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Partitioning Beta Diversity at Two Spatial Resolutions Reveals Biotic Homogenisation With Habitat Degradation

Faith A. M. Jones¹  | Alwin A. Hardenbol² | Anne-Maarit Hekkala¹ | Albin Larsson Ekström¹ | Mari Jönsson³ | Matti Koivula⁴ | Joachim Strengbom³ | Jörgen Sjögren¹

¹Department of Wildlife, Fish and Environmental Studies, Swedish University of Agricultural Sciences, Umeå, Sweden | ²Natural Resources Institute Finland, Joensuu, Finland | ³Department of Ecology, Swedish University of Agricultural Sciences, Uppsala, Sweden | ⁴Natural Resources Institute Finland, Helsinki, Finland

Correspondence: Faith A. M. Jones (faith.jones@slu.se)

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ABSTRACT

Aim: Understanding the effects of habitat degradation on biodiversity is essential for undertaking conservation initiatives, but commonly used metrics of biodiversity, like species richness and beta diversity, can miss important signals of change. Greater insights can be gained by partitioning beta diversity into nestedness, which relates to species loss, and turnover, which relates to species replacement. To obtain a more comprehensive understanding of biodiversity change with habitat degradation, we investigate how nestedness and turnover vary when comparing assemblages from the same or different habitat degradation levels, and how assemblage aggregation resolution influences this relationship.

Location: Sweden.

Methods: We used beta diversity partitioning to assess lichen, fungi and bryophyte species composition from 120 forest sites across Sweden, from three different habitat degradation levels, and at two aggregation scales (pairwise local assemblages and assemblages pooled at the habitat degradation level across our study sites). We examined how pairwise total beta diversity, nestedness and turnover varied when comparing assemblages from sites of either the same or different habitat degradation levels. In addition, we examined the relationship between total beta diversity, nestedness and turnover when assemblages pooled at the habitat degradation level were compared.

Results: We detected a small increase in pairwise lichen total beta diversity (Cliffs delta 0.40) and nestedness (Cliffs delta 0.19), but not in any other pairwise comparisons. In contrast, for all taxa, comparisons between assemblages pooled at the habitat degradation level showed higher values of nestedness and lower values of turnover than the corresponding pairwise comparisons, suggesting biotic homogenisation in highly degraded sites.

Main Conclusions: Our results highlight the importance of considering biodiversity change across multiple spatial resolutions to fully capture the effects of local species replacements in highly degraded habitats on biotic homogenisation.

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1 | Introduction

Biodiversity is under unprecedented threat from anthropogenic activities (Pereira et al. 2010), leaving many habitats in degraded conditions. This degradation, where the quality rather than quantity or connectivity of a habitat decreases, interacts with habitat loss and fragmentation, which in turn influences biodiversity (Heinrichs et al. 2016). Biodiversity change in response to habitat degradation is a complex phenomenon, as habitat modifications can affect taxa differently (Johnson and Hering 2009; Kirby et al. 2017) and species are not usually lost or gained randomly (Villéger et al. 2010). Composition and functioning of species communities can be affected when habitat degradation causes declines in resource availability, which favours generalist rather than specialist strategies and compromises the capacity of habitats to support individuals and populations of species (Calizza et al. 2017).

The concept of biodiversity is multifaceted, and its varied responses to environmental pressures depend on which aspect is measured (McGill et al. 2015). Traditionally, assessments of biodiversity change have focused on species richness, but this aspect of biodiversity is insensitive to shifts in assemblage composition (Dornelas et al. 2014; Hillebrand et al. 2018). The largest biodiversity responses to environmental disturbance are not usually at the assemblage level, but rather at the species level (Supp and Ernest 2014). This means assessments focusing on species richness may underestimate biodiversity change. There is also a disconnect with conservation goals by focusing on species richness, as conservation actions more commonly aim to support species that are declining than to increase local species richness.

Quantification of beta diversity, that is, the differences in species composition between sites (Koleff et al. 2003), provides an alternative approach to species richness-focused assessments, as it captures changes in species identities. Focusing on beta diversity can therefore improve our understanding of how biodiversity is changing with increasing anthropogenic pressures on habitats. For example, studies focusing on beta diversity have found evidence for non-random species losses with habitat loss (Püttker et al. 2015), species community responses to habitat complexity (Klein et al. 2021) and have been used to weigh the relative importance of local versus landscape factors on biodiversity conservation (Häkkinen et al. 2018; Schall et al. 2018).

Beta diversity is composed of two distinct processes: turnover and nestedness (Figure 1). Turnover refers to the total beta diversity attributable to species replacement and is assumed to relate to mechanisms controlling species sorting, dispersal and stochastic processes (Baselga 2010). Nestedness refers to species losses or gains, where the smaller assemblage is a subset of the larger and originates from processes of non-random species losses along habitat or resource availability gradients (Ulrich et al. 2009). These two components reflect disparate processes, meaning that overlooking them can mask changes in assemblage composition if the two components change with opposite responses to environmental drivers (Ribeiro et al. 2020; Tatsumi et al. 2020). Explicit comparisons of the responses of these two components of total beta diversity to

habitat degradation will support efforts to understand how the underlying biological processes contribute to biodiversity change.

Habitat degradation causes the quality and quantity of resources to decline, meaning that the degraded habitat supports fewer species and a lower number of individuals (Heinrichs et al. 2016). Nestedness and turnover are expected to respond differently to these processes. Degraded habitats support fewer species than their more intact counterparts due to lower quality resources and an increased probability of extinction, allowing for less specialisation between species (Heinrichs et al. 2016). Habitat degradation is consequently expected to lead to sequential losses of specialist species, meaning more degraded communities will be the subset of less-degraded communities that are more generalist. For example, nestedness may increase following habitat degradation from glaciation (Baselga 2010; Dobrovolski et al. 2012). It is less straightforward to predict the effect of habitat degradation on turnover. On the one hand, turnover may increase with habitat degradation if more new habitat niches become available in the altered systems to replace niches lost to degradation. On the other hand, turnover may remain stable, or even decline, if new habitats do not become available to replace those lost to degradation.

An additional layer of complexity when seeking to understand how habitat degradation affects species composition is that beta diversity patterns can vary depending on which spatial resolution the assemblages are compared (Callaghan et al. 2024). One reason for this is that assemblage composition is a result of stochasticity as well as environmental drivers like habitat degradation, especially at larger scales (Shoemaker et al. 2020). Pairwise, smaller spatial-resolution comparisons between local assemblages from different habitat degradation levels will likely be more influenced by stochasticity and have higher turnover. Comparisons of assemblages pooled within habitat degradation levels, conversely, should have lower turnover values for the same comparisons due to the decreasing influence of stochasticity on species presence. Aggregated assemblages will encompass all the species found within the habitat-degradation-level pool, thereby minimising the stochastic and dispersal filtering contribution to turnover that may dominate smaller spatial-resolution scale comparisons.

Habitat degradation can trigger biotic homogenisation (Püttker et al. 2015). This process occurs when habitat degradation favours a smaller set of disturbance-tolerant species, leading to the replacement of specialists with generalist species (Myers et al. 2015). The spatial resolution at which we compare assemblages from different habitat degradation levels can affect nestedness values if degraded habitats experience biotic homogenisation. However, small-resolution comparisons may not result in high nestedness if the same few generalists replace many different specialists across different local assemblages. In contrast, habitat-level pooled assemblages are likely to display higher nestedness because the degraded habitats host only a limited number of generalist species, resulting in a much smaller species pool compared to the more diverse pool of specialists in the less-degraded habitat. Hence, comparing how beta diversity, nestedness and turnover vary when assemblages are

A) Beta Diversity (Jaccard dissimilarity, β_{jac})

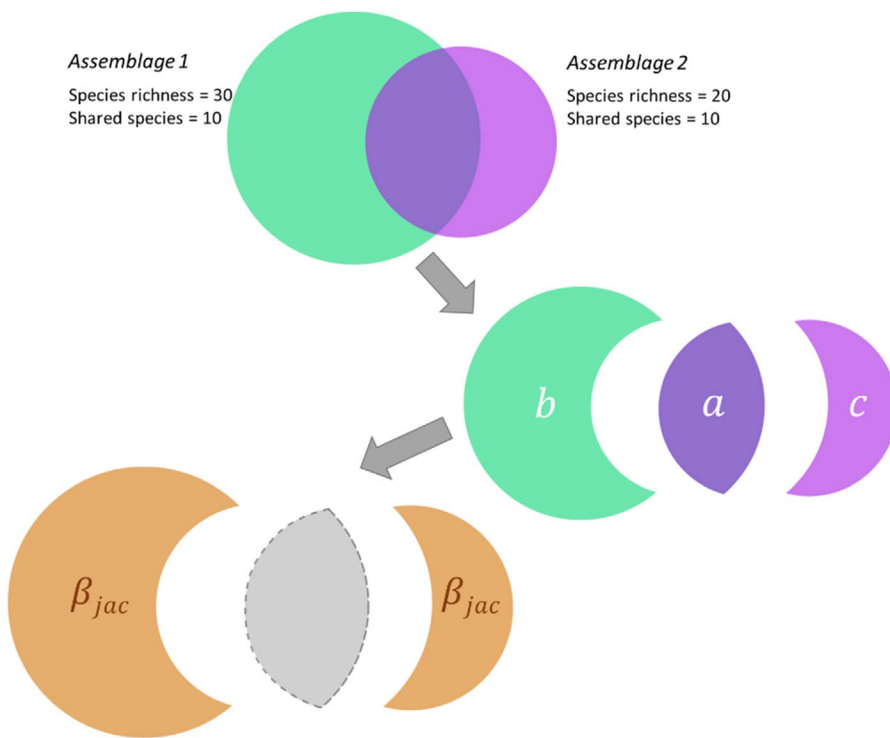
Assemblage 1 has 30 species, and Assemblage 2 has 20 species.

Beta diversity quantifies how different these two assemblages are by splitting them up into three parts:

- a – the number of shared species
- b – the number of species only found in Assemblage 1
- c – the number of species only found in Assemblage 2

In this example, the equation is

$$\beta_{jac} = \frac{b + c}{a + b + c} = \frac{20 + 10}{10 + 20 + 10} = 0.75$$



B) Partition dissimilarity (β_{jac}) into turnover (β_{jtn}) and nestedness (β_{jne})

Proportion of beta diversity due to species replacement (Turnover, β_{jtn})

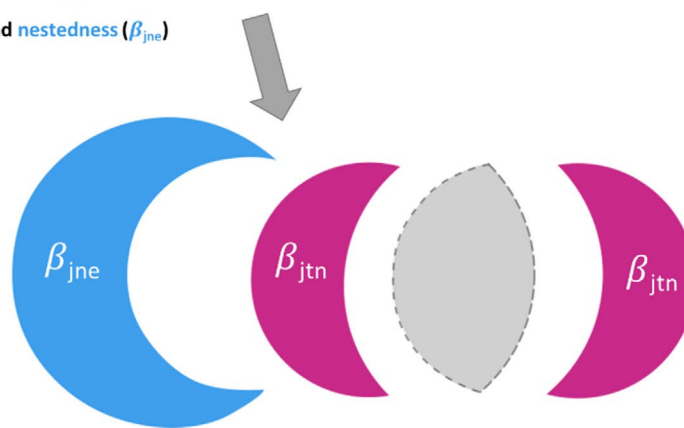
This value describes the amount of beta diversity (Jaccard dissimilarity) that is due to species replacements rather than one assemblage having lower species richness than the other.

$$\beta_{jtn} = \frac{2 * \min(b, c)}{a + 2 * \min(b, c)} = \frac{2 * 10}{10 + 2 * 10} = 0.67$$

Proportion of beta diversity due to differences in species richness (Nestedness, β_{jne})

This value describes the amount of beta diversity (Jaccard dissimilarity) that is due to the difference in species richness between the two assemblages.

$$\beta_{jne} = \beta_{jac} - \beta_{jtn} = 0.75 - 0.67 = 0.08$$



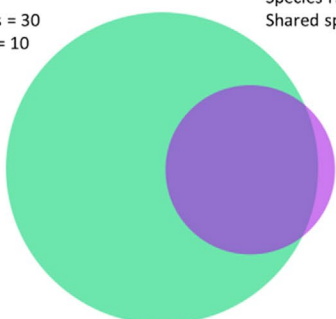
C) High Nestedness, Low Turnover

Assemblage 1

Species richness = 30
Shared species = 10

Assemblage 2

Species richness = 11
Shared species = 10



$$\beta_{jac} = 0.68 \quad \beta_{jtn} = 0.17 \quad \beta_{jne} = 0.51$$

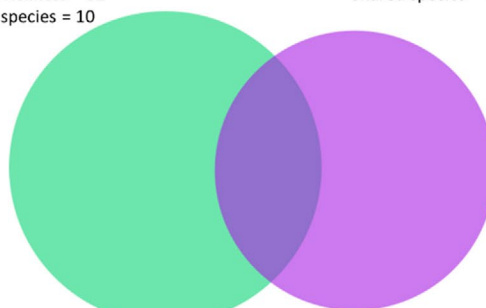
D) Low Nestedness, High Turnover

Assemblage 1

Species richness = 32
Shared species = 10

Assemblage 2

Species richness = 30
Shared species = 10



$$\beta_{jac} = 0.807 \quad \beta_{jtn} = 0.80 \quad \beta_{jne} = 0.007$$

FIGURE 1 | Legend on next page.

FIGURE 1 | A description of partitioning total beta diversity into nestedness and turnover using Jaccard dissimilarity. We show a simulated, illustrated example of how total beta diversity is calculated from two different assemblages (A) and how nestedness (dissimilarity due to differences in assemblage size, in this case species richness) and turnover (dissimilarity due to species replacements) components of total beta diversity contribute to Jaccard dissimilarity (B). See (Baselga and Leprieur 2015; Koleff et al. 2003) for full details of the equations, including a separate equation for independently calculating nestedness. We use a simplified equation using β_{jac} and β_{jtn} to calculate β_{jne} for brevity and to keep the explanation as simple as possible. We also show two examples of extreme cases with high nestedness and low turnover (C) and with low nestedness and high turnover (D).

aggregated at different spatial scales provides an opportunity to elucidate the mechanisms driving biodiversity change with habitat degradation.

Here, we address the knowledge gap of how total beta diversity and its components, nestedness and turnover, respond to habitat degradation in boreal forest landscapes. Boreal forests are under heavy pressure from harvesting activities, so they have experienced substantial habitat degradation including reductions in the overall amount and diversity of key habitat structures and microhabitat conditions (Baker et al. 2016; Fridman and Walheim 2000; Gossner et al. 2019). The most recent red-list assessment of forest habitat types in Finland, for example, highlighted the deterioration of the ecological quality of forests, especially in terms of scarcity of deadwood, veteran trees, and broadleaf species (Hyvärinen et al. 2019). The most widely used forestry practice across Fennoscandia is retention forestry, where some trees are retained during clearcutting. Retention forestry was developed to reconcile the conflicting demands of this timber production system and biodiversity conservation (Gustafsson et al. 2020), and involves retaining trees, often in small groups, during the harvest. Retention patches represent an intermediate disturbance condition between two extremes. At the degraded extreme, young forests are single-age stands with low tree-species diversity, low amounts of deadwood, and limited shelter from climate extremes. At the least degraded extreme, mature forests host abundant large older trees that offer shelter, longer habitat integrity history, and often high tree species richness and deadwood availability (Baker et al. 2016; Bartels et al. 2018; Curzon et al. 2020; Fedrowitz et al. 2014; Gustafsson et al. 2012). In combination with the other common practice in Sweden of leaving larger areas uncut for biodiversity conservation, retention forestry offers a unique opportunity to explore biodiversity change across three levels of habitat degradation.

Our study uses a dataset of three sessile taxa that inhabit woody structures in the boreal forest:

- Lichens—Including both epiphytic (on living trees) and epixylic (on deadwood) species, surveyed on the standing live and dead trees up to 2 m in height.
- Fungi—Including deadwood-inhabiting fungi and a pre-defined set of corticioid fungi (Table S1), recorded on both standing and lying deadwood.
- Bryophytes—Epixylic bryophytes recorded on a subset of lying deadwood

Boreal forest biodiversity is heavily reliant on mature forest conditions, including stable microclimates and substrate availability (Baker et al. 2016; Fossetøl and

Sverdrup-Thygeson 2009; Koivula and Vanha-Majamaa 2020; Parajuli and Markwith 2023; Yang et al. 2021; Zhang et al. 2024). Although we expect all three taxa to be sensitive to the harvesting-caused habitat degradation, they may differ in responses to habitat degradation (Nirhamo et al. 2025). Bryophytes, for example, have been found to be more sensitive than lichens to the type of habitat degradation in our study, namely felling activities (Hautala et al. 2011) and exposure to extreme climate conditions in retention patches (Perhans et al. 2009). Bryophytes may therefore display more extreme changes in species composition with habitat degradation in our study. Wood fungal assemblages typically experience high levels of turnover between sites and deadwood substrates and can be sensitive to dispersal limitations causing specialised species to be expatriated from local species pools in more degraded forests (Hart et al. 2024). As a result, turnover may play a larger role in their beta diversity patterns than other taxa.

In our study, we seek to characterise the relationships between total beta diversity and its components, nestedness and turnover, over a gradient of habitat degradation within boreal forests. Specifically, we assess beta diversity, nestedness and turnover values at two spatial resolutions: the local site assemblage level, resulting in multiple pairwise comparisons of sites (Figure 2a), and habitat degradation level pooled species assemblages (Figure 2b). Our main goal is to test whether there are greater differences when comparing between habitat degradation levels than within habitat degradation levels, signalling the effects of the habitat modifications on species composition. Second, we aim to better understand the effects of habitat degradation on species composition by comparing results across different spatial resolutions of assemblage aggregation.

To this end, we ask three related questions:

1. How does pairwise total beta diversity vary among assemblages from different habitat degradation levels compared to assemblages within the same degradation level?
2. Are nestedness and turnover greater when comparing pairwise assemblages from different levels of habitat degradation compared with assemblages within the same level of habitat degradation?
3. How is the relationship of nestedness and turnover between levels of habitat degradation affected by assemblage aggregation resolution?

In each analysis, we assess the relationship between habitat degradation and species compositional change. We hypothesise that total beta diversity will be higher among assemblages from different habitat degradation levels than within

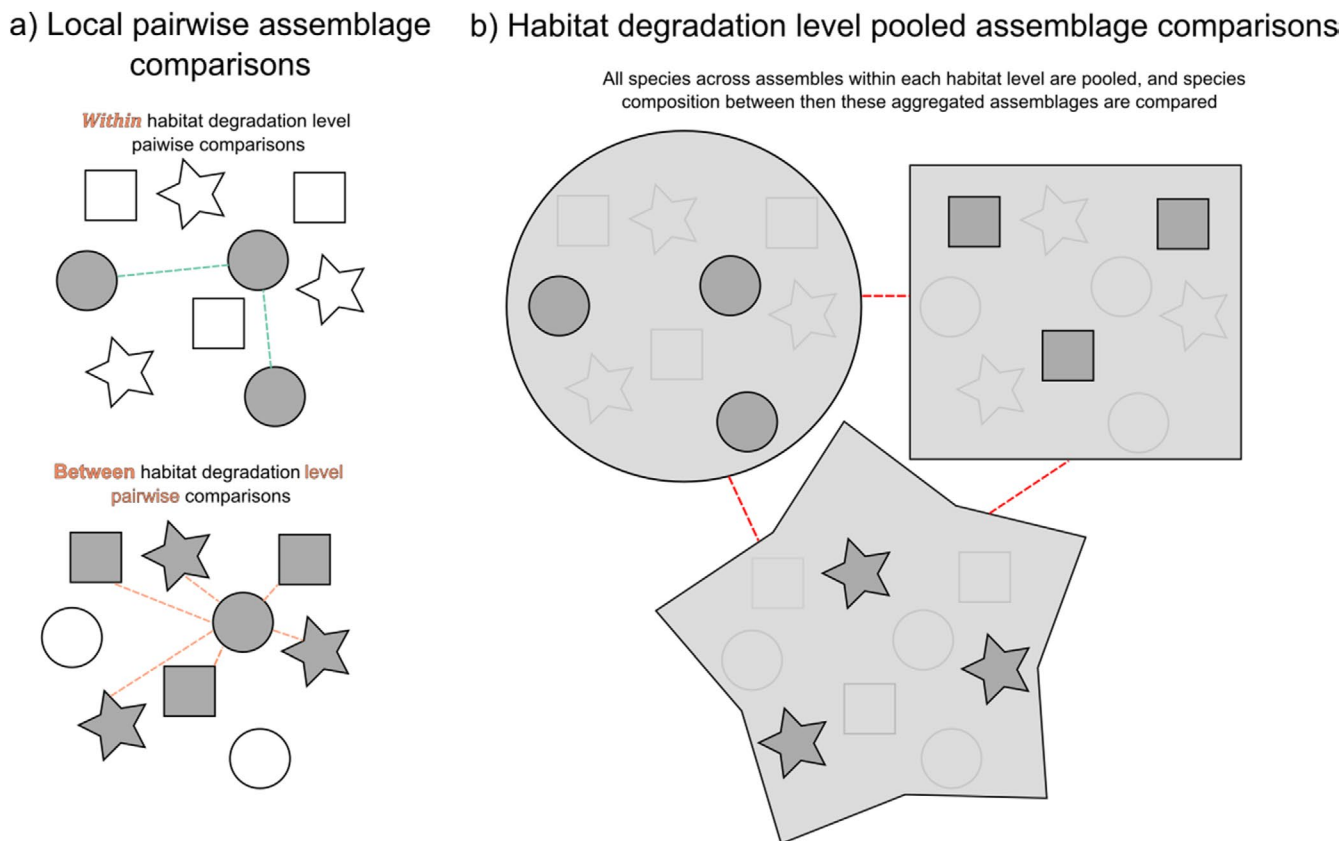


FIGURE 2 | A conceptual diagram showing the two different aggregation scales at which we assess total beta diversity, nestedness and turnover between assemblages. In line with our study design, we illustrate three habitat degradation levels, represented by three different symbols: Squares, circles and stars. In Questions 1 and 2 (a), we undertake pairwise comparisons of local assemblages from the 120 sites surveyed in our study and categorise these comparisons as either comparing within (e.g., two low habitat degradation level sites) or between (e.g., a low and a high habitat degradation site) habitat degradation level. These pairwise comparisons are illustrated by either green dashed lines between with the same habitat degradation level (between circles in our illustration) or orange dashed lines between different habitat degradation levels (between a circle and all other symbols in our illustration). In Question 3, we also pool local assemblages into three larger, pooled assemblages, one for each habitat degradation level (b). These are visually represented by larger symbols matching the dark grey symbols within them. We then compare the total beta diversity, nestedness and turnover values of these large habitat degradation level pooled assemblages (represented by dashed red lines) to the corresponding pairwise values (e.g., all the pairwise low–high values to the pooled low–high value).

assemblages from the same degradation level, indicating that habitat degradation promotes species turnover and nestedness due to non-random species losses in the more degraded forest. We also hypothesise that total beta diversity and turnover will be lower for the comparison of assemblages pooled at habitat degradation level, due to decreasing effects of stochastic and demographic processes at this scale. In contrast, we expect nestedness to be greater due to biotic homogenisation in more degraded habitats.

2 | Methods

2.1 | Study Area and System

We studied species composition of lichens, fungi and bryophytes in boreal forests located in Sweden (Figure 3). All of our forests had similar tree species compositions. They were dominated by Norway spruce (*Picea abies* (L.) Karst) and Scots pine (*Pinus sylvestris* L.) and contained some silver birch (*Betula pendula* Roth.) and downy birch (*B. pubescens* Ehrh.). There were also limited

occurrences of other deciduous trees including European aspen (*Populus tremula* L.), rowan (*Sorbus aucuparia* L.), goat willow (*Salix caprea* L.) and grey alder (*Alnus incana* (L.) Moench).

Our analysis contains three forest management types translating to three habitat degradation levels. Low-degraded habitat was mature forests not managed for timber production for several decades. Medium-degraded habitat was small retention patches of approximately 0.053 to 0.447 ha of mature forest left unharvested on clearcuts after final harvest. Both low and medium-degraded forests contained trees with diameters of up to 50 cm at breast height (1.3 m), with median densities of 1234 trees per ha and 1494 per ha, respectively, and living wood volumes of 237 m³ per ha and 230 m³ per ha, respectively. Both habitat types also contained a median of 230 items of deadwood per ha, although the median volume per ha was higher in low-degradation habitats (19 m³ per ha) than medium-degradation habitats (14 m³ per ha). The medium-degradation forests therefore had similar living tree structure to low-degradation habitats, but less deadwood. Another difference is that the medium-degraded habitats are

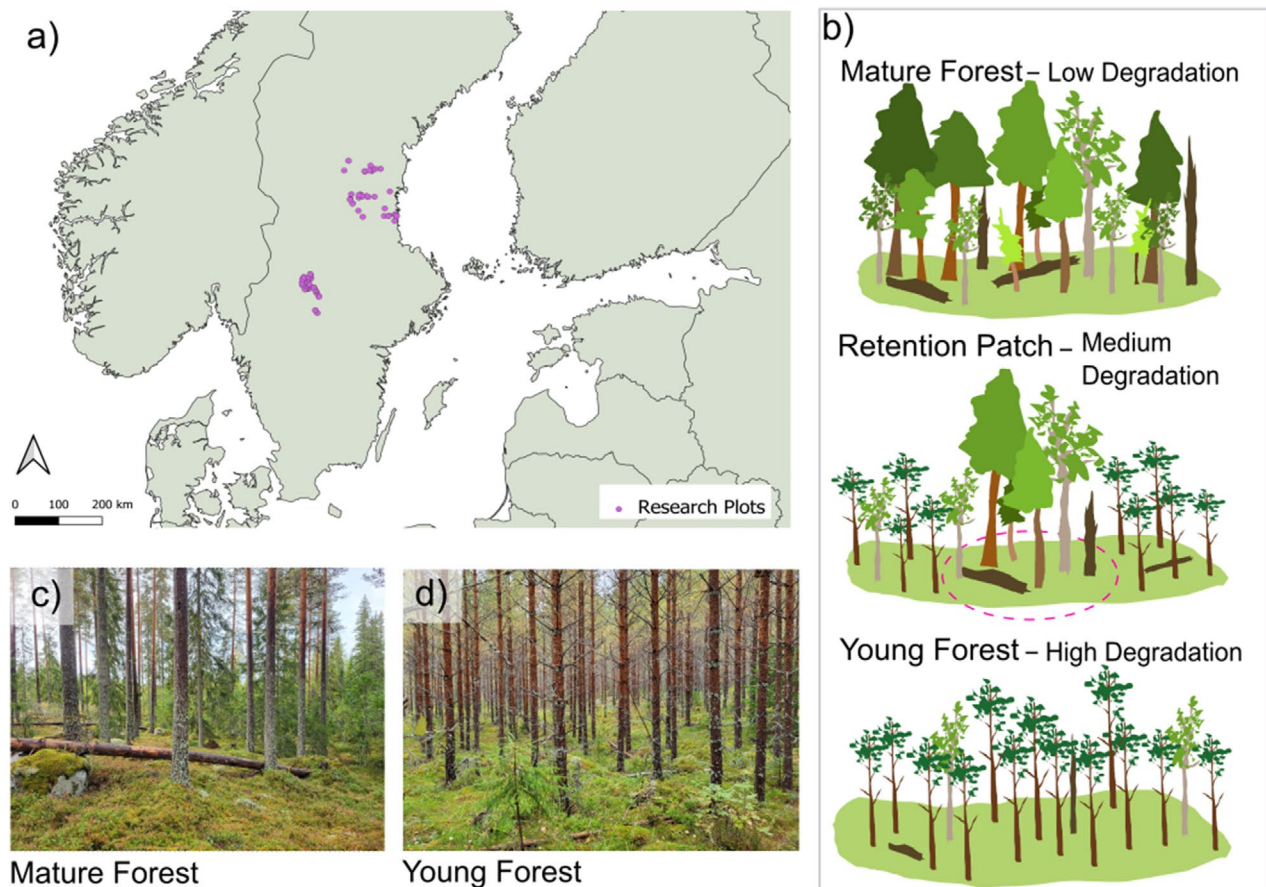


FIGURE 3 | The location of the sample sites in Sweden (a). Plots were situated in three forest types of different habitat degradation levels (b), ranging from low-degradation mature forests set aside from harvesting, often due to valuable ecological structures (c), medium-degradation retention patches, where small areas of unharvested forest were left within otherwise clearcut areas, and highly degraded young forests that were clearcut and replanted 20–30 years ago (d). The 120 plots are equally split between habitat degradation levels.

much smaller patches of forest, making them more exposed to disturbances from, for example, wind, more exposed to harsher climatic conditions, and representing a more fragmented habitat.

Highly degraded forests were young stands, clearcut about 20–30 years ago and subsequently managed for timber production. They were dominated by high densities of planted saplings and smaller trees (diameters at breast height below 20 cm), as demonstrated by the higher densities (2760 trees per ha) and lower volumes (98 m³ per ha) of living wood. They also harboured fewer deadwood items (23 per ha) with lower volumes (2 m³ per ha) than the medium- and low-degradation habitats. These high-degradation habitats have also experienced significant disturbance during harvest, and they lack mature canopy trees that provide the microclimate conditions typical of mature forests.

2.2 | Data Acquisition

We undertook an extensive survey of 120 sites within Sweden, distributed evenly between the three different habitat degradation levels (low degradation: mature set-aside forests, medium degradation: retention patches and high degradation: young

forests, clearcut in ca 30 years ago, Rudolphi et al. 2014). At each site, we inventoried the presence of species from all three taxonomic groups in circular plots with a 20-m diameter. When retention patches were smaller than this, we surveyed the entire area of the retention plot, here defined as the area covered by the canopy layer of the dominant tree species.

Lichens were surveyed up to 2 m in height on all standing dead trees within the plot. A subset of living trees was also surveyed: three small (diameter at breast height of between 5 and 15 cm) trees and seven large (diameter at breast height of at least 15 cm) for each dominant tree species (either Norway spruce or Scotch pine). If insufficient trees from one size class were available, we surveyed more from the other size class to maintain a constant subsample of 10 living trees per plot. Most lichens were visually identified to species in the field, but some unclear specimens were further assessed in the laboratory.

For the fungi survey, three small (diameter at breast height of between 5 and 15 cm) lying items of deadwood and three small standing trees per dominant tree species were surveyed in each plot. Then, all dead wood with either a diameter at breast height of at least 15 cm, for standing trees, or for lying deadwood, a maximum diameter of 15 cm and a minimum length of 1.3 m, for all tree species including deciduous trees, was inventoried.

Standing trees were surveyed up to a height of 3 m. Species identification of fungi was based on the appearance of fruiting bodies.

Bryophytes were surveyed on all deadwood with a minimum diameter greater than 15 cm and an additional five smaller deadwood items per dominant tree species. Highly decayed wood (Decay stage 5, Renvall 1995) was considered part of the organic topsoil layer and not surveyed.

2.3 | Analysis

We calculated beta diversity, quantified using the Jaccard dissimilarity index, using the R package *betapart* (figure 1, Baselga and Orme 2012). This index quantifies the proportion of species that are not shared between two assemblages, with 0 being all species shared and 1 being no species shared. We used the same *betapart* R package to partition the beta diversity values into nestedness and turnover (Figure 1). The higher the nestedness or turnover value, the greater its contribution to the overall beta diversity.

For Question 1, where we assessed differences in beta diversity of between-compared with within-assemblage pairs, we calculated the beta diversity value for each local assemblage where at least one species was present. Lichens were found in all 120 sites, giving a matrix of 7140 beta diversity values. Fungi were found in 86 sites, giving a matrix of 3916 beta diversity values, and bryophytes were found in 111 sites, giving a matrix of 6105 beta diversity values (Table S1). These values were then grouped into either assemblage pairings within a given level of habitat degradation, for example, a pair of assemblages in medium-degradation forests (within-degradation pairs), or pairings of assemblages in different levels of habitat degradation, for example, an assemblage in a medium-degradation forest compared with an assemblage in a high habitat degradation forest (between-degradation pairs). Due to the non-parametric nature of the beta diversity values, we used the Wilcoxon Rank Sum tests in R (R Core Team 2022) to test significance. However, as we had such large numbers of comparison datapoints in our analyses, statistical significance was insufficient to distinguish between biologically significant results. We therefore used Dunn test from the R package *rstatix* (Kassambara 2023) to calculate Cliff's delta values, which are the associated effect size between groups, and better reflect biological significance for large sample sizes. Cliff's delta is a non-parametric, unitless effect-size measure that quantifies the difference between two groups by estimating the probability that a value selected from one group is greater than a value from the other group (Macbeth et al. 2010). Cliff's delta values vary between -1 and 1 , with more similar groups having Cliff's delta values approaching 0 . Negative values mean the first of the two groups compared is smaller, and positive values mean the first of the two groups is larger. Values between -0.147 and 0.147 are considered biologically negligible, values between -0.147 and -0.33 and between 0.147 and 0.33 are small, values between -0.33 and -0.47 and 0.33 and 0.47 are medium, and values below -0.47 or above 0.47 are large (Hess and Kromrey 2004).

For Questions 2, where we assessed differences in nestedness and turnover in assemblage pairs from between compared with within local assemblage pairs, we repeated the steps described for Question 1. We grouped nestedness and turnover into between or within degradation assemblage pairs and then used Wilcoxon Rank Sum tests to test for a significant difference between habitat degradation pairings, and a post hoc Dunn test to calculate Cliff's delta to estimate effect size.

Nestedness values reflect differences in species richness, but do not give information on which of the two samples being compared has the lower species richness value. To aid in interpretation, we therefore also tested differences in species richness between habitat degradation levels using the non-parametric Kruskal-Wallis test in base R combined with Cliff's delta values.

For Question 3, where we sought to understand the influence of assemblage aggregation scale on beta diversity, nestedness, and turnover, we aggregated all species detected within a habitat degradation level into three large pooled assemblages (see Figure 2). We calculated beta diversity between each of these pooled assemblages using the Jaccard dissimilarity index and partitioned the values into nestedness and turnover using the R package *betapart*. We then assessed whether total beta diversity, nestedness, and turnover of the assemblages for the three levels of habitat degradation were different from the mean of the local pairwise comparisons among sites. We deemed them different if they fell outside the expected range of values from the local comparisons.

3 | Results

During our field-based substrate surveys, we found a total of 304 lichen, 149 bryophyte and 66 polypore species across our 120 sites distributed equally between the habitat degradation levels. Habitat degradation influenced species richness between sites, as demonstrated by a Dunn test revealing that high-degradation habitats had significantly lower species richness across all taxa (Figure S1, Table S2). For lichens, there was no significant difference in species richness between medium- and low-degradation habitats (Figure S1, Table S2). In contrast, for fungi and bryophytes, medium habitat degradation had intermediate species richness, while low-degradation habitats exhibited the highest species richness (Figure S1a, Table S3).

3.1 | How Does Pairwise Beta Diversity Vary Within vs. Between Habitat Degradation Levels?

We found that lichen assemblages showed higher beta diversity when assemblage pairs were from different levels of habitat degradation compared with assemblage pairs from the same level of habitat degradation (Cliff's delta: 0.40 , $p < 0.001$, Figure 4a). Fungi and bryophyte assemblages, conversely, showed a statistically significant but negligible higher beta diversity when assemblage pairs were from different levels of habitat degradation (fungi Cliff's delta: 0.09 , Figure 4d, bryophytes Cliff's delta: 0.10 , Figure 4g). These results suggest that the effects of habitat degradation on community composition can be detected using beta diversity, but not consistently across all taxa.

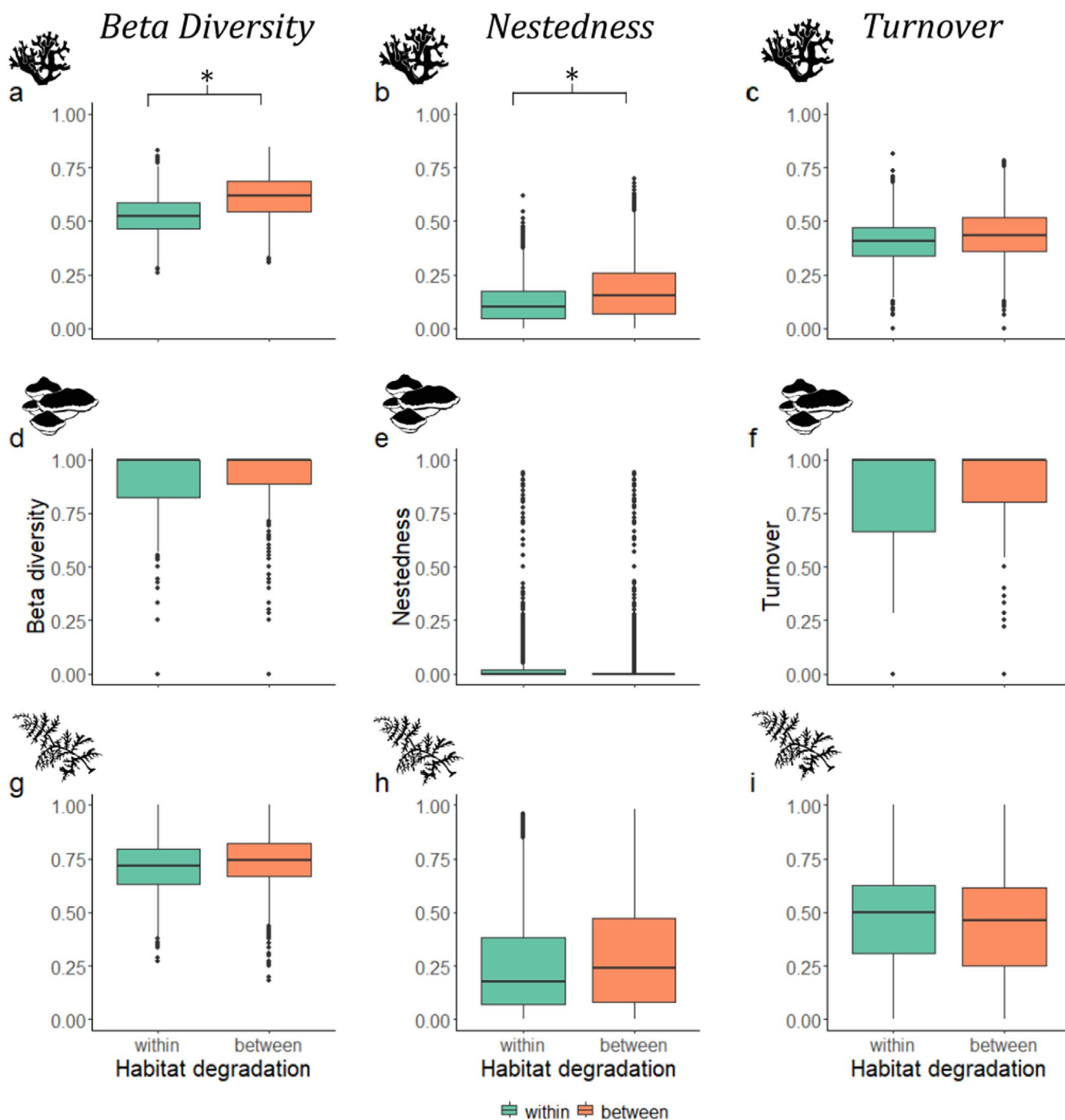


FIGURE 4 | The Jaccard beta diversity, nestedness and turnover values, respectively, for lichens (a, b, c), fungi (d, e, f) and bryophytes (g, h, i), split between comparisons of pairs of assemblages within the same level or between different levels of habitat degradation. Asterisks are shown where comparisons were significant, and effect sizes were not very low (statistical significance above 0.05 according to Wilcoxon non-parametric test combined with a Cliff's delta effect size of below -0.147 or above 0.147).

3.2 | How Do Pairwise Nestedness and Turnover Values Vary With Habitat Degradation Levels?

We found an increase in nestedness when comparing pairs of lichen assemblages from different habitat degradation levels as opposed to pairs of assemblages within the same habitat degradation level (Cliff's delta: 0.19 , $p < 0.001$, Figure 4b). In contrast, fungi and bryophytes differences were significant, but the corresponding Cliff's delta effect sizes were below the threshold for biological significance (0.147), indicating a negligible effect

of habitat degradation level (fungi Cliff's delta: 0.05 , $p < 0.001$, Figure 4e; bryophytes Cliff's delta: 0.08 , $p < 0.001$, Figure 4h). The inconsistencies in pairwise nestedness comparisons between taxa, similar to the pairwise beta diversity results above, indicate that local scale species losses do not consistently occur with habitat degradation across taxa.

Across all taxa, we found statistically significant differences in pairwise turnover between habitat types (lichens: $p < 0.001$, fungi: $p < 0.001$, bryophytes: $p < 0.001$). As with the fungi

and bryophyte nestedness comparisons, however, the corresponding Cliff's delta effect sizes were below the threshold for biological significance (0.147), indicating negligible differences (lichens: 0.14 and Figure 4c, fungi: 0.08 and Figure 4f, bryophytes: 0.04 and Figure 4l). This result suggests that, at the local pairwise scale, habitat degradation did not consistently influence species replacement patterns across taxa. Turnover also represented a greater proportion of total beta diversity than nestedness in all taxa and comparison groups (Figure 4), indicating that differences in pairwise communities were dominated by species replacements rather than losses across all comparison types.

3.3 | Spatial Scaling of the Relationship of Beta Diversity, Nestedness and Turnover to Habitat Degradation

We found clear evidence for spatial resolution affecting the relationship between habitat degradation and beta diversity, as our results for the habitat degradation level pooled assemblage comparisons were different from our pairwise results. Across all taxa, we found lower total beta diversity values when pooling species within habitat degradation levels than in corresponding pairwise comparisons, which was generally a consequence of lower turnover (Figure 5, Figure S2). The only exception to this was in the bryophyte assemblages between high and medium-degradation levels, where the values for assemblages pooled at the habitat degradation level were lower than the pairwise comparison values for both nestedness and turnover (Figure 5e,f, Figure S2g-i). Nestedness values in the pooled comparisons were higher than pairwise values for all fungi assemblage comparisons (Figures 3e and 5c,d) and the high-low bryophyte comparison (Figures 3h and 5e,f). Only nestedness in the lichen medium-low assemblage comparisons was lower in the pooled rather than the corresponding pairwise comparisons (Figures 3b and 5a,b). These findings suggest that the processes influencing species community composition at different habitat degradation levels are sensitive to the spatial resolution at which they are investigated.

4 | Discussion

By partitioning total beta diversity and comparing values from assemblages aggregated at two different spatial resolutions, we found evidence for biotic homogenisation within the most highly degraded forest habitats. At the local aggregation scale, where we compared assemblages pairwise across the study sites, only lichens showed evidence for higher beta diversity and nestedness when comparing assemblages from different habitat degradation levels. Even in this case, differences in beta diversity were mainly due to differences in turnover rather than nestedness. This result suggests that species replacements overwhelm the influence of species losses at the local scale. This result held true even when comparing assemblages from high- and low-degradation habitats with notable differences in species richness. Conversely, at the resolution of the habitat degradation level rather than individual sites, we found evidence across all three taxa that nestedness values were higher when comparing between habitat degradation levels, especially in the most

extreme habitat quality comparisons. The contrast between our results at the two spatial resolutions suggests that biotic homogenisation contributes to species replacements in assemblages with extreme differences in habitat degradation, but the effects appear weak in comparison to other local drivers of species replacement, such as differences in habitat type and demographic processes (Chase and Myers 2011; Shoemaker et al. 2020). Our results highlight the need for conservation studies to consider multiple spatial resolutions when planning and evaluating species communities, as well as emphasising the importance of considering the effects of biotic homogenisation with increasing habitat degradation.

4.1 | Turnover as the Dominant Driver of Beta Diversity

To our knowledge, our study is the first that, across multiple taxa, empirically tests the expectation that nestedness is higher when comparing paired assemblages from different levels of habitat degradation and lower when comparing assemblages from the same level of habitat degradation. This expectation derives from the understanding that degradation leads to substantial non-random local extinctions, as species less able to adapt to the harsher environment are lost (Berglund and Jonsson 2003; Táborská et al. 2017). Our results are, however, contrary to this expectation for local assemblage comparisons. While nestedness was higher for lichen assemblage pairs comparing between habitat degradation levels than within degradation levels, turnover rather than nestedness remained the larger contributor to overall beta diversity. For fungi and bryophytes, we did not find higher nestedness when comparing assemblages from different levels of habitat degradation than when comparing assemblages from the same level of degradation. However, we also found significantly lower assemblage species richness values for all taxa in more degraded habitats. This result suggests that change in species identities can overwhelm the effects of species losses even when assemblages have statistically different species richness values. These findings highlight the complexity in understanding the effects of habitat degradation on species communities, emphasising the need for conservation initiatives to avoid over-reliance on single or few aspects of biodiversity to understand and monitor change.

Ecological theory suggests that turnover is the result of two filters operating at different spatial scales, combining to influence which species from the regional pool are present at a specific site (Vellend 2010). When comparing local assemblages in different locations, at a small spatial resolution, dispersal and stochastic events dominate by influencing which species are present at a site (Chase 2014). When aggregating assemblages at larger spatial resolutions, for example, assemblages pooled at a habitat level, the effects of stochasticity and dispersal are minimised so that niche-based processes play a strong role as environmental and species differences filter, determining which species persist and thrive (Chase 2014). In line with previous results (Soinin et al. 2018), turnover was substantially lower in our study when we aggregated assemblages at the habitat degradation level rather than at the local site level. This result suggests that stochasticity and dispersal play an important role in the observed high local turnover rates in our data, even when comparing

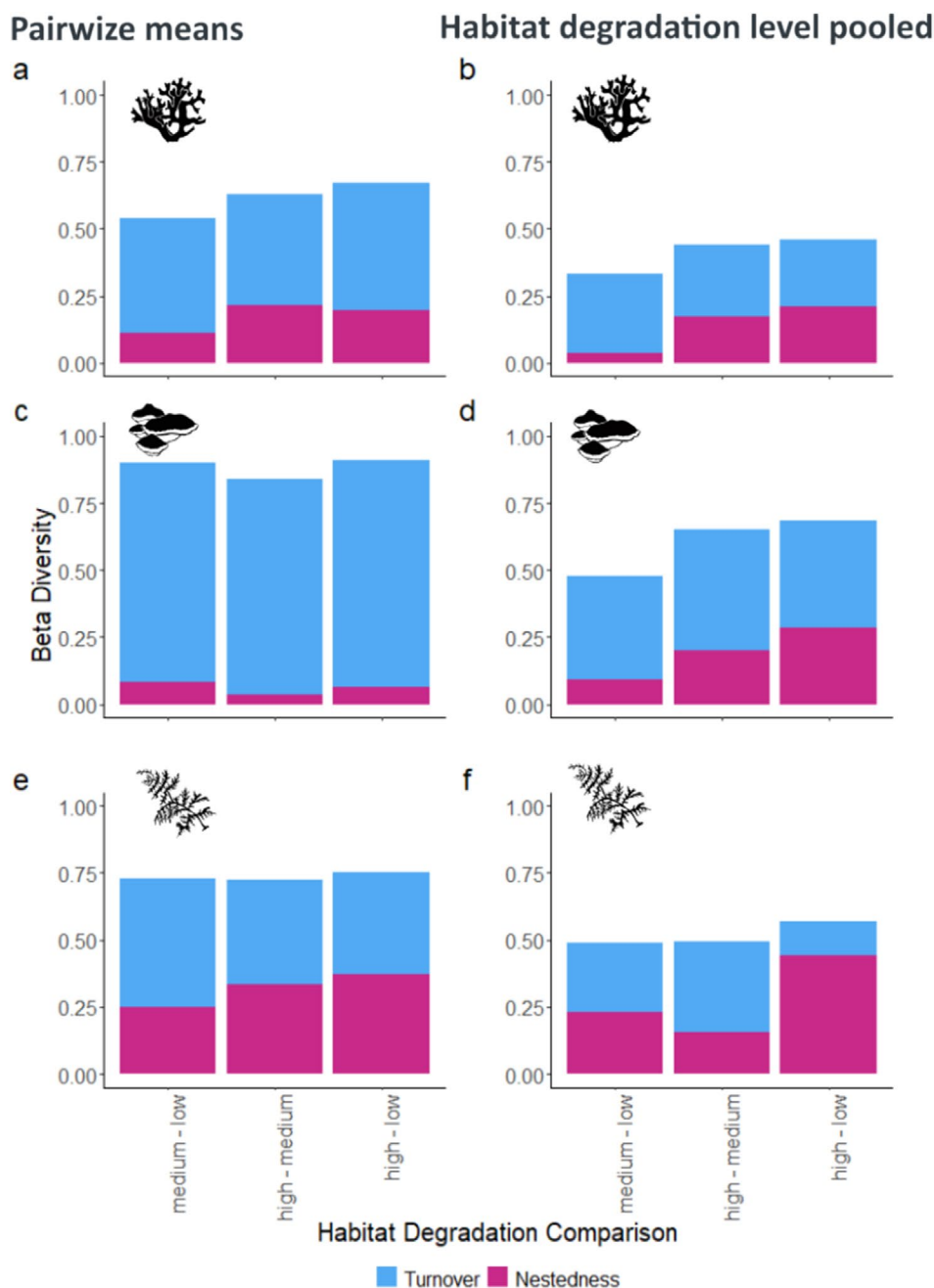


FIGURE 5 | The two components of total beta diversity, turnover (blue) and nestedness (pink), when comparing between different habitat degradation levels for lichens (a, b), fungi (c, d) and bryophytes (e, f). Pairwise means plots (a, c, e) show the mean of each pairwise turnover and nestedness value for site-pairs when comparing across habitat degradation levels. Full distributions of these data are shown in Figure S2. Habitat degradation pooled plots (b, d, f) show the turnover and nestedness values when comparing assemblages containing all species found within a habitat degradation level, so there is one value per beta diversity part, taxa and habitat degradation comparison.

between high and low-degradation habitats. Conservation assessments focusing on local, pairwise comparisons therefore risk underestimating the effects of habitat degradation on species composition due to the stronger influence of turnover at this scale.

4.2 | Support for Biotic Homogenisation

Although a previous study found nestedness to be invariant across spatial scales (Soininen et al. 2018), it did not account for

habitat degradation levels. The non-random replacement of specialist species with generalists in highly degraded habitats can result in high local turnover, while simultaneously limiting the aggregated species pool. Biotic homogenisation due to local species replacements of many specialists with few generalists would lead to high nestedness when comparing pooled assemblages of different habitat degradation levels, even if local pairwise comparisons show low nestedness. Biotic homogenisation is common globally (McGill et al. 2015), and there is evidence that this process is important in the degradation of boreal forests, where rare species are more prevalent in higher quality habitats

(Berglund and Jonsson 2003). When assemblages were pooled at the habitat degradation resolution, nestedness comparisons between habitat degradation levels for all three taxa were higher than the corresponding pairwise nestedness values between sites. By contrasting spatial resolution habitat-degradation comparisons, we therefore found evidence of biotic homogenisation within our study system, especially in the most degraded sites. This result could explain why local turnover rather than nestedness was so influential in our results even when comparing between habitat degradation levels.

An additional reason why we did not see strong signals for higher nestedness when comparing pairwise assemblages from different habitat degradation levels is that all the forests in our study are situated in landscapes experiencing significant anthropogenic disturbances. In such landscape contexts, for example habitat matrix quality and site connectivity, can drive biodiversity patterns (García-Navas et al. 2022; Leite et al. 2013). Even the least degraded forest habitats in our study are far from pristine primary forest; they have experienced some level of habitat degradation from human activities (Lundmark et al. 2013). Subsequently, these low-degradation habitats may experience species extirpations due to historical or ongoing fragmentation and a broader general environmental degradation of the surrounding landscape. It is possible that the effects of habitat degradation on nestedness would have been stronger at the pairwise scale if the comparisons had included pristine forests with more intact species assemblages than our sites. Nevertheless, our results reflect the current range of habitat degradation available in lowland Swedish boreal forests and demonstrate that within this system, biotic homogenisation is taking place.

The biotic homogenisation we detected raises concerns for decreased functional diversity (Mori et al. 2015) and consequently threatens ecosystem functioning (Hallett et al. 2017). That we found evidence for biotic homogenisation in our study, especially when comparing with more heavily degraded commercial forestry stands that make up the largest proportion of forests in Fennoscandia (Gustafsson et al. 2010), demonstrates the risk to forest sustainability if more conservation and restoration activities are not undertaken to support mature boreal forest communities.

4.3 | Taxonomic Variation

Lichens often grow on living trees and range from light- and temperature-sensitive, old-forest requiring species to more hardy species able to thrive on clearcuts with higher levels of light and greater fluctuations in temperature (Perhans et al. 2009). In our study, lichens were the only taxa where Cliff's delta effect sizes indicated differences between habitat degradation comparisons. These results are in line with previous studies that found that species richness of lichen assemblages increases with larger tree dimensions (Klein et al. 2020), which match conditions typically found in low and medium-degradation forests. In addition, the microclimatic conditions in small mature forest patches, typical to our medium-habitat degradation conditions, provide unsuitable microclimate conditions for the most sensitive lichen species (Koivula and Vanha-Majamaa 2020). In line with these previous studies of lichen ecology and habitat requirements, our

results suggest that lichen species composition is strongly influenced by habitat degradation. Specifically, retention patches did support lichen conservation in boreal forests to some extent, but they did not replace the conservation value of larger mature forest patches.

By contrast, pairwise bryophyte and fungi assemblage assessments did not show higher total beta diversity across habitat degradation levels, which is somewhat unexpected. A possible explanation is that the high overall turnover in these groups may have masked the effects of habitat degradation. Indeed, pairwise total beta diversity and turnover values were consistently higher for fungi and bryophytes than for lichens, regardless of habitat pairing. This result may partly be due to low habitat availability in high habitat degradation habitats increasing stochastic variation due to low sample sizes for bryophytes and fungi. We sampled only deadwood for these taxa to target obligatory and facultative deadwood species. Even highly degraded sites in our study had many living trees that had been present for multiple decades, whereas they often contained fewer deadwood substrates. The low deadwood counts in highly degraded sites may therefore also conflate the influence of available habitat with increased stochastic variation due to smaller sample sizes. This sampling effect may explain why the regional analysis showed higher nestedness when comparing high and low regional species pools despite no corresponding pattern when comparing local assemblages. Such regional species-pool-level analyses avoid the dominance of stochastic processes seen at local scales (Chase and Myers 2011), allowing a clearer view of the effects of habitat degradation. Our pairwise results suggest that further investigation into the effects of deadwood availability in highly degraded forests is needed to fully categorise the effects of retention forestry on wood fungi and polypore conservation. As with the lichen analysis, though, the high nestedness values at the pooled habitat-level resolution data, especially for extreme bryophyte comparison, underlines the conservation value of the low-degradation mature forests in ensuring larger scale biodiversity is maintained.

For fungi, an additional factor potentially contributing to high pairwise turnover values is the fruiting bodies' ephemeral nature. The fruiting bodies used to identify reproducing species may not be present even when a species is active in the wood. Consequently, deadwood-inhabiting fungi show very high total beta diversity and turnover in managed forests (Halme et al. 2013). Although we undertook surveying at peak fruiting season to maximise detection, additional sampling approaches involving repeated surveys or the incorporation of DNA barcoding may improve the representation of species with less robust or rarer fruiting. Yet, fruitbody-based community surveys have been shown to yield species-environment relationships (Ovaskainen et al. 2013) and species-to-species associations (Saine et al. 2020) that are consistent with findings from DNA-based community surveys. In addition, fungi communities were found to be more sensitive to substrate type and availability than forest patch naturalness (Dawson et al. 2024), suggesting our results are not simply an artefact of sampling design.

Together, these results highlight the importance of considering taxon-specific responses and spatial scale when assessing the impacts of habitat degradation on biodiversity and biotic

homogenisation. Future studies incorporating landscape variables, functional traits and repeated or multi-method sampling could help further disentangle these effects and better inform conservation strategies in degraded forest landscapes.

Author Contributions

Faith A.M. Jones chose the analysis approach and question, analysed the data and led the writing of the manuscript. Alwin A. Hardenbol and Albin Larsson Ekström contributed to developing the questions and interpreting the results. Anne-Maarit Hekkala, Mari Jönsson, Matti Koivula and Joachim Strengbom supported project conception, set-up, field methodology and data collection, as well as assisting with interpreting the results. Jörgen Sjögren led the project conception, set-up and data collection, assisted with choosing the analytical approach and questions, and contributed to interpretation. All authors contributed critically to the drafts and gave final approval for publication.

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Conflicts of Interest

This work was funded by a research grant from Stora Enso AB. The authors have no other conflicts of interest to declare.

Data Availability Statement

Data is available at DOI: [10.5061/dryad.fttdz093x](https://doi.org/10.5061/dryad.fttdz093x).

Peer Review

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** ddi70080-sup-0001-AppendixS1.docx.