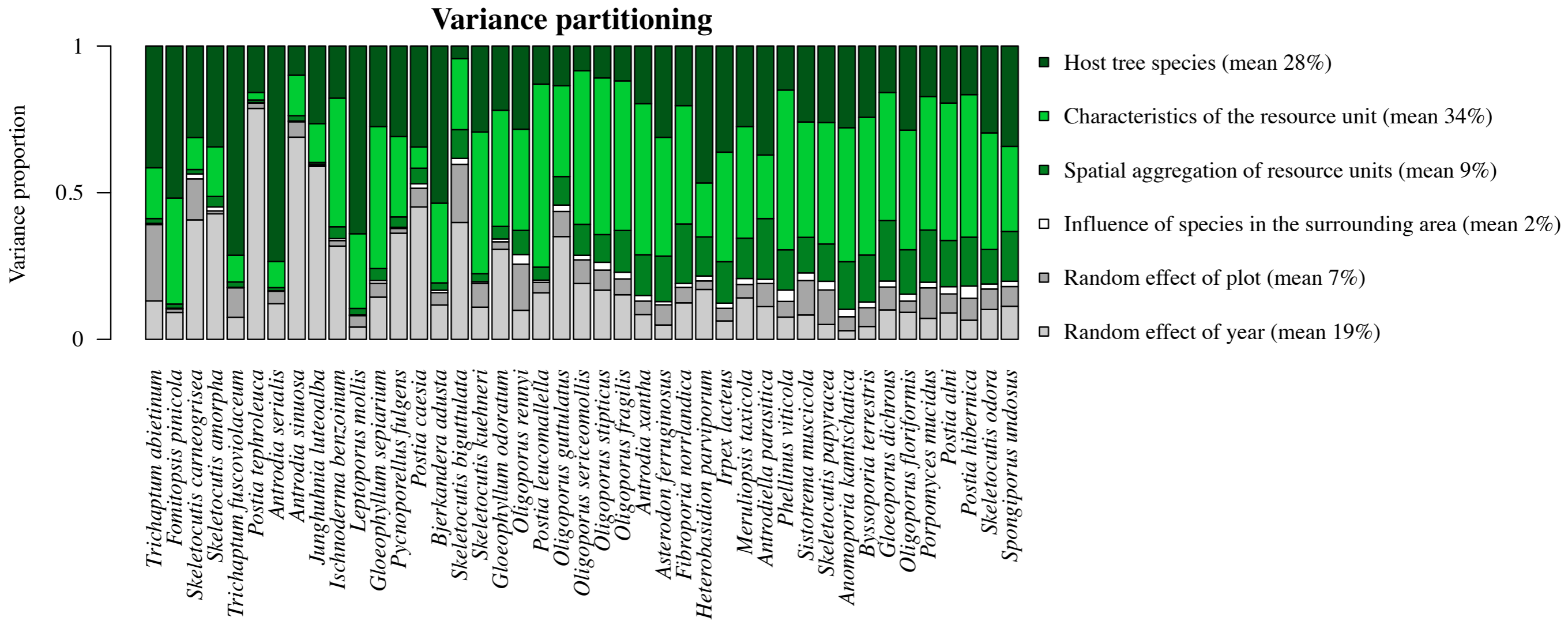
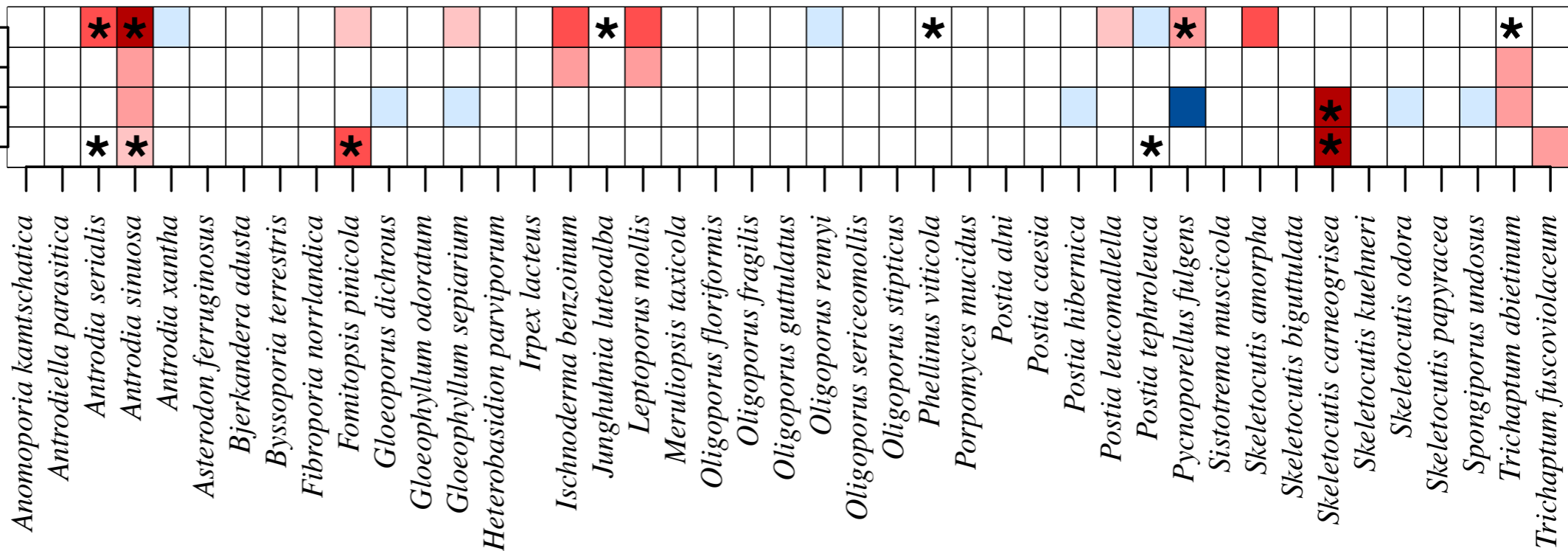


Figure 3

Primary colonisers

Fomitopsis pinicola
Skeletocutis amorpha
Trichaptum fuscoviolaceum
Trichaptum abietinum



Later-arriving species

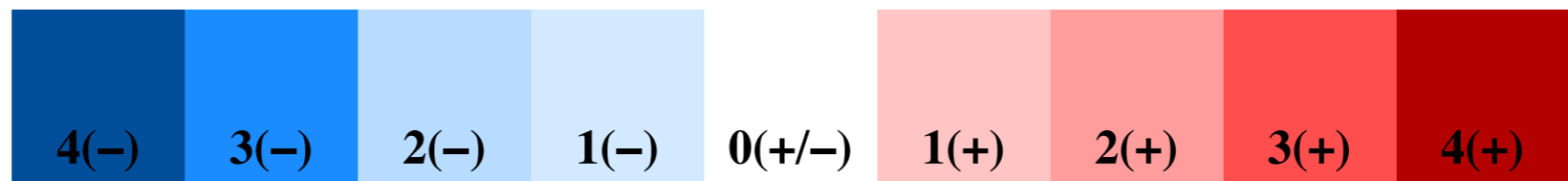
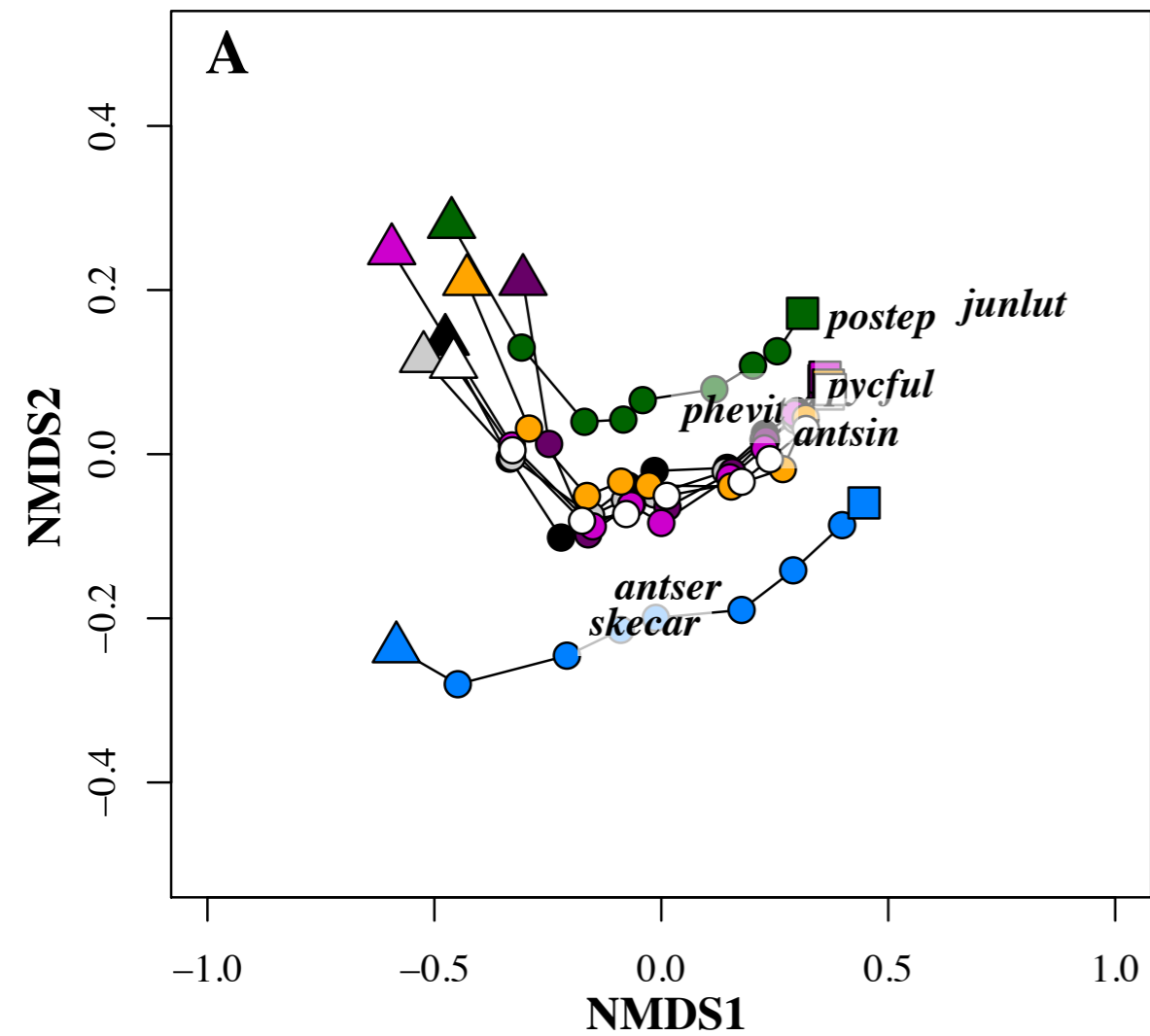
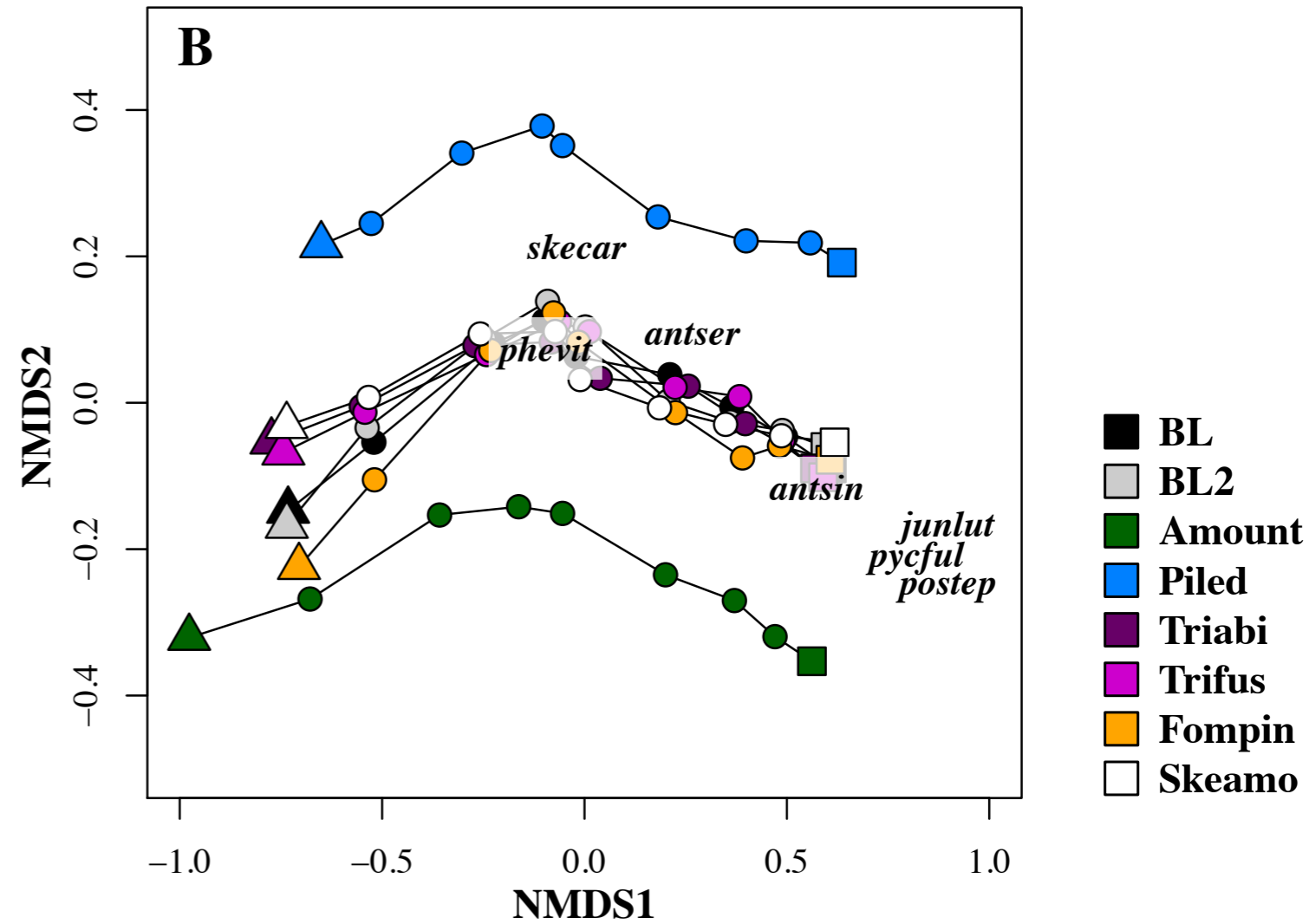


Figure 4

Spruce plot



Pine plot



antser: *Antrodia serialis*
antsin: *Antrodia sinuosa*
junlut: *Jughuhnna luteoalba*
phevit: *Phellinus viticola*
postep: *Postia tephroleuca*
pycful: *Pycnoporellus fulgens*
skecar: *Skeletocutis carneogrisea*

■ BL
 ■ BL2
 ■ Amount
 ■ Piled
 ■ Triabi
 ■ Trifus
 ■ Fompin
 ■ Skeamo

Figure 5

Tables

Table 1. Description of the scenario simulations. The other scenarios are described only in terms of how they differ from the baseline scenario (BL). All eight scenarios were simulated separately for plots with spruce or pine resource units, resulting in total 16 simulated scenarios.

Scenario	Description
BL. Baseline scenario.	The artificially produced dead wood was assumed to be of volume 5 m ³ and to have a spread spatial distribution. We followed in the simulation 100 resource units the characteristics and initial species composition of which was randomised from the real data.
BL2. A replicate of the baseline scenario.	Identical to BL .
Amount. Large amount of artificial dead wood produced	As BL , except the amount of artificial dead wood produced was increased to 10 m ³ .
Piled. Piled distribution of artificial dead wood produced	As BL , except the spatial distribution of the artificial dead wood produced was changed to piled distribution.
Triabi. Primary coloniser <i>Trichaptum abietinum</i>	As BL , except the first coloniser of the resource unit was set to be <i>T. abietinum</i> for all resource units.
Trifus. Primary coloniser <i>Trichaptum fuscoviolaceum</i>	As BL , except the first coloniser of the resource unit was set to be <i>T. fuscoviolaceum</i> for all resource units.
Fompin. Primary coloniser <i>Fomitopsis pinicola</i>	As BL , except the first coloniser of the resource unit was set to be <i>F. pinicola</i> for all resource units.
Skeamo. Primary coloniser <i>Skeletocutis amorpha</i>	As BL , except the first coloniser of the resource unit was set to be <i>S. amorpha</i> for all resource units.

Table 2. Associations between focal study species reported in previous studies. Species pairs that have been found to co-occur especially more (respectively, less) often than by random are indicated by “A+B” (respectively, “A-B”). Species pairs for which co-occurrence patterns have been tested but not found to deviate from random expectation indicated by “A<>B”. Experimentally verified competitive superiority of species A over species B is indicated by “A>B” or “A>>B”, the latter indicating a stronger level of evidence. Field-evidence based expert opinion on species B following species A is denoted by A→B. The shortenings of species names are formed by taking the first three letters of their genus and species names (triabi = *Trichaptum abietinum*). A three-lettered name refers to the whole genus (tri = *Trichaptum*).

Predecessor	Follower	Expert opinion(s)	Field survey(s)	Field experiment(s)	Laboratory Experiment(s)	This study
<i>Trichaptum</i> sp.	<i>Antrodia serialis</i>		triabi+antser ¹			+
	<i>Antrodia sinuosa</i>		triabi+antsin ¹			+
	<i>Fomitopsis pinicola</i>		triabi+fompin ^{1,2}	triabi-fompin ⁴	triabi<<fompin ³	+
	<i>Skeletocutis carneogrisea</i>	tri →skecar ⁵	triabi+skecar ¹			+
	<i>Postia tephroleuca</i>		triabi+postep ⁶			+
	<i>Junghuhnia luteoalba</i>				triabi<>junlut ³	(-/+)
<i>Fomitopsis pinicola</i>	<i>Antrodia serialis</i>		fompin+antser ^{1,6}			+
	<i>Antrodia sinuosa</i>		fompin+antsin ¹			+
	<i>Junghuhnia luteoalba</i>		fompin-junlut ¹		fompin>>junlut ³	+
	<i>Phellinus viticola</i>		fompin-phevit ²		fompin<<phevit ⁷	-
	<i>Pycnoporellus fulgens</i>	fompin →pycful ⁵			fompin<<pycful ⁸	+
	<i>Trichaptum abietinum</i>		fompin+triabi ¹		fompin>>triabi ³ fompin<triabi ⁸	+

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E-COMPONENT 1

Table E1. Environmental explanatory variables used in the models.

Input variable	Hierarchical level	Type	Temporal variability	Source
1) Resource unit size	Resource units	Continuous: 0.04 – 2.1 m ³ ; ln-transformed	Static	Measured on site in the beginning of the study (missing values set to median value)
2.1) Resource units decay stage	Resource units	Continuous: 1-4 (with 0.5 unit intervals)	Varies in time	Measured on site during all study years
2.2) Resource units decay stage to the power of two	Resource units	Continuous	Varies in time	The quadrate of the decay stage (variable 2.1)
3) Resource unit bark cover	Resource units	Continuous: 0-100%	Varies in time	Measured on site in the beginning of the study and year 2015 and interpolated
4) Resource unit sunkenness	Resource units	Continuous: 1-5 (with 1-unit intervals)	Varies in time	Measured on site in the beginning of the study and year 2015 and interpolated
5) Host tree species	Resource units	Categorical: Scots pine or Norway spruce	Static	Decided before producing the dead wood and implemented accordingly
6) Spatial distribution of the resource units	Plot	Categorical: piled or spread	Static	Predefined and implemented accordingly
7) Amount of artificial dead wood produced	Plot	Categorical: 5 m ³ or 10 m ³	Static	Predefined and implemented accordingly
8) Species surrounding occurrences	Plot	Categorical: present or absent	Varies in time	Observed on site during all study years
9) Species occurrences during the previous years	Resource units	Categorical: previously colonised or not previously colonised	Varies in time	Observed on site during all study years

Table E2. The posterior mean values for the regression coefficients describing the effects of the environmental explanatory variables used in the best performing model (Model 4 with sparse interactions). The coefficients for which the 75% central credible interval did not intersect zero are displayed with bold font.

	<i>Anomoporia kamschatica</i>	<i>Antrodiella parasitica</i>	<i>Antrodia serialis</i>	<i>Antrodia sinuosa</i>	<i>Antrodia xantha</i>	<i>Asterodon ferrugi- nosus</i>	<i>Bjerkan- dera adusta</i>	<i>Byssoporia terrestris</i>	<i>Fibroporia norrlandica</i>	<i>Fomitopsis pinicola</i>	<i>Gloeo- porus dichrous</i>	<i>Gloeo- phyllum odoratum</i>	<i>Gloeo- phyllum sepiarium</i>	<i>Hetero- basidion parviporum</i>
Intercept	-4,324	-3,8	-7,865	-2,335	-5,274	-5,143	-7,585	-3,978	-3,285	-3,862	-4,871	-9,047	-2,861	-5,15
Decay stage	0,416	0,349	0,429	0,168	0,333	0,591	0,166	-0,148	-0,05	0,131	0,161	0,671	-0,078	0,42
Decay stage ²	-0,038	-0,122	-0,12	-0,022	-0,083	-0,096	-0,141	-0,07	-0,111	-0,038	-0,085	-0,022	-0,023	-0,078
Bark cover	0,001	-0,003	0,003	-0,003	-0,015	-0,011	0,004	-0,002	-0,005	-0,015	0	-0,012	0,001	0,004
Volume	-0,15	-0,05	0,589	0,107	0,37	0,052	0,595	0,055	-0,029	0,495	0,131	0,659	0,153	0,066
Sunkenness	0,223	-0,069	-0,104	-0,143	-0,116	0,132	-0,24	0,152	0,13	-0,084	0,039	0,02	-0,144	-0,108
Spatial distribution of resource units	0,238	-0,441	-0,193	-0,139	-0,197	-0,359	-0,248	-0,293	0,453	-0,204	-0,283	0,183	0,032	-0,466
Amount of artificial dead wood produced	-0,23	0,292	-0,141	0,009	0,345	-0,406	0,092	-0,275	-0,271	0,015	0,121	-0,02	-0,002	0,079
Host tree species	-0,452	0,759	2,601	-0,683	-0,134	1,245	1,608	-0,154	-0,353	1,323	-0,664	1,089	-0,491	1,003
Species surrounding occurrences	0,123	0,036	0,098	-0,013	-0,163	0,026	-0,28	0,122	0,039	-0,077	0,05	-0,025	-0,016	0,223

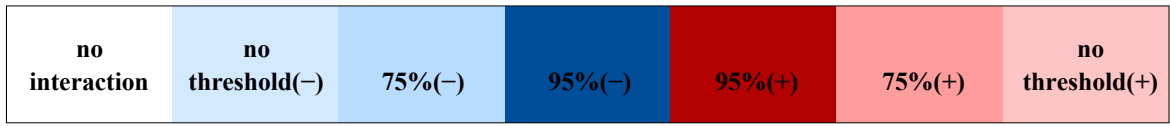
Table E2. (Continues)

	<i>Irpex lacteus</i>	<i>Ischnoderma benzoinum</i>	<i>Junghuhnia luteoalba</i>	<i>Leptoporus mollis</i>	<i>Merulioopsis taxicola</i>	<i>Oligoporus floriformis</i>	<i>Oligoporus fragilis</i>	<i>Oligoporus guttulatus</i>	<i>Oligoporus rennyi</i>	<i>Oligoporus sericeomollis</i>	<i>Oligoporus stipticus</i>	<i>Phellinus viticola</i>	<i>Porpomyces mucidus</i>	<i>Postia alni</i>
Intercept	-1,64	-5,382	-3,495	-3,126	-4,28	-4,854	-5,033	-4,062	-5,332	-5,144	-5,901	-3,098	-5,284	-4,449
Decay stage	-0,062	0,414	-0,109	0,029	0,103	0,116	0,258	0,276	0,062	0,06	0,153	0,588	0,365	0,126
Decay stage ²	-0,082	-0,083	0,032	-0,028	-0,069	-0,1	-0,018	0,068	0,078	0,015	-0,11	-0,014	-0,056	-0,112
Bark cover	0,005	-0,005	-0,007	-0,012	-0,005	-0,002	-0,006	0,002	0,001	-0,002	0,001	0	0,001	-0,003
Volume	-0,214	0,469	0,127	0,304	0,185	0,182	0,271	-0,116	0,248	0,205	0,345	-0,361	0,086	0,037
Sunkenness	-0,199	-0,023	0,257	-0,173	-0,139	0,078	-0,14	0,191	0,142	0,232	0,221	0,041	0,102	0,183
Spatial distribution of resource units	-0,219	-0,164	-0,1	-0,17	0,326	-0,242	0,139	-0,194	0,208	0,029	-0,029	-0,324	-0,229	-0,26
Amount of artificial dead wood produced	0,301	-0,008	-0,03	0,064	-0,02	0,097	0,129	0,247	-0,164	-0,207	-0,136	-0,159	0,158	0,118
Host tree species	-0,968	0,43	-1,219	-1,596	-0,765	-0,414	-0,261	-0,566	-0,998	-0,033	-0,22	0,254	-0,669	-0,124
Species surrounding occurrences	0,021	0,072	0,221	-0,017	0,009	0,069	-0,036	0,192	0,213	0,047	0,203	0,291	0,066	0,119

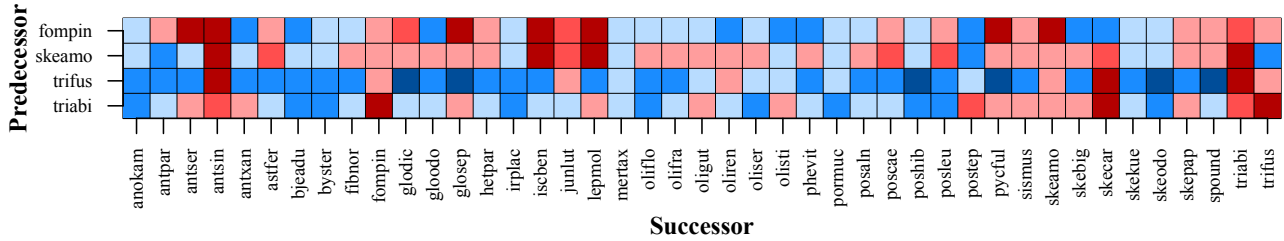
Table E2. (Continues)

	<i>Postia caesia</i>	<i>Postia hibernica</i>	<i>Postia leucomallella</i>	<i>Postia tephroleuca</i>	<i>Pycnoporellus fulgens</i>	<i>Sistotrema musicola</i>	<i>Skeletocutis amorpha</i>	<i>Skeletocutis biguttulata</i>	<i>Skeletocutis carneogrisea</i>	<i>Skeletocutis kuehneri</i>	<i>Skeletocutis odora</i>	<i>Skeletocutis papyracea</i>	<i>Spongiporus undosus</i>	<i>Trichaptum abietinum</i>	<i>Trichaptum fuscoviolaceum</i>
Intercept	-3,621	-7,825	-4,54	-2,818	-4,633	-5,596	-2,159	-3,979	-3,334	-6,629	-6,392	-6,91	-5,27	0,982	-1,919
Decay stage	0,205	0,538	0,145	-0,202	0,098	0,402	-0,34	0,065	0,111	0,403	0,353	0,394	0,349	-0,7	-0,306
Decay stage ²	-0,086	-0,016	-0,067	0,002	0,003	-0,041	0,015	-0,048	-0,093	-0,02	-0,112	-0,045	-0,111	-0,019	-0,014
Bark cover	0	0,003	-0,024	0,001	-0,009	-0,001	-0,006	-0,009	-0,001	-0,018	-0,006	0,001	-0,004	-0,012	0,002
Volume	0,005	0,398	0,273	0,085	0,351	0,139	0,266	0,219	0,136	0,441	0,23	0,388	0,156	0,139	0,185
Sunkenness	-0,043	0,071	0,066	-0,014	-0,198	0,107	-0,034	0,028	-0,08	-0,027	0,138	0,15	-0,021	-0,2	-0,175
Spatial distribution of resource units	-0,171	-0,268	0,111	-0,11	-0,264	0,046	-0,231	-0,264	-0,041	0,081	-0,406	-0,056	-0,241	-0,061	-0,144
Amount of artificial dead wood produced	0,226	-0,189	0,08	-0,107	-0,13	-0,116	0,038	0,091	-0,072	0,025	0,023	-0,149	-0,182	-0,164	-0,206
Host tree species	0,975	0,272	0,458	0,882	0,434	-0,403	-0,855	0,042	1,014	0,987	0,878	-0,594	0,773	1,767	-2,106
Species surrounding occurrences	0,236	0,302	-0,062	0,094	-0,036	0,199	-0,191	0,193	0,288	0,011	0,086	0,154	0,104	-0,273	0,042

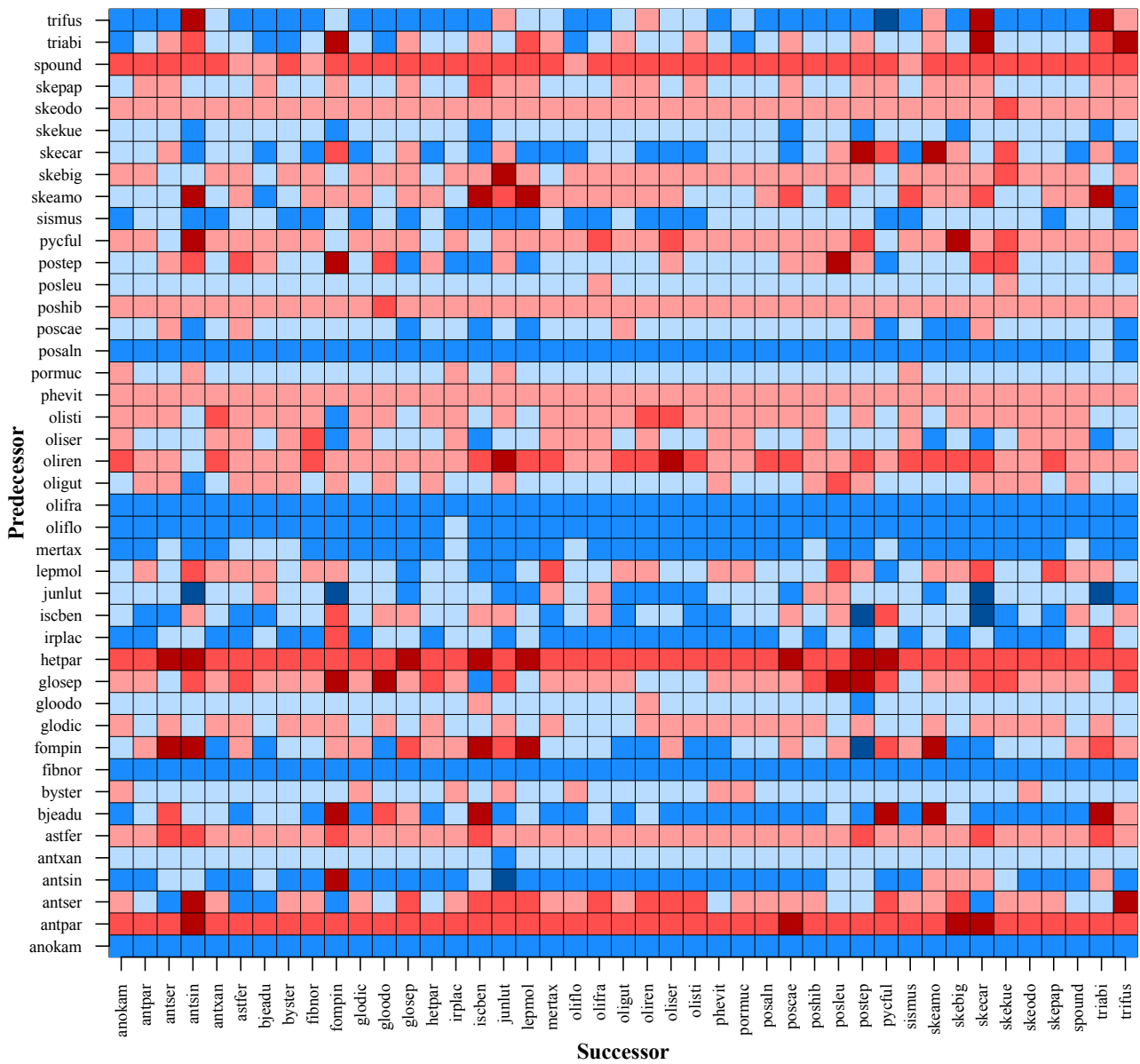
E-COMPONENT 2



Model 2



Model 3



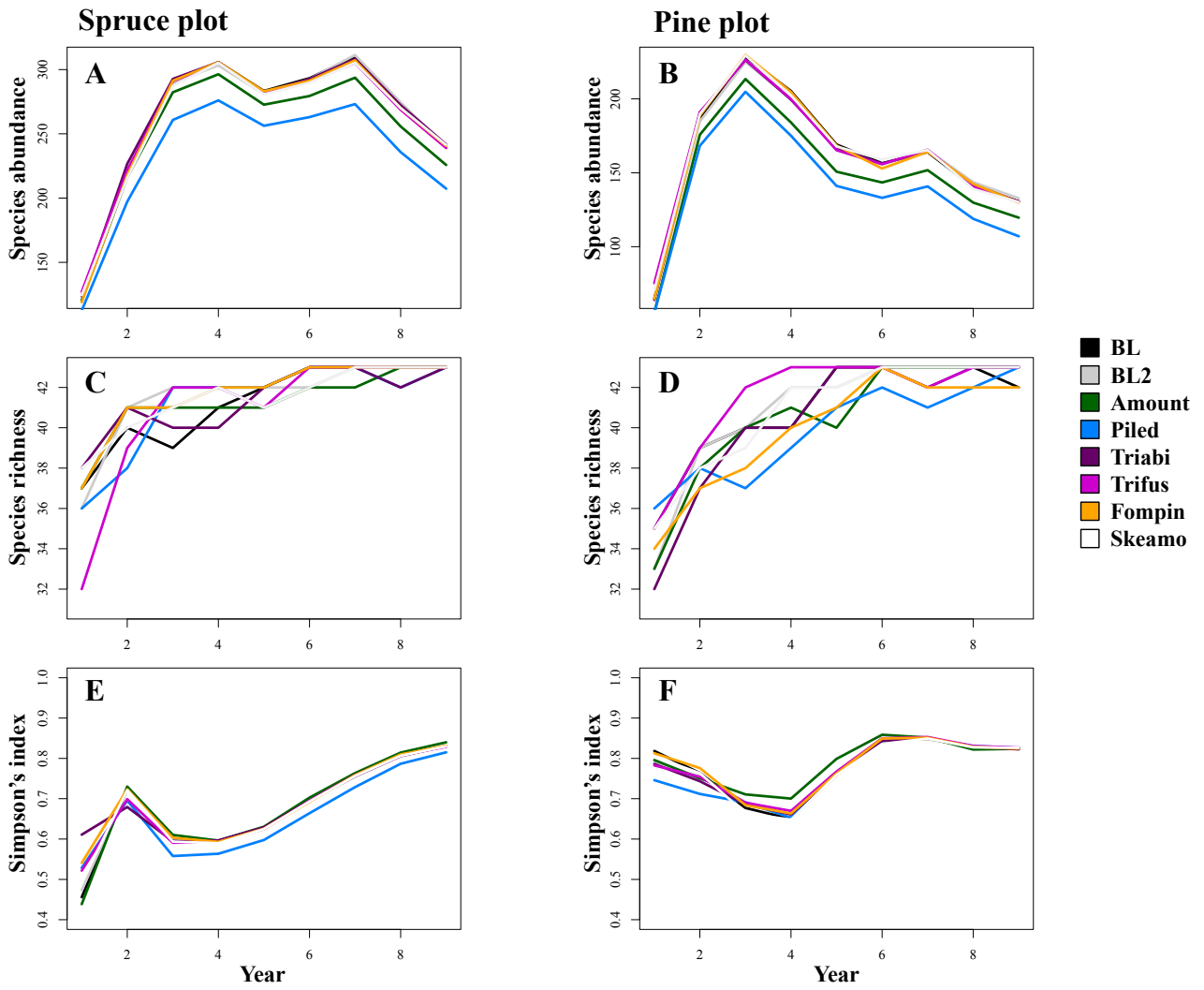


Figure E2. Species abundance (A and B) and richness (C and D) patterns of the simulated community scenarios, shown separately for the spruce (A and C) and pine plots (B and D).

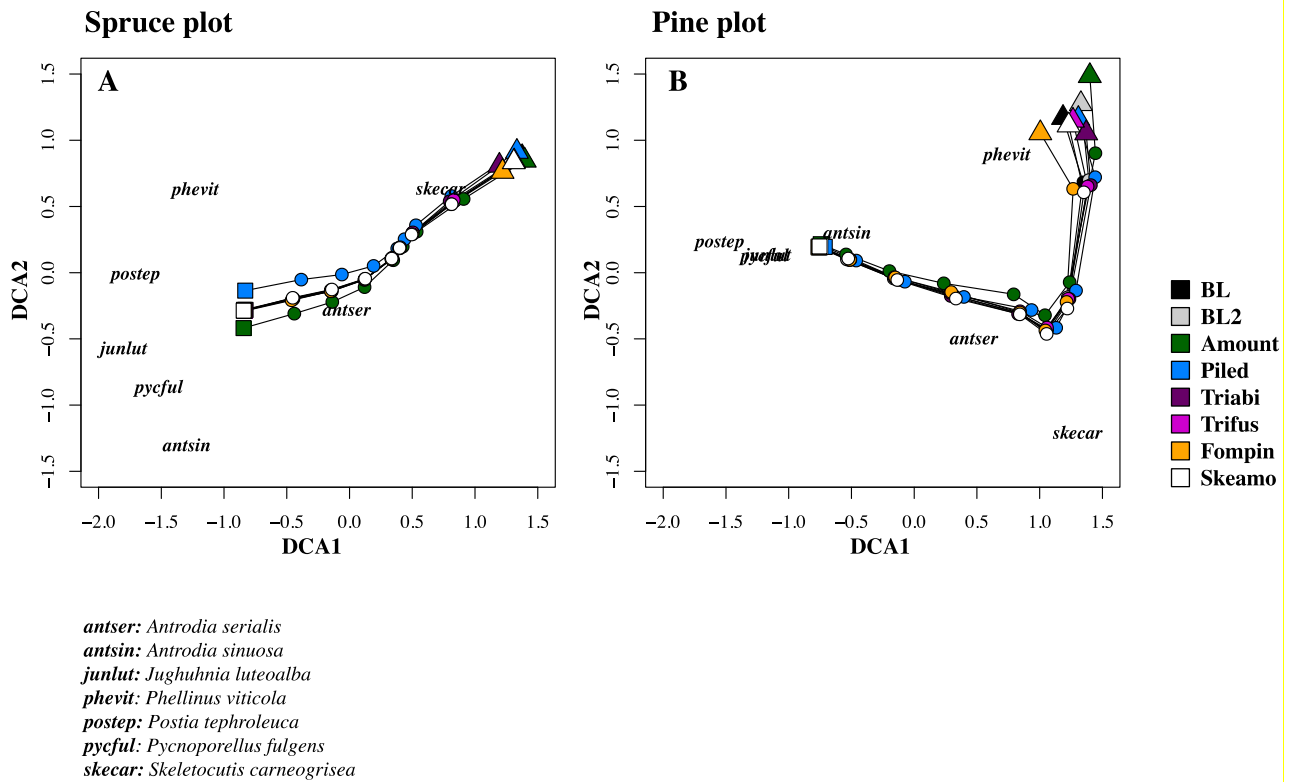


Figure E3. Detrended correspondence analysis for abundance patterns of the simulated community scenarios, shown separately for the spruce (A) and pine plots (B). The overlapping species labels in B are *junlut* and *pycful*.