Policy analysis

Convergence of fungal traits over time in natural and forestry-fragmented patches

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ABSTRACT

Setting aside small remnant patches of high biodiversity forest within managed forest landscapes is often used as conservation measure to provide a refuge and future source population of forest biodiversity, including wood-inhabiting fungal communities. Yet little is known about the long-term fungal community assembly, how these small, isolated patches change through time and how forest management in the surrounding landscape impacts traits and community functionality housed within.

We applied a joint species distribution model to compare how fungal traits and communities changed over two survey periods undertaken ~20 years apart in boreal forest set-aside and natural patches. Natural patches in naturally fragmented landscapes were considered reference forests for small, remnant, near-natural forest patches in intensively managed forest landscapes.

We found the majority of fungal traits converged over time between set-aside and natural patches, without changes in overall species richness. Red-listed species occurrence was initially lower in set-aside patches, but reached a comparable level of natural patches over time as a result of opposing changes in both patch types.

Functional trait changes were larger in set-aside patches, but convergence was also related to opposing changes in natural patches.

This is the first study to directly measure and test wood fungal community trait-environment relationships over time in small, high-conservation value forest patches. The long-term functional trait and red-listed species values of set-asides, coupled with their capacity for old-growth recovery, make them valuable focal areas for conservation.

1. Introduction

Habitat loss and fragmentation caused by expansive human development and resource extraction has resulted in much of the Earth's vegetation and biodiversity existing as small isolated patches (Haddad et al., 2015; Wintle et al., 2018). While small isolated patches often have been shown to have important and representative conservation values (Timonen et al., 2011; Wintle et al., 2018), the long-term viability of species and communities remain uncertain in such patches (Haddad et al., 2015). Few studies have investigated the long-term effects of land-use changes on functional traits in communities of small isolated patches, despite some evidence that such changes may be even more pervasive than changes in species richness and composition (Zambrano et al., 2019).

Functional traits are physiological, morphological and phenological traits, which impact the fitness of an individual and influence ecosystem functioning (Violle et al., 2007). To date, functional trait studies in patches have mostly focused on dispersal traits impacted by habitat loss and fragmentation, while traits related to persistence remain understudied (Zambrano et al., 2019). Superior colonizers and inferior competitors may benefit over more specialised species in small and isolated communities (Nordén et al., 2013). However, traits relating to environmental tolerance and resource use may become more influential than dispersal and establishment traits when considering long-term persistence.

In the Nordic countries, where intensively managed forests make up

Table 1
Traits chosen, their assumed relationship with fungal function and hypotheses as to trait characteristics in small set-aside vs. natural patches at a single point in time. Our hypotheses are based on the literature where it is available (Nordén et al., 2013; Bässler et al., 2014; Norros et al., 2014, 2015; Abrego et al., 2017b). * indicates traits which require a higher resource investment.

Trait measurement	Relationship with fungi function	Predicted relationship
Fruit-body size (volume)	Larger fruit bodies require high quality and quantity of local wood resources and produce more spores*	Decrease in set-asides
Dry fruit-body density	Higher density = tolerate harsher environmental conditions and fluctuations*	Increase in set-asides
Spore size (volume)	Hypothesis: smaller spores = better dispersers benefit colonization in managed forest landscapes	Dual hypothesis: Increase or decrease in set-asides
	Alternative hypothesis: larger spores = tolerate harsher environmental conditions and fluctuations*	
Rot/decay type (hypothesis of brown rotters increase = up arrow)	Preferential consumption of cellulose or lignin where brown rotters may be adapted to less competitive pressure (e.g. early decay wood or forest patches with fewer species)	Increase in set-asides
Fruit-body lifespan (hypothesis of perennials increase = up arrow)	Longer-lived fruit bodies require high quality and quantity of local wood resources and produce more spores*	Decrease in set-asides
# red-listed individuals	N/A *not a functional trait*	Decrease in set-asides

the majority of the total land area, much of the remaining high conservation areas exist as small forest patches (Timonen et al., 2011; Svensson et al., 2019). Various conservation measures are in place to protect such high-value patches, in accordance with forest certification systems and (inter)national conservation area targets. Measures include formal or voluntary protection of patches in naturally fragmented habitat matrices (e.g. mire islands; hereafter called natural patches) and patches in dynamic, clear cut and intensively managed forest matrices (hereafter called set-aside patches; Berglund and Jonsson, 2005; Hottola and Siitonen, 2008). The assumption is that set-aside patches will conserve and provide a refuge or source population of old-growth forest specialist species (Timonen et al., 2011). These remnant high-value forests are not true representatives of larger intact pre-industrial forests, but despite some historical selective logging, represent the last vestige of near-natural and naturally regenerated forests with long continuity (Jönsson et al., 2009). Natural patches have remained forested and unmanaged for millennia in a naturally fragmented landscape and host species rich communities with more specialised species than recently established set-aside patches (Berglund and Jonsson, 2008). With increasing time since isolation and selective cutting, the species richness and composition of community members and functional traits in set-aside patches can be expected to change due to structural old-growth recovery and species dynamics (Jönsson et al., 2017). Adjacent clear-cutting can also influence occupancy patterns of generalist and specialist species in forest edge environments of set-aside patches (Ruete et al., 2017). Communities in natural patches will likely change less over time, and mostly in relation to forest patch size, natural disturbance dynamics or by random population turnover.

Wood fungi, along with many other old-growth forest species, have declined as a result of intensive forest management and habitat loss of old-growth forests (Heilmann-Clausen et al., 2015). Not only does forestry threaten the wood fungi, but also the vital ecosystem services they perform (Lonsdale et al., 2007; Valentín et al., 2014; Heilmann-Clausen et al., 2015). In the Nordic countries, wood fungi represent > 1/3 of species associated with deadwood (2500 out of the 6500 known species; Dahlberg and Stokland, 2004), and many wood fungi are red-listed (i.e. vulnerable, near-threatened or threatened) in Sweden (Artdatabanken, 2020). Understanding the efficacy of small conservation-area measures for protecting fungal community diversity, red-listed species, and functional traits is crucial.

The community composition of polyporoid wood fungi and their traits are affected by increasing management intensity and isolation within the landscape (Nordén et al., 2013; Bässler et al., 2014; Abrego et al., 2017b). Intensively managed forest landscapes are associated with simplification of fungal communities, reduced species richness, in particular a reduction of more specialised species sensitive to habitat

fragmentation (Nordén et al., 2013) and reduced longer-lived and larger fruit body types (e.g. pileate fruit bodies; Bässler et al., 2014; Abrego et al., 2017b). Further, intensive forest management has been linked with decreases in fungal functional diversity, likely resulting from forestry-induced increased environmental filtering, or trait selective pressures (Bässler et al., 2014).

In this work, we re-visit the forest patches of Berglund and Jonsson (2005) after almost two decades to assess how the diversity and functional traits of fungal communities in set-aside patches have changed over time compared to natural patches. This is the first study to examine the long-term efficacy of small forest patches as a conservation measure (but for shorter-term changes in diversity see also Jönsson et al., 2017) and accompanying trait changes across old natural and recent near-natural patches. We hypothesised natural patches were at a stationary state and thus experienced only natural disturbance dynamics and species turnover without a directional trend in species richness, red-listed species occurrence, and fungal traits. In contrast, for set-aside patches we formulated two alternative hypotheses for diversity and trait changes. One hypothesis was that diversity decreased and traits diverged, due to set-aside patches not yet reaching a stable state in the first survey and possibly housing species that could not locally persist because of edge effects (Ruete et al., 2017) and small population sizes (Haddad et al., 2015). We hypothesised how each trait would differ between patch types with this hypothesis (Table 1). Our alternative hypothesis was that no extinction debt existed (sensu Berglund and Jonsson, 2005) and set-aside patches remained stable or moved towards a more natural state as a result of old-growth recovery (Jönsson et al., 2009). As the first study to examine wood fungal trait change over time, we hypothesised that if set-asides were successfully performing the role of conserving fungal communities, traits would either remain stable or converge with natural patches (the alternative hypothesis). Divergence would indicate that alternative states of fungal communities would arise (Suding et al., 2004).

2. Methods

2.1. Study area

This study is based in Northern Sweden, where intensive forest management is one of the largest economic activities and old-growth forest has been significantly reduced since the 1950s (Svensson et al., 2020). We surveyed 46 old natural patches (0.17–12 ha) in a mire complex and 32 recent set-aside patches (0.08–6.7 ha) in intensively managed forest landscapes (Berglund and Jonsson, 2003, 2005). Natural patches were located in the Granlandet Nature Reserve, one of the largest forest reserves in Northern Sweden (ca 27,000 ha), and set-aside

patches were located in the surrounding landscape (Berglund and Jonsson, 2003, 2005). All forest patches were dominated by Norway spruce (*Picea abies*), with moist to mesic ground conditions on moraine soil.

2.2. Species occurrence

We conducted a repeated survey of the forest patches in the autumn (August–September) with a 17–20 year return interval. The first surveys were in 1997–1998 for natural patches and in 2000 for set-aside patches (hereafter the 2000 survey; Berglund and Jonsson, 2005). In 2017, we resurveyed all of the 27 set-aside patches that had not been cut and 29 randomly selected natural patches. Circular plots (0.1 ha) situated in the center of each patch were surveyed for all fungal fruit bodies on logs with ≥10 cm diameter and ≥1 m length of decay classes one to five according to McCullough (1948). We registered the length, as well as large-end and top diameters for all deadwood originating within the plot.

We surveyed all fruiting polyporous wood fungi and six corticoid species (*Asterodon ferruginosus, Cystostereum murrai, Laurilia sulcata, Phlebia centrifuga, Stereum sanguinolentum* and *Veluticeps abietina*; nomenclature following Ryvarden and Melo, 2014). This species list matched the original survey and consists of important wood decomposers generally confined to spruce forests (Berglund and Jonsson, 2003, 2005).

Between-survey bias was minimised by the participation and calibration with Håkan Berglund who conducted the first surveys. Calibration was achieved through all surveyors examining the first logs on the first three sites together to confirm identifications and techniques. Additionally, a random sub-sample of five patches were repeat surveyed by individual surveyors, with no significant differences in the number of logs (median = 10 both groups; Mann-Whitney U = 11.5, n1 = n2 = 5, P < 0.05 two-tailed) or species (median = 27 and 30; Mann-Whitney U = 12, n1 = n2 = 5, P < 0.05 two-tailed) detected between surveyors. Analyses were done at plot (and not log) level as the original species data from the set-aside patches were available at this level.

2.3. Environmental measurement methods

We used five environmental variables in our analyses; patch type (natural vs set-aside), patch area, log volume per hectare, recent clear cutting within 1 km of the patch (clear cutting) and change in old-forest cover over time within 10 km radius (forest change). Log volume was calculated from deadwood inventories of the survey year using the conic–paraboloid formula by Fraver et al. (2007). Changes in the landscape cover of old-growth forests have never been studied jointly with changes in fungal communities before. We hypothesised that a local change in trait composition would result from a change in the surrounding landscape providing dispersal sources to the patches. At a more local scale, nearby clear cuts may increase occupancy of generalist species and decrease occupancy of interior old-growth forest specialist species (Ruete et al., 2017).

Patch areas were calculated for each survey using geospatial analyses and aerial imagery, as three set-aside patches had been reduced in size by 2017. For our measure of recent clear cutting around the forest patch, we calculated the proportion of the area within 1 km of the patch that had been clear-cut in the decadal time period immediately preceding each survey. For the historical measure forming the basis for calculating change in old forest area (forest change), we used the proportion of the area within 10 km of the patches that was forested in the 1950s (at the onset of modern forestry and clear cutting), from which we subtracted the proportion that was forested in the decade immediately preceding each survey. This represented the change in old forest cover (never clear-cut) from the 1950s to the time of survey. Hence, all landscape measures were specific to the time of the two

individual surveys (for detailed information on the geospatial analyses, see Supporting information S1).

2.4. Trait measurement methods

Fruit body traits were measured at every set-aside patch and at 11 of the 29 natural patches (for details see: Dawson and Jönsson, in press). Measurements were taken from fruit bodies on the log of intermediate decay class 3 or 4 (wood hard or starting to soften, < 50% bark remaining; McCullough, 1948) that was closest to the central point of the plot. If no log of decay classes 3 or 4 were present in the plot, a decay class of 2 (wood hard, ≥50% bark remaining; McCullough, 1948) was used. In cases where no suitable log was present inside the plot, we took the closest log outside the plot that was of decay class 3 or 4. For each log and species, we took measurements for up to three randomly selected fruit bodies, or all fruit bodies if there were three or less. We measured two fruit body traits: fruit body size and dry fruit body density, following the methods of (Dawson et al., 2018). Measuring these traits directly in the field better captured trait values in the local environmental settings than those based on literature sources.

We sourced spore size, fruit bodies lifespan (annual vs. perennial) and fungal rot-type (brown vs. white rot) from Nordén et al. (2013). Rot-type is based on whether fungi primarily break down cellulose or lignin and the physical results of each decay type on the wood (Dawson et al., 2018). Finally, we included a conservation attribute; the red-list status of a species. Although this attribute is not a functional trait, it is central to our question of understanding how threatened and non-threatened species differ in response to forest conservation measures. We ensured that no traits or attribute were strongly correlated prior to analyses.

We subset the survey data to those species that occurred on more than three patches (for model stability; 38 out of 53 species) and then further subset to the 19 species for which we had complete trait information. The final data subset contained 81% of the occurrences, which is above the 80% rule of thumb for trait analyses (Pérez-Harguindeguy et al., 2013). One of the set-aside patches in 2017 had no species recorded and this was removed from the model as trait values were required for every species and 'no species' could not be accounted for.

2.5. Statistical methods

We applied Hierarchical Modelling of Species Communities (HMSC; Ovaskainen et al., 2017) for analysing the data. HMSC is a joint species distribution modelling framework (Warton et al., 2015) that enables the integration of data on species occurrences, environmental covariates, species traits and phylogenetic relationships, as well as the spatio-temporal nature of the study design (Ovaskainen et al., 2017).

The HMSC included the data from both surveys at the plot level. In the HMSC, the $n_y \times n_s$ response matrix **Y** consisted of presence-absences of the $n_s = 19$ species observed in the $n_y = 134$ forest patch plots from the 1998/2000 survey (78 patches) and the 2017 survey (56 patches). We modelled **Y** with probit-regression, including in the predictor matrix **X** of environmental covariates at the level of the forest patch and survey period; the study variables. At the forest patch level, we included the deadwood log volume per hectare, patch area, and the forest management intensity, captured by forest change and recent clear cutting. At the level of study variables, we include the indicator variables describing if a patch was natural or set-aside, and whether the survey period was the first or second. We also included the interaction of patch type and survey period to test whether the fungal communities changed over time differently within the set-aside patches compared to the natural patches, one of our main study questions. Each forest patch was included as a community-level random effect, implemented through a latent variable approach (Ovaskainen et al., 2016, 2017).

We modelled the relationship between **X** and **Y** as a function of
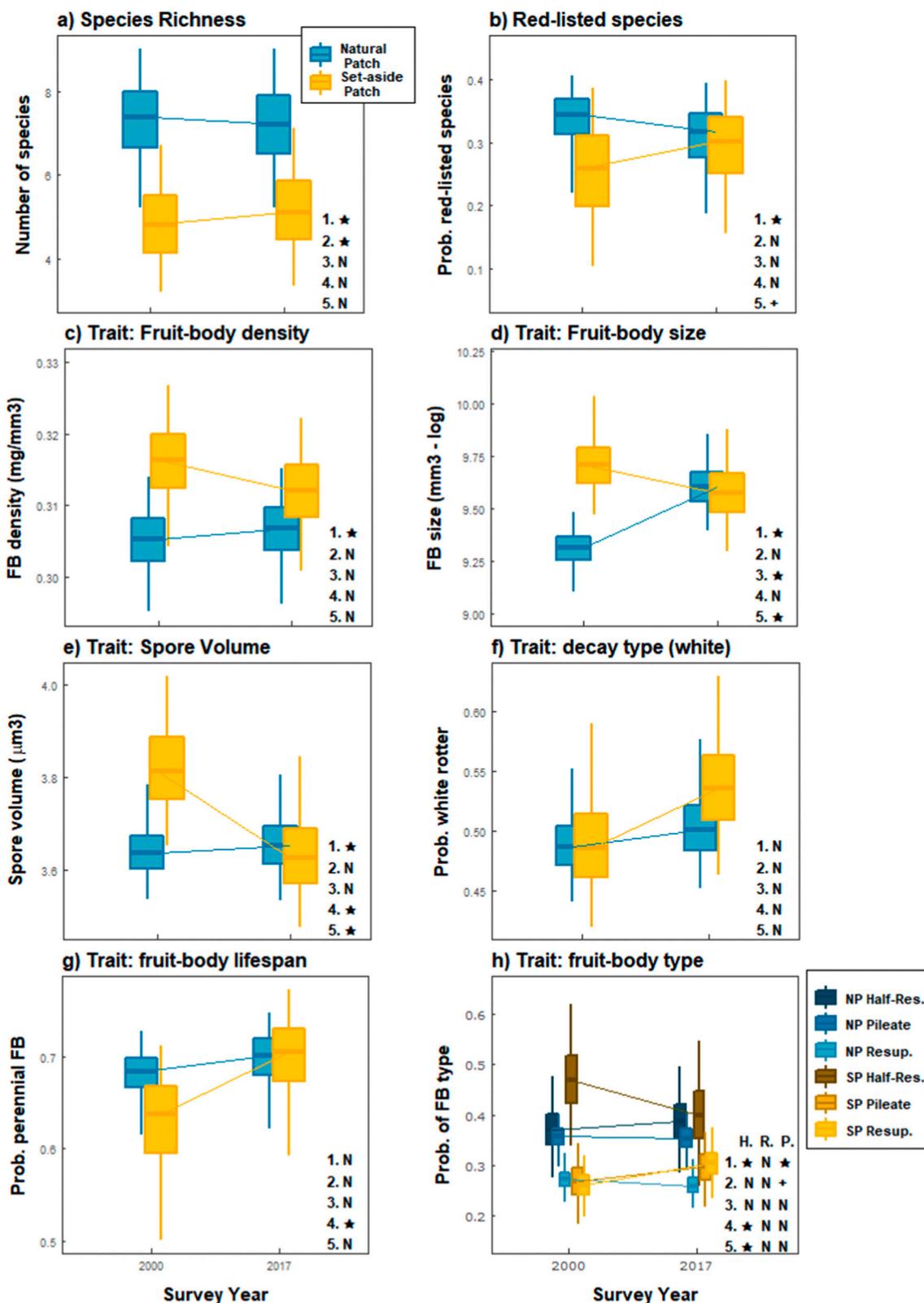
Fig. 1. The model-predicted change in species richness, red-listed species and community-weighted mean traits between patch types and survey period. Box and whiskers indicate the distribution (0.025, 0.25, 0.5, 0.75 and 0.975) of the predicted species communities from the draws of the joint posterior distribution. Tests for differences are shown by the numbers; 1. Difference between patches in 2000 survey, 2. Difference between patches in 2017 survey, 3. Change over time in natural patches, 4. Change over time in set-aside patches, 5. Difference in the slopes over time between patch types. ★ = strongly supported difference, + = supported difference and N = not supported. Prob.: probability of that trait occurring, FB: fruit body, NP: natural patch, SP: set-aside patch, Half-Res: half resupinate, Resup.: resupinate.

species traits and phylogenetic relationships following Abrego et al. (2017a) and Ovaskainen et al. (2017). We included in the matrix of species traits **T** dry fruit-body density, fruit-body size (log-transformed to normal distribution), spore volume, decay type (brown or white), fruit-body lifespan (annual or perennial), fruit-body type (pileate, re-supinate, or half-resupinate), and red-list category (least concern or red-listed). In the absence of a quantitative phylogeny, we followed Abrego et al. (2017a) and used a taxonomical correlation matrix as a proxy for the phylogenetic correlation matrix **C**, constructed from the five levels of class, order, family, genus and species, and assuming equal branch length for each level.

We fitted the model using the R package Hmsc (Tikhonov et al., 2020). We assumed the default prior distributions, and sampled the posterior distribution with 100,000 MCMC iterations, out of which the first 50,000 iterations were discarded as burn-in. We thinned the MCMC by 100 and thus approximated posterior distribution by a sample size of 1000. We assessed the convergence of the MCMC chains visually. The predictive power of the model was evaluated by cross-validation (for details see Supporting information SI2).

To assess the relative roles of the explanatory variables, we performed a variance partitioning, where we partitioned the explained variation among the fixed effects included at the levels of the study variables, as well as the random effect at the forest patch id level.

We aimed to answer five general questions with our analysis: did the communities in natural and set-aside patches differ between study period (1) 2000 and (2) 2017, was there a change over time in (3) natural and (4) set-aside patches, and (5) were these changes different between natural and set-aside patches? To answer these questions, we predicted species communities on 2000 draws (1000 draws from each chain) from the joint posterior distribution of the fitted model for four set conditions. For each of these, we predicted species occurrence probabilities for patches with the environmental covariates set to their case-specific mean values. For example, when making the prediction for set-aside patches during the first study period, we set the intensity of forest management to the mean value in this subset of the data. We compared predictions per patch of each species occurrence, number of species, probability for a red-listed species occurrence, as well as community weighted mean trait values. We considered an observed difference to have moderate or strong statistical support if the parameter of interest was greater in one case than in another with at least 90 or 95% posterior probability, respectively.

3. Results

Species occurrences were recorded with a high frequency, with a total of 852 observations of individual species in plots. All species were found in both types of patches, however *Meruliopsis taxicola* and *Skeletocutis stellae* were only found in set-aside patches in 2017. The highest number of occurrences (338) was recorded in natural patches during the 2000 survey, however this subset also had the largest number of plots. The lowest number of plots and species occurrences was in set-aside plots in 2017, with only 143 species recorded. *Trichaptum abietinum* was the most frequent species, found 110 times across all surveys and *S. stellae* was the most infrequent, with only five occurrences. Largely, species occurred much more frequently than *S. stellae*; 45 was the mean and 50 the median number of occurrences.

Mostly, the environment in the natural patches was more favourable for wood fungi. Natural patches had higher deadwood volume per hectare; 25.4 m^3/ha in 2000 and 30.7 m^3/ha in 2017 versus 15.2 m^3/ha and 18.5 m^3/ha respectively. Further, they had lower proportions of the surrounding area affected by historical and modern clear cutting. Patches surveyed in 2000 had slightly larger area, due to some larger natural patches not included in the 2017 survey and clear cutting into the edges of set-aside patches over time.

The explanatory power of the HMSC model was on average AUC = 0.804 and the predictive power (based on cross-validation) was

on average AUC = 0.655, and thus the model was successful in capturing a large proportion of the variation in the data (S3). Based on variance partitioning, the study variables (patch type, survey year and their interaction) had the second highest explanatory power (mean = 0.23), after deadwood volume per hectare (SI3).

Generally, traits of the natural and set-aside patches were more similar in 2017 than 2000, despite there being no change in the overall species richness (Fig. 1). Across time, species richness was lower in set-aside patches, with both patch types being stable in the number of species housed. The number of red-listed species occurring in set-aside patches, however, changed over time from being lower in 2000 to no difference in 2017. The species composition changed in both natural and set-aside patches, but the shift was greater in set-aside patches. Fruit body size and density was lower in natural patches in 2000, but by 2017 this changed with patches becoming more similar. The change in size was largely due to increases in natural patches, although set-aside patch size was also decreasing. Spore volume was likewise lower in natural patches in 2000, but then set-aside spore volume decreased by 2017 to converge with natural patches. The proportion of decay types remained relatively stable over time in both patches. In set-asides, patches fruit body lifespan increased over time, making it more similar to natural patches. The outcome for fruit body type is subtler, with changes largely confined to half resupinates decreasing in set-aside patches to become more similar to natural patches.

Over time, traits generally changed so that natural and set-aside patches converged. Of the six traits/attribute that were either continuous or binary (all but fruit body type) there was convergence over time in five, with varying levels of support (Fig. 1). Although this was often due to changes in both patch types, the greater change was largely in set-aside patches, supporting our hypothesis that natural patches are more stable. When comparing our hypothesised relationships between natural and set-aside patches, all except for fruit body size were supported (Table 2). There was no evidence for or against a phylogenetic signal on the species' response to the environmental conditions beyond that explained by the traits, with the phylogenetic signal parameter having posterior mean (0·67). This is not unexpected given we only have 19 species in the dataset.

The predicted change in individual species between survey periods and patch types shows that the trait results are not attributable to a particular species (Fig. 2). Any species with different occupancy between natural and set-aside patches in the 2000 survey, but a reduced or changed occupancy in the 2017 survey, is contributing to the trait trends (9 of the 19 species; e.g. *Antrodia sinuosa*; Fig. 2). Likewise, any species where the biggest change was in the set-aside patches over time is also contributing to observed trends (7 species; e.g. *Amylocystis lapponicia*; Fig. 2).

Table 2

A comparison of our trait hypotheses and the modelled trait differences of set-aside patches in 2000 (natural patches as reference), as well as the direction of trait change over time in set-aside patches.

Trait measurement	Hypotheses of set-aside compared with natural patches	Modelled 2000 relationship	Modelled change
Fruit body size	↓	↑	↓
Dry fruit body density	↑	↑	↓
Spore size	↓↑	↑	↓
Rot/decay-type (brown rot)	↑	NA	↑
Fruit body lifespan	↓	↓	↑
# red-listed individuals	↓	↓	↑
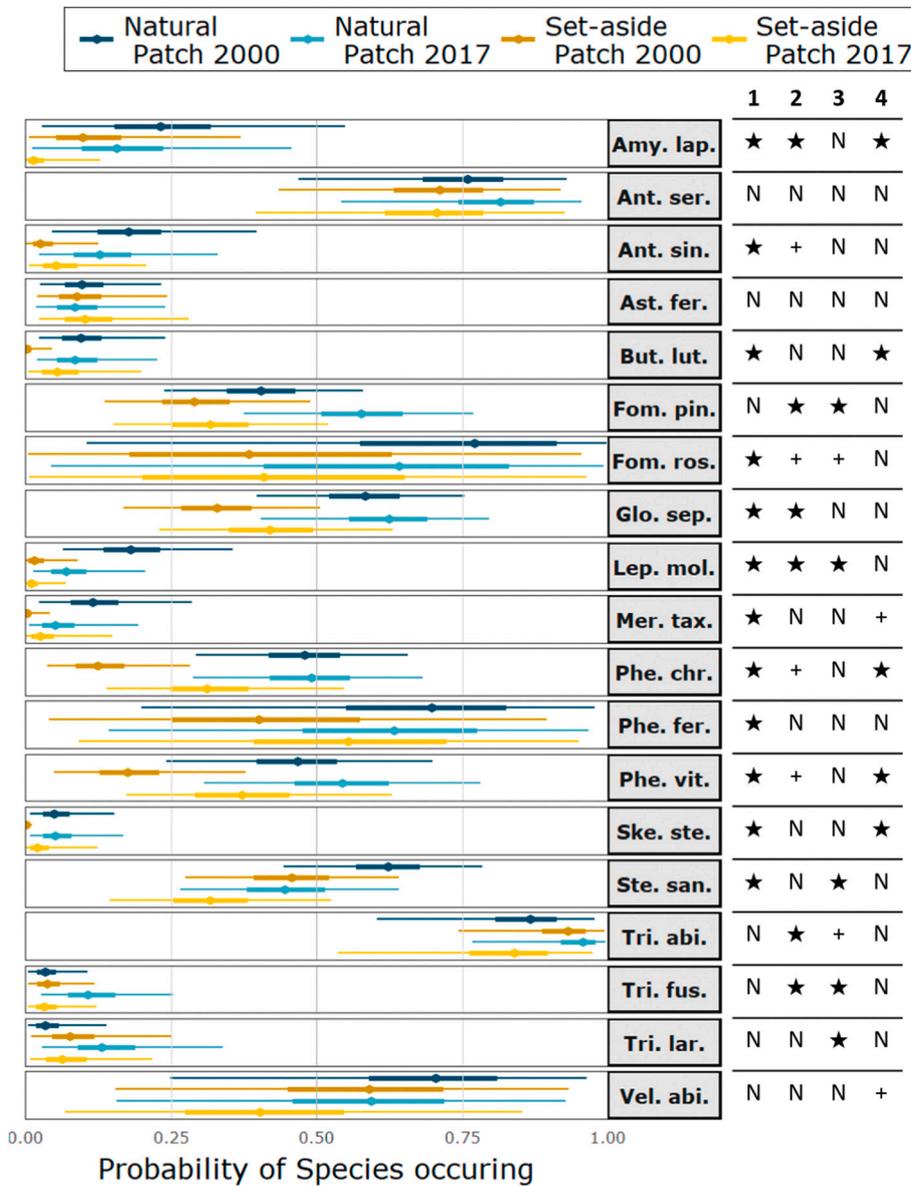
Fig. 2. Predicted probability of a species occurring in each of the four cases. Dots, thick and think lines indicate the distribution (0.025, 0.25, 0.5, 0.75 and 0.975) of the predicted species communities from the draws of the joint posterior distribution. Tests for differences are shown by the numbers; 1. Difference between patches in 2000 survey, 2. Difference between patches in 2017 survey, 3. Change over time in natural patches, 4. Change over time in set-aside patches, ★ = strongly supported difference, + = supported difference and N = not supported. Species shorthand names are (* denotes red-listed): Amy. lap. = *Amylocystis lapponicia**, Ant. ser. = *Antrodia serialis*, Ant. sin. = *Antrodia sinuosa*, Ast. fer. = *Asterodon ferruginosus**, But. lut. = *Butyrea luteoalba**, Fom. pin. = *Fomitopsis pinicola*, Fom. ros. = *Fomitopsis rosea**, Glo. sep. = *Gleophyllum sepiarium*, Lep. mol = *Leptoporus mollis**, Mer. tax. = *Meruliopsis taxicola*, Phe. chr. = *Phellinus chrysoloma**, Phe. fer. = *Phellinus ferrugineofuscus**, Phe. vit. = *Phellinus viticola*, Ske. ste. = *Skeletocutis stellae**, Ste. san. = *Stereum sanguinolentum*, Tri. abi. = *Trichaptum abietinum*, Tri. fus. = *Trichaptum fuscoiolaceum*, Tri. lar. = *Trichaptum laricinum**, Vel. abi. = *Veluticeps abietina*.
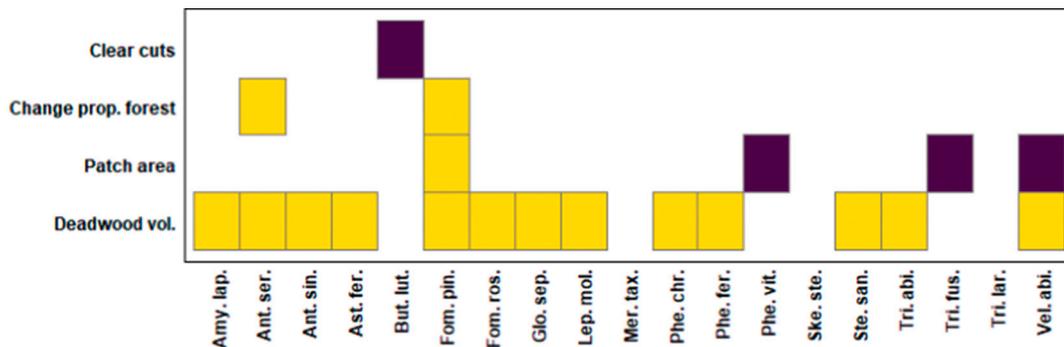
Fig. 3. Relationships between species occurrence and environmental variables with positive relationships in yellow and negative interactions in dark blue. Only relationships with strong support are shown; posterior probability of a relationship > 95%. Species full names can be found in Fig. 2 caption. The full names of the environmental variables are as follows: proportion of clear cutting within 1 km of the site, change in the proportion of old forest area within 10 km between 1950s and survey, the area of the forest patch and the deadwood volume per hectare within the patch. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

In regards to the other explanatory environmental variables, the probability of occurrence for most species increased with increasing deadwood volume (Fig. 3). There were relatively few other species-specific relationships, but increasing proportions of cut forest area in the landscape was positively related to increased occupancy of *A. serialis* and *Fomitopsis pinicola*, while clear cuts in the immediate

surrounding correlated with reduced *B. luteoalba* occupancy. Increasing patch area was related with reduced occupancy of a few species but increased occupancy by *F. pinicola* (Fig. 3).

4. Discussion

Fungal community trait values and the probability for red-listed species occurrence of natural and set-aside patches became more similar over time, despite overall species richness remaining stable. The convergence occurred across five of the seven traits/attributes studied and was not the result of changes in any particular one, or few, species. The functional trait changes were larger in set-aside patches (i.e. decreasing spore volumes, increasing fruit-body lifespans, and changes in fruit-body types), but convergence was also related to opposing changes in increasing fruit-body size in natural patches. Converging occurrence probabilities of red-listed species further support long-term positive trends, although this was the result of opposing changes in both patch types. These long-term functional trait and red-listed species values of set-asides, coupled with their capacity for old-growth recovery, make them valuable focal areas for conservation.

4.1. Functional trait convergence

It is encouraging that functional traits of set-asides and natural patches are converging, even without convergence in overall species richness. Previous research has shown that fungal communities in managed forests are functionally different from old-growth forests (Nordén et al., 2013; Bässler et al., 2014; Abrego et al., 2017a). For example, fragmented and managed forests had less red-listed species (Nordén et al., 2013), more early decay fungi with small fruit bodies (Abrego et al., 2017a) and were functionally less diverse with stronger environmental filtering (Bässler et al., 2014). These studies imply that forest management changes the functionality of fungal communities leading to altered outcomes from natural correlates. Our study is the first to show that although small patches of set-aside near-natural forests were initially functionally different from old-growth natural patches, such differences converged over time. Particularly species with smaller spores and longer-lived fruit bodies increased in set-aside communities, suggesting that trait mechanisms relating to both dispersal and persistence were important. Species with smaller spores may have increased in occupancy of set-asides in managed matrices because they are better dispersers. Longer-lived fruit bodies likely benefit the local persistence in set-asides over time, and these species may also have increased as an effect of old-growth recovery and increasing deadwood resources. The community convergence includes the probability of finding a red-listed species, which increased in set-aside patches. As hypothesised, old-growth recovery may be causing this stable or slight positive trend for red-listed occurrence. These results are supported by decadal re-inventories of old-growth forest fungi in set-asides in central Sweden (Jönsson et al., 2017) and national-scale projections of increasing future habitat suitabilities for six species of red-listed wood fungi (Mair et al., 2018).

The converging of patch types is encouraging for the use of set-aside patches as a measure to conserve or provide refuge for species and community traits (Timonen et al., 2011), especially given that larger trait changes took place over time in set-aside patches. These larger changes in traits when compared to the natural patches, suggests that fungal traits in set-aside patches are responding to an environmental change, as opposed to natural variation. This is supported by the lack of phylogenetic signal, suggesting that trait responses are more closely related to the environment (Webb et al., 2002). Overall improvements could be partly explained by set-aside forest maturation with increasing mean volumes of deadwood (increase in 66% of stands; from 15 to 18 m^3/ha). The magnitude of adverse edge effects may also have declined in set-aside patches with increasing time since set-aside and isolation (Ruete et al., 2017). Such a reduced need for resistance to harsher

environmental edge conditions was indicated by the reduced fruit body densities and spore sizes observed in our set-aside communities. These findings support the use of set-aside patches in the future, and also provide timely advice to management, as the use of these small patches is currently debated in the management/policy realm (Bjärstig et al., 2019). Critics argue that woodland key habitats threaten ownership rights, their inventory is subjective, their general value in regions with a large fraction of set-aside areas is negligible and the negative economic aspects of setting aside too much forest in North-western Sweden. Advocates for the program, however, cite their use in conservation of threatened species and communities and preservation of species in fragmented landscapes.

It is important to acknowledge that we do not contrast our findings of community diversity and functional traits to that of larger intact forests, from which many set-aside patches may have originated (Jönsson et al., 2009). The reference natural patches are also small forest patches and may host different communities compared to larger natural intact forests. However, as the last small vestiges of near-natural forest, coupled with their capacity for old-growth recovery, our finding suggests that set-aside patches represent valuable complementary focal areas for fungal conservation. As our study focused on fungal traits, we did not include some of the rarest species lacking trait data, meaning some red-listed species were overlooked. Further, as we have surveys from only two points in time, it is possible that stochastic differences are contributing to the observed trends.

4.2. Individual trait performance

Larger fruit body size in set-aside patches did not support our hypotheses or what has previously been found or expected for wood fungal traits in managed vs natural forests (Nordén et al., 2013; Bässler et al., 2014; Abrego et al., 2017b). However, this may be due to other studies being based on size categorisation (S,M,L; Nordén et al., 2013), fruit body type as a size proxy (Abrego et al., 2017b) or literature-based mean sizes (Bässler et al., 2014), as opposed to our field measurements of size and density. For instance, if we examine our results based on the definition of Abrego et al. (2017a) where pileate fruit bodies were considered large, then in 2000 there was a higher probability of pileates occurring in natural, rather than set-aside patches. One alternative explanation to larger fruit body sizes in 2000 set-aside patches could be more occurrences of generalist least concern species, characterised by fast resource acquisition and growth (Nordén et al., 2013). The greatest changes in fruit body sizes, however, occurred in natural patches, where this was the only trait to change substantially. This may be related to the increase in mean deadwood volumes (46% of stands; from 25 to 31 m^3/ha).

Fruit body dry density was higher in set-asides in 2000, supporting our hypothesis, but then changed to become similar to natural patches in 2017. This indicates that the fruit bodies in the communities of the first survey had more internal structure and skeletal hyphae, which are more often associated with resistance to harsh environmental conditions (Abrego et al., 2017a; Dawson et al., 2018). Fruit body density changes in set-aside patches may be related to increased environmental tolerance to the more dynamic managed matrix and edge effects (Ruete et al., 2017), or alternatively past selective cuttings and old-growth recovery of set-aside patches.

Contrary to expectations from the literature that have not found spore size as a critical trait (Nordén et al., 2013; Bässler et al., 2014; Abrego et al., 2017b), we found that spore size was larger in set-aside patches than in natural patches in 2000. This was in agreement with our alternative hypothesis that larger spores have greater environmental tolerance and a higher germinability under harsh conditions than small spores (Norros et al., 2015) and are therefore more likely to be found in recent set-aside patches of managed matrices. However, spore size differences between patch types converged by 2017, which instead aligns more closely with our first hypothesis that smaller spores

benefit dispersal and occupancy in managed fragmented matrices (Norros et al., 2014).

4.3. Species-environment relationships

Aside from deadwood volume which was positively related to most species, our results supported few species-environmental relationships. This is perhaps not surprising since much of the variation explained in the model was due to either deadwood volume or study design variables (patch type, survey period and their interaction; Supporting information SI3). Deadwood volume, which had the highest explanatory power, had positive relationships with most of the species. This is expected, as wood is the basic resource for wood fungi (Junninen and Komonen, 2011). There was no particular species that responded exceptionally strongly to low or high deadwood resources.

The occupancy of the common generalist species *A. serialis* and *F. pinicola* increased with larger area removal of old-growth forest over time. This indicates that these species can either withstand the new conditions in recently isolated habitats and managed matrices better than other fungi, and/or are out-competed by other fungi in more favourable habitats and stable matrices (Boddy and Heilmann-Clausen, 2008). Surprisingly, *B. luteoalba* occupancy decreased with increasing adjacent recent clear cutting. This species was taken off the Swedish red-list in 2015 based on molecular information that it could persist as mycelia in cut stumps on clear cuts (Kubart et al., 2016). However, the species seem unlikely to form fruit bodies on cut stumps, so even when cut stumps represent an open and easily colonizable substrate for fungal spores they may not be contributing to the sexual reproduction and dispersal to the surrounding.

This is the first study of wood fungal trait-environment relationships over time in small and isolated high conservation value forest patches. The results that five out of six fungal traits and probabilities for finding red-listed species in set-aside patches converged with those of natural patches, coupled with a capacity for structural old-growth recovery, make set-aside patches valuable complementary focal areas for conservation. This is nonetheless surprising given that previous studies have predominately shown declines of biodiversity in small and isolated habitat fragments (Haddad et al., 2015). Yet the overall species richness of set-aside patches remained lower than natural patches over time, indicating a species richness deficit. Many of the traits and attributes of natural patches did not change over time, suggesting that old and small naturally fragmented old-growth forests are relatively stable in terms of functional and compositional change.

Data availability

Once accepted all data will be available on Dryad.

CRediT authorship contribution statement

SKD and MJ conceived the study; SKD, MJ and HB undertook the surveys; OO and SKD designed and conducted the analyses; SKD, MJ, HB, OO, BJ and TS wrote the manuscript with writing led by SKD.

Declaration of competing interest

The authors have no conflicts of interest to declare for the manuscript:

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108789.

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