Occupancy versus colonisation-extinction models for projecting population trends at different spatial scales

Jenni Nordén[1], Philip Harrison[2], Louise Mair[3], Juha Siitonen[4], Anders Lundström[5], Oskar Kindvall[6], and Tord Snall[7]

[1]Norwegian Institute for Nature Research Oslo
[2]Uppsala University
[3]Newcastle University
[4]Natural Resources Institute Finland
[5]Swedish University of Agricultural Sciences
[6]Calluna AB
[7]Sveriges lantbruksuniversitet

May 5, 2020

Abstract

Understanding spatiotemporal population trends and their drivers is a key aim in population ecology. We further need to be able to predict how the dynamics and sizes of populations are affected in the long term by changing landscapes and climate. However, predictions of future population trends are sensitive to a range of modelling assumptions. Deadwood-dependent fungi are an excellent system for testing the performance of different predictive models of sessile species as these species have different rarity and spatial population dynamics, the populations are structured at different spatial scales and they utilize distinct substrates. We tested how the projected large scale occupancies of species with differing landscape-scale occupancies are affected over the coming century by different modelling assumptions. We compared projections based on occupancy models against colonization-extinction models, conducting the modelling at alternative spatial scales, and using fine or coarse resolution deadwood data. We also tested effects of key explanatory variables on species occurrence and colonization-extinction dynamics. The hierarchical Bayesian models applied were fitted to an extensive repeated survey of deadwood and fungi at 174 patches. We projected higher occurrence probabilities and more positive trends using the occupancy models compared to the colonisation-extinction models, with greater difference for the species with lower occupancy, colonization rate and colonization:extinction ratio than for the species with higher estimates of these statistics. The magnitude of future increase in occupancy depended strongly on the spatial modelling scale and resource resolution. We encourage using colonisation-extinction models over occupancy models, modelling the process at the finest resource-unit resolution that is utilizable by the species, and conducting projections for the same spatial scale and resource resolution at which the model fitting is conducted. Further, the models applied should include key variables driving the metapopulation dynamics, such as the availability of suitable resource units, habitat quality and spatial connectivity.

Introduction

Understanding spatial and temporal population trends and the drivers behind them is a key aim in population ecology (Turchin 2003). Such knowledge is also necessary when planning actions to mitigate the pervasive effects of habitat loss, fragmentation and climate change (Pressey et al. 2007). In fragmented landscapes, large-scale population trends often result from metapopulation dynamics, through the local processes of

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colonisation and extinction (Hanski 1999). Theoretical studies suggest that metapopulation viability strongly depends on landscape features and processes such as the availability, size and longevity of suitable habitat patches (e.g. old stands or appropriate tree structures in forest landscapes), spatial connectivity, patterns of patch destruction and creation, and interactions between these (Johst et al. 2011).

Habitat patches naturally appear and disappear through succession and disturbance, but in production landscapes these processes are largely replaced by management and conservation actions (Kuuluvainen 2009). A continuous local supply of new resource units is critical for the persistence of species that are confined to ephemeral resource units such as living or dead trees. These species need to balance the local extinctions (stochastic or resulting from resource unit disappearance) with local colonisations of new resource units. These units need to have high enough density in space and frequency through time to allow regional persistence (Gourbiere and Gourbiere 2002, Snäll et al. 2003).

It is important that forecasts of the long-term effects of management and conservation actions on species populations are realistic and accurate, because today's decisions may give rise to adverse or unexpected consequences that may be difficult to overturn (Guisan et al. 2013). To parameterise models of spatially realistic metapopulation dynamics (Hanski 1999) to be used as a basis of forecasts, one should ideally have collected data repeatedly on the size and distribution of all habitat patches and local populations, and information about the dispersal rate and range of the species (Higgins and Cain 2002). Such data are usually lacking and thus other solutions must be sought.

A common method to predict species responses to future environmental changes is to use Species Distribution Models (SDMs) fit to a single (static) snapshot of presence/absence data across the landscape (Elith and Leathwick 2009). These include occupancy models which we evaluate for projection herein. SDMs associate the spatial pattern of a species' occurrence across a subset of the populations in the landscape with habitat and climate data. Such models fitted to snapshot pattern data, however, assume that the current occurrence pattern of the species is at metapopulation equilibrium with its environment. Violations of this assumption can produce biased results as at disequilibrium, occupancy-environment relationship are expected to vary over time and space (Yackulic et al. 2015). For species with high colonization-extinction dynamics, e.g. many mammals, birds and insects, the species distribution pattern can indeed be assumed to much depend on the current landscape structure (Ovaskainen and Hanski 2002). If the landscape structure changes, e.g. due to management operations, the species distribution will promptly adjust to the new structure. For such species, SDMs may produce reliable projections of future population trends. In contrast, for sessile species with slow colonization-extinction dynamics, such as probably many fungi and plants, the distribution patterns may not reflect the present spatial structure of the landscape (Ovaskainen and Hanski 2002). With changing landscape structure, the species distribution patterns will reflect the past rather than the current landscape structure (Snäll et al. 2004, Paltto et al. 2006). Thus for sessile species, a SDM may be inappropriate for predictive modelling, e.g. resulting in overly optimistic projections in situations where the area and connectivity of the habitat have decreased over time.

When data are available over multiple time points it is preferable to acknowledge the temporal change and model the processes which generated the patterns (Gimenez et al. 2014), for instance using what we refer here to as colonisation-extinction models (aka dynamic occupancy models, occupancy dynamics models or multiseason occupancy models) (MacKenzie et al. 2003). Under models for colonisation-extinction dynamics, the past landscape structure becomes less influential, because colonisation events that take place between the two surveys reflect the current locations of the dispersal sources. Especially for species with slow colonization-extinction dynamics, SDMs based on occupancy–environment relationships can be expected to produce biased future occupancy patterns (Ovaskainen and Hanski 2002), and it should be better to base predictions on models that incorporate both rates of local colonization and extinction and their dependence on environmental conditions (Yackulic et al. 2015). Projections of future population development have focused on changes in the distribution patterns (del Rosario Avalos and Hernandez 2015), while estimates of the future summed occupancies or population sizes have to date received little attention.

A major issue in predictive ecology is the scale at which ecological processes should be considered (Chave

2013, Evans et al. 2013, Mouquet et al. 2015). Predictions made from models fit to data at different spatial modelling scales can lead to drastically different conclusions (León-Cortés et al. 1999). When modelling is performed at too large a spatial modelling scale, local heterogeneities in resource quality and quantity relevant for the species in question will go undetected (Mouquet et al. 2015). SDM model performance has been shown to depend on the chosen grain size, especially for systems that can be relatively accurately modelled, but the direction and strength of this effect depends strongly on the type of species (Guisan et al. 2007).

In studies of species that are restricted to a particular resource unit in the habitat patch, such as living trees or deadwood, field surveys often involve a trade-off between resource resolution, i.e. the minimum size or the types of the resource unit to be included (e.g. minimum deadwood diameter), and the survey area covered (Zotz and Bader 2011). If small or particular kinds of resource units are abundant, including them in the survey may make it difficult to attain a survey design that would cover the within-habitat heterogeneity and give information about the occupancy-environment relationship that is general for the focal species and habitat type. It is justifiable to exclude the small resource units from the survey if they are seldom used by the species and if they therefore do not significantly influence its population dynamics (Zotz and Bader 2011, Loos et al. 2015).

There were four aims with our study. The first aim was to test for differences in the future occupancies of (1) species with different landscape-scale occupancy when using occupancy versus colonisation-extinction models. The occupancy models are based on data from one point in time while the colonisation-extinction models are based on data from two points in time. As data suitable for occupancy models are available and frequently used for many species and many geographical areas, it is important to find out how the trends and magnitudes of change that occupancy models reveal differ from the ones revealed by colonisation-extinction models for which data are currently scarce. Colonisation-extinction models are expected to be more realistic for predicting changes as they focus on rate of changes (of occupancy). We hypothesise that the difference in the projected future occupancy between occupancy and colonisation-extinction models is greater for a species with lower landscape-scale occupancy because rare species can be expected to have slower colonization-extinction rates and therefore track changes in forest landscapes with a greater delay than common species. We further test for differences in projected future occupancies between modelling the data at (2) three different spatial modelling scales (cell, plot or patch), and (3) two resource-unit resolutions (two different minimum diameters for deadwood to be included) to find out how scale and resolution influence predictions of future population trends. Inferences were made based on projections of occupancy of two model species in forest production land and in land set aside from production across the whole boreal zone of Sweden. The projections were obtained through stochastic simulations using the occupancy and colonization-extinction models fitted at different spatial scales and resource-unit resolutions. Building the models was part of our fourth aim, specifically (4) to test which local and regional environmental variables explain the occupancy and colonization-extinction dynamics at different spatial scales and resource-unit resolutions.

Materials and methods

STUDY PATCHES AND DATA COLLECTION

We obtained the large-scale, extensive data on colonization-extinction dynamics by surveying spruce deadwood and fruit bodies of the focal polypore fungi in 174 forest patches across southern and central Finland once in 2003-2005 (Nordén et al. 2013) and then resurveying them in 2014. These two surveys revealed the colonisation and extinction events that had taken place between the first and the second survey and constituted the data to estimate (parameters for) rate of change in occupancy in the colonization-extinction models. Data from the first survey formed the basis for the occupancy models.

A forest patch is a contiguous and homogeneous forest area that is surrounded by other land types or forests of different age or tree species (Fig. 1). The survey plot was of the size 20 m x 100 m and subdivided into

survey cells of 20 m x 20 m. All patches were dominated by Norway spruce (*Picea abies*) and covered a range of forest types: clear-cuts with retention trees (53 patches, 16 of which had a plot, 16 x 5 cells), woodland key habitats (56 patches, 56 plots, 56 x 5 cells); and managed forests (65 patches, 65 plots, 65 x 5 cells). In each forest patch, in both surveys (2003-2005 and 2014), we surveyed the two fungal species (*Phellinus ferrugineofuscus* and *P. viticola*) and deadwood both in each cell and in the remaining patch area. See Appendix S1 for a detailed description of the data collection and the focal species.

MODELLING OCCUPANCY AND COLONISATION-EXTINCTION

For each species, we fitted hierarchical Bayesian state-space models to the presence-absence data of the species at three spatial modelling scales (cell, plot and patch) and two deadwood resource resolutions (diameter [?]5 cm or [?]15 cm). We included covariates collected for different spatial modelling scales that we hypothesised would explain the occupancies and colonization-extinction dynamics of the focal species (Appendix S1). For the comparison with the colonisation-extinction models, we also fitted occupancy models to data from the first survey.

A detailed description of the occupancy and colonisation-extinction models at the cell level is provided in Appendix S1. The number of colonisations and extinctions recorded allowed including the effects of covariates on colonisation probability of mature patches. For the extinction probability and the colonisation probability of clear-cut patches, only intercepts (i.e. the rate parameters) were estimated.

The covariates to retain in the final fitted models were determined with forwards stepwise model selection. This model selection was based on overlap of 95% credible intervals with 0, reduction in deviance and biological knowledge on the species, as suggested by Gelman and Hill (2007). The models were fit using OpenBUGS (Lunn et al. 2009) in R through the library R2OpenBUGS (Sturtz et al. 2005). The data and computer code used for models, simulations, and statistical analyses are archived in the Swedish National Data Service, https://snd.gu.se/en.

PROJECTING POLYPORE OCCUPANCIES THE COMING CENTURY

To answer our study questions, we utilized available projections of forest conditions on National Forest Inventory (NFI) plots in adjacent boreal Sweden between 2010 and 2110, the nationwide Forestry Scenario Analysis by the Swedish Forest Agency (Claesson et al. 2015, Eriksson et al. 2015; Appendix S1). Next we projected the occupancy dynamics of the species for the same time period. For each polypore species, the final fitted occupancy model was utilised to initialise the occupancy states in the first time step, here 2010. We used 10-year time steps to simulate the subsequent colonisation and extinction dynamics on the NFI plots until 2110 using the final fitted colonisation-extinction model with its estimated parameter values. For investigating the effect of making projections based on occupancy models, the final fitted occupancy model was instead used for each time step.

All projections were made based on drawing 1000 values from the joint posterior distribution of the parameters from the fitted models. All NFI plots with no dead spruce or those with ages 26-63 were given an occupancy probability of zero, because of the typical absence of spruce deadwood suitable for the species in forests of this age range (Mair et al. 2017).

Results

COLONISATION AND EXTINCTION EVENTS

We observed several colonization events, especially in the mature patches/plots/cells, and several extinction events, especially in the clear-cut patches/plots/cells (Table 1). The clear-cut forests lost almost all of their occurrences between the two surveys, and very few colonisations took place.

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The species with the highest occupancy in the landscape, *P. viticola* , had higher colonization rates and higher ratios of colonization/extinction than the less frequent species, *P. ferrugineofuscus* at all spatial modelling scales and both resource resolutions (Table 1). We observed the highest extinction rates for *P. viticola* at the fine resource resolution ([?]5 cm) and the smallest spatial modelling scale (20 x 20 m). For *P. ferrugineofuscus,* the colonisation and extinction rates were comparable between the fine resource resolution at the smallest spatial modelling scale and the coarse resource resolution at the largest spatial modelling scale. At the fine resource resolution, the colonization rate increased and extinction rate decreased with increasing spatial modelling scale. Similarly, at the coarse resource resolution, the largest spatial modelling scale had the highest colonisation rates and the lowest extinction rates. Extinctions resulted both from host logs disappearing due to decomposition and stochastically where suitable logs were recorded in both surveys.

SUMMARIES OF FITTED MODELS

For *P. ferrugineofuscus* , the responses – probabilities of occurrence and colonisation – were explained by the volume of spruce logs at the cell scale (here reflecting the presence of large logs), whereas the plot-scale responses were explained by stand age, and the patch-scale responses by stand age or connectivity (Table S2-1). The amount of data available allowed estimating the effects of one or two covariates (Table S2-1) and hence only one or two rounds of model selection were required. For *P. viticola,* the same responses were explained by the density of spruce logs (here reflecting many small logs) and connectivity at the cell and plot scales, and the density of spruce logs at the patch scale. The best fitting measure of connectivity for *P. ferrugineofuscus* was the presence/absence of old ([?]120 years) spruce forests within a distance that corresponds to a mean dispersal distance of 1 km. For *P. viticola* , two measures of connectivity were important: the volume of spruce or presence/absence of spruce in old forests within a distance that corresponds to a mean dispersal distance of 10 km. Deadwood resource resolution had an influence on whether the density of logs was selected or not in the models for *P. viticola.*

FUTURE PROJECTIONS

We predicted higher occurrence probabilities and relative changes from the projections based on the occupancy models than the colonisation-extinction models. The general probability of our model species increasing across all forest land was higher using the occupancy models than the colonization-extinction models. The main reason for this was the predicted smaller decrease in production land when using the occupancy model (Figs. 2 and 3, Table 2, Figs. S3-1-4). For both model species, the probability of an increase over all forest patches was unity for the projections based on the occupancy models but ranged from 0.59 to 0.96 for *P. ferrugineofuscus* and from 0.88 to 1 for *P. viticola* based on the colonisation-extinction models. Occupancy models were more sensitive to the chosen resource resolution and spatial modelling scale than colonisation-extinction models. Specifically, there was larger variation among the projection trajectories when using the occupancy models (Figs. 2 C-D, 3 C-D) than when using the colonisation-extinction models (Figs. 2 A-B, 3 A-B).

For both model species we projected an increase in the set-asides across all spatial modelling scales and resource resolutions, owing to increasing density and volume of deadwood, stand age and connectivity for set-asides (Figs. S4-1 and S4-2). The relative change in occurrence across all the forest patches depended on the degree to which the positive trends in the set-asides could compensate for the declines (where predicted) in the production land (Figs. 2 and 3, Table 2, Figs. S3-1-4). We predicted higher occurrence probabilities for *P. viticola* than for *P. ferrugineofuscus* , and an increase in future occupancy was more likely for *P. viticola* than *P. ferrugineofuscus* across the two types of models, spatial modelling scales and resource resolutions.

The differing forecasts of the occupancies of the two polypore species resulted from a combination of the general occupancies or colonization-extinction rates (Table 1) and the forecasts of the covariates of the fitted models (Table S2-1). For a description of these links, see Appendix S1.

The magnitude of future increase in occupancy depended strongly on the spatial modelling scale (cell, plot,

patch) (Figs. 2 and 3). For both model species in mature forests, colonisation rates were the lowest at the cell scale and increased going up via plot to patch scales, while the opposite was true for the extinction rates (Table 1). In clear-cut forests, colonisation events were rare and extinction events were common at all spatial modelling scales (Table 1). The consequence of these overall colonization and extinction rates were that the probability of future increase across all forest land was higher for both model species when the projections were conducted using the plot- or patch-scale models than using the cell-scale model (Table 2, Figs. S3-1-4). Applying the fine resource resolution ([?]5 cm) colonisation-extinction model for *P. viticola* , the probability of a decline in the production land was much lower using the cell- than the plot-scale models (0.08 versus 0.66). However, here the 0.08 probability of decline also means a 1-0.08=0.92 probability of increase, which is thus detected by the fine resource resolution.

Resource resolution (all or only large deadwood included) had a great impact on the future predictions. For *P. viticola* , we predicted clearly a more positive future population development with the fine resource resolution ([?]5 cm) than with the coarse resolution ([?]15 cm), and the precision of the prediction was higher for the coarse resolution (Table 2, Figs. S3-3-4). For *P. viticola* we predicted, probably erroneously, a decline in the production land when we did not account for the small resolution deadwood units. For *P. ferrugineofuscus* , future decline in production land seemed certain based on the coarse resolution (both model types) but less probable (0.47 and 0.38) based on occupancy models that used the fine resolution. Projections based on the occupancy models for *P. ferrugineofuscus* showed a decline in the production land only for the models based on the coarse resource resolution; for the fine resolution the trends were more stable (Fig. 2; Table 2, Fig. S3-2). Projections based on the occupancy models for *P. viticola* similarly showed an almost certain (probability [?]0.99) decline in the production land only when we modelled at the coarse resource resolution; at the fine resolution the probability of decline was zero (Fig. 3; Table 2, Fig. S3-4). We predicted the greatest increase in future occupancy when modelling at the fine resource resolution. The effect of resource resolution was less pronounced in the colonisation-extinction models than in the occupancy models.

Discussion

When making predictions for ecological systems it is seldom clear from the outset which models to use and at what scale and resolution the modelling should be performed (Evans et al. 2013). Based on the joint posterior parameters distribution from hierarchical Bayesian models fitted to an extensive colonisation-extinction dataset on deadwood-dependent fungi, combined with realistic forest projection data, we show that the future trends predicted were sensitive to all four questions addressed – to the type of modelling performed, the landscape-scale occupancy of the model species which affects their colonization-extinction rates, the spatial scale of model fitting and the resolution of the resource-unit data. For our model species, the resource-unit resolution had a strong impact on the predictions especially for the species that frequently uses the smaller deadwood that were excluded from the coarse resolution data. Type of model (occupancy vs. colonisation-extinction model) substantially affected the magnitude of the predicted change, while the effect of the spatial scale of model fitting was also considerable. We encourage the use of colonisation-extinction models over occupancy models (or more generally, Species Distribution Models, SDMs), modelling the process at the finest resource-unit resolution that is utilizable by the species, and conducting projections for the same spatial scale and resource resolution at which the model fitting is conducted.

COLONISATION-EXTINCTION MODELS PRODUCE MORE REALISTIC PREDICTIONS

The occupancy models, corresponding to the frequently applied SDMs (Franklin and Miller 2010), predicted what we believe is unrealistically positive population development. Our conclusion is based on knowledge about the study system and population development of the focal species during the recent decades. Compared to the colonisation-extinction models, the occupancy models predicted higher occurrence probabilities and

less steep future declines in the production land leading to more positive increases across all the forest land combined. Future declines are thus underestimated with occupancy models, especially if habitat amount is decreasing and the distances to dispersal sources are consequently increasing. Many of these species have slow life history which is often associated with rarity (Pilgrim et al. 2004). The occupancy models reflect the species distribution patterns which reflect the past rather than the current amount and connectivity of the habitat. Even more, occupancy SDMs often use data collected over a long time period during which the environment may change. The colonisation-extinction models are more realistic because they reflect the rate of change from one time step to another. Their higher realism, that they more mechanistically model the process leading to the occupancy pattern, may also explain why they were less sensitive to the spatial scale modelled and the resource resolution. Limitations of their use may be the costs of making another survey of the system, and the time span necessary for changes to take place.

The colonization-extinction rates observed at the patch and plot scales in this study were surprisingly high. Several local colonisations and extinctions had taken place during just 9-11 years, which challenges the view of very long time lags, from decades to much over hundred years, before a new equilibrium between the metapopulation and its environment is reached (Sverdrup-Thygeson et al. 2014). The high turnover rate may be partly explained by the ecology of our focal species which are not confined to very large or slowly decomposing dead trees. However, our results also suggest that in many species of deadwood-dependent fungi, the delay in response to environmental change is shorter than previously thought. Despite this, metapopulation equilibrium cannot be assumed as the colonization-extinction models project lower future species occurrence than the occupancy models. This is especially so for *P. ferrugineofuscus* with a lower ratio of colonization/extinction. The species is thus tracking the changes in its environment with a delay, especially in the production forest with the highest rate of forest stand and deadwood turnover. The colonisation-extinction models account explicitly for the temporal change, while occupancy models assume that the current occurrence pattern is at metapopulation equilibrium with the environment.

CONSIDERATIONS OF APPROPRIATE SPATIAL SCALE OF MODEL FITTING

The predictions of the future population development depend strongly on the chosen spatial scale of the statistical model fitting. For the less frequent *P. ferrugineofuscus* the predicted population increase by the year 2110 ranged from 0% to 42%, depending on which of the three models were applied in the projections. We generally recommend conducting model fitting and simulation at a small spatial scale. This allows modelling and projecting the dynamics at the level at which the local population dynamics take place, including accounting for proximal variables within each patch and among patches. However, this recommendation of simulating detailed dynamics ignores the computational power required. Moreover, for making projections for a landscape or region, simulation of complete deadwood and population dynamics across the chosen spatial scale is required, ideally including dispersal between patches. However, for rare species with slow colonization-extinction dynamics and few occurrences on a small proportion of logs in each patch (here especially *P. ferrugineofuscus*), simulating detailed, small-scale deadwood dynamics may be inefficient. For such species, model fitting and projection simulation at a larger scale (here plot or patch) may be more appropriate, especially if the general question of the study concerns a landscape or region. Thus, conducting modelling and projection simulations at a more aggregated spatial resolution is acceptable. On the other hand, when modelling at a larger spatial scale, more distal predictors (e.g. stand age) are selected – these affect the species more indirectly than the proximal predictors they replace (Merow et al. 2014). The use of the more distal predictors may bring a higher level of uncertainty into the analyses, as it assumes a strong correlation between the distal predictors and the resources they replace. Moreover, if there is bias in this assumed correlation, then this bias is transferred into biased projections.

APPROPRIATE RESOURCE RESOLUTION DEPENDS ON THE ECOLOGY OF THE STUDY SPECIES

Resource-unit resolution can have a considerable influence on the predictions of future population development. For *P. viticola* the most striking difference in the projections was between using the fine or coarse resolution deadwood data. Excluding the smaller deadwood units resulted in the conclusion that this species will decline in the production land, while when including them the decline was much reduced. For *P. ferrugineofuscus* the population trends based on the coarse and fine deadwood data were more similar. This is because of the preference of *P. ferrugineofuscus* for larger-diameter dead trees and consequently the models for this species having deadwood volume (influenced mostly by larger trees) as the significant covariate of resource availability. With different minimum sizes of deadwood inventoried, the deadwood quantities such as density and volume of deadwood – the measures of resource availability used as covariates in the models and projections – may also change (Hottola et al. 2009). However, it may also be wise to choose the resource-unit resolution of analysis during the initial exploratory analysis. For example, a species may occur on a substrate of subordinate quality (e.g. small diameter logs) in a high-quality area (old-growth forest with high species abundance) resulting from mass effect. If erroneously assuming that it may occur on such substrate also in low-quality areas (albeit at low probability) and if this substrate is very common in these lower-quality areas, then one is likely to overestimate the future occupancy of this species, especially in low-quality areas. This may be the case for *P. ferrugineofuscus* whose colonization probability increases with diameter (Jonsson et al. 2008), but which only occasionally occurs on the very common 5-10 cm logs. It may thus be justified to exclude the small resource units from the survey or analyses as their influence on population dynamics is minor (Loos et al. 2015). Another option, if data quantity allows, is to include the interaction between substrate size and forest age. See Appendix S1 for more discussion on resource resolution and species ecology.

RELIABLE PREDICTION OF FUTURE OCCUPANCY

Despite the differing occurrence probabilities and rate of change in future occupancies produced by the occupancy and colonisation-extinction models, the direction of the change was usually the same. This is partly explained by the fact that the covariates selected for the colonisation probabilities were, in most cases, the same as those selected for the occupancy probabilities. Arguably, precise predictions of biological responses to environmental change, especially if extrapolating beyond current conditions and into the future, require elaborate mechanistic process-based models, driven by the detailed life history of the species (Evans et al. 2013). However, for essentially all species, including deadwood-dependent fungi, the data required to parameterise such models are still lacking. Inaccurate estimation of the rate of change in occupancy will lead to severe bias in future projections, e.g. when addressing the effects of global change (Dietrich et al. 2012) that may increase habitat turnover rates, making population persistence more dependent on a high number and good connectivity of habitat patches (Johst et al. 2011). The potential sources of bias in our predictions that we identified are detailed in Appendix S1. Nevertheless, with models for colonisations and extinctions accounting for key variables driving these metapopulation dynamics, such as the availability of suitable resource units, habitat quality (e.g. forest age) and spatial connectivity, we may detect the true future patterns and trends if they are strong.

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Table 1. Numbers recorded for each type of colonisation-extinction history for different forest age classes across the varying spatial modelling scales and resource resolutions. A history of '11' means that the patch was observed to be occupied at each survey event, whereas a history of '10' means that the patch was observed to be occupied at the first survey event but not the second. Rates are number of events observed divided by the number of events possible and occupancy is the proportion of modelling units occupied in the second survey.

Species	Age class	Spatial modelling scale	Resource resolution (diameter limit) (cm)	Colonisation-extinction history	Colonisation-extinction history	Colonisation-extinction history	Colonisation-extinction history	Colonisation rate	Extinction rate	Colonisation rate/extinction rate	C
				11	**10**	**00**	**01**				
P. ferrugineofuscus	mature	cell	5	0	5	357	17	0.05	1.00	0.05	(
			15	0	4	170	14	0.08	1.00	0.08	(
		plot	5	1	4	79	12	0.13	0.80	0.16	(
			15	1	4	61	10	0.14	0.80	0.18	(
		patch	15	4	7	66	17	0.20	0.64	0.32	(
	clear-cut	cell	5	0	10	127	0	0.00	1.00	0.00	(
			15	0	4	38	0	0.00	1.00	0.00	(
		plot	5	1	5	29	0	0.00	0.83	0.00	(
			15	0	5	15	0	0.00	1.00	0.00	(
		patch	15	2	4	23	1	0.04	0.67	0.06	(
P. viticola	mature	cell	5	1	10	338	30	0.08	0.91	0.09	(
			15	1	3	168	16	0.09	0.75	0.12	(
		plot	5	3	6	69	18	0.21	0.67	0.31	(
			15	3	3	55	15	0.21	0.50	0.43	(
		patch	15	7	6	61	20	0.25	0.46	0.53	(
	clear-cut	cell	5	1	11	124	2	0.02	0.92	0.02	(
			15	1	3	38	0	0.00	0.75	0.00	(
		plot	5	1	7	26	1	0.04	0.88	0.04	(
			15	1	6	12	1	0.08	0.86	0.09	(
		patch	15	2	8	18	2	0.10	0.80	0.13	(

Table 2. Mean change in occupancy across all forest land and in production land between 2020 and 2110 based on 1000 simulations from the full posterior distributions of the fitted models. Shown are also

95% Bayesian credible interval and probability of increase on all forest land and probability of decrease in production forest. All model types and resource resolutions predicted that there would be an increase in the set-asides with a probability of 1.00.

Species	Model type	Spatial modelling scale	Resource resolution (diameter in cm [?] value)	Resource resolution (diameter in cm [?] value)	Covariates and associated parameter estimates (95% Bayesian credible interval)
P. ferrugineo-fuscus	colonisation-extinction	cell	cell	5	deadwood volume 1.32 (0.47-2.54)
				15	deadwood volume 0.68 (-0.18-1.82)
		plot	plot	5	stand age 0.46 (-0.19-1.21)
				15	stand age 1.25 (0.12-3.42)
		patch	patch	15	connectivity* 0.45 (-0.06-1.05)
	occupancy	cell	cell	5	deadwood volume 1.23 (0.44-2.32)
				15	deadwood volume 0.66 (-0.22-1.82)
		plot	plot	5	stand age 0.51 (-0.10-1.18)
				15	stand age 1.02 (0.17-2.02)
		patch	patch	15	stand age 0.57 (0.06-1.14)
P. viticola	colonisation-extinction	cell	cell	5	density of dead trees 1.20 (0.48-2.20) and connectivity+ 0.99 (0.13-2.19)
				15	connectivity++ 2.91 (-0.02-1.01)
		plot	plot	5	density of dead trees 0.47 (0.75-6.58)
				15	connectivity++ 0.58 (-0.11-1.48)

Species	Model type	Spatial modelling scale	Resource resolution (diameter in cm [?] value)	Resource resolution (diameter in cm [?] value)	Covariates and associated parameter estimates (95% Bayesian credible interval)
		patch	patch	15	density of dead trees 1.14 (0.46-2.03)
	occupancy	cell	cell	5	density of dead trees 1.08 (0.49-1.79) and connectivity+ 0.77 (0.04-1.63) [connectivity+ 1.31 (0.50-2.35)]
				15	connectivity++ 2.02 (0.47-4.58) [connectivity++ 2.05 (-0.98-6.40)]
		plot	plot	5	density of dead trees 0.54 (0.08-1.03) [connectivity+ 0.71 (0.16-1.30)]
				15	connectivity++ 0.56 (-0.05-1.28)
		patch	patch	15	density of dead trees 0.90 (0.45-1.38)

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FIGURES
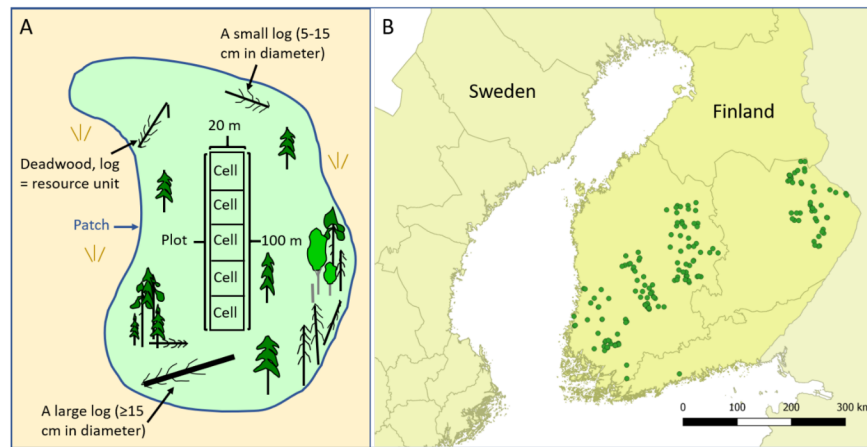
Fig. 1. (A) The three spatial scales of data collection and modelling with a sample *plot* with five *cells* (20 x 20 m) in a forest *patch* . Small logs were only surveyed within the sample plot while the large logs were surveyed across the whole patch. (B) The repeated survey data collected in 174 forest patches across boreal Finland used to build the occupancy and colonization-extinction models.
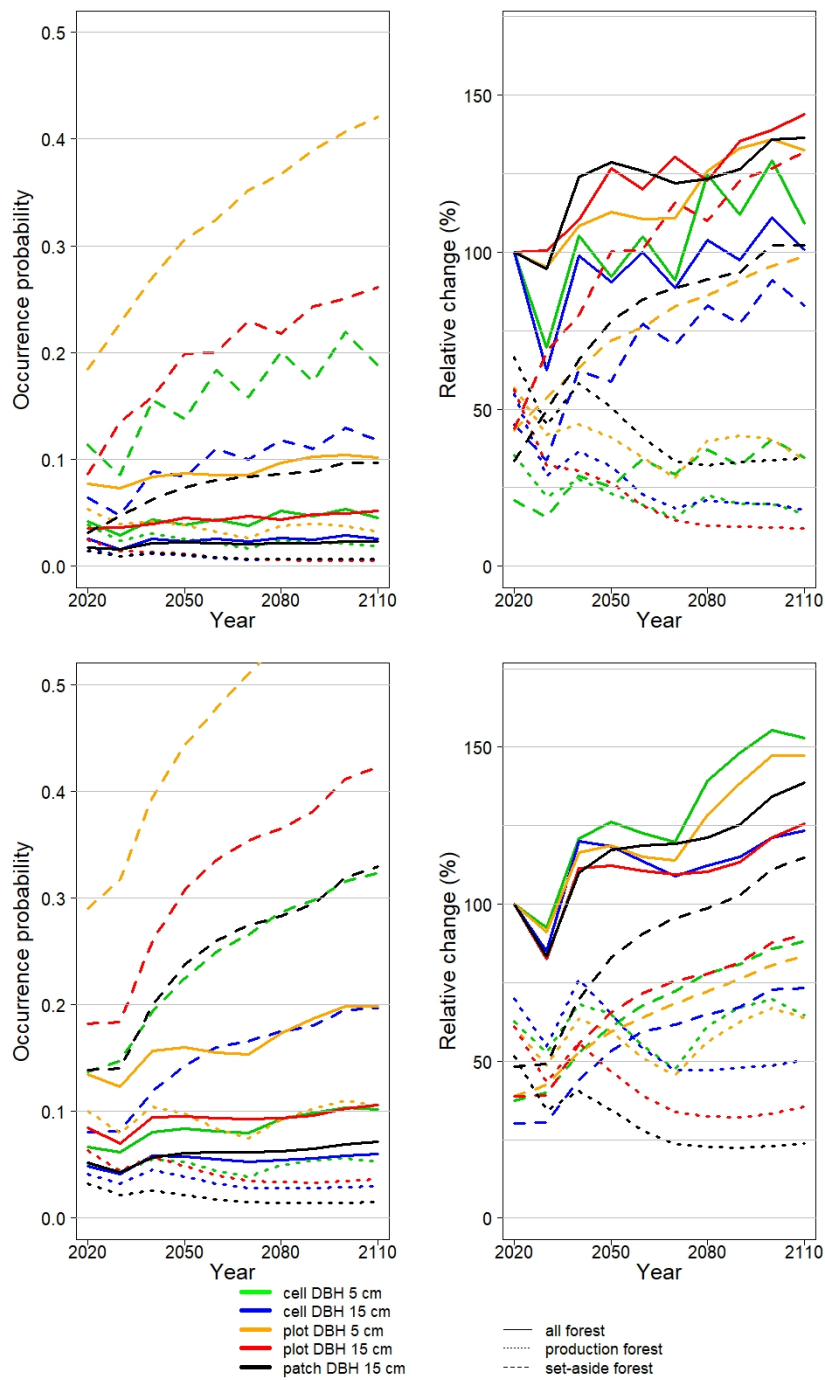
Fig. 2. Projections of mean occurrence probability and relative change in occurrence for *Phellinus ferrugi-neofuscus* over the present century in response to forest management. Panels A-B are for projections based on the colonisation-extinction models (*Col-ext*) and panels C-D for those based on the occupancy models (*Occ*). The projections are based on averaging the results based on 1000 simulations from the full posterior distributions of the fitted models.
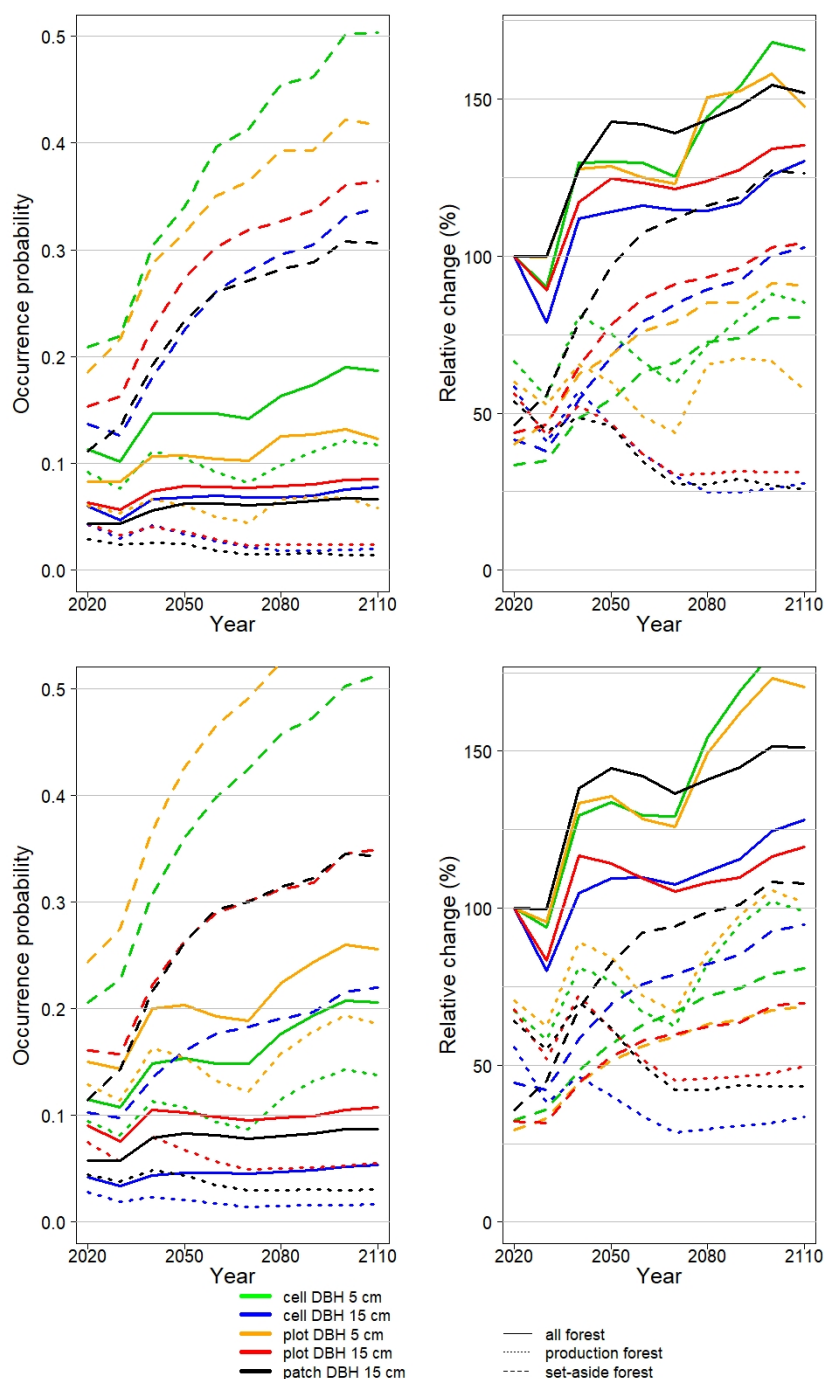
Fig. 3. Projections of mean occurrence probability and relative change in occurrence for *Phellinus viticola* over the present century in response to forest management. Panels A-B are for projections based on the colonisation-extinction models (*Col-ext*) and panels C-D for those based on the occupancy models (*Occ*). The projections are based on averaging the results based on 1000 simulations from the full posterior distributions of the fitted models.

Data Accessibility Statement

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The data are archived in the Swedish National Data Service, https://snd.gu.se/en.

Competing Interests Statement

There are no competing interests to report.

Authors' contributions

Acknowledgments

APPENDICES

APPENDIX S1.

Supplementary introduction

THE STUDY SYSTEM: DEADWOOD-DEPENDENT FOREST FUNGI

Forest-living, deadwood-dependent decomposer fungi are an excellent system for testing the performance of different kinds of predictive models, including occupancy versus colonisation-extinction modelling, and the effects of spatial modelling scale and resource resolution on species projection performance. Wood-decomposer fungi are sessile species that may respond to environmental change with a delay (Gu et al. 2002, Paltto et al. 2006, Sverdrup-Thygeson et al. 2014). Snapshot occupancy data on wood-decomposer fungi are abundant, but in the current study we also utilize a large dataset on colonization-extinction dynamics collected over a wide ecological gradient. The resource units of the wood-decomposer fungi are dynamic in the sense that they have a lifespan of years to decades and even centuries (depending on tree species, tree size and environmental conditions). Wood-decomposer fungi must therefore balance extinctions from resource units with colonisations elsewhere to ensure metapopulation persistence (Gourbiere and Gourbiere 2002). In production forests, and especially for rare species, rates of local colonisation are expected to be lower and rates of local extinction higher than in natural-like forests, because production forests have much less deadwood (<10%) than natural-like forests (Jonsson et al. 2016) and the quality of the deadwood present usually does not meet the requirements of specialised species (Nordén et al. 2013). In more common species, the differences in colonisation and extinction rates between production and natural-like forests can be assumed to be smaller, and therefore the bias in projection when using occupancy models instead of colonization-extinction models can be assumed to be smaller. As deadwood rich set-aside forests are typically small in area and few in the landscape, many species of wood-decomposer fungi have small local populations and appear to be limited by dispersal (Edman et al. 2004, Norros et al. 2012). Furthermore, these fungi occur in hierarchically structured systems: they are restricted to resource units (dead trees) located in forest patches (Fig. 1 in the main text). Empirical data have usually been collected in sample plots of varying size, i.e. survey data that usually cover only a part of each forest patch. The fungi are to a varying extent specialised with respect to resource-unit

characteristics, such as deadwood tree species, size, type and stage of decomposition (Nordén et al. 2013), and this gives an opportunity to test the effects of resource resolution on population projections.

Supplementary material and methods

DATA COLLECTION

In each forest patch, in both surveys (2003-2005 and 2014), we surveyed fungi and deadwood both in a survey plot and in the remaining patch area. The survey plot was of the size 20 m x 100 m and subdivided into survey cells of 20 m x 20 m (Fig. 1 in the main text). Within the cells we inventoried all deadwood with a diameter at breast height or base (depending on the deadwood type; referred to henceforth simply as diameter) [?]5 cm and length [?]1.3 m. For each spruce deadwood resource unit, we recorded the presence of fruit bodies of the focal species, spruce log diameter, length and decay stage. In the rest of the forest patch, i.e. in the remaining area outside the plot, we followed the same procedure but used a log diameter threshold of [?]15 cm. The lower resource-unit resolution in the remaining patch area was for covering the whole patch and for reaching a greater total number of patches than would have been possible if small-diameter deadwood was included everywhere.

All patches were dominated by Norway spruce (*Picea abies*) and covered a range of forest types: clear-cuts with retention trees (53 patches, 16 of which had a plot, 16 x 5 cells, Fig. 1 in the main text), age of dominant trees 5-20 years at the time of the second survey; brook-side and herb-rich woodland key habitats (56 patches, 56 plots, 56 x 5 cells), age 64-163 years, representing natural-like set-asides; and managed forests (65 patches, 65 plots, 65 x 5 cells) of varying age, 66-134 years, and intensity of management. Patch area ranged from 0.2 ha to 4.3 ha (mean 1.1 ha). We recorded the forest stand variables living spruce volume and stand age in the first survey. Stand age in the second survey was the number of years in between the two surveys added to the age in the first survey. Volume of living stand in 2014 was predicted based on the stand characteristics measured during the first inventory using the MOTTI forest stand simulator (Salminen et al. 2005, Hynynen et al. 2014). MOTTI is a stand-level forest management and decision support tool which includes tree-level models for predicting growth and mortality. Prediction models for stand dynamics and underlying data sets are presented in detail in Hynynen et al. (2014).

Focal polypore species

Our two focal polypore species have spruce deadwood as their main resource (Berglund et al. 2011), are very rarely found in patches 20-60 years old (because such forests lack suitable deadwood; H. Moor et al., unpublished data) which our empirical data did not cover; are absent on stumps and living trees (Berglund et al. 2011), and were expected to have differing occupancies and colonisation-extinction rates because of differing ecologies (see below). *Phellinus viticola* has fairly large and easily recognized perennial fruit bodies leading to high detectability (Halme and Kotiaho 2012). *Phellinus ferrugineofuscus* has annual-biennial fruit bodies but as they are large and also well recognizable long (up to years) after the fruit bodies have died, this species also has high detectability. Both species further usually produce many fruit bodies per log during many years so that the total fruiting period is several years, even >10 years (Ovaskainen et al. 2013). *Phellinus viticola* occurs on both small- and large-diameter logs (Juutilainen et al. 2011, Norden et al. 2013). *Phellinus ferrugineofuscus* occurs more frequently on larger logs but occasionally also on the thinner logs (Norden et al. 2013). *Phellinus ferrugineofuscus* is ecologically relatively specialised while *P. viticola* is rather generalised in its resource use. This likely explains the different proportions of occupied patches by the two species – *P. ferrugineofuscus* in 17% and *P. viticola* in 24% of the patches in 2014.

COVARIATES EXPLAINING OCCUPANCIES AND METAPOPULATION DYNAMICS

We hypothesised that covariates collected for different spatial modelling scales would explain the occupancies and colonization-extinction dynamics of the focal species. The resource unit covariates were density (ha^{-1}) and volume (m^3 ha^{-1}) of spruce logs, their mean diameter and stage of decomposition. The patch-level covariates were living spruce volume, age of the living stand (range 4-206 years), wetness, slope and aspect, measured as in Mair et al. (2017). Landscape-scale covariates were connectivity to potential dispersal

sources in the surrounding landscape, and annual temperature and precipitation (Mair et al. 2017). For our relatively rare and specialized focal species we hypothesised positive effects of all resource-, patch- and large-scale covariates on occupancy and colonization probability but negative effects on extinction probability. Two exceptions are stage of decomposition and wetness for which we expected a unimodal relationship. These hypotheses are supported by a large number of studies (e.g. Heilmann-Clausen and Boddy 2008, Abrego et al. 2017, Norden et al. 2018). Connectivity was calculated using satellite-based estimates of spruce volume and forest age in the form of 25 m grid cell layers (Tomppo et al. 2008). We followed the procedure of Mair et al. (2017), weighing the volumes of spruce in surrounding grid cells up to 20 km from the focal patch by $\exp(-\alpha d)$, where d is the distance to the focal patch and alpha is the relevant spatial scale of connectivity. We tested two different thresholds in forest age for inclusion of grid cells in the connectivity calculation (grid cells with stand ages [?]100 years or [?]120 years). We also tested replacing the spruce volumes in the connectivity measure with the presence or absence of forest exceeding the age threshold in each grid cell. As there is limited information available on species' dispersal distances we further tested three different values for α (0.1, 0.2 and 1), representing a mean dispersal distance of 10, 5 and 1 km, respectively. All covariates were log transformed, centred and standardised to have a mean of zero and a variance of unity.

Estimating the detection probability

One potential pitfall in models based on survey data is failing to account for unobserved species presences which can result in biased estimates of population trends and extinction probabilities (Kery et al. 2006, Rhodes et al. 2006). Non-detection has likely a minimal effect on our projections as we accounted for it in several ways. Imperfect detection because of species characteristics, surveyor behaviour or sampling design can result in incorrect conclusions about population trends if not accounted for with the sampling and model design (MacKenzie et al. 2003, Altwegg et al. 2008). Firstly, in fungi, the species might not be fruiting at the time of the survey even if it is present as mycelia inside the dead tree. However, our focal species have similar mycelial and fruit-body prevalences as well as short time delays from mycelial colonisation to fruiting (Ovaskainen et al. 2013) which makes fruit body data meaningful and reliable. Secondly, the species might go non-detected even if it is present and fruiting, but we accounted for this in our models. Finally, a subset of the resource units may be included in the survey (e.g. based on minimum diameter), which we show can result in an opposite conclusion as compared with including all resource units: *P. viticola* was predicted to decrease in production forests when its smallest resource units were excluded, but predicted to increase when all the resource units were included.

A further hierarchical level in Bayesian modelling allows the unobserved "true" state of the population to be linked to the observed state via a model for the observation process and thus accounting for detectability (Harrison et al. 2011). For estimating the detection probability of the fruit bodies of the two polypore species, a larger survey plot of 4 ha (64 cells of the size 25 m x 25 m) in an old-growth forest patch in southern Finland was first surveyed in 2002 and partly (15 cells) resurveyed twice in 2014. The principle for detectability data collection is similar as in the general survey, and hence the detectability estimate obtained was used in the modelling, see below. In 2014, a field team of two experts first carried out a regular resurvey without knowledge about the subsequent second resurvey. In the second resurvey, the 'intensive resurvey', the task was to do as thorough a survey as possible, taking the time needed, in a team of four experts that now knew the purpose of the intensive resurvey was to collect data for estimating detectability. We fit detectability models to these data assuming the occupancies recorded during the intensive resurvey represented the true occupancies of the polypore species encountered during the surveys. As the density of deadwood is considerably larger overall in this old-growth forest than in a typical managed forest, we included deadwood density as a covariate in the detectability models. The mean detection probability across all polypore species recorded in the intensive resurvey was estimated to be 0.9 for the mean deadwood density in managed forests, and >0.9 in forests with a low density of dead wood. In the colonisation-extinction and occupancy models, we therefore used a patch-specific detection probability 0.9.

MODELLING OCCUPANCY AND COLONISATION-EXTINCTION

For each species, we fitted hierarchical Bayesian state-space models to the presence-absence data of the species

at three spatial modelling scales (cell, plot and patch) and two deadwood resource resolutions (diameter [?]5 cm or [?]15 cm). We included covariates collected for different spatial modelling scales that we hypothesised would explain the occupancies and colonization-extinction dynamics of the focal species. For the comparison with the colonisation-extinction models we also fitted occupancy models. We used data from the second survey (174 patches surveyed both in 2003-2005 and 2014), and, for obtaining more reliable estimates of occupancy (but not colonization-extinction requiring two surveys) on clear-cuts, especially in relation to clear-cut age, we further included data from 19 patches from the first survey (2003-2005) that were not re-surveyed in 2014, and 22 patches that were cut between the two surveys and therefore only surveyed in the first survey.

In the modelling of species occupancy in clear-cuts, we only tested the effects of stand age and connectivity, and used all first-survey and resurvey data from clear-cut patches. We hypothesized (i) a negative age effect with time since cutting, and (ii) a positive effect of connectivity to surrounding dispersal sources. We did not test for the effect of deadwood quantity in clear-cut patches as most of the dead wood in these patches is made up of logging residues which, based on our data, are very seldom used by the focal species.

The response variables in the models (probabilities of occurrence, colonisation and extinction) were adjusted to a time scale of 10 years (only colonisation and extinction concerning change through time) and a spatial modelling scale of one hectare (Appendix S1). This was conducted by offsetting for the differing numbers of years between the surveys and the varying survey areas (cell, plot or patch). In the cell-level models, we included a random effect for the patches, which was assumed to be normally distributed with mean zero and a variance that was estimated during model fitting. In the projections we assumed a colonisation probability of zero and extinction probability of unity at such locations.

We fitted separate models at each of the cell-, plot- and patch scales and we detail the cell-scale model. The plot- and patch-scale models are simplifications of this model with the finest level indexing instead at the plot and patch scale, respectively.

For the cell-scale models we define $Z_{i,j,t}$ as the occupancy state of the focal species in cell i in patch j during survey period t. We assume that $Z_{i,j,t} \sim \text{Bernoulli}(\psi_{i,j,t})$. For the first survey period $\psi_{i,j,t} = \omega$ and in the following period:

$$\psi_{i,j,t} = (1 - Z_{i,j,t-1}) c^*_{i,j,t} + Z_{i,j,t-1} (1 - e^*_{i,j,t}),$$

where $c^*_{i,j,t}$ and $e^*_{i,j,t}$ give the colonisation and extinction probabilities, respectively. They have been offset to correct for the different numbers of years between the surveys and the different cell areas (20 m x 20 m or 25 m x 25 m), such that:

$$c^*_{i,j,t} = 1 - (1 - c_{i,j,t})^{n_{i,j,t} a_{i,j,t}}$$

$$e^*_{i,j,t} = 1 - (1 - e_{i,j,t})^{\frac{n_{i,j,t}}{a_{i,j,t}}}$$

where $n_{i,j,t}$ gives the number of years between the surveys divided by 10 (i.e. scaled by the typical number of years) and $a_{i,j,t}$ gives the cell area divided by 400 (i.e. scaled by the typical cell size in m^2). For a cell with ten years between the two surveys and an area of 400 m^2, $c^*_{i,j,t} = c_{i,j,t}$ and $e^*_{i,j,t} = e_{i,j,t}$. If the forest in the cell had not been clear-cut we assumed that:

$$\text{cloglog}(c_{i,j,t}) = \delta_2 + \sum_k \beta_k^{(C)} X_{k,i,j,t}^{(C)} + \sum_l \beta_l^{(P)} X_{l,j,t}^{(P)} + \gamma_{j,t}$$

and that $\text{cloglog}(e_{i,j,t}) = \varepsilon_2$. We chose to use the complementary log-log link function, cloglog, as due to its asymmetrical nature it is better suited than the more conventional logistic link function to cases where the probabilities are very large or very small (Golding et al., in preparation). Due to data limitations we could

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not include covariates or random effects in the models for the extinction probabilities or the colonisation probability for cells in forest patches that had been clear-cut (either before the first survey or between the two survey events) and intercept only models were used in these cases. Specifically, we estimated separate parameters for clear cuts, $\text{cloglog}(c_{i,j,t}) = \delta_1$ and $\text{cloglog}(e_{i,j,t}) = \varepsilon_1$. The k cell-scale covariates used in the model for the colonisation probability are given by $X_{k,i,j,t}^{(C)}$ with corresponding parameter values $\beta_k^{(C)}$. The l patch-scale covariates are given by $X_{l,i,j,t}^{(P)}$ with corresponding parameter values $\beta_k^{(P)}$. We also include a patch-scale random $\gamma_{j,t}$ which was assumed to be normally distributed with mean zero and variance σ^2. In cases where colonisation and extinction probabilities were observed to be 0 and 1, respectively (see Table 1), we used these probabilities in the simulations.

Finally, we define $Y_{i,j,t}$ as the observed occupancy state of cell i in patch j during survey period t. For the observation model we assume that $Y_{i,j,t} \sim \text{Bernoulli}(Z_{i,j,t}p)$ where p gives the detection probability. This detection probability was estimated based on an intensive control study (see *Estimating the detection probability* above) and a value of 0.9 was used.

For the cell-scale models it was necessary, due to statistical non-independence, to include a random patch effect term. At the higher spatial modelling scales (plot and patch) it was not possible to include such random effects. This random effect term has the advantage that it will capture between patch variation that is not explained by the covariates included in the models, for instance due to unmeasured covariates, habitat differences at the time of establishment but not necessarily at the time of the inventories, or competitive exclusion by species already established on some patches (Berglund et al. 2009b). True absences on some suitable patches can also be a consequence of stochasticity in the dynamics of either the species (Snäll et al. 2005) or their host trees (Jonsson 2000) or both. Not accounting for such variability has been shown to bias model-based predictions (Berglund et al. 2009a), especially for resource-unit restricted species such as wood-decomposer PROJECTING fungi.PROJECTING FOREST CONDITIONS THE COMING CENTURYTHE COMING CENTURY

We made projections of the distribution of the resource of our focal species on 17,383 National Forest Inventory (NFI) plots spread across the boreal zone of Sweden between 2010 and 2110 under a 'business as usual' scenario utilizing the recent nationwide Forestry Scenario Analysis by the Swedish Forest Agency (Claesson et al. 2015, Eriksson et al. 2015). In this scenario, 16% of forest land is protected in state reserves, patches voluntarily protected by individual landowners or areas set aside from forestry, retention patches. We refer to the collection of these non-production patches as set-asides in what follows. The set-asides are situated in forest landscapes otherwise dominated by clear-cutting forestry. The NFI plots are circular and have a diameter of 7 or 10 m but for all the projections we first scaled all variables to values at one hectare.

Projections of forest management and dynamics were made using the multiple-use forestry planning tool Heureka (Wikström et al. 2011). For the projections the RegWise software (version 2.2) was used. RegWise is a software component within the Heureka suite of forest decision support tools (Wikström et al. 2011). The core of Heureka is made up of empirical individual models for tree growth (see Fahlvik et al. 2014), ingrowth (Wikberg 2004) and mortality (Elfving 2014) together simulating tree layer development in five-year time steps. In RegWise forest management actions are steered by a rule-based simulation framework. The harvest level – and consequently the development of the forest – is controlled by specified management programmes (silviculture and harvest activities) and the actual growth in each time period. Different management programmes are specified for, e.g., different forest owner categories, tree species mixtures and site factors. Tree retention practices at final felling were also included. The forest projection output data included stand age, a covariate used in the modelling, living spruce volume which was utilised in our connectivity calculations and spruce deadwood production generated by natural tree mortality. We initialized the projections with the amounts and properties of spruce deadwood observed on the NFI plots during 2008-2012. We simulated decomposition of the deadwood based on the one-time chronosequence method described in Harmon et al. (2000). When deadwood enters the fourth stage of decomposition (based on the Swedish decay stage classification (Sandström et al. 2007), it is removed from the simulations as our focal species do not produce fruit bodies on such highly decomposed wood. We do not differentiate between standing (snags) and downed

(logs) deadwood in the simulations but used the proportion of spruce logs (out of all dead spruce) in the NFI data to determine how much to multiply the deadwood quantities by in the covariates for our focal species. These multipliers were estimated as 0.59 for the volume of spruce dead wood and 0.64 for the density of dead spruce trees. Forest connectivity projections were done as in Mair et al. (2017).

All the model parameters were given priors with a mean of zero and a standard deviation of 0.01, except for sigma which was given a uniform prior between zero and five. In all cases three MCMC chains were run for 3000 iterations with a burn-in of 1000 iterations and a thinning of 100. Convergence was assessed visually based on the results of the three chains. In all cases convergence was reached after 3000 iterations.

PROJECTING POLYPORE OCCUPANCIES THE COMING CENTURY

We projected the occupancy dynamics of our focal species for 2010-2110. For each polypore species the final fitted occupancy model was utilised to initialise the occupancy states in the first time step, here 2010. As the average time between our surveys was 10 years, we used 10-year time steps to simulate the subsequent colonisation and extinction dynamics in the NFI plots until 2110 using the final fitted colonisation-extinction model with its estimated parameter values. Offsets were used on the occupancy and colonisation and extinction probabilities to account for the different sizes of the NFI plots (7 and 10 m radii). Finally, area factor scaling, accounting for different densities of NFI tracts across Sweden, was used to compute means and totals of these hectare-scale values. Although our model fitting, projections and decomposition modelling are in terms of deadwood with diameter [?]5 cm at the finest resolution, the NFI data used for initialising the projections are in terms of deadwood with diameter [?]10 cm. Visual inspection of the modelling output showed that after ten years the effect of the missing small pieces (<10 cm) on the deadwood projections was minimal and we thus show the results between 2020 and 2110.

Supplementary results

FUTURE PROJECTIONS

The differing forecasts of the occupancies of the two polypore species resulted from a combination of the general occupancies or colonization-extinction rates (Table 1 in the main text) and the forecasts of the covariates of the fitted models (Table S2-1). Projections for the density of logs showed an increase in the production land when based on the fine resolution deadwood data, but a decrease when based on the coarse resolution data. However, the deadwood volume was predicted to decline in the production land at both resolutions (Fig. S4-1). This was because of a declining stand age in the production land over the coming decades, with the steepest decline between 2020 and 2050 (Fig. S4-2). The clear-cutting of old (>120 years) unprotected forests resulted in fewer large logs that would contribute to the deadwood volumes, whereas the density of logs in the production land would still increase owing to the self-thinning of younger forests. This abrupt initial decline in the ages in the production land had a strong influence on the connectivity measures which affected both the production land and the set-asides. After 2050 the connectivity was predicted to increase again, returning or exceeding the initial levels.

Supplementary discussion

APPROPRIATE RESOURCE RESOLUTION DEPENDS ON THE ECOLOGY OF THE STUDY SPECIES

Local dynamics of wood-decomposer species are influenced by the characteristics and abundance of the resource units the species primarily uses. Of the cell-scale covariates selected in our fitted models for the colonisation probability, *P. viticola* responded to the density of logs, whereas *P. ferrugineofuscus* responded to the volume. At this smallest spatial modelling scale (20 m x 20 m cells) a large volume at one cell, relative to that at other cells, will often be caused by one or two large logs. Higher log densities, on the other hand, will often be made up of several smaller deadwood units. In a previous study of colonisation and extinction events at the individual log level, Jonsson et al. (2008) found that for *P. viticola,*colonisation probability increased with connectivity to occupied logs regardless of log size, whereas for *P. ferrugineofuscus,*colonisation probability increased with log diameter. During the first round of model selection, we found a positive effect

of mean log diameter for *P. ferrugineofuscus* when based on the cell-level fine scale deadwood data (results not shown), but once volume had been included in the model this effect was no longer significant. At the level of individual dead trees, Jonsson et al. (2008) found that *P. viticola* had a substantially lower log-level extinction risk than *P. ferrugineofuscus* (with annual mortality rates of 13.1% and 29.6%, respectively) on similar-sized logs, probably reflecting the longer fruiting period and later peak in fruiting in *P. viticola* than *P. ferrugineofuscus* (Jonsson et al. 2008, Norden et al. 2013, Ovaskainen et al. 2013). In our data, *P. viticola* had higher extinction rates than *P. ferrugineofuscus* at the cell, plot and patch scale especially when including also 5-15 cm logs. The difference is likely because in our data *P. viticola* occurs on average on smaller, fast-decomposing logs than P. *ferrugineofuscus* that leads to more frequent extinctions in *P. viticola* . The rate of deterministic extinction due to log disappearance increases with decreasing log size.

POTENTIAL BIAS IN MODEL PREDICTIONS

Our predictions of the future population trends may be biased for several reasons. Firstly, connectivity decreases for 20 years after 2020 (Fig. S4-2). Some populations acting as dispersal sources will disappear during that time which will slow down the colonization rates more than what is expected by our models. Secondly, the forest currently voluntarily set aside may in fact not be set aside until the year 2100. For example, the mean length of private landownership is 22.5 years (Ingemarson et al. 2006) and new owners often start by cutting the oldest forest (Eriksson 2008). Thirdly, we ignored edge effects from clear cuts into set-asides which will have a negative effect on sensitive wood-decomposer fungi (Ruete et al. 2017). Fourthly, we may have misestimated the colonisation and occurrence probabilities in deadwood-rich forests as our models are based on field data from forests with low or intermediate amounts of deadwood. Fifthly, we assumed that *P. ferrugineofuscus* colonizes all dead trees with diameter [?]5 cm with the same probability while other studies have shown that the colonization and occurrence probabilities increase with log diameter for this species (Jonsson et al. 2008, Norden et al. 2013). Finally, future climate is likely to be adverse for our model species (Mair et al. 2018) even if our data lacked the power to detect climate effects.

APPENDIX S2

Table S2-1. Covariates and associated parameter estimates in the final fitted models. For the colonisation-extinction models, the covariates are for the colonisation probability only. Covariates enclosed in square brackets were those selected for the occupancy models on cut patches. All covariates were standardised to have a mean of zero and standard deviation of one.

[*] connectivity based on presence/absence of spruce forests (according to a GIS-based layer for spruce volume (Tomppo et al. 2008)) [?]120 years (according to a GIS-based layer for forest age (Tomppo et al. 2008) and an α value of 0.1

[+] connectivity based on volume of spruce (according to a GIS-based layer for spruce volume (Tomppo et al. 2008) in forests [?]120 years (see [*] above) and an α value of 1

[++] connectivity based on presence/absence of spruce forests (see [*] above) [?]120 years (see [*] above) and an α value of 1
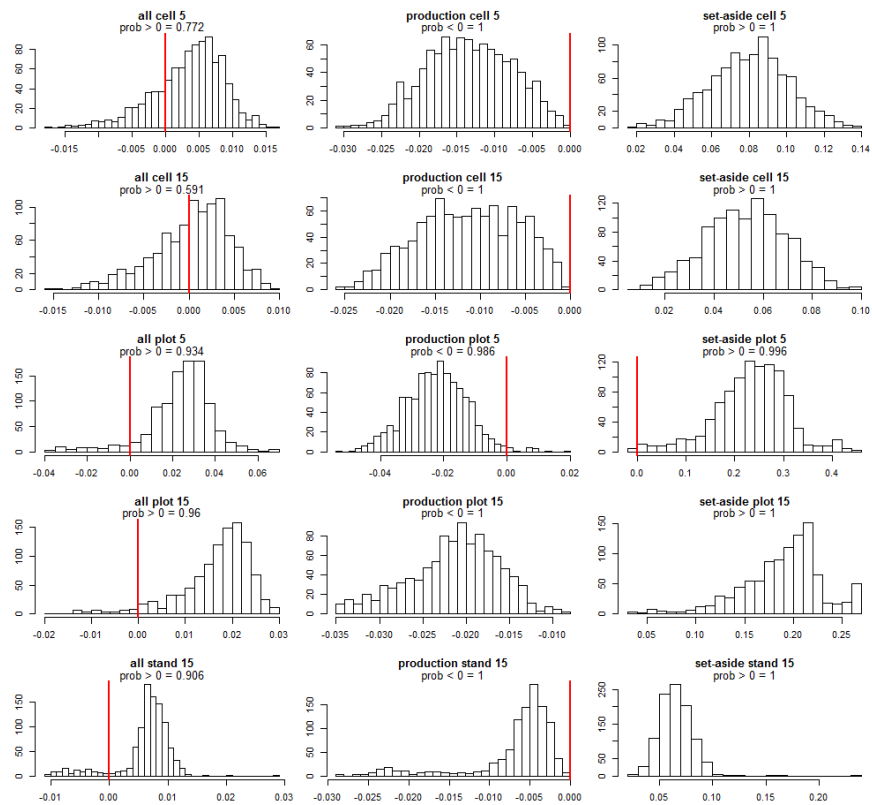
APPENDIX S3

Fig. S3-1. Probability of an increase over all patches (left), a decrease in the production land (middle) and an increase in the set-asides (right) based on the colonization-extinction models for *Phellinus ferrugineofuscus* .
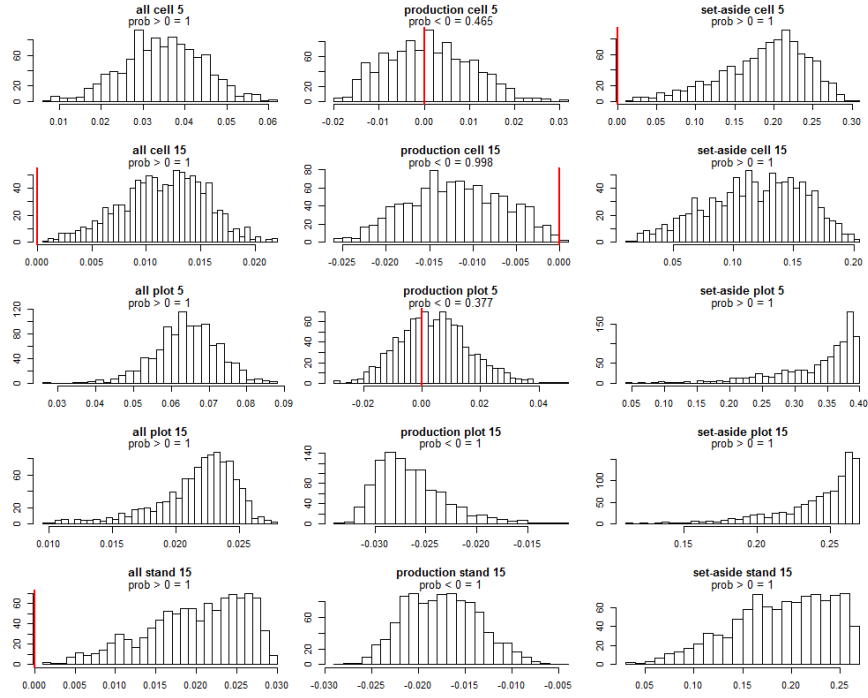
Fig. S3-2. Probability of an increase over all patches (left), a decrease in the production land (middle) and an increase in the set-asides (right) based on the occupancy models for *Phellinus ferrugineofuscus* .
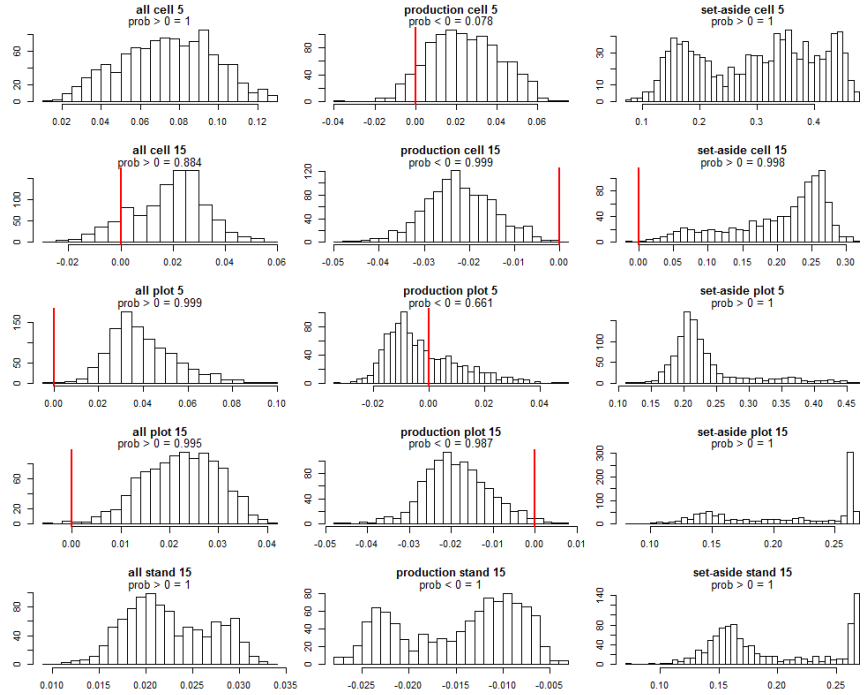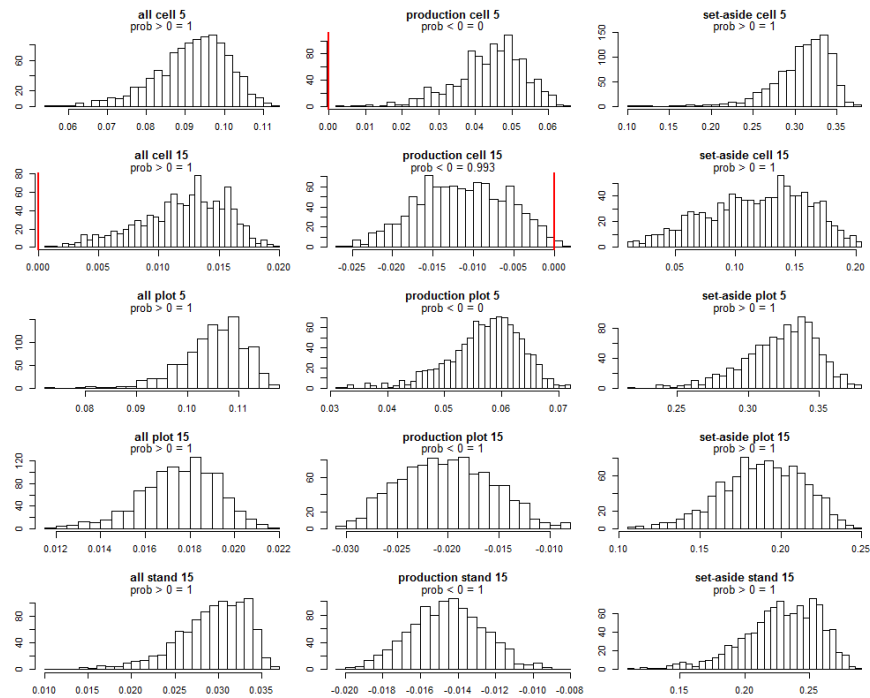

Fig. S3-3. Probability of an increase over all patches (left), a decrease in the production land (middle) and

an increase in the set-asides (right) based on the colonization-extinction models for *Phellinus viticola* .

Fig. S3-4. Probability of an increase over all patches (left), a decrease in the production land (middle) and an increase in the set-asides (right) based on the occupancy models for *Phellinus viticola* .
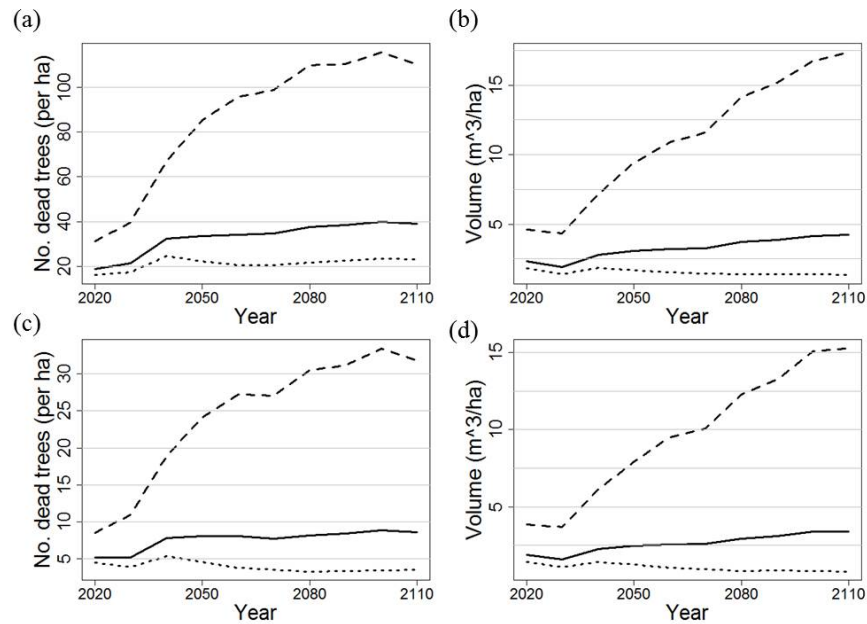
APPENDIX S4

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Fig. S4-1. Projections of the spruce deadwood covariates driving the species projections using the colonisation-extinction and occupancy models (see Table S2-1). Panels a and b give respectively the density and volume of logs with a diameter [?]5 cm in all forest land (solid lines); production forests (dotted lines); and set-asides (dashed lines). Panels c and d give the corresponding values for the coarse resolution dead-wood data (diameter [?]15 cm). Note that when deadwood reaches the fourth stage of decomposition (based on the Swedish decay stage classification (Sandström et al. 2007), it is excluded. We do not differentiate between standing (snags) and downed (logs) deadwood in the simulations but used the proportion of spruce logs (out of all dead spruce).
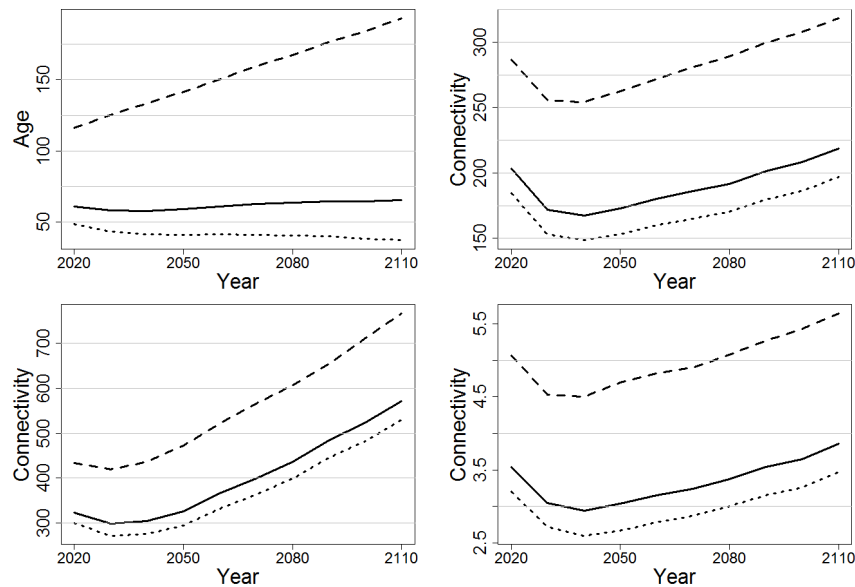

Fig. S4-2. Projections of stand age and connectivity covariates driving the species projections using the fitted colonisation-extinction and occupancy models (see Table S2-1). Panel a gives the stand age in all forest land (solid lines); production forests (dotted lines); and set-asides (dashed lines). Panel b-d give the connectivity measures used in the final models: (b) connectivity based on presence/absence of spruce forests [?]120 years and an α value of 0.1; (c) connectivity based on volume of spruce in forests [?]120 years and an α value of 1; and (d) connectivity based on presence/absence of spruce forests [?]120 years and an α value of 1.

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