RESEARCH ARTICLE

Journal of Ecology | BRITISH ECOLOGICAL SOCIETY

Long-term effects of colonization–extinction dynamics of generalist versus specialist wood-decaying fungi

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Abstract

1. Long-term metapopulation persistence is mediated by the dynamics of colonization and extinction. To understand and predict future species occupancy in changing landscapes, we must account for the dynamic rates that shape the occupancy and disentangle their dependence on environmental conditions. Specialist and generalist species may differ in their dynamics in systematic ways.

2. Using an extensive, large-scale repeat survey dataset for wood-decaying fungi, we fitted dynamic metapopulation models for ten species, ranging from generalists to specialists with differing resource requirements. We first estimated base rates of colonization and extinction and tested their relationships to species' degree of specialization. We then tested for effects of local and landscape scale variables on the colonization and extinction rates. Finally, using the fitted models and a scenario of future forest development we projected future colonization–extinction dynamics over 100 years to test for differences in species occupancies between production stands and set-aside stands.

3. Our study revealed a striking pattern of decreasing colonization rates with increasing degree of specialization across species, along with concomitantly increasing extinction rates. Strong sensitivity of colonization probabilities to local habitat quality (dead wood volume and stand age) in specialist but not generalist species constrained the regional occupancy of specialists, especially in production forest. We found evidence for short-range dispersal limitation in two specialists, but no effect of our measure for landscape-scale connectivity on colonization rates. Simulations of future metapopulation dynamics resulted in decreasing and lower final occupancy in production forest than in set-asides, especially of specialist species. In set-aside stands, however, specialists increased over time to relatively high occupancies.

4. *Synthesis*. Colonization–extinction dynamics of wood-decaying fungi varied with species' degree of specialization. Increasing specialization was associated with increasing sensitivity of colonization rates to habitat conditions, and partly local connectivity, as well as with increasing extinction rates. Low landscape-scale occupancies of specialist as compared to generalist wood-decaying fungi are thus

maintained by a combination of lower colonization rates, particularly in production forest, and higher extinction rates.

1 | INTRODUCTION

The landscape-scale occupancy of spatially structured populations (metapopulations) is the result of their colonization–extinction dynamics (Yackulic et al., 2015). Landscape-scale or regional occupancy is the proportion of all suitable patches that are occupied, that is, the average probability of a suitable patch being occupied. Metapopulation theory explains patch occupancy through the interactive effects of landscape and species properties on colonization–extinction dynamics (Hanski, 1999; Hanski & Ovaskainen, 2003). While theoretical studies on the subject abound, empirical data of metapopulation dynamics at the landscape scale are more difficult to obtain (but see Ovaskainen & Saastamoinen, 2018).

Landscape properties affecting metapopulation dynamics include the area and quality of patches, as well as their connectivity, that is, the distance to surrounding occupied patches that constitute dispersal sources (Hanski, 1999). Extensive evidence for a positive effect of connectivity on colonization rates and patch occupancy suggests that dispersal limitation often plays an important role in metapopulation dynamics (Hanski, 1999; Jönsson et al., 2008), although this has recently been discussed for species dependent on dead wood (Komonen & Müller, 2018; Ranius et al., 2019). In dynamic landscapes, where suitable patches change over time, the rates of patch creation and destruction additionally influence metapopulation dynamics (Bennie et al., 2013; Keymer et al., 2000; Snäll et al., 2003). Variable patch turnover rate and changing habitat quality may affect colonization and extinction rates differentially, which can result in nonlinear metapopulation responses. Simulations are therefore required to fully appreciate the implications of colonization–extinction dynamics. They are also needed to answer applied questions on future species viability, given societally relevant scenarios of future land-use (IPBES, 2016).

Species properties that are of key relevance to colonization–extinction dynamics include local abundance, population growth rate and dispersal capacity (Johst et al., 2002). The latter two properties remain elusive for many fungal species (Heilmann-Clausen et al., 2017), but they may covary with species' degree of specialization (Verberk et al., 2010). Specialist species have narrower ecological niches than generalist species, that is, more specific ecological resource requirements (the Grinnellian niche sensu Devictor et al., 2010), but are thought to perform better within their niche, for example, through greater competitive ability (Clavel et al., 2011; Hiscox et al., 2016). Among wood-decaying fungi, highly specialized species, such as *Amylocystis lapponica*, require a particular type of dead wood (e.g. typically large diameter dead wood at a particular

decay stage) and may be sensitive to local microclimate and other environmental factors. Generalist species, such as *Trichaptum abietinum*, can utilize a broad variety of dead wood of different diameters and decay stages in a wide variety of environments. Specialists may be more vulnerable to environmental change and to habitat loss and fragmentation than generalists (Clavel et al., 2011). Indeed, the loss of specialists and their replacement with generalists has been observed in many disturbed environments (Banks-Leite et al., 2014; Brückmann et al., 2010; Devictor et al., 2008), also among wood-decaying fungi (Abrego et al., 2015; Nordén et al., 2013; Pouska et al., 2017).

In the context of metapopulation dynamics, generalists are expected to have higher landscape-scale occupancy than specialists, which leads to higher connectivity and higher colonization probabilities of generalists in a positive feedback loop (Johansson et al., 2012; Verberk et al., 2010). Their local extinction rates may be lower either due to larger local populations that are less sensitive to environmental stochasticity, or due to rescue effects, where the local extinction risk is decreased through immigration (Gonzalez et al., 1998; Verberk et al., 2010). At the scale of forest stands, where dead wood of different quality is available for colonization by generalist fungi, these mechanisms are likely to dominate their extinction dynamics. In contrast, the lower landscape scale occupancy of specialists could cause lower colonization rates due to weaker regional propagule pressure or longer distance to disperse between their suitable substrates. Their local extinction rates may be higher due to smaller local populations that are more sensitive to demographic and environmental stochasticity (Clavel et al., 2011; Ramiadantsoa et al., 2018).

A key component of colonization is dispersal, which may be related to the degree of specialization. Theory suggests that specialists have lower dispersal capacity than generalists (Nurmi & Parvinen, 2011; Poisot et al., 2011), as a result of evolution in homogeneous and stable natural habitats that favoured the joint selection for specialization and decreased dispersal capacity (Büchi & Vuilleumier, 2014). In wood-decaying fungi, successful colonization depends on both dispersal and establishment, the latter increasing with spore size and deposition density (Norros et al., 2012, 2015). The density of spore deposition is strongly distance-dependent and increases with the proportion of old forest in the surrounding landscape (Edman, Gustafsson, et al., 2004; Edman, Kruys, et al., 2004). We therefore expect specialists to be dispersal-limited already at short, within-stand distances (Jönsson et al., 2008; Norros et al., 2012).

We here identify drivers of current and future landscape-scale colonization–extinction dynamics of generalist versus specialist species inhabiting dynamic patches. We study wood-decaying

fungi, ranging from common generalists to rare specialists with wide to narrow habitat and substrate niches. Wood-decaying fungi are functionally important components of forests with a major role in wood decomposition and carbon and nutrient cycling (Harmon et al., 1986; Stokland et al., 2012), yet the dispersal and population ecology of many of these species are still poorly understood (Heilmann-Clausen et al., 2017). As it is not trivial to predict future metapopulation dynamics in landscapes where the key drivers change in dynamic and mutually dependent ways, we use scenario simulations to understand long-term effects of the estimated colonization–extinction dynamics. To test how long-term metapopulation occupancy responds to future forest usage, we simulated realistic future forest development and future fungal colonization–extinction dynamics for the coming 100 years. As particularly specialists have experienced recent population declines in Fennoscandian forests (Hyvärinen et al., 2019; SLU Artdatabanken, 2020), a key applied question is their future occupancy development in production versus set-aside forest.

Specifically, we ask: (a) Is there a difference in the rates of colonization and extinction between generalists and specialists? We expect decreasing colonization rates and increasing extinction rates with increasing degree of specialization. (b) Is there a difference between specialists and generalists in how local environmental conditions and connectivity at local and landscape scales affect rates of colonization and extinction? We expect colonization and extinction rates of specialists to be more affected by local habitat conditions and connectivity than the rates of generalists. (c) What are the future long-term effects of the estimated colonization–extinction dynamics in production versus set-aside stands? We expect lower future occupancy for specialists in production stands than in set-asides due to the greater sensitivity of their colonization and extinction rates to environmental conditions.

2 | MATERIALS AND METHODS

2.1 | Data

The extensive dataset analysed here was collected through two large-scale surveys of dead wood objects and wood-inhabiting fungi in 258 forest stands sized 0.17–4.3 ha across the southern and middle boreal vegetation zones in Finland (a subset of the stands described in Nordén et al., 2013). Initial surveys were conducted between 2000 and 2005 (Nordén et al., 2013), resurveys in 2014, 2016 and 2017. The mean time interval between the first and second survey was 11 years (range 9 to 16 years). The stands were dominated by Norway spruce (*Picea abies*; a majority of the stands) or Scots pine (*Pinus sylvestris*; minority) and comprised both managed production forests of different ages and semi-natural and natural old forests. Stand ages (in the second survey) ranged from 10 to 243 years. The youngest stands, aged 10 to 20 years, were recent clear-cuts with a few retention trees and typically some dead wood originating from the pre-cutting stand, while older, mature stands had a minimum age

of 64 years. Stands aged 21 to 63 years (henceforth referred to as *young production stands*) were surveyed once, confirming their lack of suitability for most species (Table S1). For all species, the main model was fitted for *mature stands* only. Where the data permitted, separate models were additionally fitted for *recently clear-cut stands* for use in projections into the future (Table S1). See Supporting Information, section *Projections of future dynamics and occupancy* for the use of models based on these different data for projections.

In each stand, all dead trees (of minimum diameter 5 cm) and fruit body occurrences of focal polypore species were inventoried in a sample plot (of size 20 × 100 m in 98% of stands; across all stands, plot size ranged from 0.08 to 0.94 ha, mean 0.2 ha). Dead trees were measured to determine diameter at breast height, volume and decay stage, classified into five categories via physical (with a knife) and visual inspection (following Hottola & Siitonen, 2008; Table S2). In most stands (83%), also the remaining stand area outside the sample plot was surveyed for fruit body occurrences on larger logs (minimum diameter 15 cm), to quantify local connectivity to living fruit bodies of focal species.

The studied species include nine polypores (poroid Aphyllophorales) and one corticioid (*Phlebia centrifuga*, corticioid Aphyllophorales; Table 1). Species' degree of specialization in the boreal forests of Finland is a dimensionless measure estimated by Nordén et al. (2013, their measure R7) based on species occurrence on 100,000 dead trees in 500 sites in Finland. Nordén et al. (2013) first predicted the occurrence probabilities of each species in dead trees representing different tree types (e.g. uprooted log, broken log, cut log, snag), tree species, tree diameters and decay stages, and in sites representing different levels of naturalness, canopy closure, dead-wood connectivity at the local (forest stand), landscape and regional scales. Specialization was then measured by the fraction f of resource units that were needed to include 50% of the predicted occurrences, selecting first those resource units with the highest occurrence probabilities. The specialization level was defined as $-\log f$, so that a high value represents specialization, that is, that a small fraction of the real resource units (dead wood pieces) in the forest constitute a suitable resource for the focal species. Specialization was not related to spore size across our 10 species (Figure S1).

As we could not trace individual dead trees through time, species data were aggregated to presence/absence per plot. We used only data from stands where the plot contained at least one suitable dead tree at both time points since otherwise the species cannot be present. A suitable dead tree was a downed spruce log of a minimum diameter that depended on the species modelled. For *T. abietinum*, *Gloeophyllum sepiarium* and *Phellinus viticola*, which commonly use small logs, a minimum diameter of 5 cm was used, resulting in a dataset of 214 stands, comprising 65 recently clear-cut stands and 149 mature stands. For the remaining species a minimum diameter of 10 cm was used, resulting in a dataset of 184 stands, comprising 52 recently clear-cut stands and 132 mature stands. The occupancy histories in all suitable mature stands formed the basis for the analysis (Table 1).

Explanatory variables were quantified at the level of the plot, stand and region. *Plot-level variables* were total downed spruce

TABLE 1 Overview of the 10 study species with their acronyms, ordered by increasing degree of specialization with regard to resource requirements as estimated by Nordén et al. (2013). Colonization–extinction history shows the observed occurrence histories in mature stands (occurrence 0 or 1 in the first and second survey, respectively). An occurrence history of '01' corresponds to a colonization event, while an occurrence history of '10' corresponds to an extinction event. N gives the total number of stands included in the analysis, that is, with suitable dead wood at both time points. *Trichaptum abietinum*, *G. sepiarium* and *Phellinus viticola* occurred on dead wood of minimum diameter 5 cm (149 suitable stands), while the remaining species required dead wood of a minimum diameter of 10 cm (132 suitable stands). Base colonization and base extinction rates are median rates [with 95% credible interval (CI) limits] estimated with intercept-only models, that is, dynamic occupancy models where colonization and extinction rates are estimated as intercepts only without including effects of environmental variables

Species[a]	Acronym	Degree of specialization[b]	Colonization–extinction history '00'	'01'	'10'	'11'	N	Base colonization rate (95% CI)	Base extinction rate (95% CI)
Trichaptum abietinum	tricabie	2.4	7	30	10	102	149	0.83 (0.67, 0.97)	0.06 (0.03, 0.11)
Fomitopsis pinicola	fomipini	2.5	26	38	11	57	132	0.62 (0.48, 0.78)	0.09 (0.04, 0.17)
Gloeophyllum sepiarium	gloesepi	2.9	103	23	16	7	149	0.20 (0.14, 0.28)	0.55 (0.36, 0.72)
Antrodia serialis	antrseri	3.1	54	33	12	33	132	0.41 (0.31, 0.53)	0.17 (0.08, 0.28)
Phellinus viticola	phelviti	3.1	76	33	9	31	149	0.33 (0.24, 0.43)	0.14 (0.06, 0.25)
Phellinus ferrugineofuscus	phelferr	4.0	87	28	3	14	132	0.26 (0.19, 0.35)	0.16 (0.06, 0.31)
Phellinus nigrolimitatus	phelnigr	4.3	96	20	5	11	132	0.19 (0.13, 0.27)	0.23 (0.09, 0.42)
Phlebia centrifuga	phlecent	5.2	119	11	1	1	132	0.10 (0.06, 0.15)	0.49 (0.18, 0.8)
Fomitopsis rosea	fomirose	5.3	113	14	0	5	132	0.13 (0.08, 0.18)	0.22 (0.07, 0.46)
Amylocystis lapponica	amyllapp	5.5	115	9	1	7	132	0.09 (0.05, 0.14)	0.21 (0.07, 0.42)

[a]Taxonomy following (Niemelä, 2016).

[b]Degree of specialization corresponds to measure R7 in Nordén et al. (2013), estimated from the fraction of 100,000 surveyed dead-wood units that would be suitable for the target species. Higher specialization values indicate that a smaller fraction of studied dead-wood units represented suitable substrate.

dead-wood volume (m³/ha), mean diameter (cm) and mean decay stage of downed spruce dead-wood objects per plot. *Stand-level variables* were the age of the stand (at the time of the second survey), the volume of living spruce (m³/ha; extracted from the 2013 Finnish Multi-source National Forest Inventory data; © Natural Resources Institute Finland, 2015; Mäkisara et al., 2016), and local connectivity, defined as the presence of an active dispersal source (a living fruit body) in the same stand, recorded during initial surveys in 215 of the 258 stands during 2000–2005. For 18 stands, data on local connectivity were missing, but we could fill some data gaps with (presence-only) data from records from the Finnish Biodiversity Information Facility (FinBIF, 2019a, 2019b). Missing data were replaced by a presence in case of a FinBIF record within 1 km of the plot. The remaining missing data were estimated during model fitting via so-called data imputation within the Bayesian modelling framework (Gelman et al., 2004). In models used for projections, local connectivity was excluded from the model selection procedure, as we did not have information on future local connectivity. *Landscape-level variables* were measures of connectivity to old spruce-dominated forest with the minimum age of 100 years (potential dispersal sources), assuming different dispersal ranges (following Mair et al., 2017), and, lastly, climatic variables (mean annual temperature and the sum of precipitation through May to November; for details see Supporting Information).

To estimate detection probability, intensive repeat surveys were conducted in 30 smaller plots (0.04 ha) across four stands in 2014 and 2016. Detection/non-detection data were pooled across all

species for modelling, except for three common generalist species with sufficient species-specific data (Table S3).

2.2 | Dynamic colonization–extinction modelling

For each species, we fitted a hierarchical Bayesian state-space model of colonization and extinction to presence–absence data at the plot level, while accounting for imperfect detection (dynamic occupancy models, Royle & Kéry, 2007; details in Supporting Information section *Model structure*). These models relate the true occupancy status z in plot i at time t, imperfectly observed with detection probability p_{det}, to the the observed occurrences y as

$$y_{i,t}|z_{i,t} \sim \text{Bernoulli} \left\{ z_{i,t} p_{det} \right\}, \qquad (1)$$

and estimate local colonization probability c and extinction probability e from changes over time in the true occupancy status z of each plot i as

$$z_{i,t} \sim \text{Bernoulli} \left\{ \left(1 - z_{i,t-1} \right) c_{i,t} + z_{i,t-1} \left(1 - e_{i,t} \right) \right\}. \qquad (2)$$

A colonization event, that is, the observation of fruit bodies in a plot in the resurvey but not in the initial survey, encompasses arrival of the species through dispersal, establishment, growth to sufficient size, mating and fruiting. However, theoretically, it can also result from establishment before the initial survey and fruit

bodies forming between the surveys, or from multiple such events (colonization, extinction and recolonization). An extinction event on the other hand records the absence of fruit bodies in a plot in the second survey where they were recorded in the first survey, which necessarily results from both a failure to persist (due to natural mortality/demographic stochasticity) and a failure to re-colonize.

Effects of environmental variables on c and e can be modelled using linear models with an appropriate link function. To estimate base rates of colonization and extinction irrespective of environmental conditions, we first fitted intercept only models for all species. We related the estimated base rates to species' degree of specialization, testing linear and log-linear relationships. To establish effects of environmental variables on colonization and extinction, we then fitted the main models, successively including variables on first colonization rate, then extinction rate, as

$$\text{cloglog}\left(c_{i,t}\right) = \alpha_c + \sum_k \beta_k X_{k,i,t},$$

$$\text{logit}\left(e_{i,t}\right) = \alpha_e + \sum_k \gamma_k X_{k,i,t}, \qquad (3)$$

for k variables with associated parameters β_k for colonization probability and γ_k for extinction probability. In a forward stepwise model selection procedure, variables were conservatively added to the model starting with the most proximate plot level dead-wood variables, subsequently adding increasingly distal variables (stand level and then landscape level). Possible unimodal responses (quadratic terms) were tested for dead-wood volume, mean decay stage and stand age. For *P. nigrolimitatus* the effect of local connectivity could not be tested due to insufficient data. Landscape-scale connectivity to old forest was not tested in the four least specialized species, as these are not confined to old forest. Figure S2 shows correlations between key plot-level and stand-level variables. All variables were scaled to mean zero and unity variance prior to analysis (Table S4).

Forward stepwise model selection was performed based on a combination of ecological knowledge, 95% credible intervals of parameter posterior distributions, deviance reductions for comparison of models with the same number of parameters, and posterior predictive checking (Bayesian *p*-values; Gelman et al., 2004; Mackenzie et al., 2018). The Deviance Information Criterion was used with caution, as it is not appropriate for complex hierarchical models (Hooten & Hobbs, 2015) where calculating the number of effective parameters in the model becomes difficult. More weight was given to credible intervals for assessing individual parameters and posterior predictive checks for comparing entire models.

We used the Bayesian approach to fit the models. It relies on Markov chain Monte Carlo (MCMC) simulations for model fitting and parameter estimation. Uninformative prior distributions (specifically a normal distribution with mean zero and variance 100) were used for all parameters except intercept-only models, where a normal distribution with mean zero and variance 1 was used to facilitate convergence. For each model, we estimated the posterior distributions using three MCMC chains, with a burn-in of 200,000 discarded iterations, and subsequent 100,000 iterations thinned by 300, resulting in final posterior distributions of 1,000 iterations on which inferences were based. Parameters were summarized by the median and 95% credible intervals. Models were fitted in JAGS, run through R version 3.5.0 using library jagsUI (Kellner, 2019; Plummer, 2003; R Core Team, 2018).

2.3 | Projections of species colonization–extinction dynamics for representative example stands

To explore long-term colonization–extinction dynamics and the resulting occupancy over time, we used a random sample of production stands and set-asides from a boreal landscape simulated for 100 years into the future (Moor et al., in prep), using the PlanWise application of Heureka (Wikström et al., 2011). PlanWise is a forestry decision support tool that allows projection of stand conditions into the future based on empirical tree growth functions, ingrowth of new trees, mortality and management decisions. Dead wood is continuously supplied, resulting from tree mortality and decomposes following the one-time chronosequence method (Harmon et al., 2000). Starting conditions were taken from boreal Swedish National Forest Inventory plots (Fridman et al., 2014), and projected into the future assuming Nordic business as usual clearcutting forestry (Supporting Information section *Scenario of future forest development*). Set-asides are stands that are left unmanaged, that is, they are set aside from forestry actions and allowed to develop naturally. To compare future metapopulation dynamics and occupancy between production stands and set-asides, we utilized an age-stratified random sample from the simulated landscape (>10,000 stands) consisting of 100 production stands and 100 set-asides, where the initial age was chosen to be uniform, specifically 20 stands each in five 40-year age classes between 0 and 200 years. Note that in spite of the initial uniform age distribution [mean (*SD*): production stands = 99 years (56), set-asides = 97 years (59)], production stands were characterized by lower amounts of dead wood [mean (*SD*): production stands = 2.9 m³/ha (3.1), set-asides = 11.5 m³/ha (8.4)] and living spruce volume [mean (*SD*): productions stands = 55.9 m³/ha (66.3), set-asides = 82.2 m³/ha (90)] (Figure S3). Based on the Swedish National Forest Inventory data, these conditions reflect the current state of a subset of the Nordic forests.

To initialize the projections, species occurrence was predicted using a model for species occurrence that included the same variables that affect colonization probability (Table S5). Projections into the future were simulated using the main models and, where available for the different species, auxiliary models for clear-cut stands (Table S6; Figure S4). In stands of ages for which our models did not apply, mechanistic assumptions were used: (a) in stands with no suitable dead wood, species could not occur (i.e. $p_{occ} = 0$, $p_{col} = 0$, $p_{ext} = 1$); (b) specialist species could not occur in recently clear-cut stands (*P. ferrugineofuscus* to *A. lapponica*, Tables S5 and S6), nor in young production stands (*P. viticola* to *A. lapponica*, Tables S5 and

S6). The inclusion of assumptions based on expert knowledge on species' ecology beyond the scope of models can improve forecasts through greater ecological realism and is preferable over extrapolation beyond the available model's range (Kearney & Porter, 2009).

3 | RESULTS

3.1 | Colonization and extinction rates depend on species specialization

Generalist species had higher colonization rates and a tendency for lower extinction rates than specialist species. Base rates of colonization independent of environmental conditions ($p_{col, base}$) varied from 0.83 (median, 95% CI: 0.67, 0.97) for the generalist species *T. abietinum* to 0.09 (0.05, 0.14) for the most specialized species *A. lapponica* (Figure 1a; Table 1).

Gloeophyllum sepiarium was the only exception to these general patterns, showing lower $p_{col, base}$ = 0.20 (0.14, 0.28), and higher $p_{ext, base}$ = 0.55 (0.36, 0.72) than other generalist species. For *P. centrifuga*, $p_{ext, base}$ was difficult to estimate due to data limitations (Table 1), resulting in a very uncertain estimate with a high median $p_{ext, base}$ = 0.49 (0.18–0.8).

Log-transformed base colonization rates of species decreased linearly with increasing degree of specialization ($F_{1,8}$ = 43.4, $p < 0.001$, with R^2 = 0.84; Figure 2). $p_{ext, base}$ only increased with increasing degree of specialization when *G. sepiarium* was excluded from the analysis ($F_{1,7}$ = 14.3, $p < 0.01$, with R^2 = 0.67; Figure 2b). If included, the relationship was not significant ($F_{1,8}$ = 2.6, $p = 0.14$, with R^2 = 0.25; Figure 2b).

3.2 | Effects of forest conditions on colonization and extinction probability

The colonization probability (p_{col}) of all species but *G. sepiarium* increased with increasing dead-wood volume (Figure 3a; see
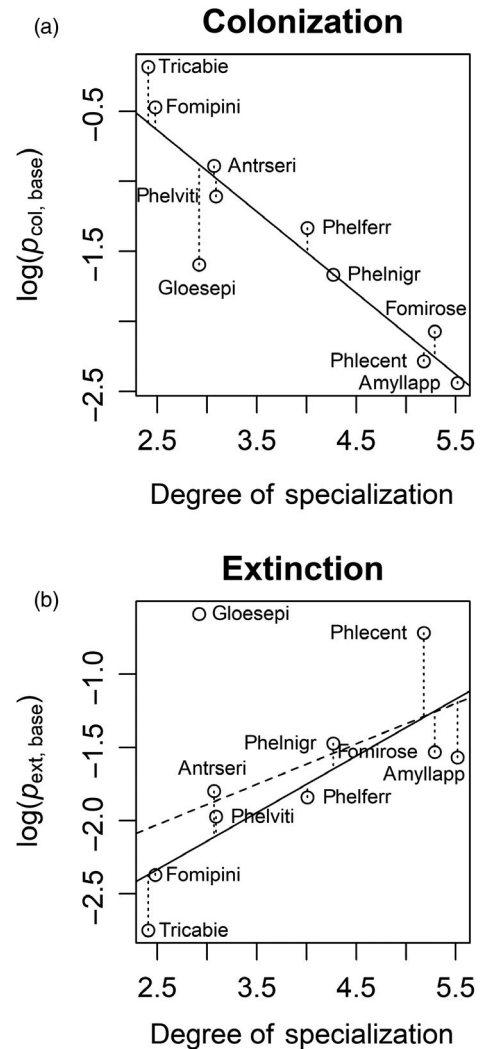

FIGURE 2 Log-linear relationships between median base rate of colonization (a) and extinction (b) and species' degree of specialization (see Table 1 for full species names). Colonization probability decreased log-linearly with increasing specialization. For extinction probability, the increase with increasing specialization was not significant (dashed line) unless the outlier species *Gloeophyllum sepiarium* was excluded (solid line)
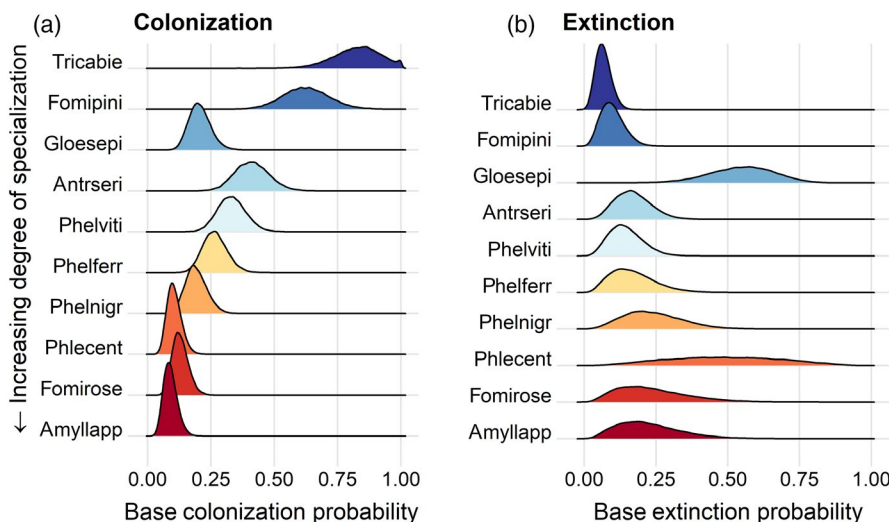

FIGURE 1 Posterior distributions of base rates of colonization (a) and extinction (b) estimated with intercept-only models. Base rates are estimated without inclusion of environmental variables and thus represent average rates across all sites. Species are ordered along increasing degree of specialization (see Table 1 for full species names)

FIGURE 3 Relationships between probabilities of colonization (a–c) and extinction (d, e) and explanatory variables, shown as partial regression plots where all other variables are at their mean value. Species are ordered according to increasing degree of specialization
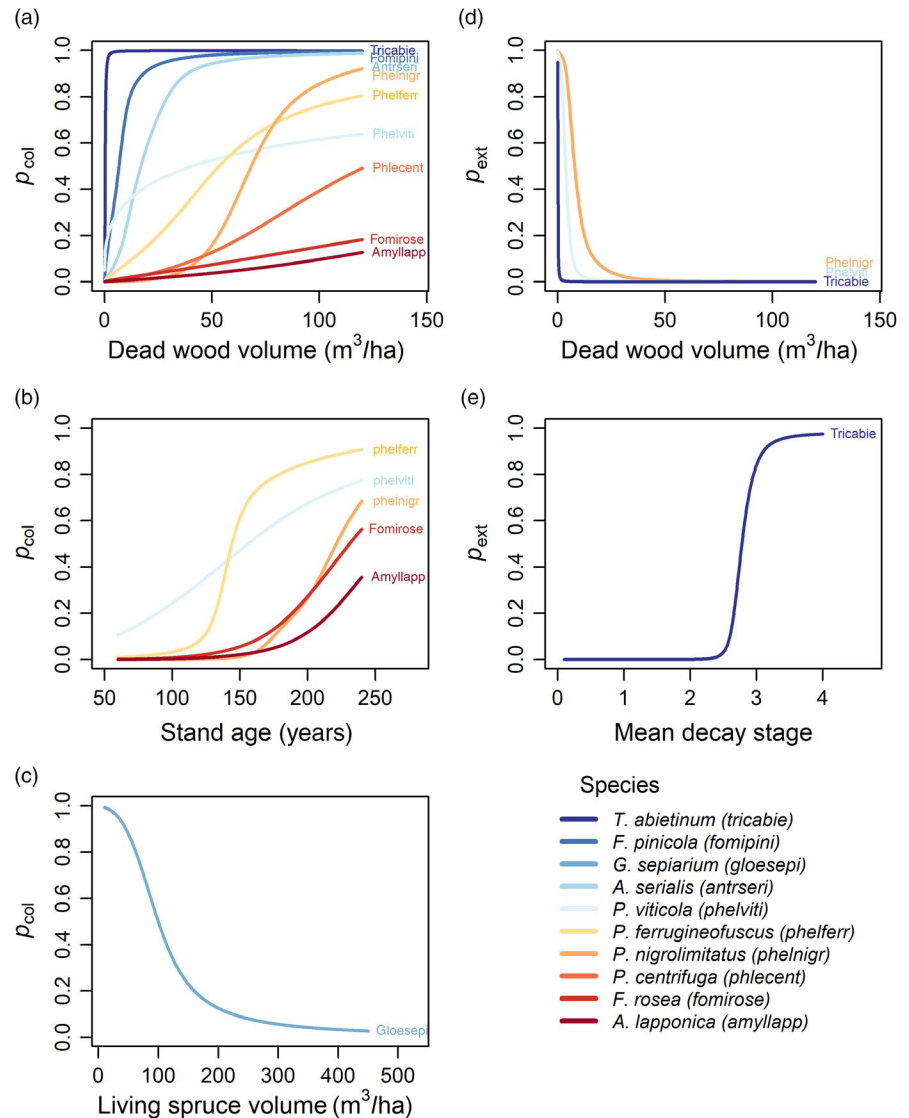

Table S7; Figure S5 for parameter estimates). Plot-level mean dead-wood diameter was not retained in any of the final models. During model selection, however, weak positive effects of mean diameter were found on p_{col} of *F. pinicola, P. viticola, P. nigrolimitatus, P. centrifuga and F. rosea*; these effects disappeared upon inclusion of either dead-wood volume or stand age and were not retained in the final models.

Similarly, weak unimodal responses to mean decay stage were present during model selection for *G. sepiarium, P. ferrugineofuscus, P. centrifuga* and *A. lapponica*, but were not retained in final models. The more specialized species, except for *P. centrifuga*, further showed increasing colonization probabilities with increasing stand age (Figure 3b). *Phlebia centrifuga* showed a weak positive response to stand age, which had, however, not sufficient statistical support to be retained in the model. *Gloeophyllum sepiarium* additionally showed decreasing p_{col} with increasing volume of living spruce in the stand (Figure 3c).

The colonization probabilities of generalist species showed a steep positive response to dead-wood volume already at low amounts, while in more specialized species the probabilities only gradually increased, even at high volumes of dead wood. Similarly, p_{col} increased at earlier stand ages for the intermediately specialized species *P. viticola* and *P. ferrugineofuscus*, while for the highly specialized species, p_{col} only increased noticeably above stand ages of 150 years.

p_{col} of two specialist species (*P. centrifuga* and *A. lapponica*) increased strongly in the presence of a local dispersal source (at least one living fruit body) elsewhere in the stand at the first survey time point (Figure 4). In models fitted without this variable (for use in projections), the other selected variables remained the same for *P. centrifuga*, while for *A. lapponica*, stand age entered the model in place of the presence of a local dispersal source (Table S7). Neither landscape-scale connectivity nor climate variables were retained in any of the final models.

Extinction probabilities (p_{ext}) were more difficult to estimate, and were modelled by an intercept only for most species, that is, the base rate was fitted. Exceptions were the generalists *T. abietinum* and *P. viticola*, and the specialist *P. nigrolimitatus* for which p_{ext} decreased steeply with increasing dead-wood volume (Figure 3d), and

T. abietinum where p_{ext} increased with mean dead-wood decay stage (Figure 3e; Table S7).

Model fit as indicated by posterior predictive checks was generally adequate (Figure S6). The worst, albeit still acceptable, Bayesian *p*-values for predictions of occupancy at the second time point were 0.18 for *A. serialis* and *P. viticola*. For both of these relatively common species, this underestimation of occupancy in the second survey resulted largely from a concurrent overestimation of extinction events; for *A. serialis* in conjunction with an underestimation of colonization events (Figure S6).

As a result of the dependencies of species' p_{col} on dead-wood volume and stand age, expected p_{col} were substantially lower in a

typical managed production stand than a natural stand with old-growth characteristics (Figure S7). p_{ext} was the same for most species (corresponding to the base extinction rate), except for three species with higher p_{ext} in production stands (Figure S7).

3.3 | Projected future occupancy in a dynamic landscape

In set-asides, occupancy probabilities (p_{occ}) of all species (except *G. sepiarium*) were stable or increased over time (Figure 5a). p_{occ} of generalist species (*T. abietinum*, *F. pinicola*, *A. serialis*) remained
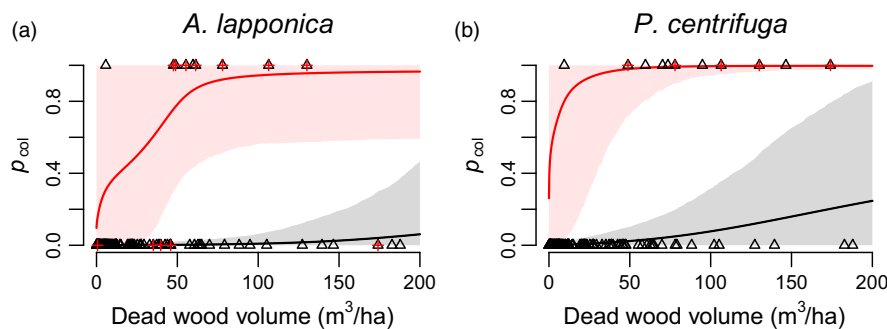

FIGURE 4 Effect of local connectivity on colonization rates of the two specialist species *Amylocystis lapponica* (a) and *Phlebia centrifuga* (b). Shown is the response of p_{col} (with 95% credible intervals) to dead wood volume without (black line) and with (red line) the presence of a local dispersal source. Black triangles show colonization events (at $y = 1$) and no colonizations (at $y = 0$) in all stands; red crosses show the presence of a local dispersal source in these stands
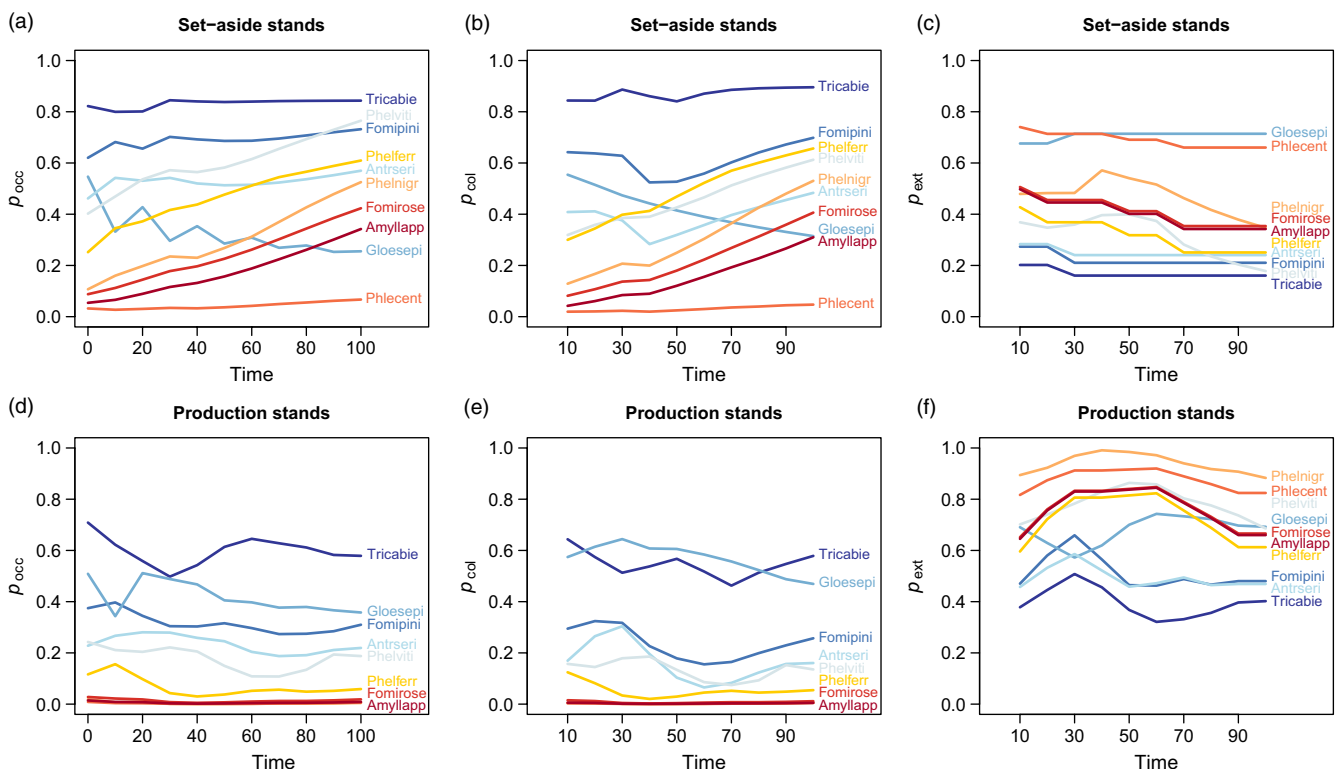

FIGURE 5 Predicted average occupancy (a, d), colonization (b, e) and extinction probability (c, f) in a set of 100 set-aside stands (a–c) and 100 production stands (d–f) simulated over 100 years. For species colour key, see Figure 2

relatively stable or decreased (*G. sepiarium*), while p_{occ} of specialist species increased steadily, apparently without reaching a ceiling (Figure 5a). In production stands, p_{occ} was lower than in set-asides for all species (Figure 5b). p_{occ} of all species here first decreased slightly, but then remained relatively stable over time.

These trajectories were driven by the combination of higher colonization rates and lower extinction rates in set-asides than in production stands, with the exception of *G. sepiarium* (Figure 5a,d). In set-asides, species had generally higher colonization rates that further increased over time, as well as lower and decreasing or stable extinction rates (Figure 5b,c). In production stands, colonization rates remained relatively stable or decreased intermittently, while extinction rates generally increased over the first few decades to then decrease again, but always at higher levels than in set-asides (Figure 5e,f). The initial increase in p_{ext} here was mainly a result of an increase in the proportion of recently clear-cut stands early in the simulation, after the oldest production stands were harvested.

During simulations, mean stand age, dead-wood volumes and the volume of living spruce increased gradually in set-asides, while in production stands, these variables decreased first and then stabilized or rebounded (Figure S3). In spite of the uniform stand age distribution in the beginning, initial species occupancies were generally higher in set-asides than in production stands (Figure 5a) due to higher starting dead-wood volumes in set-asides [mean (*SD*) [m³/ha]: production = 2.9 (3.1), set-aside = 11.5 (8.4)].

4 | DISCUSSION

We have estimated the dynamic rates of colonization and extinction for 10 species of wood-decaying fungi ranging from generalist to specialist species, using an extensive large-scale repeat-survey dataset. Our study revealed a striking pattern of decreasing colonization probability with increasing degree of specialization across species, along with concomitantly increasing extinction rates. Given the high, observed plot-level turnover rates, this suggests that the low occupancy of specialists in the landscape is largely maintained by their lower colonization rates, which strongly depended on local habitat quality. The high sensitivity of colonization probability to habitat quality, in combination with a tendency for higher local extinction probability, lead to very low predicted future occupancies of specialist species in production forest. In contrast, specialist occupancies increased continually in set-asides, suggesting a potential for relatively high future occupancies in these umanaged stands.

4.1 | Mechanisms shaping colonization–extinction dynamics

Sessile species occurring on ephemeral patches must maintain a dynamic equilibrium to persist in the landscape. We show that the low landscape-scale occupancy of highly specialized species results mainly from low colonization probabilities, but also slightly higher local extinction rates. Three mechanisms are likely to be involved in shaping these dynamics. First, the high sensitivity of colonization probability to patch quality in specialists. Second, a positive feedback between low colonization rates and low landscape-scale occupancy. Third, potential dispersal limitation of specialist species.

First, the high sensitivity of colonization probability to patch quality of specialists restricts successful colonizations to a smaller subset of the potentially suitable patches. While generalists' colonization probabilities responded to increases in dead-wood volume already at low amounts, specialist species required much higher dead-wood volumes, as well as older stands for increases in colonization probability. Rather than an effect of stand age per se, this is likely due to a higher likelihood of the presence of suitably large logs of the right decay stage with increasing total dead-wood volume and stand age. The specialists studied here are known to require large-diameter dead wood of natural origin (Berglund et al., 2011; Norberg et al., 2019; Nordén et al., 2013) and at a particular decay stage (intermediate for most specialists, advanced for *P. nigrolimitatus*; Stokland & Kauserud, 2004). While neither mean diameter nor mean decay stage explained colonization rates in any of the species, this may be attributed to the plot-level data aggregation. If a lot of dead wood is required for the presence of large and late decay stage logs, then the mean across all dead wood will not reflect the presence of a few such logs. With increasing stand age, however, the amount of dead wood and the density of large diameter and late decay stage logs should increase. For the key unit in landscape scale studies, that is, the stand as represented here by the plot, forest age and total dead-wood volume are thus the main variables explaining the colonization probability of wood-decaying fungi.

Second, a feedback loop between low colonization rates and low landscape-scale occupancy likely maintains the latter via decreased connectivity to dispersal sources and thereby constrained colonization rates, in accordance with theory (Hanski, 1999). This also prohibits rescue effects, where local populations are rescued from extinction by immigration, and thereby increases local extinction rates (Eriksson et al., 2014; Gonzalez et al., 1998). The observed higher extinction rates of specialists further imply the absence of a colonization–extinction trade-off, as has been described at the patch-scale for plants (Verheyen et al., 2004). The specialist fungi we studied are characterized by both low colonization probabilities *and* higher extinction probabilities at the plot-scale, which emphasizes their sensitivity to environmental stochasticity. At the scale of individual dead-wood objects, established wood-decaying fungi are thought to persist until the object becomes unsuitable (Jönsson et al., 2008). Specialists may achieve a large mycelial mass through superior competitive abilities on their preferred substrate (Nordén et al. unpublished data), but that may not be reflected at the plot-scale. Persistence at the plot-scale may also result from colonization of other, potentially newly formed, logs within the plot. The higher extinction probabilities of specialists thus probably also reflect the scarcity of suitable substrate within the plot, preventing recolonization and persistence. Pre-emptive competition from species with

locally higher abundance and priority effects may further mediate local recolonization success (Fukami, 2015; Norberg et al., 2019).

Third, dispersal limitation of specialist species may further limit the potential for successful colonization if suitable substrates are rare and scattered. The strong positive effect of a local dispersal source on the colonization rates of two specialist species (*P. centrifuga* and *A. lapponica*) is consistent with previous results that show strong dispersal limitation for specialist wood-decaying fungi already at distances of tens to a few hundred meters from the nearest fruit body (shown for *P. centrifuga* by Norros et al., 2012). In a study within a 7.5 ha old-growth Norway spruce stand, Jönsson et al. (2008) also demonstrated small-scale distance-dependence of colonization probability on individual, occupied dead-wood objects for *P. centrifuga*, *P. ferrugineofuscus* and *P. viticola*. These studies support the proposition that, in these species, a high density of spore deposition is required for successful colonization of new substrate as a very small fraction of the spores manage to establish, rather than greater dispersal distance of individual spores per se (Edman, Gustafsson, et al., 2004; Norros et al., 2014). Note that all of our species had relatively small spores (4.3–9 μm in length, no relationship with the degree of specialization), which all could be expected to potentially disperse far (Kuparinen et al., 2007; Norros et al., 2014). However, the hyaline spores of our focal species lose their viability quickly when exposed to UV light and cold temperatures during dispersal (Norros et al., 2015). If spore survival and mass deposition of spores is restricting successful colonization to short distances, then contiguous forest with high-quality dead wood may be required for the landscape-scale persistence and spread of specialist fungi.

Our measure of landscape-scale connectivity did not affect colonization probabilities of specialists. This measure integrates the distance-weighted volume of old spruce-dominated forest, but does not account for the actual amount of dead wood present or for the occurrence of fruit bodies producing dispersal propagules in the surrounding landscape. It may thus be too coarse a metric to detect true connectivity dependence. Occurrence of a rare bryophyte in forest stands, for example, was explained by the landscape-scale connectivity to stands occupied by the species (presumably producing dispersal propagules), but not by connectivity to stands assumed suitable for the species (Snäll et al., 2004). However, other work found effects of landscape-scale connectivity to surrounding old forest on the occurrence probability of rare specialist fungi (e.g. Abrego et al., 2017; Nordén et al., 2018). For the same spruce specialists as studied here, Nordén et al. (2018) found higher occurrence probability in sites with higher landscape-scale connectivity. It is thus also probable that we did not achieve the statistical power to detect effects of landscape-scale connectivity on colonization probabilities of specialist species, for which we had less data. Due to our forward stepwise model selection procedure, the effects of local habitat quality were included first, such that less power remained to estimate responses to subsequently added variables from larger spatial scales. We are confident, however, that the colonization probability of generalist species is not explained by connectivity, as shown by Nordén et al. (2018). Generalist wood-decaying fungi are able to persist also in managed production forest, which for specialists represents an unhospitable matrix, such that for generalists, the proximity and density of old and natural forests is not vital (Berglund et al., 2011; Penttilä et al., 2006).

Gloeophyllum sepiarium deviated from the overall pattern by comparatively lower colonization and higher extinction probabilities than other species of a similar degree of specialization. The distinct ecology of this species may account for this. Unlike most other species, it favours open forests or canopy gaps and sunny, exposed dead wood (Jönsson et al., 2008), which is reflected in the negative response of its colonization probability to the volume of living spruce in the stand. It also frequently occurs on clear-cuts (Junninen et al., 2006), which may contribute to its higher predicted occupancy in production forests than in old-growth forests.

4.2 | Future dynamics in production and set-aside stands

Predicting potential future species occupancy in landscapes where relevant conditions change in dynamic and mutually dependent ways necessitates simulations. Our projections for *P. ferrugineofuscus* were very similar to forecasts by Mair et al. (2017) under a possible national forest management scenario for Sweden for 2020–2110. Also using a dynamic colonization–extinction model, Mair et al. (2017) estimated a mean relative change in occurrence probability of −41% in production stands and an increase of +129% in set-aside stands, compared to our estimates of −49% and +142%. Our projections for *P. ferrugineofuscus* and our scenario of forest development under management approximating business as usual thus align well with expectations derived from national scale policy analysis.

We found consistently lower future occupancies of all the studied species (with the one exception of *G. sepiarium*) in managed production stands than in set-aside, unmanaged stands. Lower occupancies resulted largely from substantially lower colonization probabilities, which were sensitive to forest conditions especially for specialist species, in combination with higher extinction probabilities in production stands. The projection results are in line with assessments of occurrence probability of wood-decaying fungi based on correlative habitat suitability models (Berglund et al., 2011; Mair et al., 2018; Nordén et al., 2013). Frequent disturbance from clear-cutting, the absence of large old trees and large diameter dead wood of natural origin and in advanced decay stages is known to negatively affect the occupancy of specialist wood-decaying fungi in production forest (Berglund et al., 2011; Junninen & Komonen, 2011; Norberg et al., 2019; Nordén et al., 2013). Note that our models do not include spatially explicit, realized connectivity to species occurrences in the surrounding landscape that constitute active dispersal sources, but instead imply a background spore deposition rate contained in the estimated colonization rate (in the intercept parameter quantifying the base rate). Regional extinction after a drop of occupancy below a threshold (Ovaskainen & Hanski, 2003) can therefore not occur in our forecasts, but is possible in reality. The projected occupancy of *A. lapponica*,

F. rosea, *P. centrifuga* and *P. nigrolimitatus* in production stands is so low that regional extinction resulting from low landscape-scale occupancy is possible in landscapes dominated by production forest.

In set-asides, specialist species (especially *A. lapponica*, *F. rosea* and *P. nigrolimitatus*, but also *P. ferrugineofuscus* and *P. viticola*) continually increased, suggesting the potential for high occupancy under suitable conditions. Our findings using colonization–extinction models further strengthens the trust in the findings of Mair et al. (2018), which were based on habitat suitability models. Their results similarly predicted monotonous increases of suitability in legally protected set-asides, which however plateaued after 70 to 80 years. Time lags in the response of species' colonization–extinction dynamics to altered conditions might explain the projected continual increase in occupancy of set-asides in our projections. Wood-decaying fungi have been shown to respond to changing availability of suitable patches with considerable time lags (Berglund & Jonsson, 2005; Gu et al., 2002). It is therefore imperative to consider the dynamic rates of colonization and extinction that underlie observed occurrence patterns to accurately assess the effect of environmental conditions (Nordén et al., 2020; Yackulic et al., 2015) or the impact of different forest management options. Accounting for these dynamics, our projections illustrate the potential for rather high occupancies of these species if forests would consist of natural undisturbed habitat throughout.

5 | CONCLUSIONS

In summary, our study of the dynamics of wood-decaying fungi has shown that landscape-scale occurrence probabilities are mainly constrained by the colonization process. Disentangling the dynamic processes that result in occupancy sheds more light on the actual mechanisms that determine species' occupancy, and the rarity of many specialist species. Compared to the commonly used correlative species distribution models or occupancy models, dynamic colonization–extinction models enable more realistic projections of future responses of species to changes in their environment. Quantitative estimates of the effect of different environmental variables on the dynamic rates of colonization and extinction are critical for realistic predictions of species' responses to land-use change. In specialist but not generalist species, colonization probability was highly sensitive to local habitat quality, and for two species to the presence of active nearby dispersal source. Low colonization rates of specialist species maintain their low landscape-scale occupancy. Projections of long-term dynamics clearly showed potential for high occupancy even for specialist species in set-aside stands, but not in production stands. This demonstrates the need for adequate amounts of dead wood and the continued presence of old stands in forest landscapes to ensure the persistence of specialist wood-decaying fungi.

AUTHORS' CONTRIBUTIONS

T.S., J.N. and H.M. conceived the ideas and designed methodology; J.N., R.P., J.S. and T.S. designed the data collection; H.M. and T.S. analysed the data; H.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.13526.

DATA AVAILABILITY STATEMENT

Data and code are archived on Zenodo https://doi.org/10.5281/zenodo.4081059 (Moor et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.