



Bryophytes of conservation concern decline and traits change in retention patches during two decades following forest harvest

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ABSTRACT

Setting aside tree retention patches at final harvest is a common forest conservation measure, but the long-term responses of species of conservation concern to different types of forest retention remain unknown. This is the first long-term study of the dynamics of bryophytes of conservation concern and associated traits in small forest retention patches (0.01–0.53 ha) over almost two decades and in relation to environmental drivers. We applied joint species distribution models to compare how bryophytes changed in terms of occurrence, abundance, species richness and traits between year 2000, 2006 and 2018, and in relation to five different retention patch types, patch area, retained living tree volume per hectare, structural heterogeneity, and surrounding habitat openness. Bryophytes responded mostly negatively to the long-term environmental change, although with considerable variation depending on retention patch type. Only negative trends were detected for individual species. Still, no regional extinctions (loss of species from all local patches) occurred and there was a tendency for recovery of a few species. Bryophytes with predominantly asexual reproductive modes and small colony size (<100 cm²) increased in occurrence probability over time, indicating that these traits were beneficial for the long-term persistence of species in small and exposed forest patches. We recommend forest managers to create large (preferably up to 0.5 ha) and variable retention patches, both in terms of patch type (i.e. buffer zones and free-standing groups of different dominant tree species and ground moisture) and structural heterogeneity (i.e. living tree volumes, large and small trees, and deadwood).

1. Introduction

The retention of living trees, as single trees or aggregated into forest patches at final harvest, has become a widespread forest conservation measure (Gustafsson et al., 2012; Lindenmayer et al., 2012; Gustafsson et al., 2020a). The underlying motivation is that tree retention increases the structural diversity of homogenous managed forests and thereby better mimics the variable forest structural dynamics of natural forests (Franklin et al., 2002; Gustafsson et al., 2012; Lindenmayer et al., 2012). Tree retention has the potential to increase the availability of key forest structures (e.g. large old trees and dead trees) that are scarce in even-aged forest production landscapes (Jonsson et al., 2016). Furthermore, the long-term objective of green tree retention is that the retained trees provide refuges ('life-boats') and source populations of forest-dwelling biodiversity that may not survive in the harvested areas.

A meta-analysis by Fedrowitz et al. (2014) suggest that clear-cuts with retained trees (retention cuts) support higher richness and abundance of 'forest species' than traditional clear-cuts, but results also indicate that certain forest-interior species may not survive in retention cuts. Forest-dwelling bryophytes (liverworts and mosses) seem particularly vulnerable to increased exposure by clear-cutting (Hylander et al., 2005; Åström et al., 2007). Bryophyte species of conservation concern (i.e. red-listed species and species indicating forests with high conservation value) (Gårdenfors, 2000; Swedish Forest Agency, 1994) have been shown to decline in richness and abundance in retention patches shortly after clear-cutting (Perhans et al., 2009), but the long-term life-boating of species of conservation concern has not been studied. Further knowledge gaps include the long-term effectiveness of different retention patch types (i.e. free-standing tree groups, buffers to both dry and wet site types), how the regenerating surrounding forests may provide

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shelter against adverse edge effects, and the long-term persistence of species, diversity and functional traits in retention patches.

Joint studies of species distributions, diversity and traits in relation to retention patch environmental drivers (e.g. type, size and quality) have not been conducted, but could improve our understanding of the life-boating efficacy of small forest patches and provide guidelines for forest managers. Investigations of physiological, morphological and phenological traits has the advantage that they can directly link species' performance (e.g. growth, reproduction and survival) to environmental conditions, facilitating a deeper understanding of the mechanisms that control species distributions and changes over time (Violle et al., 2007). Research have so far mostly focused on dispersal traits of vascular plants impacted by habitat loss and fragmentation, while traits related to persistence generally remain understudied (Zambrano et al., 2019). Traits relating to environmental tolerance, competition and resource use may become more influential than dispersal and establishment traits when considering the long-term persistence of species (as in the case of studying life-boating objectives with retention patches). Given their small size and lack of water-conducting stem central strands, bryophytes represent an alternative strategy and interesting study case for species survival in terrestrial environments (Proctor, 2000). Bryophytes of conservation concern are a particularly important target group for study, given their sensitivity to desiccation stress associated with increased solar radiation, temperatures, wind and lower relative humidity in exposed forest environments (Busby et al., 1978; Stewart and Mallik, 2006). Morphological traits that may be related to bryophyte species persistence, such as size (e.g. shoot height, colony size), have been suggested to be interrelated to climatic variation and competitive capacity (Virtanen, 2014; Löbel et al., 2018). Variation in life-history longevity (i.e. the potential life span) will likely also have importance for bryophyte distribution and persistence (During, 1979). Bryophyte trait-environment relationships have not been studied in a retention forestry context, but could provide valuable information on traits that are particularly important for the long-term persistence of species of conservation concern in small and exposed forest patches.

The main aim of our study is to improve the understanding of the long-term dynamics of species of conservation concern in small patches retained at forest harvest, and associated species trait changes, and environmental drivers. We re-survey a broad range of forest retention patches (Perhans et al., 2009) to assess how the species occurrence, abundance, richness and functional traits of bryophytes changed over almost two decades. More specifically, retention patches were surveyed shortly 0–3 years after harvest in 2000 and again 6–9 years after harvest in 2006 (Perhans et al., 2009), and re-surveyed in this study 18–21 years after harvest in 2018. This is the first study to examine the long-term changes of species and traits in varied retention patch types. Our null hypothesis is that bryophyte occurrence, abundance, species richness and traits in retention patches in 2018 recover towards the state directly following harvest in 2000 (reflecting near pre-harvest conditions). We base this assumption on the 'life-boating objective', evidence for stronger bryophyte declines within the first few years of harvesting (Hylander and Weibull, 2012), and older cut edges having a weak edge influence on the understorey in boreal forests in Canada and Fennoscandia (Harper et al., 2015; Harper et al., 2016). This evidence for recovery over time may however be nuanced by our focus on species of conservation concern (e.g., dependent on continuous tree cover, deadwood, large old trees, being disturbance-sensitive species) and the small and isolated retention patches in our study, exposed to edge effects (Jönsson et al., 2017). An alternative hypothesis is therefore that these sensitive bryophytes will continue to decrease and traits change from the original state. We expect that species with predominantly asexual vegetative propagules, large size, and perennial life history, will persist or recover due to such traits being beneficial for maintenance, stress tolerance, competitive capacity and frequent short-distance reproduction and dispersal (During, 1979; Löbel and Rydin, 2009; Virtanen, 2014; Löbel et al., 2018). Lastly, we assume that responses of bryophyte species to

environmental variation depends on species' traits or phylogenetic relationships, since closely related species with shared evolutionary history tend to retain their ancestral niche-related traits (Crisp and Cook, 2012). Assessing whether closely related species are more similar in their responses to environmental variation (after accounting for the effects of the measured traits), may indicate the importance of unmeasured traits (Ovaskainen et al., 2017). Because of this we test for the effects of taxonomic relatedness, but hypothesize that it will not have a major influence on the communities in our study system since we studied a limited number of species of conservation concern and included several ecologically relevant traits as explanatory variables.

2. Materials and methods

2.1. Study area and types of retention patches

This study was conducted in central Sweden (62°30'N, 17°15'E), where commercial forest management and even-aged stands in different rotation stages dominate and old-growth forests have been significantly reduced (Jonsson et al., 2019). The dominating tree species in the region are Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), with birch (*Betula* spp.) and aspen (*Populus tremula*) as subordinate species. As mentioned above, retention patches were surveyed in 2000 (0–3 years after harvest) and 2006 (6–9 years after harvest) by Perhans et al. (2009), and re-surveyed in this study in 2018 (18–21 years after harvest). Following Perhans et al. (2009), we surveyed 74 retention patches (0.01–0.53 ha, minimum tree density of 650 stems >8 cm diameter at breast height per ha), distributed over 37 harvested areas (mean size 10.8 ha) located in a region of approximately 80 × 70 km (see online Appendix A1 and Fig. A1 for a map). However, in 15 of the 74 retention patches we did not record any bryophyte species of conservation concern any year and too few ($n = 4$) rocky outcrop buffers hosted species for this retention type to be included in analyses. Subsequently, over the whole period we analysed data from 55 unique retention patches, excluding the 15 unoccupied patches and 4 occupied rocky outcrop buffers. We further subset the retention patch data by removing stands which were unoccupied a specific survey year, resulting in 45 retention patches with species records in 2000, 44 retention patches in 2006, and 41 retention patches in 2018 (together representing 55 retention patches occupied at least one year between 2000 and 2018). The analysed retention patches were classified into five main types with short name and sample size (for all years and individual survey years) in parenthesis: spruce/pine dominated buffer zone to open mire (hereafter 'mire buffer'; 2000–2018: 18, 2000: 14, 2006: 15, 2018: 13), spruce-dominated buffer zone to stream or lake ('water buffer'; 2000–2018: 14, 2000: 13, 2006: 11, 2018: 12), free standing tree group dominated by spruce or pine ('free-standing coniferous'; 2000–2018: 7, 2000: 6, 2006: 6, 2018: 6), free standing tree group dominated by deciduous trees ('free-standing deciduous'; 2000–2018: 9, 2000: 6, 2006: 7, 2018: 5), and moist-wet paludified forest patches, with roughly equal amounts of spruce, pine and deciduous trees ('wet forest'; 2000–2018: 8, 2000: 6, 2006: 5, 2018: 5).

2.2. Species surveys

We surveyed red-listed bryophyte species and bryophytes that indicate high nature conservation value in 2000, 2006 and 2018, matching the original species list by Perhans et al. (2009). We followed the same method as Perhans et al. (2009) with recording bryophyte species of conservation concern on all substrates, i.e. on the ground, logs, trees and cliffs, up to a height of 2 m. The same bryologist and co-author LA, performed all surveys. In each retention patch, species were recorded in 5 m wide belt transects, covering the whole retention patch. We measured abundance of each species as the number of 5 × 5 m squares in which each species occurred (see online Appendix A2 for details on abundance changes in retention patches). The nomenclature followed

the Swedish taxonomic database (Dyntaxa; www.dyntaxa.se).

2.3. Environmental variables

We used five environmental variables in our analyses; retention type (the five types described above), patch size, living tree volume per hectare, a 'conservation value score', and area of open land within 100 m of the retention patch. To calculate the living tree volume (standing timber), the diameter at breast height of all trees >8 cm was measured in the field at the onset of the study in 2001 (Perhans et al., 2011). The conservation value score was also estimated at this time, as the sum from evaluating 50 different forest structural and dynamics characteristics of whole patches (e.g. diameter and age distributions of trees, deadwood, seasonal flooding regime, degree of sun-exposure) (Perhans et al., 2011). This method has been used extensively by Swedish forest companies and owners associations to assess forest conservation values (Perhans et al., 2011). Retention patch sizes and areas of open land within 100 m were also calculated at the onset in 2000, using geospatial analyses and aerial imagery. All continuous explanatory variables were scaled to improve model performance and facilitate interpretability of model outputs.

2.4. Trait measurements

The size of individual species records in 5 × 5 m squares were estimated in the field according to an ordinal scale for bryophyte cover: (1) < 10 cm², (2) 10–100 cm², and (3) >100 cm². The mode of these size classes based on all survey years was used in analyses, pooled as two categories *small* <100 cm² vs *large* >100 cm² bryophyte colony size. The community members' mode size classes correlated (Pearson's R² = 0.8) with the community members' maximum shoot lengths derived from the trait literature (Hallingbäck, 2016; Löbel et al., 2018). Estimating traits directly in the field may better capture trait values in the local environmental settings than those based on literature sources, and we therefore opted to only use estimated small vs large bryophyte colony size classes in our analyses. We sourced dominant reproductive mode (asexual vs sexual) and bryophyte life history (colonist vs perennial) from the bryophyte trait literature (Bernhardt-Romermann et al., 2018; Löbel et al., 2018). We defined a species as predominantly asexual when production of asexual diaspores occurs at least occasionally, and production of sporophytes is lacking and rare. In contrast, a species was defined as sexual when production of sporophytes occurs at least occasionally, and production by asexual diaspores is lacking or rare, or sexual reproduction occurs rarely, and asexual reproduction is lacking. We ensured that no traits were strongly correlated (Pearson's R² ≤ 0.6) prior to analyses.

2.5. Statistical methods

We aimed to answer the following main questions with our analyses: did the total species richness, occurrence probability of individual species, and probability of colony size class, dominant reproductive mode, and life history trait, change with time since clear-cutting in different retention types and all retention types pooled? To answer these questions, 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 or abundances, 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 all three surveys at the retention patch level. We subset the survey data to those species that occurred on more than five retention patches across all patch types; 15 out of 20 species (omitting five species distributed across five different forest types, see online Appendix A3 for details). In the HMSC for occurrences,

the $n_y \times n_s$ response matrix \mathbf{Y} consisted of presence-absences, respectively, of the $n_s = 15$ species observed in the $n_y = 130$ forest retention patches from the 2000 survey (45 retention patches with species records), the 2006 survey (44 retention patches), and the 2018 survey (41 retention patches). We modelled \mathbf{Y} for occurrences with a probit-link function and included a matrix \mathbf{X} of environmental covariates at the level of the forest retention patch and survey year (as factors). At the retention patch level, we included the retention type (except in the simplified 'pooled model' which did not include retention type, see below), living tree volume per hectare, conservation value score, retention patch size and area of open land within 100 m of the retention patch. We also included the interaction of retention type and survey year to test whether the bryophyte communities changed over time differently within the different retention types. Each forest retention patch ID was included as a community-level random effect, implemented through a latent variable approach (Ovaskainen et al., 2016; Ovaskainen et al., 2017).

We modelled the relationship between \mathbf{Y} and \mathbf{X} as a function of species traits and phylogenetic relationships following Abrego et al. (2017) and Ovaskainen et al. (2017). We included in the matrix of species traits \mathbf{T} , bryophyte colony size class (small vs large), dominant reproductive mode (asexual vs sexual), and bryophyte life history (colonist vs perennial). In the absence of a quantitative phylogeny, we followed (Abrego et al., 2017) and used a taxonomical correlation matrix as a proxy for the phylogenetic correlation matrix \mathbf{C} , constructed from the five levels of class, order, family, genus and species, and assuming equal branch length for each level.

We fitted two occurrence models, one with retention type included and one simplified model not including retention type, using the R package Hmsc (Tikhonov et al., 2020). We assumed the default prior distributions and sampled the posterior distribution with two Markov chain Monte Carlo (MCMC) chains and 150000 iterations, out of which the first 50000 iterations were discarded as burn-in. We thinned the MCMC by 100 and thus approximated posterior distribution by a sample size of 1000 per chain and 2000 posterior samples in total for inference and predictions. We assessed the convergence of the MCMC chains visually and model fit while successively building up model complexity to the full models with all the environmental variables of interest (online Appendix A4 and Table A1). To evaluate the predictive power of the full occurrence model, we performed a 5-fold cross-validation (online Appendix A5) and we assessed the relative roles of the explanatory variables with variance partitioning (online Appendix A6).

An important feature of the HMSC model is the ability to predict community composition along environmental gradients described by the environmental covariates included in the model (\mathbf{X} matrix). HMSC comes with predict functions for generating predictions over the studied environmental gradients (Tikhonov et al., 2020). In this study we used the predict function to make predictions both at the species level for occurrence probabilities of individual species and at the community level for species richness and occurrence probabilities for categorical community trait values. We predicted species occurrences and communities on 1000 draws from the 2000 posterior samples (see above) of the fitted models, for each survey year and the five different retention types and retention types pooled. When making predictions for each year and/or patch type, we set the other environmental covariates to their case-specific mean values. We considered an observed difference to have moderate or strong statistical support if the parameter of interest was greater in one year than in another with at least 90 or 95 % posterior probability, respectively.

3. Results

The species of conservation concern were recorded with a total of 1003 observations across the three survey years, with on average two species and six observations per retention patch (see online Appendix A7 and Table A2 for details of survey data).

3.1. Trends in species richness and abundance

The mean richness of species of conservation concern per retention patch declined already after the first survey and remained at a lower level after ca 20 years (Fig. 1a). However, the changes in species richness depended on the retention type (Fig. 1b–e). Spruce-dominated water buffers (Fig. 1b), experienced the largest total declines in species richness over the longer term. In contrast, the species richness remained stable in free-standing coniferous and deciduous tree groups while it declined already after the first survey and remained at a lower level after ca 20 years in conifer-dominated buffers to open mires (Fig. 1e). Wet forest patches (Fig. 1e), recovered in richness over the long term. The abundance generally followed the same temporal pattern as that for species richness, although in contrast to species richness trends, the total abundance of bryophytes had declined already by year 2006 in water buffers and did not change as strongly in wet forests (online Appendix A2 and Fig. A2).

3.2. Trends in functional traits

Even in our relatively small community of 15 specialised bryophyte species, we found some support for a decreasing probability of species with large colony size occurring in all retention types pooled from 2006 to 2018 (Fig. 2a). The greatest trait-related change was the increase in the occurrence of asexual reproductive modes for all retention types pooled in 2018 (Fig. 2b), supported for water buffers and wet forests (online Appendix A8 and Fig. A5). Perennial life history was the dominant functional trait in communities over time (Fig. 2c). However, in wet forests the probability of a perennial life history decreased in bryophyte communities in 2018 (online Appendix A8 and Fig. A5d).

For the full occurrence model, there was no evidence for or against a phylogenetic signal on the species' presence-absence response to the environmental conditions beyond that explained by the traits, with the phylogenetic signal parameter having posterior mean (0.68). With only 15 species in the dataset this was expected, and the traits explained a fair amount of the variation in species niches and occurrences ($R^2 = 0.36$) after having accounted for environmental variables. The results thus indicate that the 15 species included in our analyses respond mostly individually through the studied traits to environmental variation,

without dependences on additional phylogenetic relationships (and potential unmeasured traits).

3.3. Trends for individual species

The predicted change in individual species between survey years shows that the diversity and trait changes were not attributable to a particular species (Fig. 3; for all retention types pooled). In total six mosses declined in occurrence probability in the long term (Fig. 3). All of these except the deadwood species *H. turfacea* are ground-living. The epixylic liverwort *Lophozia ascendens* was the only species to decline initially and to recover in the long term. For occurrence probabilities in different retention patch types, six species in buffers to water declined between 2006 and 2018, 12 species declined over the whole study period in buffers to mires, while as many as five species in wet forests initially declined 2000 to 2006 and later increased between 2006 and 2018 (online Appendix A9 and Fig. A6). No individual species in coniferous or deciduous free-standing groups changed in species occurrence (online Appendix A9 and Fig. A7).

The probability of occurrence for several species increased with increasing tree retention area, tree volume, and conservation value score (Fig. 4). There were relatively few negative species-specific environmental relationships, but the occurrence probability for *P. cinclidioides*, *H. seligeri* and *Geocalyx graveolens* decreased with increasing proportions of open land within 100 m of the retention patch. Unlike many other species, the occurrence probability of *Crossocalyx hellerianus* was lower in retention patches with higher tree volumes and higher in retention patches with more open land in the surrounding.

3.4. Model performance

The explanatory power of the full HMSC occurrence model was on average AUC = 0.94, and thus the model was successful in capturing a large proportion of the variation in the full data (online Appendix A5, Fig. A3). Based on variance partitioning for bryophyte occurrence probabilities (online Appendix A6 and Fig. A4), the study design variables (retention type, survey year and their interaction) had the highest explanatory power (mean = 0.30), followed by the random variable for the site (mean = 0.29) and the tree volume per hectare (mean = 0.13).

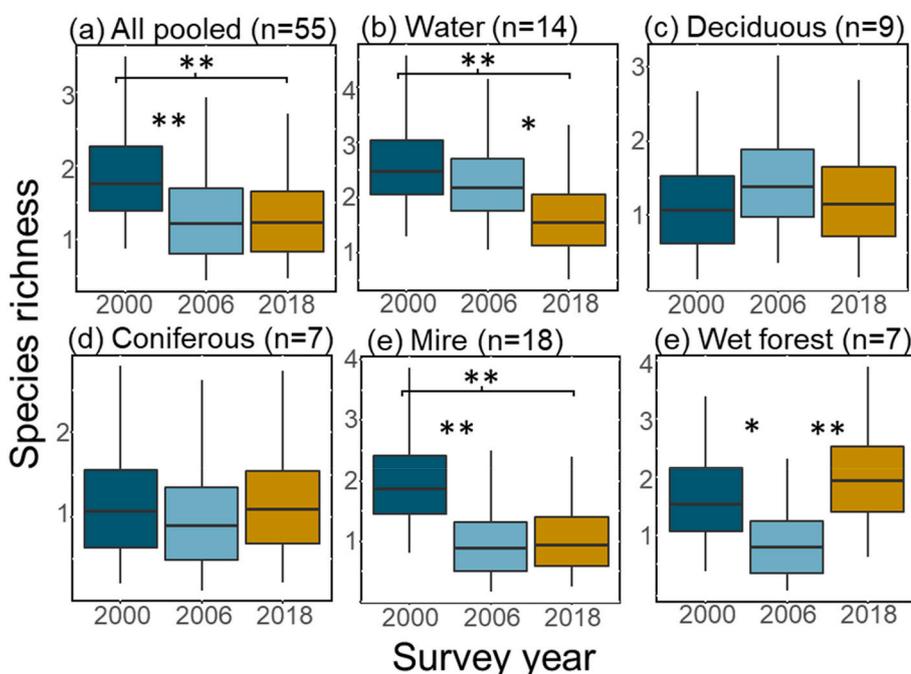


Fig. 1. The model-predicted change in species richness between survey years for (a) all retention types pooled, (b) buffer zones to water, (c) free-standing deciduous tree groups, (d) free-standing coniferous tree groups, (e) buffer zones to open mires, and (f) wet forests. Box and whiskers indicate 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. Differences between survey years; ** = strongly supported difference, and * = supported difference.

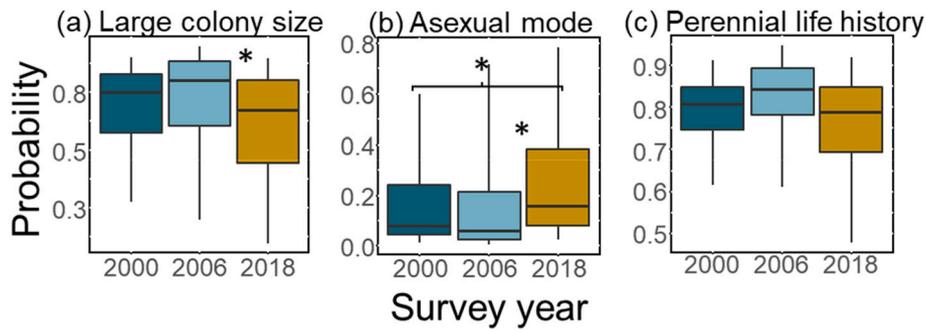


Fig. 2. The model-predicted change in the probability of (a) large bryophyte colony size, (b) dominant asexual reproductive mode, and (c) perennial life history, for all retention types pooled across survey years. Box and whiskers indicate the distribution (0.025, 0.25, 0.5, 0.75 and 0.975) of the predicted species communities from the draws of the joint posterior distribution.

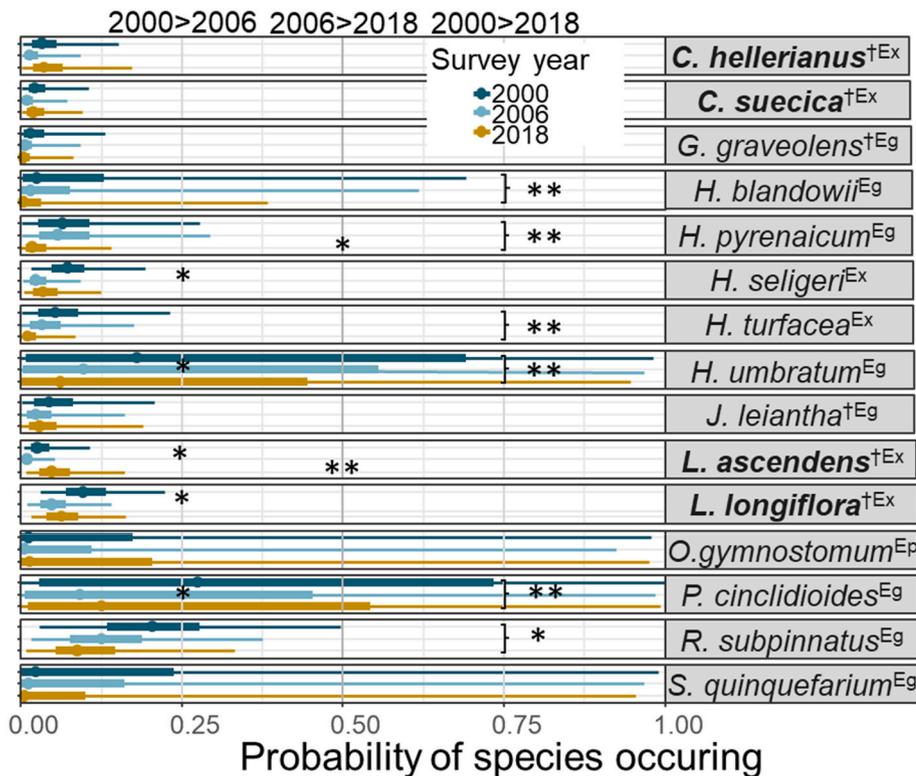


Fig. 3. Predicted probability of a species occurring for all forest types pooled in each study year. Dots, thick and thin lines indicate the distribution (0.025, 0.25, 0.5, 0.75 and 0.975) of the predicted species communities from the draws of the joint posterior distribution. Red-listed species are marked in bold, liverwort species by [†], deadwood living (epixylic) by ^{Ex}, tree-living (epiphytic) species by ^{Ep} and ground-living (epigeal) species by ^{Eg}. For full species names see Fig. 4. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

The open land within 100 m, retention patch area and conservation value scores had the lowest explanatory power, ranging between 7 and 11 % (online Appendix A6). The random site effect had a high explanatory power for the occurrence of *H. blandowii*, *H. umbratum*, *Orthotrichum gymnostomum*, *P. cinclidioides* and *Sphagnum quinquefarium*.

4. Discussion

Our study extends the knowledge on the dynamics of species of conservation concern in retention patches beyond the first decade after harvesting and adds to an improved evidence-base on the conservation efficiency of the growing forestry practice of tree retention. Our observations over two decades point to an ongoing negative trend for bryophytes, agreeing with a development found already after six years (Perhans et al., 2009), but still all species remain over patches as a whole. We also identified a change in traits, pointing to a sensitivity of species being associated with large colony size and dominant sexual reproductive modes.

4.1. Temporal trends in diversity

Our results did not adhere to our null hypothesis that bryophyte species richness, occurrence and abundance in retention patches would recover towards the state directly following clearcutting, reflecting pre-harvest conditions, in accordance with the overall life-boating objective (Franklin et al., 1997). Instead, sensitive bryophyte diversity continued to decrease and traits changed in occurrence over two decades, in agreement with our alternative hypothesis. Experimental studies have predominantly shown declines of biodiversity in small and isolated habitat fragments (Haddad et al., 2015), although synthesis research also points to isolated patches as inordinately important for biodiversity conservation (Wintle et al., 2019). Substantial declines in bryophyte richness and/or abundance of species of conservation concern have been reported in retention patches within a few years after harvesting (Hylander et al., 2005; Perhans et al., 2009; Rudolphi et al., 2014). Hylander and Weibull (2012), contrary to our results, observed a stabilization of red-listed bryophyte species richness and abundance

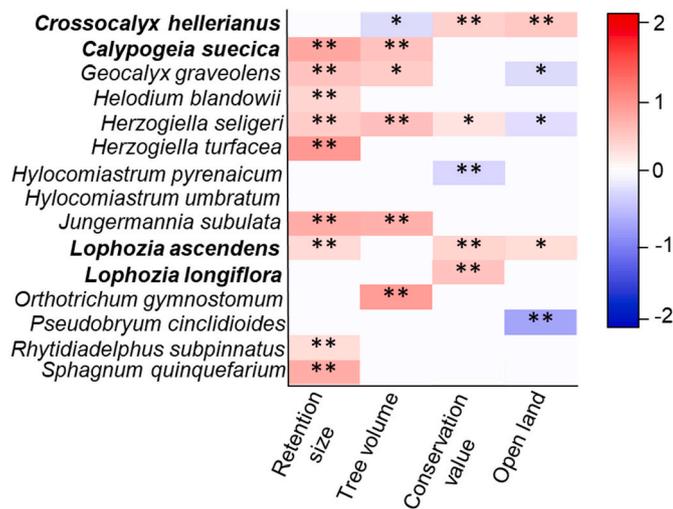


Fig. 4. Heatmap of estimated species niches, based on occurrence models for all retention types pooled. Red and blue colour indicates environmental variables that are estimated to be positive and negative, respectively, with at least 0.90 (= *) or 0.95 (= **) posterior probability. The intensity of the colour represents the posterior mean estimate of the parameter; the stronger the colour the stronger the relationship (variables were scaled for comparison). Red-listed species are marked in bold. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(typically species growing on deadwood) in riparian buffers strips after a decade, after an initial decline. The tendency for recovery of some of the bryophyte species living on deadwood (e.g. five liverwort species in wet forests) could have been caused by increasing amounts of suitable logs over time or increased shading and wind protection from the surrounding regenerating forest. Tree-fall from wind exposition can be large in retention patches (Hallinger et al., 2016), with forests on wet soils especially sensitive (Hautala and Vanha-Majamaa, 2006). Since bryophytes depend on air humidity for water supply (Proctor, 2000), their negative reaction to clearcutting in surroundings likely depends on desiccation caused by increased irradiation and evaporation stress (Busby et al., 1978). Sensitive bryophytes of conservation concern, such as our study species *H. umbratum*, have been shown to have reduced shoot growth and vitality in exposed forest edges (Hylander, 2005). The lack of phylogenetic signal also support that trait responses were mostly related to the environment (Webb et al., 2002).

4.2. Forest retention type

The forest retention type is according to our results an important driver of the long-term persistence of bryophytes in retention patches. Species adapted to moist-wet conditions in buffer zones to water and mires underwent the greatest declines in species occurrence and changes in traits. Buffer zones to streams and lakes were also highlighted as most sensitive by Perhans et al. (2009) and Hylander and Weibull (2012) also detected a rapid decrease in bryophytes in a buffer strip experiment along a stream. The elongated shape of the buffer zones implies an increased risk of desiccation; microclimatic edge effects may affect bryophytes negatively as far as 40–50 m from a forest edge (Hylander, 2005). Unfortunately, we could not include the shape of patches in our analyses due to a high correlation with retention type. Although the free-standing tree groups hosted fewer species, many species remained stable over the study period (online Appendix A9). The lack of change in free-standing tree groups probably relates to their more rounded shape implying lower edge effects and species may already have acclimatised to the drier conditions in these patches compared to the more humid retention types. The epiphyte *O. gymnostomum* even increased in total numbers recorded in the deciduous tree groups (unsupported increase

from 6 in 2000, 14 in 2006 and 22 in 2018). In wet forest patches, the only forest type that adhered to our null hypothesis with signs of recovery, five epixylic liverworts and three epigeal bryophytes increased from 2006 to 2018. This may relate to the increase in ground-water level following clearcutting (Farooqi et al., 2020) compensating for desiccation due to edge effects. Liverworts are considered as more sensitive to harvesting disturbance than mosses through higher demands on substrate quality, shading and air humidity (Fenton et al., 2003; Nelson and Halpern, 2005) but humidity in wet forests evidently was high enough for them to recover long-term. This agrees with Bartels et al. (2019), that site wetness may mediate bryophyte responses to forest harvesting. Therefore, leaving retention patches (including deadwood) on wetter sites may be more effective for conserving bryophytes.

4.3. Traits

The observed trait changes in moister retention patch types suggest that bryophyte traits were responding to an environmental change, as opposed to natural variation, which was also supported by the lack of phylogenetic signal (Webb et al., 2002). Our expectations of dominance of asexual vegetative propagules and a perennial growth-form over the time-period were supported, especially in the moister forest types. Asexuality may have a local competitive advantage over sexual reproduction due to more frequent short-distance dispersal and higher germination and establishment rates (Pohjamo and Laaka-Lindberg, 2004; Löbel and Rydin, 2009; Löbel and Rydin, 2010). In moister retention types, the wetter conditions may have further facilitated the release of asexual gemmae (Pohjamo et al., 2006). Vegetative propagules are also less sensitive to habitat quality compared to vulnerable early developmental stages following spore germination (i.e. protonema) (Löbel and Rydin, 2010). Caners et al. (2013b) in the only other bryophyte trait analysis in relation to retention patches, revealed that rare sporophyte production and species that require greater moisture or shade were affiliated with higher proportional retention area and forest moisture. The high probability for perennial species may be due to longer-lived species likely investing less resources in reproductive effort and more resources in gametophyte longevity, competitive capacity and/or stress tolerance (Löbel and Rydin, 2009). In contrast to what we expected, the occurrence probability for species with larger colony sizes decreased over the long term. Colony size and morphology are important in controlling dehydration rate essential for desiccation tolerance induction in bryophytes of different environments (de Carvalho et al., 2019). A reduction in occurrence of large colony size in bryophyte communities may point to negative influence of environmental stressors and/or loss of competitive capacity.

4.4. Species-environment relationships

Year, retention type, and the random site variable explained most of the variance of the models for bryophyte occurrences and abundances, but varied much across species. The high explanation of the random site variable suggests that some unmeasured site-level covariate or stochastic effect may be important for a few species. The increase in probability of occurrence for many species with increasing patch area, tree volume, and conservation score agrees with established insights into the species-area relationship (Berglund and Jönsson, 2001; Patino and Vanderpoorten, 2018), microclimate moderation from increasing tree volumes and canopy cover (Fenton and Frego, 2005; Caners et al., 2013a), and variation in forest structures promoting habitat diversity (Paillet et al., 2010). Although the patch-area surveyed (= patch size) did not vary over time for the different retention patch types, the free-standing coniferous, mire buffers, and water buffers were generally larger than free-standing deciduous and wet forest types (online Appendix A10, Fig. A8). In larger patches, as for free-standing coniferous, mire buffers, and water buffers, one may expect greater environmental heterogeneity, i.e. structurally and in terms of micro-sites where the

bryophytes may persist even when the overall quality of a patch decreased after the harvest. Another possibility is that in larger patches the pre-harvest occurrence, abundances and colony size was larger for some species, which were then less likely to be lost over time (Rudolphi et al., 2014). The occurrence of species was both positively (*C. hellerianus* and *L. ascendens*) and negatively (*G. graveolens*, *H. seligeri* and *P. cinclidioides*) related to the proportion of open land in the surrounding, which could result from mixed responses to edge influence (Harper et al., 2015). Less dense forests and open surrounding may have promoted the dispersal of asexual diaspores of *C. hellerianus* and *L. ascendens* (Pasiche-Lisboa et al., 2019). Our type of study does not allow deep analyses of causal relationships between individual species and the environment but point to a need of species-specific studies on population dynamics of species of conservation concern. There is also a need for further long-term studies of retention patches across other organism groups, to understand if our results for boreal forest bryophytes are representative of other taxonomic groups. Long-term studies of small conservation areas focused on species of conservation concern are uncommon (Johansson et al., 2018) but form an important evidence-base for species-oriented nature conservation.

5. Conclusions for practice

Overview of research on retention practices in north Europe show that retention patches have an important role for forest species with benefit increasing with retention level and patch size (Gustafsson et al., 2020b). Our study points to large importance also of smaller patches. In terms of management, retention patches can host many bryophyte species of conservation concern long-term, since there were no extinctions over all patches during the 18-year period. Still, ongoing negative trends for most species indicate that a high reliance on this conservation instrument for this taxonomic group may be risky. Based on our results, however, we recommend forest managers to create large (preferably up to 0.5 ha) and variable retention patches, both in terms of patch types and structural heterogeneity. Save areas where there are both conifers and deciduous trees, large and small trees, and deadwood. Remember to save both edge zone buffers and free-standing retention patches on dry and wet site types, they have long-term life-boating benefits even if some of the trees blow down. The long-term conservation of bryophytes in retention patches will also benefit from retaining more trees per unit area within patches. This is because many bryophytes of conservation concern live directly on the trees, or because ground-living species benefit indirectly from the micro-climatic buffering of trees.

CRedit authorship contribution statement

Mari Jönsson: Conceptualization, Methodology, Data curation, Analyses, Visualization, Investigation, Writing- Original draft preparation, Writing- Reviewing and Editing. **Karin Perhans:** Conceptualization, Methodology, Writing- Reviewing and Editing. **Leif Appelgren:** Inventory, Data curation, Writing- Reviewing and Editing. **Lena Gustafsson:** Conceptualization, Methodology, Investigation, Writing- Original draft preparation, Writing- Reviewing and Editing.

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Declaration of competing interest

The authors have no competing financial interests or personal relationships.

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Appendix A. Supplementary data

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