Title: Experimentally induced community assembly of polypores reveals the importance of 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

Introduction

Assembly history can be a key factor affecting the dynamics of species communities (Diamond 1975, Drake 1991, Chase 2003, Schröder et al. 2005, Fukami et al. 2010), e.g. through so called priority effects (e.g. Alford and Wilbur, 1985; Chase, 2010; Fukami et al., 2016; Hiscox et al., 2015; Leopold et al., 2017; Sarneel et al., 2016; Weslien et al., 2011), which refer to the influence of an occupying species on the probability of establishment of following colonisers (Fukami et al. 2010). Priority effects induce historical contingency in the structure and function of communities, which can lead to alternative stable states, transient states, or compositional cycles (Fukami 2015). Studying when these effects take place is difficult as the arrival order of species is often difficult to manipulate or to reconstruct in sufficient detail (Fukami et al. 2016; but see e.g. Ejrnaes et al., 2006, Sarneel et al., 2016).

Extensive spatial variability in both the quantity and quality of dead wood is a characteristic feature of natural boreal coniferous forests, and it influences the possibilities for colonisation of dependent organisms (Jonsson and Siitonen 2012a). It has for long been recognised that the community assembly (Zobel 1997, Götzenberger et al. 2012, Ovaskainen et al. 2017b) of wood-inhabiting fungi does not result in a deterministic one-dimensional pathway, but may follow different trajectories (Stokland and Siitonen 2012). The way the host tree has died (e.g. storm, pathogens or fire) is generally considered to be the most influential filter in the very beginning of community assembly, creating variability in the community structure during the early stages of the decomposition process (Boddy and Heilmann-Clausen 2008, Stokland and Siitonen 2012, Komonen et al. 2014). The characteristics of the forest stand affect the development of the community e.g. due to differences in the microclimatic conditions (Boddy and Heilmann-Clausen 2008) or contact to the forest floor allowing the colonisation through

mycelia in soil (Fricker et al. 2008, Stenlid et al. 2008). The spatial distribution of dead wood influences colonisation through for example distance-dependent dispersal (Norros et al. 2012) but these effects are not necessarily expected to be seen at the level of individual forest stands (Edman and Jonsson 2001).

Pulsed accumulation of dead wood is a natural part of boreal forest ecology (Kuuluvainen 2002, Jonsson and Siitonen 2012b). In natural boreal forests e.g. wind, insect outbreaks and forest fires are some of the main mortality factors of trees, creating resource pulses for deadwood inhabiting species. However, in Fennoscandia more than 90% of the productive forests are under intensive forest management (Anon. 2014a, 2014b). Consequently, from the point of view of wood-inhabiting organisms, both the mean availability of resources and their spatial and temporal variability has undergone a major change (Siitonen 2001, Jonsson et al. 2005, 2016). In parallel with research from other habitats suggesting that mitigating the global biodiversity crisis calls for active ecological restoration (Dobson et al. 1997, Young 2000, Hobbs and Harris 2001, Brudvig 2011), halting the decline of dead-wood dependent species in boreal forests also calls for active restoration measures (Jonsson and Siitonen 2012c). Artificial creation of dead wood has been a common restoration practice in Fennoscandia (Similä and Junninen 2012, Halme et al. 2013a), and several studies have examined the potential of this method in aiding dead-wood dependent fungi. Studies have focused on surveying dead wood generated by cutting or killing trees (Olsson et al. 2011, Komonen et al. 2014, Pasanen et al. 2017), by controlled forest fires (Penttilä et al. 2013), or by a combination of these restoration methods (Vanha-Majamaa et al. 2007, Berglund et al. 2011). In addition to its relevance for the conservation context, time-series data on fungal community structure on restored sites provides opportunities for advancing the fundamental understanding of processes underlying community assembly.

In addition to environmental filtering (Kraft et al. 2015), biotic interactions (Wisz et al. 2013), such as predecessor-successor associations, have been suggested to be important for fungal community assembly (Niemelä et al. 1995, Stokland and Siitonen 2012, Boddy and Hiscox 2016, Hiscox et al. 2018). Interactions are likely to occur between dead-wood-inhabiting organisms, of which fungi and insects are the first ones to colonise. Insects may disperse fungi and hence facilitate their colonisation (Rayner and Boddy 1988, Boddy and Jones 2008, Strid et al. 2014). Wood-inhabiting fungi are known to be an highly interactive group of species, especially through competition, but also facilitative interactions (Woodward and Boddy 2008, Hiscox et al. 2018).

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

The aim of this study is to analyse the roles of environmental filtering and biotic interactions as well as stochastic processes in the community assembly of polypores, a polyphyletic morphological group of wood-inhabiting fungi, over an 11 yr period, which starts from seemingly unoccupied resource units. This time series data set, combined with the recent progress in the field of joint species distribution modelling for studying associations between

species in multispecies communities (Warton et al. 2015, Ovaskainen et al. 2017b, 2017a), provides an excellent opportunity for studying both the effects of the environment as well as potential interactions between species during the early development of the community.

Specifically, we ask: (1) how well the future colonising species can be predicted based on knowledge of the environmental characteristics of the dead wood unit and the preceding community; (2) is there evidence of priority effects, either through species-to-species influences or more generally through groups of species influencing each other; and (3) is it possible to determine distinct successional pathways of community assembly initiated by specific environmental conditions and/or by the identity of the primary colonisers.

Material and Methods

Study area and data collection

The study was conducted in Leivonmäki National Park in Central Finland ($62^{\circ}N$, $26^{\circ}E$). Like many of the currently protected areas of southern Finland, it consists of forests with a long history of intensive forest management. Therefore, before the establishment of the park in 2003, the study area was a low-resource environment with the amount of dead wood not different from typical managed forests of Finland, i.e. generally not exceeding 10 m³/ha while a typical amount for a natural forest in the geographic area would be 50 - 80 m³/ha (Siitonen 2001).

We established 40 study plots within the park's forests. The plots were of rectangular shape and of 0.25 ha (50 m \times 50 m) area, and all the plots were located within a 2 \times 3 km area. The dominant tree species on the plots was either Norway spruce (*Picea abies*) or Scots pine

(*Pinus sylvestris*), along with some deciduous admixture, mainly birches (*Betula* spp.), grey alder (*Alnus incana*) and rowan (*Sorbus aucuparia*). The age of the dominant tree layer on the plots was 80 – 120 yr.

On the study plots, we manipulated the amount of dead wood such that approximately 5 m^3 or 10 m^3 of dead wood was added by felling trees with chain saw. In each plot, we produced either spruce or pine dead wood according to the dominant tree species of the plot. As exception, in one plot we downed pine logs due to their large volume, even if ecosystem-wise the dominant tree was spruce. The created dead wood was either evenly distributed (later referred to as 'spread') on the plot or aggregated to form a stack at the centre of the plot (later referred to as 'piled').

We included 10 replicates of each amount × distribution combination. The plots were selected in autumn 2003, the treatments were randomised among the plots, and the felling was conducted during winter 2003-2004. The realised amounts of created dead wood in the 5 m^3 and 10 m^3 treatments were $5.00 \pm 0.56 m^3$ (range $3.69 - 6.62 m^3$) and $10.02 \pm 1.02 m^3$ (range $8.12 - 11.57 m^3$). We measured the following characteristics of the created dead wood units: diameter, decay stage according to the five-stage classification of Renvall (1995), bark cover and how sunken it is to the ground (see details of the resource unit characteristic from Appendix S1). The volume of whole trees was calculated with the tree-specific equations of Laasasenaho (1982).

We collected polypore data yearly during 2004-2014 on the artificially produced resource units (i.e. the added dead wood) as well as on all naturally formed dead wood with > 5 cm diameter and > 1.3 m length. The inventories were conducted in October — early November each year. All fruit bodies of a given species on one dead wood unit were regarded as one occurrence. Most of the polypore species were identified in the field. In case of doubt of the

correct identity of the species, we collected specimens for microscopic identification. The voucher specimens are deposited in the Natural History Museum of the University of Jyväskylä (JYV). In the classification of species, we used the Nordic concept of polypores, i.e. all poroid Aphyllophorales (Niemelä 2005).

Statistical analyses

We calculated the yearly, cumulative (across resource units) occurrences of the species for all the resource units included in the study, as well as abundances at the plot level. We illustrate the plot level species abundances of the cumulative community resulting from the whole study period with a non-metric multidimensional scaling (NMDS), applying the 'metaMDS' function (Oksanen et al. 2015), We used Bray-Curtis dissimilarities between the plots and global monotone regression as basis for the NMDS.

We fitted a joint species distribution model (JSDM) called Hierarchical Modelling of Species Communities (HMSC, Ovaskainen et al., 2017a), adjusted for identifying species associations from time-series data (Ovaskainen et al. 2017a). JSDMs not only allow inference of how species respond to their environment but also capture co-occurrence patterns related to unmeasured environmental variables or biotic interactions (see Warton et al. 2015). As response variable, we used the species colonisations. We considered the species absent (absence = 0) until the first observed presence on a resource unit (colonisation = 1), after which we disregarded its occurrences (no information = NA). Hence, the response vector for a particular species on a particular resource unit was e.g. of the form [0 0 1 NA NA... NA] if the species colonised the resource unit during the third study year. Utilising species colonisations rather than their occurrences as response allows us to better address our study questions, as we are interested in the emergence patterns of the species, and not their yearly fluctuations afterwards, which, in addition to biological reasons, can be due to variation in detection (Halme and Kotiaho 2012, Abrego et al. 2016).

As environmental explanatory variables at the resource unit level we included variables characterising the host tree species (Scots pine or Norway spruce), log-transformed resource unit size ($0.04 - 2.1 \text{ m}^3$), decay stage (1-4, see e.g. Hottola and Siitonen (2008)) and its square, bark cover (0-100%), and how sunken the resource unit is to the ground (0-100%). At the plot level, we included variables describing the spatial distribution of the resource units (piled or spread), and the amount of dead wood produced to this study plot ($5 \text{ or } 10 \text{ m}^3$). In line with the study design, we included community-level random effects (Ovaskainen et al. 2017b) to the model at the levels of plots and years. In addition, we included an indicator variable describing whether the focal species was observed in any of the previous years in the plot (including occurrences on both natural and artificially produced resource units). This variable describes the effect of the surrounding occurrences of the species on its probability of colonisation. For more details about the explanatory variables used, see Appendix S1.

We modelled the colonisation of species *j* on resource unit *h* in year *t* with probit regression, with

$$y_{hjt} = \mathbf{1}_{L_{hjt} > 0} \tag{1}$$

$$L_{hjt} = L_{hjt}^{K} + L_{hjt}^{A} + L_{hjt}^{R} + \epsilon_{hjt}, \qquad (2)$$

where the linear predictor L_{hjt} is modelled as a sum of fixed (*K* and *A*) and random (*R*) terms (Ovaskainen et al. 2017b, 2017a). The environmental term *K* models the effects of the environmental covariates, the association term *A* models the effects due to occurrences of the

other species in the previous years, and the random effect term *R* models the residual variation in species colonisations at the level of plots and years, and $\epsilon_{hit} \sim N(0,1)$.

We fitted 10 model variants to the data by varying the way the components *K*, *A* and *R* (eq. 2) were included. The environmental variables (*K*) and the random effects (*R*) were both either simultaneously included or excluded. Regarding the association term (A), i.e. how the influences of the species in the previous years were accounted for, we followed the modelling strategies of Ovaskainen et al. (2017b) to either exclude this component completely (Model 1), or to include it in four different ways (Models 2-5). This enabled us to examine how we can construct the interaction network most accurately. In Model 2, we used the occurrences of the most common primary colonising species (all the rest of the study species were among the first colonisers on at most 17 resource units): Trichaptum abietinum (first coloniser on 497 resource units), Trichaptum fuscoviolaceum (133), Skeletocutis amorpha (128) and Fomitopsis pinicola (72). In Model 3, we used the full interactions model and thus included the whole species community of the previous year as predictors. In Model 4, we used the sparse interactions model and thus assumed that only some species pairs interact with each other. In Model 5, we used the community-level drivers model and thus assumed the influence of species groups rather than of individuals species. This resulted in total $2 \times 5 = 10$ model variants, ranging from an intercept-only null model (K, R and A all excluded) to the full model (K, R and A all included, varying regarding the component A). The implementation of the general structure of the model, including terms *K* and *R* are described in detail in Ovaskainen et al. (2017a) and for the term A in Ovaskainen et al. (2017b). We fitted the model to the data with Bayesian inference, using the posterior sampling scheme described by Ovaskainen et al. (2017b). We ran all the models for 80,000 MCMC iterations and used the last guarter (thinned to every 100th iteration) for inference and predictions.

For comparing the predictive performances of the models, we performed a two-fold crossvalidation. We first split the data into two sets, of which both contain a randomly selected half of the resource units for each plot. We then fitted the models to both sets of data and used the fitted models to predict the colonisations in the half of the data not used in model fitting, resulting in predictions for the whole data set based on independent data sets used for training. We integrated the species (*j*), resource unit (*h*) and year (*t*) -specific colonisation probabilities p_{hjt} over the n_t study years as the total probability p_{hj} that the species *j* will ever colonise the resource unit *h* as

$$p_{hj} = 1 - \prod_{t=1}^{n_t} (1 - p_{hjt}). \tag{3}$$

Separately for each species, we measured the predictive performances of the models against the validation data at the levels of resource units by the Tjur R² coefficients of discrimination (Tjur 2009), and at the plot level by the Spearman's correlation (ρ) between the predicted and observed numbers of colonisations.

Scenario simulations

For examining the captured signal of different community assembly trajectories, we used the model variant showing best predictive performance to simulate different colonisation scenarios for hypothetical plots of 100 resource units (Table 1). In the scenario simulations, the model parameters were sampled from their posterior distribution, with the random effect term R being set to its year-specific effect. We conducted the simulations separately for spruce and pine plots by first sampling 100 resource units randomly from the data. Next, we modified the characteristics of the plot to construct eight scenarios that vary regarding the plot level variables (Table 1).

As a baseline (scenario **BL**), we created a plot with a small amount of artificial dead wood with spread distribution. For comparing whether the differences between the scenarios were greater than due to just random variation in the predictions, we produced a replicate of the baseline (scenario **BL2**), i.e. another realisation of a plot with the same characteristics. To investigate how an increase in the aggregation of the dead wood affects the colonisation process, we created a plot with a large amount of artificial dead wood (scenario **Amount**; but also in this case we simulated their dynamics only on 100 plots to keep the survey effect the same among the scenarios), as well as a plot with piled distribution of the artificial dead wood (scenario **Piled**). Finally, we wanted to see how the identity of the primary coloniser affects the colonisation process, so we created plots with either *Trichaptum abietinum*, *T. fuscoviolaceum*, *Fomitopsis pinicola* or *Skeletocutis amorpha*, i.e. one of the four most common primary colonisers as the sole first coloniser of all the resource units (scenarios, we assumed all resource units to be initially empty.

In the course of the simulations, the values of the covariates related to the resource units were assumed to change according to the data, so that e.g. the decay stage of the resource units increased as a function of time. Species that had occurred in the same resource unit in previous years were employed as predictors in the species-association part of the model, whereas species that had occurred in any resource unit of the same plot were employed as predictors for the surrounding occurrences.

We calculated the yearly, cumulative (across resource units) abundances of the species for each simulated plot. We illustrate the simulated community structures based on abundances with a non-metric multidimensional scaling NMDS, applying the 'metaMDS' function (Oksanen et al. 2015), We used Bray-Curtis dissimilarities between scenario-year-combination as basis

for the NMDS, and independent monotone regressions were used for all the resulting points. We also calculated the species total abundance (sum over all abundances, across species), species richness (number of species with abundance > 0), as well as the alpha diversity (Simpson's diversity index) for all the scenario-year-combinations, for which the results are displayed in Appendix 2.

Results

In total 43 species fruited on the resource units during the study period. The amount of yearly new fruitings varied between species, as the primary species emerged on the resource units intensely during the first few years (descending lines in Fig. 1A), whereas secondary coloniser species gained territory towards the end of the study period (ascending lines in Fig. 1A). The total number of new species emerging on any particular substrate unit was greater during the second half than the first half of the study period (Fig. 1B), reflecting the higher species diversity of secondary colonisers over the primary colonisers. The cumulative species richnesses were uniform across dead wood addition treatments (Fig. 1C), and there were no striking patterns in the plot level abundances either (Fig. 1D).

Of the primary colonisers, the most common one was *Trichaptum abietinum* (first coloniser in 77% of the resource units), followed by *Trichaptum fuscoviolaceum* (21%), *Skeletocutis amorpha* (20%) and *Fomitopsis pinicola* (11%). The percentages sum over 100% as in some cases more than one of these species emerged on the same resource units. Of these four primary colonisers, *F. pinicola* produces brown rot and the other species white rot. All other species were among the first colonisers for less than 3% of the resource units.

Predecessor species and environmental characteristics provide explanations of community assembly

The cross-validation exercise suggested that fungal community assembly is highly stochastic, as the average predictive power of even the best model variant was only ca. 10% at the resource unit level (Fig. 2A). A comparison among the model variants showed that the joint influence of environmental and random effects (components *K* and *R*, eq. 2) was greater than the influence of predecessor species (*A*). While accounting for the predecessor species clearly improved the prediction of colonising species in the null model (Fig. 2A, difference between Model 1 and other Models, open symbols), their added value in the full model that utilised the environmental predictors was only minor (Fig. 2A, difference between Model 1 and other Models, filled symbols). Models 2-5 produced essentially equally good predictions both on average (Fig. 2A) and for individual fungal species (Figs. 2BC), and thus the data was not informative on the structural properties of the interaction network. The overall best model (though with a small margin) was Model 4, with sparse interactions. The posterior mean effects of the environmental variables are shown in Appendix 1.

The partitioning of explained variance among the environmental factors, plot identity and study year shows that the host tree species and the measured characteristics of the resource unit accounted for the largest part of the variation (Fig. 3). The spatial aggregation of the artificially generated resource units (amount per plot and whether they were piled or spread) also accounted for a substantial part of the variation, whereas the influence of the surrounding species occurrences was negligible.

Links from the primary colonisers to the later-arriving species

As there were no major differences in predictive performance among Models 2-5, we extracted species pairs that influenced each other by comparing the results for all Models. Reassuringly, the models yielded, for most cases, consistent results in which secondary colonisers were positively or negatively influenced by the primary colonisers (Fig. 4). Many of the captured associations were also supported by previous findings in the literature (asterisks in Fig. 4 and Table 2).

Succession pathways

The NMDS illustrates the compositional dissimilarity between all the scenario-yearcombinations (Fig. 5). As the NMDS simply maps the configuration of the sites and species averages on the biplot, the axes do not have a meaning *per se*. Nevertheless, by observing the sites and species averages with respect to simulation year and scenario, we can see how the communities change as a function of these two.

The first axis of variation identified by the NMDS analyses is related to the year since the dead wood was generated (Fig. 5), supporting the successional view of community development. The scenario that most deviated from the other ones was the scenario **Piled** in which dead wood was produced in a pile (Table 1), with *Antordia. serialis* and *S. carneogrisea* especially favouring this scenario. Also, scenario **Amount**, which differed from the others by having a larger amount of dead wood, differed from the other scenarios. The remaining scenarios differed from each other during the very first years of community development but showed highly convergent results during the later years. The differences between scenarios were somewhat more pronounced on pine (Fig. 5B) than spruce units of resource (Fig. 5A). The most deviating scenarios had also slightly lower species abundances in comparison to the other scenarios, but differences regarding species richness were negligible (see Fig. E2 in E-Component 2).

The curved shape of the scenario lines can be explained by the short simulation time and species abundance. In the beginning of the simulation, the species begin to colonise the resource units. As the majority of the possible species emerge quickly, there is little room for patterns of species replacement, and the abundance patterns determine the compositional dissimilarities. During the midway of the simulation, the sites differ from the beginning and end the most, as the species are most abundant, and the majority of all the possible species have emerged (see Fig. E2 in E-Component 2). At the end of the simulation, the communities start to converge, as the fruiting of the species that colonised the resource units in the beginning start to decline in abundance. Hence, the second NMDS axis relates to the differences between scenarios as well as the general patterns in species abundances (see Fig. E3 in E-Component 2 for detrended correspondence analysis for comparison).

Discussion

Our results illustrate the difficulty of predicting the stochastic community assembly of woodinhabiting fungi, as all of our model variants had only limited power to predict which species will colonise a resource unit in a given year. However, while it was difficult to make accurate predictions of the colonising species at the resource unit level, the predictions were more accurate at the plot level, where some of the stochasticity becomes averaged out. Beyond the unexplained stochastic and potentially neutral variation, we found more evidence for community assembly being structured more by environmental than biotic filtering. The predecessor community, as opposed to environmental and random effects, provides an alternative and only to a limited extent a complementary explanation to the observed colonisation patterns.

Despite of this, we identified several links between primary and secondary coloniser species supported by previous experimental and observational studies, demonstrating how the primary colonisers affect the probabilities of colonisations of secondary colonising species (asterisks in Fig. 4 and Table 2). For example, the positive influence of *Trichaptum abietinum* on *Skeletocutis carneogrisea* is in accordance with previous studies showing that *S. carneogrisea* is a successor of *Trichaptum* species, with fruit bodies often growing on top of its predecessor. As another example, the positive influence of *F. pinicola* on *Pycnoporellus fulgens* has also been recorded before. However, we did not find that different primary species to initiate distinct successional pathways, as in our scenario simulations the fungal communities converged in their composition irrespective of the primary coloniser.

One likely reason why we found biotic interactions to play only a relatively minor role is that we characterised the species community through fruit body surveys, even if ecological interactions among the species take place mainly at the mycelia stage (Fricker et al. 2008, Hiscox et al. 2018). The community visible as fruit bodies presents only part of the mycelial community (Ovaskainen et al. 2010b, Kubartová et al. 2012), and the production of fruit bodies involves a delay following the build-up of the mycelial biomass (Allmér et al. 2006, Ovaskainen et al. 2013). On the other hand, the community visible as fruit bodies has been shown to reflect the dominating part of the mycelia community (Ovaskainen et al. 2013, Runnel et al. 2015). The order of appearance of fruit bodies reflects the species succession order, but is also affected by the ecological strategy of the species (Boddy and Hiscox 2016). Given these uncertainties, the approach taken here would be expected to pinpoint only such biotic interactions that have a major structuring role in community assembly, more subtle ones remaining possibly invisible in our data. A related reason for low predictive power is that we surveyed only one morphological group of wood-inhabiting fungi, namely polypores.

It would have been better to include all other groups as well, but the survey effort of such a well-replicated long-term monitoring work would have exploded. We acknowledge the need for smaller-scale studies with corticioids, ascomycetes and other groups included.

Another difficulty in identifying biotic interactions, even from a replicated field experiment, is that the characteristics of the resource unit and the fungal community structure both influence each other. For example, fungi contribute to the decay of the wood, and thus the influence of the decay class could be either seen as part of the fundamental niche (as we did here), or as the influence of biotic interactions. This makes it difficult to quantify the relative impacts of environmental filtering and priority effects, as seen from the fact that in our modelling framework the predecessor community had a substantial effect in a null model but only a minor effect in the model where the influence of environmental covariates and the random effects of plot and year were controlled for.

Even though we used the characteristics of the dead wood and the plot as a proxy for the microclimatic conditions and included these units also as random effects, we note that more detailed data on the physicochemical conditions of the studied logs would have benefitted our study. As the wood decomposes, its physical and chemical conditions change: the density of the wood decreases, its moisture and carbon dioxide levels increase and its nutrient content alters (Rayner and Boddy 1988, Stokland and Siitonen 2012). Experimental studies have shown that resource availability in the form of e.g. nitrogen availability has an effect on the priority effects taking place (Fukami et al. 2010, Dickie et al. 2012). However, we note that as these physiochemical changes result partly from the fungal decomposition process, their separation from the effects of the biotic interactions would be challenging from observational data, even if we had measured them.

In most of our scenario simulations, fungal communities diverged from each other during the very first years of community development and converged by the end of the time series. Thus, while we identified the primary colonisers to influence several secondary colonisers, these effects did not propagate through the decay process in a way that would create primary-coloniser dependent distinct successional pathways. This finding is in line with studies showing that wood-inhabiting fungal communities increase in their similarity along the succession (Stokland and Siitonen 2012), although it has also been shown that divergence may also increase along the succession in natural forests, when entering later decay stages (Halme et al. 2013b). Since our study focuses on the early steps of the succession, it remains to be seen whether it results in divergent or convergent patterns during the later stages.

We found that whether the resource units were spread individually or on a pile had a major influence in community composition, as well as the amount of dead wood produced. One of the species which benefited most of the piled scenario was *S. carneogrisea*, a known follower of the primary colonisers of genus *Trichaptum*, and *A. serialis*, which appeared to follow both *Trichaptum* sp. and *F. pinicola*. Both *Trichaptum* sp. and *F. pinicola* are ruderal pioneer species (Niemelä 2016) that might benefit from the piled resource distribution by spreading aggressively, and thus inhibiting other species from colonising. Most likely also the potentially different physical conditions of the piled dead wood may favour these species, but this influence was at least partly accounted for in the characteristics of the individual resource units (e.g. sunkenness, decay stage and bark cover).

The way the tree has died has major influence on the wood-inhabiting fungal community development (Stokland and Siitonen 2012). Intentionally cut dead wood differs from naturally formed dead wood resulting in differences in their community development (Komonen et al. 2014, Pasanen et al. 2017). The felled trees in our study were originally living

ones, and their death was thus very sudden as opposed to the slow deterioration caused by pathogens (Similä and Junninen 2011, 2012, Stokland and Siitonen 2012). Characteristics of the felled trees might give an advantage for certain pioneer polypore species (such as the primary coloniser *T. abietinum*) at the expense of others, and the dominance of one or two primary species might decrease the diversity of the following community (Similä and Junninen 2011, 2012). As the environmental conditions can strongly influence the likelihood of priority effects taking place (Fukami et al. 2016), we hope the generality of our results will be tested with future experiments, which would ideally also characterise the mycelial state and more detailed abiotic conditions.

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E-COMPONENTS

E1. Details on the explanatory variables used in the models and their effects for the best performing model.

E2. Results regarding the associations from predecessor to successors for all species and all model variants and complementary results for the scenario simulations.

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1771 1772 1773 1774 1775 1776 1777 1778 1779 1780 1781 1782 1783 1784 1785 1786 1787 1788 1789 1790 1791 1792 1793 1794 1795 1796 1797 1798 1799

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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 m^3), and downward pointing triangles small (5 m^3), 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 \mathbb{R}^2 values > 0.9 (for both linear and non-linear fits) and stress value = 0.11.

Figure 2. A cross-validation based comparison of predictive performance among the model variants. (A) Resource-unit level and plot-level results averaged over the species; (B and C) Species-specific resource-unit level results. In A, the filled (respectively, empty) symbols refer to model variants that include (respectively, exclude) environmental covariates and random effects. In B and C, only model variants that include environmental covariates and random effects are considered. The Models 1-5 differ in the way the current community structure is assumed to influence or not to influence future colonisations (see text). At the resource-unit level, predictive performance is measured by comparing predicted colonisation probabilities to observed ones with Tjur's (2009) coefficient of discrimination. At the plot level, predictive performance is measured by comparing predicted numbers of colonisations to observed ones among the plots with Spearman's correlation. In panels BC, the Tjur R² coefficients of discrimination are plotted for all species, for Models 3 (B) and 5 (C) against those of Model 4.

Figure 3. Partitioning of the explained variation among the environmental covariates and random effects in Model 1. Different groups of variables are indicated by different colours. Characteristics of resource units include their volume, decay stage, bark cover and sunken the unit is to the ground. The spatial aggregation of resource units includes both their amount per plot (5 or 10 m³) and whether they are piled or spread. The bars show the results for each species, and the numbers in the legend show averages over the species. The species are ordered according to their prevalence in the original data, with the most common one being on the left-hand side.

Figure 4. The influences of the primary colonisers on the later-arriving species. The colours indicate the level of statistical support by which each of the four primary coloniser species (*Trichaptum abietinum, Trichaptum fuscoviolaceum, Skeletocutis amorpha* and *Fomitopsis pinicola*) influences either positively (red) or negatively (blue) the colonisation of the later-

arriving species. The level of statistical support is measured by the number of model variants (among Models 2-5 that control for environmental covariates and random effects) for which the 95% central credible interval of the association did not intersect zero. The asterisks indicate associations that have been reported previously in the literature (Table 2). Results for all species pairs are shown separately for all model variants in Appendix 2.

Figure 5. Variation in community structures among the scenario simulations summarised by non-metric multidimensional scaling (NMDS). The results are shown separately for the resource units consisting of (A) Norway spruce or (B) Scots pine. Different scenarios are indicated by the different colours (for explanations of the abbreviations, see Table 1). The triangles indicate the first year of the simulated community assembly, and the lines connect the years (points) chronologically, and the squares indicate the final years. The centroid locations of species that are strongly influenced by one of the primary colonisers based on our results (Fig. 4) or previous literature (Table 2) are shown in the figure. In both NMDS analyses, the regression for interpoint distances between pairs of communities against the original dissimilarities resulted in R^2 values > 0.99 (for both linear and non-linear fits) and stress values < 0.05. The NMDS plots are based on communities simulated with the best performing Model 4.





A Mean predictive performance

O Environmental and random effects included

O Environmental and random effects excluded



- Host tree species (mean 28%)
- Characteristics of the resource unit (mean 34%)
- Spatial aggregation of resource units (mean 9%)
- □ Influence of species in the surrounding area (mean 2%)
- Random effect of plot (mean 7%)
- □ Random effect of year (mean 19%)

Skeletocutis carneogrisea Skeletocutis amorpha Trichaptum fuscoviolaceum Postia tephroleuca Asterodon ferruginosus Fibroporia norrlandica Heterobasidion parviporum Irpex lacteus Meruliopsis taxicola Antrodiella parasitica Phellinus viticola Spongiporus undosus Gloeophŷllúm sepiarium Pycnoporellus fulgens Skeletocutis odora Oligoporus sericeomollis Oligoporus stipticus Oligoporus floriformis Porpomyces mucidus Fomitopsis pinicola Antrodia serialis Antrodia sinuosa Leptoporus mollis Postia caesia Skelėtocutis biguttulata Skeletocutis kuehneri Oligoporus rennyi Postia leucomallella Oligoporus guttulatus Antrodia xantha Sistotrema muscicola Byssoporia terrestris Gloeoporus dichrous ostia alni Postia hibernica Trichaptum abietinum Junghuhnia luteoalba Ischnoderma benzoinum Bjerkandera adusta Oligoporus fragilis Skeletocutis papyracea Anomoporia kamtschatica Gloeophyllum odoratun

Variance proportion



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

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 \rightarrow 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 experi- ment(s)	Laboratory Experiment(s)	This study
<i>Trichaptum</i> sp.	Antrodia serialis		triabi+antser ¹			+
	Antrodia sinuosa		triabi+antsin ¹			+
	Fomitopsis pinicola		triabi+fompin ^{1,2}	triabi -fompin ⁴	triabi< <fompin<sup>3</fompin<sup>	+
	Skeletocutis carneogrisea	tri →skecar ⁵	triabi+skecar ¹			+
	Postia tephroleuca		triabi+postep ⁶			+
	Junghuhnia luteoalba				triabi<>junlut ³	(-/+)
Fomitopsis pinicola	Antrodia serialis		fompin+antser ^{1,6}			+
	Antrodia sinuosa		fompin+antsin ¹			+
	Junghuhnia luteoalba		fompin-junlut ¹		fompin>>junlut ³	+
	Phellinus viticola		fompin-phevit ²		fompin< <phevit<sup>7</phevit<sup>	-
	Pycnoporellu s fulgens	fompin →pycful ⁵			fompin< <pycful<sup>8</pycful<sup>	+
	Trichaptum abietinum		fompin+triabi ¹		fompin>>triabi ³ fompin <triabi<sup>8</triabi<sup>	+

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E-COMPONENT 1

Table E1. Environmental explanatory variables used in the models.

Input variable	Hierarchical level	Туре	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.

	Anomoporia kamtschatica	Antrodiella parasitica	Antrodia serialis	Antrodia sinuosa	Antrodia xantha	Asterodon ferrugi- nosus	Bjerkan- dera adusta	Bysso- poria terrestris	Fibroporia norrlandica	Fomitopsis pinicola	Gloeo- porus dichrous	Gloeo- phyllum odoratum	Gloeo- phyllum sepiarium	Hetero- basidion parviporum
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)

	Irpex lacteus	Ischno- derma benzo- inum	Junghuh nia luteoalba	Lepto- porus mollis	Meruli- opsis taxicola	Oligo- porus flori- formis	Oligoporus fragilis	Oligoporus guttulatus	Oligoporus rennyi	Oligoporus sericeo- mollis	Oligoporus stipticus	Phellinus viticola	Porpo- myces mucidus	Postia alni
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)

	Postia caesia	Postia hibernica	Postia leuco- mallella	Postia tephro- leuca	Pycno- porellus fulgens	Sisto- trema music- cola	Skeleto- cutis amorpha	Skeleto- cutis biguttu- lata	Skeleto- cutis carneo- grisea	Skeleto- cutis kuehneri	Skeleto- cutis odora	Skeleto- cutis papyracea	Spongi- porus undosus	Trichaptum abietinum	Trichaptum fusco- violaceum
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

Successor

Figure E1. The influences of all primary coloniser species on the colonisation probabilities of all later-arriving species. As shown in the legend, blue indicates the negative and red positive influences, and the shade of the colour indicates the level of statistical support behind the interaction (e.g. 75%(-) mean negative association with statistical support based on 75% central credible interval). White colour indicates pairs with no interactions. In Model 4, only the four primary colonisers were included in the models as predecessor community.

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*.