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Stand-level modelling and mapping of a pine-dependent indicator fungus across Sweden: effects of stand structure and climate

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ABSTRACT

Keystone wood-decaying fungi affect structure and conservation value of forests. Using Bayesian regression, we modelled the stand-level occurrence of the Scots pine (*Pinus sylvestris*)-dependent *Porodaedalea pini* across Sweden using a presence–absence dataset from 1889 permanent plots of the Swedish National Forest Inventory (NFI). Using the model, we then predicted the spatial distribution of *P. pini* across the country represented by 33,474 NFI plots for which data on the explanatory variables were available. We found that *P. pini* occurrence increased with stand age, living pine volume, and mean annual temperature, and decreased with growing-season precipitation. The model showed good predictive performance and identified areas of high suitability in southeastern Sweden. Our results underscore the importance of mature pine stands and warm, relatively dry climatic conditions for *P. pini*, and demonstrate the potential of combining national forest inventory data with species distribution modelling to inform conservation about a keystone wood-decaying fungus.

1. Introduction

Old-growth forests, once perceived as relatively simple and homogeneous, are now recognized as complex systems governed by multiple, interacting biotic and abiotic processes (Ylläsjärvi and Kuuluvainen, 2009; Gauthier et al., 2015; Boudreault et al., 2018; Glasier et al., 2019). Keystone species are important components of this complexity through disproportionate effects on ecosystem structure and community composition, such that their removal can trigger major shifts in associated communities (Paine, 1969; Power et al., 1996). Subsequent work has refined the keystone concept, emphasizing that such effects may arise through multiple mechanisms, including top-down control, mutualistic interactions, and, particularly relevant to forest conservation, the creation or maintenance of habitat features upon which other organisms depend. These include cavities, snags, and microclimates that are used by diverse assemblages of organisms (Mills et al., 1993; Cottee-Jones and Whittaker, 2012; Jones et al., 1994; Tews et al., 2004).

Deadwood-associated and tree-parasitic fungi both depend on and actively contribute to the formation of dead and dying trees (Moose et al., 2019; Speight, 1989). Through decomposition processes that generate snags, cavities, and porous wood, these fungi create ecological niches that support species often absent or rare in younger forests (Majdanová et al., 2023; Ambec et al., 2023; Gilhen-Baker et al., 2022). Against this conceptual background, we use the term keystone in this functional sense. We specifically refer to species that contribute to maintaining critical habitat attributes and whose loss could plausibly lead to cascading effects on other taxa, even in the absence of direct experimental evidence of such effects.

In Europe, the heart rot fungus *Porodaedalea pini* (Hymenochaetaceae) has garnered increasing attention for its role in shaping the structure and habitat architecture of old Scots pine (*Pinus sylvestris*) stands (Lõhmus, 2016; Edman et al., 2024; Swedish Forest Agency, 2020). Historically, the name *P. pini* has been used in a broad sense (*sensu lato*) to morphologically similar taxa in both Eurasia and North America. However, phylogenetic and taxonomic revisions show that *P. pini sensu stricto* is restricted to Eurasia and does not occur in North America (Fischer, 1996; Brazee and Lindner, 2013; Wu et al., 2019). Here, we use *P. pini* sensu stricto to refer specifically to the Eurasian taxon predominantly associated with Scots pine. As a primary wood-degrader fungus of living Scots pine, *P. pini* plays a unique

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ecological role in Eurasian forest ecosystems. By decomposing the heartwood in living trees, it creates internal cavities and hollows that provide critical nesting, roosting, and foraging habitats for a wide range of organisms, including woodpeckers, owls, other fungi, and insects–among them several beetle species listed on the Swedish Red List (Tews et al., 2004; Remm and Lõhmus, 2011; Ehnström and Holmer, 2020). Trees occupied by *P. pini* may persist for decades before structural failure, eventually forming tall chimney-like snags that today are largely confined to unmanaged forests and protected areas (Saurola, 1992; Lõhmus, 2003).

Due to the widespread decline of old-growth Scots pine forests across its European range, *P. pini* is now considered near threatened to critically endangered in several countries (Senn-Irlet et al., 2007; Matzke-Hajek et al., 2017; SLU Artdatabanken, 2020; Van Vooren, 2023; SLU Artdatabanken, 2025). In Estonia, for example, *P. pini* is rarely found in managed forests but remains relatively common in natural pine forests, highlighting its sensitivity to forest management intensity (Lõhmus, 2016). A similar pattern is expected in Sweden, where the age distribution of Scots pine forests has been profoundly altered by intensive forestry. In particular, clear-cutting practices have largely replaced old forests (>150 years) with younger, more homogeneous forest landscapes (Linder and Östlund, 1998). These transformations have substantially reduced the availability of suitable habitat for *P. pini*, which typically develops over several decades on trees older than 100 years (Edman et al., 2024; SLU Artdatabanken, 2025) and depends on long rotation periods to persist at the stand level (Lõhmus, 2016). Hence, the species is increasingly confined to remnant old-growth stands and protected areas.

The aim of this study is to identify the main factors shaping the distribution of *P. pini* across Sweden. Specifically, we estimate the relative importance of climatic, edaphic, and forest stand variables in explaining its distribution across the country. We further evaluate the explanatory and predictive power of the resulting model and examine spatial patterns in predicted occurrence probability of *P. pini* across Sweden.

2. Materials and methods

2.1. Species distribution data

To model the distribution of *P. pini*, we used data from the Swedish National Forest Inventory (NFI) spanning between 2003 and 2023. We included only plots with living Scots pine volume and classified *P. pini* as present if at least one fruitbody was recorded on at least one tree within the plot. Although *P. pini* fruitbodies are perennial, and thus relatively reliable indicators of occurrence, absences may still include occasional non-detections (e.g., fruitbodies high on stems), potentially resulting in some false absences. This can be accounted for given available data on detectability (Moor et al., 2021), but since no such data exist for *P. pini*, non-detections are hereafter interpreted as absences. This filtering resulted in a presence-absence dataset of 1889 sample plots (Fig. 1), with 1462 and 452 plots surveyed during the first (t_0) and second survey ten years later (t_1), respectively. *P. pini* was recorded as present in 45 (t_0) and 14 (t_1) of these plots.

2.2. Predictor variables

Based on prior studies of spruce-associated fungi (Moor et al., 2021) and species-specific ecological knowledge of *P. pini* (Lõhmus, 2016; Edman et al., 2024), we selected seven plot-level variables as candidate predictors of occurrence: i) volume of living Scots pine (m^3/ha), ii) standing deadwood volume (m^3/ha), iii) stand age (years), iv) peat content in the soil (%), v) site productivity (an NFI-derived index of site fertility reflecting tree growth), vi) summed precipitation May 1 – November 30 (mm), and vii) annual mean temperature (°C).

We derived climate predictors from four global climate models in the CMIP5 ensemble, following the approach of Mair et al. (2018). For each plot, we extracted mean annual temperature (averaged over the preceding 10 years), and cumulative precipitation from May 1 to November 30. We calculated ensemble means by averaging the pixel-level values across all four climatic models, and finally, made spatial matching to plots using a nearest-neighbour approach.

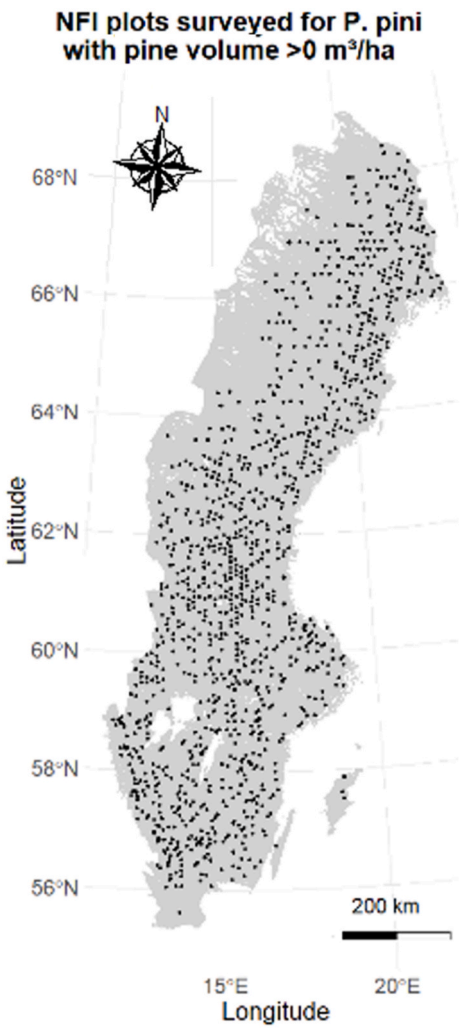


Fig. 1. Location of the 1889 Swedish National Forest Inventory plots with pine volume >0 m^3/ha for which data on absence and presence of *Porodaedalea pini* exist.

2.3. Species distribution modelling

We fitted Bayesian Bernoulli regression models with a complementary log-log (cloglog) link function for *P. pini* occurrence in the first survey (t_0). The linear predictor took the form:

$$\text{cloglog}(\psi i) = \alpha + \sum_k \beta_k X_{k,i}$$

where ψ_i is the probability of presence at plot i, and $X_{k,i}$ are the standardized (division with their standard deviation) and centered (subtraction with mean) explanatory variables.

Prior to fitting the multiple models, we assessed collinearity among retained predictors using variance inflation factors (VIFs) and pairwise correlations. Collinearity was low (VIF range = 1.01–1.17; maximum $|r|$ = 0.37), signalling that multicollinearity was unlikely to bias parameter estimates. Interaction terms were not included; we assumed additive main effects to maintain a parsimonious model and avoid over-

parameterisation given the low prevalence of *P. pini* in our dataset.

Model building proceeded in two steps. First, we fitted models with each candidate predictor, considering both linear and quadratic predictors when relevant. These single variable models (Annex 1) were used to guide the selection of candidate predictors for the multiple model. Next, we iteratively refined the multiple model based on posterior parameter estimates and ecological plausibility, following the recommendation of Gelman and Hill (2006). This led to a parsimonious core model including stand age, living pine volume, mean annual temperature, and growing-season precipitation. Finally, we re-evaluated the inclusion of living pine volume squared (Annex 1) but rejected productivity due to lacking data for a subset of the plots. Specifically, we calculated proportion of deviance explained by the models and the difference in the Deviance Information Criterion (DIC) for adding pine volume squared. We concluded negligible improvement from adding this term but show model diagnostics for adding this term (Annex 2).

Because NFI plots are sampled systematically, *P. pini* occurrences may exhibit spatial structure, potentially violating independence assumptions. However, the residual spatial autocorrelation was weak and not statistically significant (Moran's I = 0.0068, p = 0.146; 50 km neighborhood). In addition, we evaluated the predictive performance against the observations from the second resurvey (t_1) approximately ten years later (t_1), providing a temporally independent test of predictive performance.

We fitted the Bayesian models using JAGS via the *rjags* R package (Plummer, 2008). We ran two parallel Markov chain Monte Carlo (MCMC) chains with a burn-in of 100,000 iterations each and retained 3333 posterior samples per chain after thinning by a factor of 30. We assigned vague normal priors (mean = 0, variance = 10,000) to all parameters.

2.4. Model evaluation

To assess model performance, we used three complementary metrics: First, we calculated the area under the receiver operating characteristic curve (AUC) to evaluate the model's ability to discriminate between presence and absence. Second, we quantified sensitivity (the proportion of observed presences correctly predicted as presences) and specificity (the proportion of observed absences correctly predicted as absences, using a probability threshold of $\psi_i > 0.50$) to classify presences and $\psi_i \leq 0.50$ to classify absences. We calculated all three metrics across all posterior samples to account for parameter uncertainty, and we reported the median and 95% credible interval. AUC was computed using the ***pROC*** R package (Robin et al., 2011), while sensitivity and specificity were calculated using a custom R script. Model performance was evaluated both within-sample using data from the first survey (t_0), used for model fitting, and out-of-sample using data from the second survey (t_1) to assess predictive performance.

To visualize spatial patterns in predicted occurrence beyond the 1462 NFI sample plots used for model fitting, we made prediction across another larger dataset of 33,474 NFI plots surveyed during the period 2016-2020. For these plots, all explanatory variables data were available, although *P. pini* presence had not necessarily been recorded. Additionally, we generated maps of predicted occurrence probability across Sweden for a 10 × 10 km grid, excluding grid cells lacking complete explanatory variable data.

For each grid cell, we calculated the mean value of the explanatory variables and the mean predicted probability of occurrence (ψ) based on the 3333 samples. We also quantified spatial variation in predictive uncertainty by calculating the width of the 95% credible interval for probability of occurrence (i.e., the difference between the upper and lower credible limits). All spatial analyses and map production were conducted in R version 4.3.0 (R Core Team, 2020).

3. Results

3.1. Effects of climate and forest variables on P. pini occurrence

The probability of *P. pini* occurrence was explained by several forest stand and climatic variables (Fig. 2). Occurrence probability increased with stand age, volume of living Scots pine, and mean annual temperature; thus, the highest probability of *P. pini* occurrence is in mature pine stands under warmer climatic conditions. Among the predictors, particularly stand age and mean temperature had large effects, with posterior mean parameter estimates of 0.71 and 0.74, respectively. Living pine volume per hectare also increased the probability, although the effect size was smaller (posterior mean = 0.38). Conversely, increasing precipitation decreased *P. pini* occurrence (posterior mean = −0.33), suggesting less favourable conditions in wetter regions.

3.2. Predicted spatial distribution and hotspots of occurrence probability

Predictions of *P. pini* occurrence probability across the 31,585 NFI plots for which complete predictor data were available revealed pronounced spatial heterogeneity at both broad and fine spatial scales (Fig. 3). Areas with relatively high predicted probabilities (>0.20) were concentrated along the southeastern coast of Sweden and on the island of Gotland. Another notable hotspot was the Scandinavian mountain range, where the probabilities range from circa 0.10 to 0.35.

The spatial variation in the predicted occurrence probabilities of *P. pini* broadly reflect geographic patterns in the key environmental predictors (Fig. 4). Stand age is generally highest in the northern half of the country, particularly towards the Scandinavian mountain range (Fig. 4A), whereas living Scots pine volume showed an opposite gradient, with higher levels in southern regions, especially along the eastern coast, and lower values toward the north (Fig. 4B). Also climatic gradients structured predictions: mean annual temperature (Fig. 4C) follows a latitudinal pattern, while the precipitation was highest along the western coast and in parts of northwestern mountainous region (Fig. 4D). The spatial overlap of relatively warm, dry climatic conditions with structurally suitable pine stands led to relatively higher predicted occurrence probability.

Maps of mean predicted occurrence probability (Fig. 5A) and the associated 95% credible interval (Fig. 5B) showed that predictive uncertainty increased with increasing probability of occurrence. This pattern signals high confidence in predicting absences across much of the landscape, but lower precision in predicting in which forest *P. pini* will be found (i.e., ψ_i >0.20).

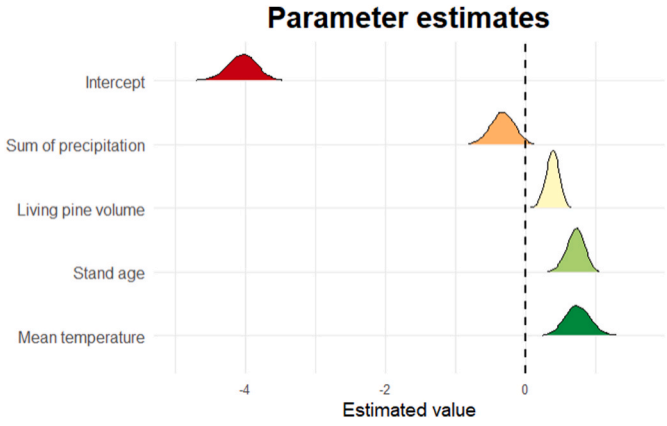


Fig. 2. Posterior distribution of parameters of the final model for *Porodaedalea pini* occurrence.

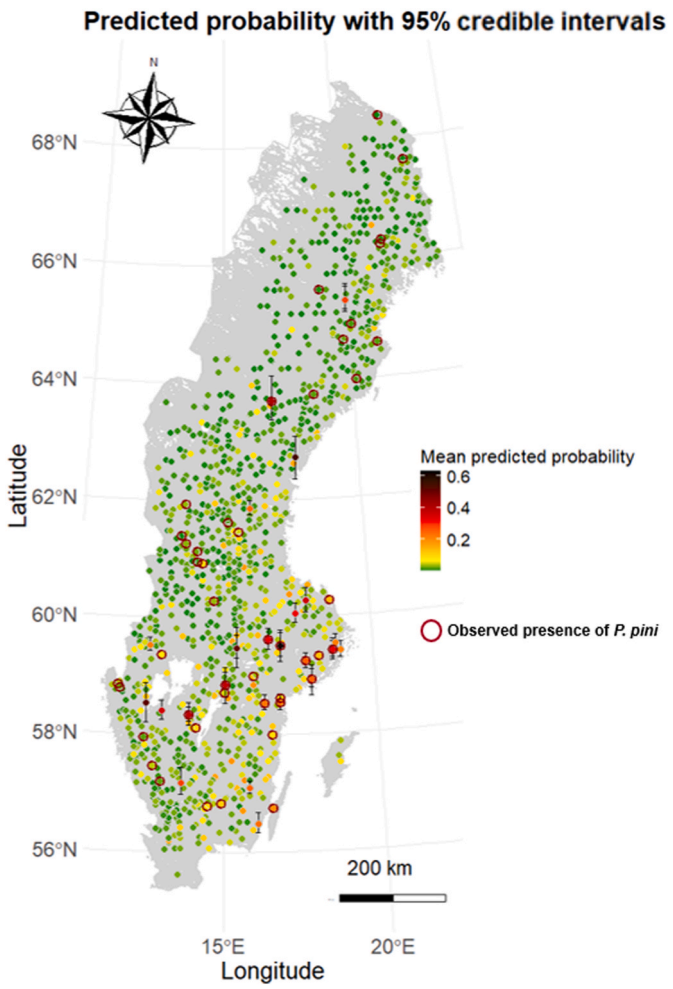


Fig. 3. Mean predicted probability of *Porodaedalea pini* across 1889 Swedish National Forest Inventory plots used for model fitting and having pine volume >0 m^3/ha. Vertical lines represent the 95% credible intervals shown only for plots with probability >0.2. The widest 95% credible interval spans 75.2 percentage points (total width) around the posterior mean.

3.3. Model performance and predictive uncertainty

Within-sample (t_0) model performance yielded an AUC of 0.76, with a mean sensitivity of 0.12 and a mean specificity of 0.97 (Fig. 6A). Out-of-sample (t_1) performance was comparable, with an AUC of 0.79, sensitivity of 0.20, and specificity of 0.97 (Fig. 6B). Together, these results indicate stable discriminatory power over time, with similar accuracy when predicting occurrences a decade after the year of data collection.

The model showed high accuracy in predicting absence (specificity) for both the data used for model fitting (t_0) and data collected ten years later (t_1). In contrast, sensitivity was low, indicating limited ability to correctly classify presences at the chosen probability threshold. Pooling presence observations from t0, the mean predicted occurrence probability was ≥0.2 for 20% of presence cases and for the remaining 80% of presence cases the predicted probabilities ranged 0.003 to 0.194. Amongst t1 data only, the mean predicted occurrence probability was ≥0.2 for 42.9% of the presence cases and for the remaining 57.1% of presence cases, the predicted probabilities ranged 0.0066 to 0.123. Spatially, the highest predicted probabilities were concentrated in southeastern Sweden (Fig. 3).

4. Discussion and conclusion

Our results demonstrate that both climate and stand level forest structure strongly shape the occurrence of *P. pini* across Sweden. Key predictors of occurrence are stand age, living Scots pine volume, mean annual temperature and precipitation, and this is consistent with the species' well-documented association with mature pine forests (Lõhmus, 2016; Edman et al., 2024; SLU Artdatabanken, 2025). The negative relationship with precipitation further suggests that relatively dry conditions are suitable for *P. pini*.

Several non-mutually exclusive mechanisms may underlie the effects of climate conditions. Competition among fungi likely plays a role primarily during the colonization stage (e.g., via wounds or broken branches), as few species are capable of establishing and persisting in the heartwood of living Scots pine. Drier conditions may reduce sapwood moisture and increase oxygen availability, thereby potentially weakening physiological barriers to colonization by heart-rot fungi. Importantly, this result does not contradict reports of *P. pini* occurrence in more humid areas (e.g. Lõhmus, 2016), but rather highlights how local climatic variation can modulate species performance within broader biogeographic zones.

The strong effects of stand age and living Scots pine volume are consistent with *P. pini* being a late-developing heart-rot fungus of Scots pine. Colonization typically occurs via wounds or broken branches on large, old trees, and subsequent mycelial growth and hollow formation may take decades (Lõhmus, 2016; Edman et al., 2024). Stands combining high pine volume with old age therefore provide both the structural availability of suitable hosts and the temporal continuity needed for establishment and persistence, explaining why *P. pini* occurrence is linked to mature pine-dominated stands.

Spatial predictions identified hotspots of relatively high occurrence probability of *P. pini* along the south-eastern coast and on Gotland island, where warm, dry climates coincide with intermediate to high volumes of living pine. These patterns reflect the combined influence of climatic gradients and forest structure shaped by both natural conditions and historical forest management. While older stands are more common in the northern half of the country, particularly in the Scandinavian mountain range, living pine volume is generally higher in the southern and eastern regions. At the same time, mean annual temperature follows a latitudinal gradient, dampened by even lower temperatures with increasing altitude in the north-western mountainous regions. Further, the precipitation is highest along the western coast and in certain mountainous pockets. Together, these gradients interact with historical differences in forest management intensity, with the mountainous areas generally experiencing less intensive forestry and larger set-aside areas, while southern and northern inland regions are dominated by younger, more fragmented production forests (Egnell, 2000; Sahlin, 2011; Swedish Forest Industries, 2023).

Overall model performance was acceptable (AUC = 0.76–0.79), but mismatches between predicted suitability and observed presences were evident. Such discrepancies are expected given the stochastic nature of the preceding processes fungal dispersal, establishment, mycelial growth, and fruiting. This is reflected in spatial variation in model performance (Fig. 3). In southeastern Sweden, several plots were predicted to have high probabilities of *P. pini* occurrence, but no presence was recorded. This may reflect dispersal limitation in landscapes where historical fragmentation has reduced regional source populations even though local conditions are favourable (Berglund and Jonsson, 2008; Norros et al., 2012; Moor et al., 2021). Alternatively, *P. pini* may have been present as mycelium without producing detectable fruit bodies at the time of the NFI survey. Since *P. pini* occurrence records are based on fruit body detection, they likely represent an imperfect proxy for true occupancy, and some absences in the data reflect non-detection rather than true absences. For example, Moor et al. (2021) found a detectability of 0.80-0.94 for spruce log fungi. On the other hand, the presence of *P. pini* in some northern plots with low predicted probabilities may

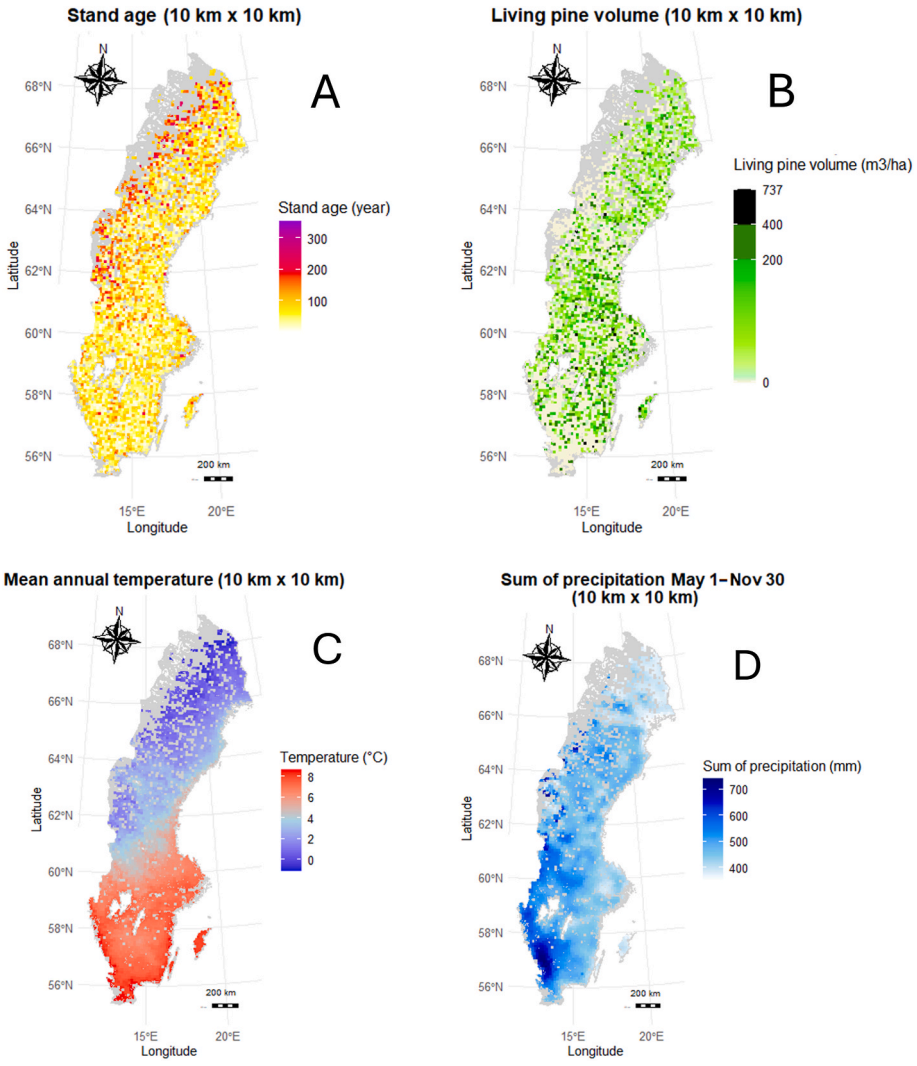


Fig. 4. Distribution of the explanatory variables aggregated from Swedish National Forest Inventory plots averaged within each 10 × 10 km grid cell (when multiple plots occurred in a cell) for (A) stand age, (B) living pine volume per hectare, (C) annual mean temperature and (D) sum of precipitation from 1st May to 30th November.

indicate persistence in legacy habitats. Our stand and climate predictors are relatively coarse and it is impossible to obtain data on all environmental explanatory variables. Moreover,population biological mechanisms are important and an explanation may be higher spore rains in regions with higher landscape-level abundance, perhaps in landscapes with landscape-level continuity of old pine stands (Remm and Lõhmus, 2011; Majdanová et al., 2023). These conditions may sustain relatively high *P. pini* occurrence even in stands with otherwise marginal structural or climatic conditions.

At the spatial scale of individual inventory plots (10 m radius), substantial uncertainty in predicted occurrence is unavoidable. While broad-scale climate and stand-structural predictors are effective for explaining and predicting general, large-scale distribution patterns and suitable forest types, actual occurrence at the plot level follows after numerous biological processes, including spore dispersal, establishment, mycelial growth affected by intra- and interspecific interactions, reproduction, and timing of fruitbody production detected by a field worker. Thus, the model is applicable for identifying clearly unsuitable sites, whereas predictions for suitable sites are inherently less precise. This pattern is consistent with field experiences when unsuitable habitats can often be ruled out confidently, but suitable habitats do not guarantee local occurrence. Altogether, this is summarized in an AUC of 0.76–0.79 whereby the model can be considered acceptable for larger-scale prediction.

Our findings underscore the importance of retaining old, living Scots pine trees as essential habitat for *P. pini*, a keystone wood-decaying fungus that contributes to the formation of veteranized wood structures supporting forest biodiversity. The clear associations with stand age, host tree volume, and climate conditions suggest that forest management strategies aiming to conserve or restore *P. pini* populations should prioritize long rotation periods and the retention of mature pine stands, particularly in regions characterized by warm and moderately dry climatic conditions. More broadly, our study demonstrates how national forest inventory data combined with Bayesian species distribution modelling can provide valuable insights into the ecology and conservation of cryptic but functionally important forest fungi.

CRediT authorship contribution statement

Nils Ambec: Writing – original draft, Visualization, Validation, Software, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Laura Chevaux:** Writing – review & editing, Data curation. **Shengmin Zhang:** Writing – review & editing. **Cristian S. Montalvo-Mancheno:** Writing – review & editing, Visualization. **Tord Snäll:** Writing – review & editing, Funding acquisition, Conceptualization.

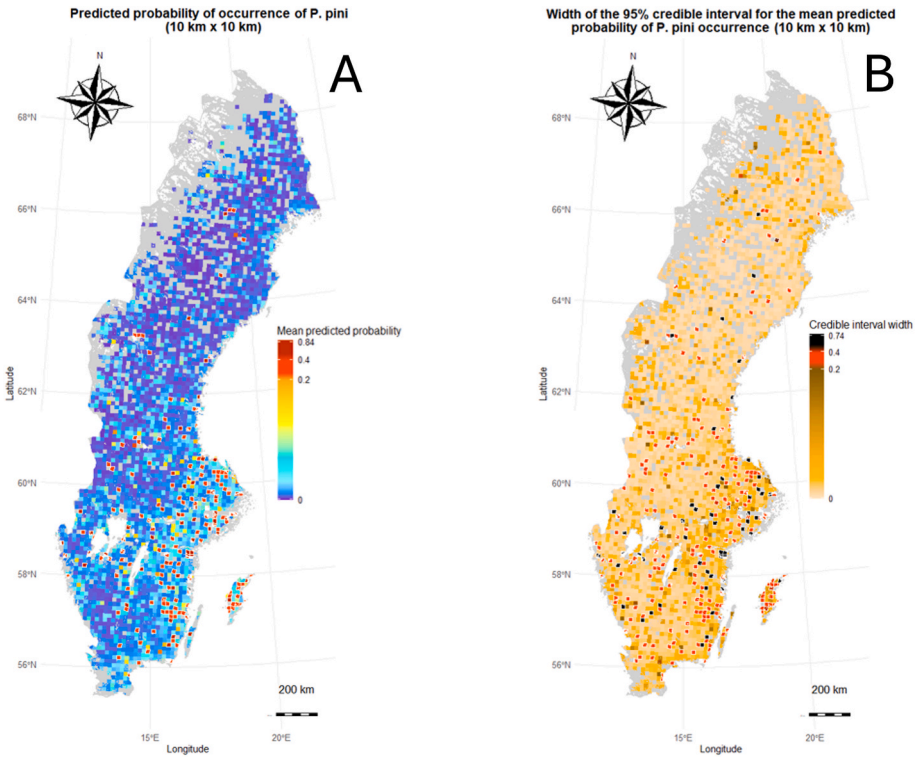


Fig. 5. (A) The mean predicted probability of *Porodaedalea pini* occurrence and (B) the width of the 95% credible interval around the mean across Sweden.

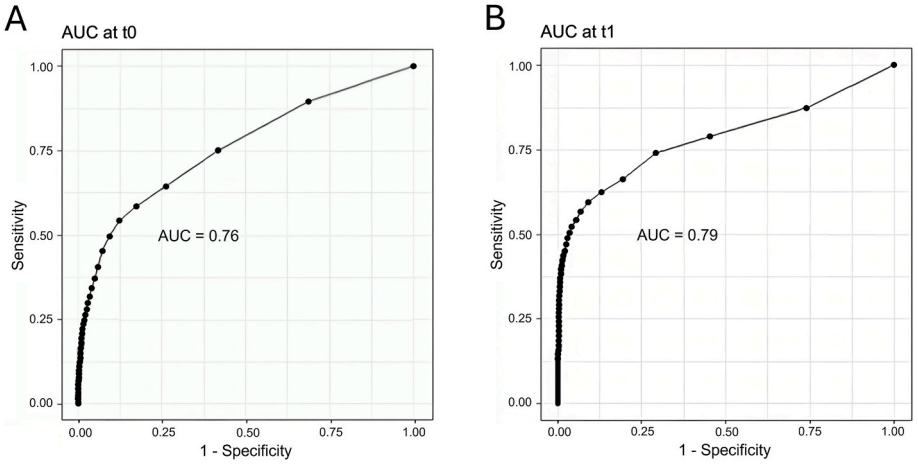


Fig. 6. AUC using the data used for (A) model fitting (t0) and (B) predicting the data collected ten years later (t1).

Data availability statement

The data are available upon request.

Submission declaration

This work has not been submitted somewhere else.

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Conflict of interest statement

The authors have no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.funeco.2026.101518.

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