Journal of Environmental Management 381 (2025) 125161

Contents lists available at ScienceDirect

Journal of Environmental Management

journal homepage: www.elsevier.com/locate/jenvman

Research article

Enhanced bryophyte communities, but challenges for lichens following translocation of deadwood in ecological compensation

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A B S T R A C T

Habitat restoration and ecological compensation are gaining attention as methods to offset habitat loss from landscape exploitation, but few studies assess their impact on species and communities, particularly in boreal forests. We evaluated a novel ecological compensation method; the translocation of deadwood and associated species from an impact area to a compensation area. Our study focused on assessing species richness and assemblage composition of epiphytic bryophytes and lichens on translocated (637 substrates) and naturally occurring Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) H. Karst) logs in a compensation area in northern Sweden. We also assessed the effects of translocated deadwood density and dead wood type on these assemblages. We recorded 52 bryophyte species and 38 lichen species. For lichens, only species confined to deadwood were included. Translocated logs significantly altered bryophyte and lichen assemblages in the translocation plots. Bryophyte richness increased over time as colonization was higher than species loss, while lichen richness remained stable with colonization of new species and disappearance of translocated species occurring at similar rates. Bryophyte colonisations mainly involved generalist forest species. Higher deadwood density in translocation plots increased bryophyte species richness but had no effect on lichens, whereas diverse deadwood types promoted conservation success for both groups. Logs of intermediate decay and snags (deadwood originating from standing dead trees) supported distinct communities, though lichen species on snags declined four years post-translocation. Our results highlight the need to include diverse substrates in conservation translocations to maximize the number of translocated species. Although translocating entire communities presents challenges, it offers a promising tool for species conservation and ecological restoration.

1. Introduction

Ecological restoration is an important strategy for mitigating negative impacts of habitat degradation and assisting in the rehabilitation of ecosystems, a practice frequently used in boreal forests (Halme et al., 2013; Hjältén et al., 2023; Tolvanen and Aronson, 2016). Restoration involves various activities aimed at restoring ecosystem structures and functions that have been degraded or lost due to anthropogenic activities (Martin, 2017). One such action is the reintroduction or reinforcement of species that have been lost or become rare, termed conservation translocations, i.e., 'the intentional human-mediated movement of species from one place to another with a primary objective of conservation benefits' (IUCN/SSC, 2013; Seddon et al., 2014). In boreal ecosystems, bryophytes (including liverworts and mosses) and lichens play important roles due to their contributions to forest biodiversity, nutrient cycling and soil formation (Campbell et al., 2010; Pizňak and Bačkor, 2019; Van Cleve and Alexander, 1981). These organisms are highly responsive to environmental changes, making them excellent bioindicators of functional ecosystems and high conservation values (Thormann, 2006). The unique ecological niches that bryophytes and lichens occupy reflect the habitat diversity, and species distribution often depend on the availability of suitable substrates. For example, different types of deadwood such as fallen logs and sun-exposed snags (standing dead trees) offer distinct ecological niches for a variety of bryophyte and lichen species (Stokland et al., 2012). Substrate type and decay stage significantly influence bryophyte and lichen diversity, with

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https://doi.org/10.1016/j.jenvman.2025.125161
Received 30 October 2024; Received in revised form 17 March 2025; Accepted 26 March 2025
Available online 3 April 2025
0301-4797/

earlier decay stages benefitting lichens and later decay stages providing more complex and moister habitats supporting greater species richness and distinct assemblages of bryophytes (Caruso and Rudolphi, 2009; Dittrich et al., 2014). A number of bryophyte and lichen species prefer old dead trees with properties that are challenging to create artificially through restoration and the time required to develop suitable substrates can well exceed 20–100 years (Hämäläinen et al., 2015; Santaniello et al., 2017), complicating restoration efforts significantly. Additionally, strategies such as creating high stumps to increase deadwood availability have been shown to have limited effect in enhancing lichen diversity (Hämäläinen et al., 2021), highlighting the need for more effective conservation measures that consider the complex dynamics and requirements of these species.

In boreal managed forest, many bryophytes and lichens, face challenges in recolonization both due to lack of old-growth source habitats and lack of suitable substrate (Belinchón et al., 2015; Ellis, 2017; Snäll et al., 2005; Sundberg, 2005). For several wood-inhabiting bryophytes, it is crucial that the wood is old and of large dimensions for them to establish (Ódor and van Hees, 2004; Rambo and Muir, 1998). Another challenge is that bryophytes and lichens exhibit limited dispersal abilities. For instance, the epiphytic lichen *Lobaria pulmonaria* has a mean dispersal distance of only 35 m (Öckinger et al., 2005) and lichen soredia and isidia (vegetative dispersal propagules) generally disperse over short distances. Sexual spores and asexual propagules of some bryophytes are capable of long-distance dispersal (>2 km) but a significant proportion disperse only short distances (100 m) (Hämäläinen et al., 2023; Pasiche-Lisboa, 2019).

Lichens' symbiotic nature requires that sexually dispersed spores pair with a compatible photobiont for the lichen to develop. The local availability of suitable photobionts may pose challenges for the establishment of certain lichens (Belinchón et al., 2015). Several studies suggest, however, that for many species establishment limitations at the stand level may be more critical than dispersal constraints (Werth et al., 2006; Sillett et al., 2000). Bryophytes and lichens on trees tend to have higher dispersal capabilities compared to species on the forest floor and on deadwood (Pasiche-Lisboa, 2019). However, some abundant ground-living generalist species can still rapidly occupy new deadwood substrates (Dittrich et al., 2014). Due to these varying species traits, restoration may not necessarily guarantee success if target species struggle to colonize and establish themselves on restored substrates (Hilderbrand et al., 2005; Palmer et al., 1997). Factors such as dispersal limitations or competiveness for these habitats, along with limited densities of restored substrates, may hinder the success of restoration.

Previous studies of bryophytes and lichens show that populations in degraded and/or restored habitats can benefit both from shorter distance to source populations and from remnant populations acting as sources for recolonization (Caruso and Rudolphi, 2009; Ellis, 2017). However, when source populations are depleted, direct translocation may be necessary. Successful translocation of old-growth forest lichens is indicated by survival of translocated species in new locations and dispersal to new substrates in the new locality (Hilmo and Såstad, 2001).

Numerous experiments of translocation and reintroduction of bryophytes and lichens have been performed (e.g., Mallen-Cooper and Cornwell, 2020; Smith, 2014), although most experiments have focused on single-species translocations. Early studies, such as those by Gilbert (1977) and Hallingbäck (1990), examined the survival of lichen species like *Bryoria fuscescens* and *Lobaria pulmonaria*, and focused on local condition sensitivity and successful translocation techniques. Hazell and Gustafsson (1999), Lidén et al. (2004) and Jansson et al. (2009) showed high survival and vitality rates for threatened lichen species like *Lobaria pulmonaria*, *Evernia divaricata*, *Ramalina dilacerata* and *Usnea longissima* when transplanted on retained trees, but success depended on microhabitat factors like tree clustering and dispersal distances. For bryophytes there has also been several translocation and reintroduction experiments, for instance Lappalainen et al. (2007) focused on ground-living bryophytes *Pleurozium schreberi* and *Dicranium viride*. Dahlberg et al. (2014) and Merinero et al. (2020) conducted studies on *Eurhynchium angustirete*, *Herzogiella seligeri*, *Barbilophozia lycopodioides* and *Hylocomiastrum umbratum* along slopes in Swedish forests, and observed complex interactions between these bryophytes and their microclimatic conditions. Mežaka (2023) explored the transplantation of the threatened liverworth *Lejeunea cavifolia* in an aspen forest, and underlined species' sensitivity to variations in substrate quality. Together these studies highlight the potential for translocation of bryophytes and lichens to restore and enhance biodiversity in various ecosystems. It also underscores the adaptability and sensitivity of bryophytes and lichens to new or changed microclimatic conditions (e.g., Cacciatori et al., 2022; Perhans et al., 2009) and the necessity of considering species-specific habitat requirements (e.g., Santaniello et al., 2017) and local conditions for successful translocation (Brooker et al., 2018; Smith, 2014).

There is still a lack of translocation studies focusing on multi-species or multi-taxon responses studies. It is known that lichens often form associations involving multiple species (Asplund and Wardle, 2017) but there is a limited understanding how these associations influence processes at community and ecosystem level. These complexities necessitate a shift from traditional single-species conservation strategies to more integrated approaches that consider the ecological roles of multiple organisms and communities (Mallen-Cooper and Cornwell, 2020; Seddon et al., 2014). The reintroduction and conservation strategies for multi-species translocations of bryophyte and lichens are however complex and have been rarely performed (Smith, 2014).

In recent studies, deadwood translocation has been suggested to circumvent some of the problems with long delivery times of some substrates and limited dispersal distances of wood-inhabiting bryophytes and lichens (Lindroos et al., 2021; Tranberg et al., 2024). The practice of deadwood translocation is the relocation of fallen or dead trees together with associated species communities from one impact area (target for exploitation) to a compensation area. The method has proven to at least locally enhance deadwood amounts and diversity of substrates, especially of substrates with long delivery times (Tranberg et al., 2024). It is essential to understand the ecological outcomes of translocating deadwood with entire species communities, as the process might influence the existing species pools, potentially affecting local species assemblages in both positive and negative ways (Seddon et al., 2014).

The aim of this study is to examine if the translocation of deadwood can serve as an effective tool for maintaining and/or enhancing bryophyte and lichen diversity. We used a novel method where whole communities of lichens and bryophytes were translocated together with their habitat and conducted a large-scale field experiment where more than 600 deadwood substrates were translocated from an impact area to a compensation area in boreal forests in northern Sweden. We surveyed bryophytes and lichens on both the translocated deadwood and naturally occurring local deadwood, immediately after translocation and again after three-four years. We aimed to answer two key questions: first, how the translocated deadwood contribute to bryophyte and lichen biodiversity in the compensation area; and second, how factors such as habitat amount (medium vs. high amounts of translocated deadwood) and substrate type impact translocation success for lichens and bryophytes.

We aim to test the predictions listed below.

a) The species assemblages on translocated deadwood will differ from those on local, naturally occurring deadwood because the locally occurring deadwood comprise mostly well-decomposed wood and decidous wood while the translocated wood comprise higher proportions of fresh wood or wood in early decay stages (Tranberg et al., 2024). Differences in deadwood qualities, micro-environment, and biotic interactions are known to influence bryophyte and lichen species assemblages on deadwood (Dittrich et al., 2014; Larsson Ekström et al., 2023).

b) Species richness will be greater in plots with higher densities of translocated deadwood than in plots with lower densities. Assemblages in plots with lower amount of translocated deadwood will comprise a subset of those found in higher-density plots (Haeler et al., 2021; Hylander, 2009).
c) Species richness, as well as community assemblage, will be closely associated with specific substrate types. Intermediate decomposition stages are expected to support greater diversity and distinct communities compared to early decomposition stages (Santaniello et al., 2017; Svensson et al., 2016).
d) For lichens, species that are highly specialized to specific substrate types, such as standing resin-impregnated and decorticated pine (kelo wood) (Larsson Ekström et al., 2023), are predicted to decline after translocation.
e) Bryophytes are expected to colonize the translocated deadwood over time, leading to an increase in species richness due to the establishment of generalist species (Dittrich et al., 2014) while for lichens we expect limited colonization (Larsson Ekström et al., 2023).

2. Material and methods

2.1. Study area and design

The study was conducted in a newly established research infrastructure adjacent to the Aitik mine (67°2′ N 20°43′E) in Norrbotten County in northern Sweden (Fig. 1). It includes two sites: an impact area and a compensation area. The impact area was destroyed during the expansion of the Aitik mine and as a result deadwood and cut living trees was translocated from the impact area to the compensation area. The impact area measured 376 ha, of which 167 ha comprised old-growth high-conservation-value forests (Swedish Standards Institute, 2014). It had an average deadwood volume of 21.1 m^3 ha^{-1} and the mean basal area of living trees was 19.7 ± 4.2 m^2 (Tranberg et al., 2024). The remaining 209 ha consisted of lower conservation value forests, non-productive lands, mires, and open water (Forsgren et al., 2016). The compensation area comprised 397 ha including 192 ha of high-conservation-value forests with moderate deadwood volumes averaging 9.3 m^3 ha-1 and mean basal area of living trees 25.2 ± 2.3 m2 (Tranberg et al., 2024) and 205 ha of lower-value forest and non-productive land (Forsgren et al., 2016). Both sites had previously been managed through selective logging, although no recent active management during the last decades. The area is situated in the northern boreal vegetation zone (Ahti et al., 1968) and are primarily composed of broadleaves-mixed-coniferous forests dominated by Norway spruce (*Picea abies* (L.) H. Karst) and Scots pine (*Pinus sylvestris* L.) with scattered occurrences of downy birch (*Betula pubescens* Ehrh.) and willow (*Salix caprea* L.).

The experimental design included translocation of 637 deadwood

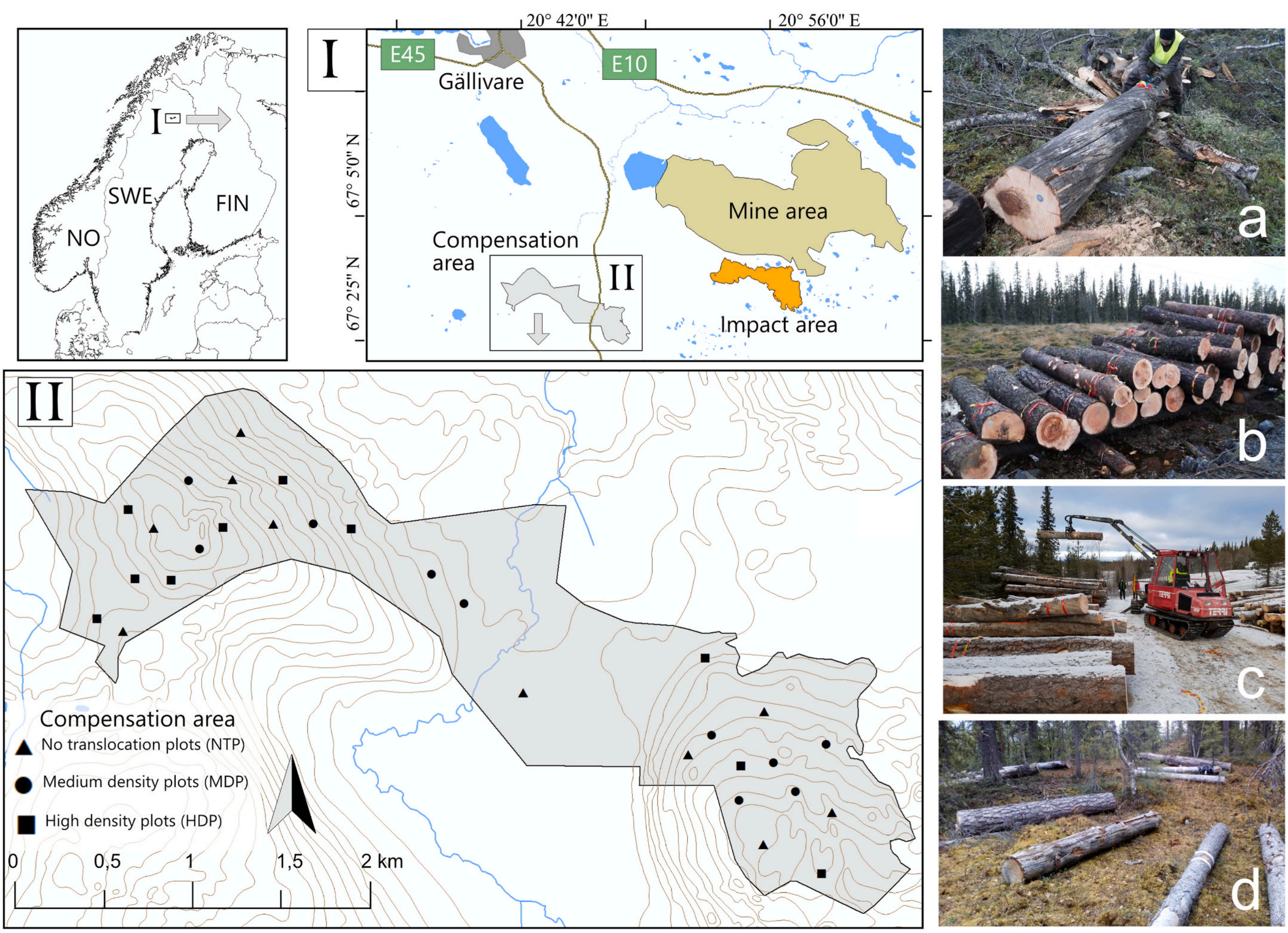

Fig. 1. Overview of research area and translocation procedure (far right). Research area (subfigure I) is shown in relation to Gällivare municipality, showing the mining area (light green), impact area (orange) and compensation area (grey). Symbols in lower figure (subfigure II) indicate plot type in the compensation area. Steps in the translocation process; a) selection of substrates, b) marking and storing of substrates, transport to the compensation area, c) forwarding to compensation plots, d) one of the high-density plots with 48 translocated substrates. Photo: Maria Nordlund (a–b), Joakim Hjältén (c) and Olov Tranberg (d).

substrates (3–5 m long, >15 cm in diameter) of both Scots pine and Norway spruce together with associated species of saproxylic (wood living) invertebrates, fungi, bryophytes and lichens, from the impact area to the compensation area. Translocation was performed in late autumn 2017. The translocated deadwood consisted of logs of different decay stages, and originated from both standing and laying deadwood. In total the translocated deadwood comprised eight substrate type categories; fresh cut nature value trees (NV), early decay logs (early), intermediate decay logs (intermediate) and cut snags (standing dead trees in decomposition classed 3–7 according to Thomas and Parker (1979)) of Scots pine and Norway spruce (Table 1).

The goal was to translocate 80 substrates from each of the eight substrate type categories, however, due to a shortage of pine logs, additional substrates were supplemented by using standing dead trees and living pine trees.

The translocation process involved careful selection, marking, and transporting of logs to ensure minimal disruption to their ecological communities. The upward facing side of the logs was in advance marked and positioned in same orientation after translocation. Due to limitations in effective methods to maintain translocated snags in the same posture (standing) post-translocation, all translocated snags were felled and laid on the ground in the compensation area. Prior to translocation, 30 experimental plots were established in the compensation area as target plots for the translocated deadwood. The plots had a radius of 50 m and translocated deadwood was placed within 25 m radius from plot center. All plots in the compensation area were randomly distributed at least 150 m apart for independence and randomly divided into three groups. Controls/no translocation plots (NTP, n = 10) received no translocated deadwood, medium-density-plots (MDP, n = 10) received 16 deadwood substrates (approximately 2 of each substrate type) and high-density-plots (HDP, n = 10) received 48 deadwood substrates (approximately 6 of each substrate type). In all plots, including control plots, one living tree of Scots pine and one Norway spruce were felled on site and left unbucked to serve as control for new colonizations (Table 1).

2.2. Bryophyte and lichen survey

Deadwood in all plots were surveyed directly after translocation in the summer of 2018 for both bryophytes and lichens (NTP were however not surveyed for lichens in 2018), followed by a re-survey in 2021 for bryophytes and 2022 for lichens. All fallen naturally occurring and translocated deadwood logs of Scots pine and Norway spruce with a maximum diameter >10 cm and length >1 m, and with the root end situated within the plots (radius 50 m) was surveyed for bryophytes and lichens. For the lichen survey on naturally occurring deadwood, only logs with at least some part of the trunk being debarked were included, branches were excluded. Species identifications were done in the field by experts and each species were noted as presence-absence for each individual log. We included obligately lignicolous lichen species, *sensu* Spribille et al. (2008) with addition of red-listed species and species that are regional indicators of high conservation value deadwood (Jonsson, 2024). Four lichen species, *Arctoparmelia centrifuga*, *Flavocetraria nivalis*, *Hypogymnia bitteri* and *Micarea melaena* were removed from further analysis following recommendation of species experts due to incomplete survey of these species in the field.

For bryophytes, all species present on the logs were recorded, regardless of their main substrate preferences. The reason for including not only obligately lignicolous bryophytes (as we did for lichens) was that the investigated dead wood substrates are not only important substrates for dead wood dependent bryophytes but also for other more generalist species to a larger extent than is the case for lichens. In addition, restricting the dataset to only obligately lignicolous bryophytes would have resulted in too few species and observations to allow

Table 1

Distribution of surveyed deadwood substrates for bryophytes and lichens, divided on tree species, translocated or naturally occurring deadwood (indicated by yes or no in the translocated column), substrate type (only set for translocated deadwood), treatment (translocation effort, control, medium or high) over years. NTP = Control/No translocation plots, n = 10, MDP = medium density plots with 16 translocated substrates, n = 10 and HDP = high density plots with 48 translocated substrates, n = 10. Type refer to type of translocated deadwood and include Pine NV and Spruce NV = fresh cut nature value trees of pine and spruce, respectively, Pine early and spruce early = early decay logs, Pine intermediate and Spruce intermediate = intermediate decay logs, Pine snag and Spruce snag = cut standing dead trees (snags) that were placed lying in the compensation area.

Tree species	Translocated	Type	Treatment	Number of surveyed substratets			
	(Yes/No)			2018	2018	2021	2022
				Bryophytes	Lichens	Bryophytes	Lichens
Translocated deadwood							
Pine	Yes	Pine NV	MDP	29	29	29	29
Pine	Yes	Pine early	MDP	10	10	10	10
Pine	Yes	Pine intermediate	MDP	19	19	19	19
Pine	Yes	Pine snag	MDP	22	22	22	22
Spruce	Yes	Spruce NV	MDP	20	20	20	20
Spruce	Yes	Spruce early	MDP	20	20	20	20
Spruce	Yes	Spruce intermediate	MDP	20	20	20	20
Spruce	Yes	Spruce snag	MDP	20	20	20	20
Pine	Yes	Pine NV	HDP	103	103	103	103
Pine	Yes	Pine early	HDP	9	9	9	9
Pine	Yes	Pine intermediate	HDP	49	49	49	49
Pine	Yes	Pine snag	HDP	78	78	78	78
Spruce	Yes	Spruce NV	HDP	61	61	61	61
Spruce	Yes	Spruce early	HDP	61	61	61	61
Spruce	Yes	Spruce intermediate	HDP	59	59	59	59
Spruce	Yes	Spruce snag	HDP	57	57	57	57
			Total	637	637	637	637
Naturally occurring deadwood logs							
Pine	No		NTP	29	–	31	27
Spruce	No		NTP	22	–	21	19
Pine	No		MDP	20	21	19	21
Spruce	No		MDP	35	38	36	38
Pine	No		HDP	24	29	25	29
Spruce	No		HDP	15	21	14	21
			Total	145	109	146	155

for proper statistical analyses. Complete lists of included species and species traits can be found in Appendix 1. Nomenclature follows Dyntaxa (Backlund, 2024).

2.3. Statistical analyses

To assess how translocated deadwood contributed to bryophyte and lichen species richness and assemblage composition on plot level we counted the number of species and summed the number of occurrences in each plot. Similarly, to assess how the different translocated deadwood substrates impacted species richness and assemblage composition we counted the number of species per individual log (substrate level). Each log was categorized into two groups within each plot, translocated and naturally occurring deadwood.

All analyses for species richness were done in R (R Core Team, 2021). To assess differences in species richness on plot level, we conducted a generalized linear model (GLM) with a Poisson distribution (package glmmTMB by Brooks et al. (2024)) with the number of species as response variable. In the GLM model on plot level, plot treatment (0, 16 or 48 added deadwood logs), year and substrate origin (translocated or naturally occurring deadwood) were set as fixed factors. On substrate level, we performed a GLM, using template model builder (glmmTMB) from "glmmTMB" package by Brooks et al. (2024) with a negative binominal distribution. This package allows us to handle the zero-inflated count data that origins from the high number of substrates with no species at first year (mainly nature value trees for both bryophytes and lichens and also snags for bryophytes). For each GLM, substrate type (Nature value trees, early decay logs, intermediate decayed logs and snags from pine and spruce, Table 1), year and plot treatment were set as fixed factors. Plot ID was first included as random factor, but the model did not converge, and the random effect structure was therefore excluded. For pairwise comparisons of species richness between treatments, substrate origins, substrate types and years, we applied a pairwise post-hoc test with Tukey adjustment to account for multiple comparisons (using the "emmeans" function from the "emmeans" package by Lenth et al. (2023)). For all models, we checked the residual plots and Q-Q plots for over dispersion, outliers and model fit.

To assess the differences in species composition between (i) treatments, years and substrate origins (translocated or not) on plot level and (ii) treatments, years and substrate types on substrate level, we performed a permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001) in PRIMER (PRIMER, 2007). We used treatment, year and substrate origin (translocated or not) as fixed factors on plot level, followed by pairwise comparisons. On substrate level, substrate type (in total eight categories, Table 1), year and treatment were set as fixed factors. Plot ID was initially included as random factor, but the model did not converge, and the random effect structure was removed from the model. We used a fourth root transformed frequency data (the number of logs on which a species occurred) at the plot level and presence-absence data at the substrate level, and calculated the resemblance matrix using Bray-Curtis dissimilarity.

To identify which species contributed most to the observed differences in assemblage compositions, we used similarity percentage analysis (SIMPER) in PRIMER, also on fourth-root transformed data. SIMPER calculates the overall percentage contribution that each species makes to the average dissimilarity between two groups and lists the species in decreasing order of their importance in discriminating the two sets of samples. The cut-off for the list was set to 90 % explained variation.

3. Results

In total we found 52 bryophyte and 38 lichen species. Naturally occurring deadwood had the highest number of bryophyte species, with 47 species compared to 32 on the translocated deadwood (21 in 2018), whereas corresponding numbers for lichens were 32 lichen species found on naturally occurring and 33 on translocated deadwood (30 in 2018). Two bryophyte species and seven lichen species were classified as red-listed. For bryophytes eight species colonized the translocated deadwood and were only present in 2022. One bryophyte species went locally extinct (i.e., disappeared from the surveyed logs entirely between survey years). Corresponding numbers of colonization for lichens were four species colonizing and four species going locally extinct (Appendix 1).

The most frequent bryophyte was *Pleurozium schreberi*, found on 194 different logs in 2018 and on 780 different logs in 2021 (naturally occurring and translocated). For lichens, the most frequent species, *Xylographa vitiligo,* was found on 117 different logs in 2018 and on 205 logs in 2022.

3.1. Contribution of translocated deadwood to bryophyte and lichen biodiversity (plot level)

For both bryophytes and lichens, naturally occurring deadwood had greater species richness compared with translocated deadwood (Fig. 2, Table 2). For both bryophytes and lichens, high-density plots had significantly greater richness compared to no translocation plots. For bryophytes, richness was also significantly higher in high-density plots than in medium-density plots. Pairwise comparisons of interacting variables explaining bryophyte species richness are shown in Appendix 2. The assemblage composition on translocated wood differed significantly from naturally occurring deadwood for both bryophytes and lichens (Table 2, Figs. 2 and 3, pairwise comparisons see Appendix 3). For bryophytes year explained most of the variation (31 %) followed by deadwood origin (translocated or not, 21 %) and the interaction of deadwood origin and year (18 %). For lichens deadwood origin explained 40 % of the variation (Table 2, Fig. 3). On naturally occurring deadwood, assemblage composition did not change between the two surveys for neither bryophytes nor lichens. Bryophyte species richness on natural deadwood increased between survey years (Appendix 2). On the translocated deadwood assemblage composition changed over time for both bryophytes and lichens. For bryophytes, changes resulted from an increase in species richness, while for lichens, species richness showed a negative trend (Table 2, Fig. 2).

3.2. Habitat amount and substrate type impact on species richness and assemblage composition (substrate level)

Substrate type had a significant effect and the different translocated deadwood types provided habitat for significantly different bryophyte and lichen assemblages (accounting for 8 % of the variation for bryophytes and 86 % for lichens) and affected species richness (Table 3, Figs. 4–6). Furthermore, assemblage composition changed from 2018 to 2021 for bryophytes (Post hoc test $p = 0.001$ for all substrate types, Fig. 6) with year accounting for 88.7 % of the variation in assemblage. For lichens, assemblages changed from 2018 to 2022 for Pine early, intermediate, and snags ($p = 0.005$, 0.042, and 0.001 respectively) as well as for Spruce intermediate ($p = 0.004$), and year only accounted for 3.7 % of variation in assemblages. For bryophytes, Pine intermediate ($p = 0.014$) and Spruce snags ($p = 0.038$) showed different assemblages also between medium- and high-density-plots. For all significant pairwise comparisons, see Appendix 4.

For bryophytes, species richness increased from 2018 to 2021 (Fig. 4, Appendix 4) and more species contributed to the differences in assemblage composition in 2021 (Fig. 7). A majority of the differences in bryophyte assemblage composition on specific substrate types was explained by species colonizations of new substrates between 2018 and 2021, for example colonization by the ground-covering moss *Pleurozium schreberi* explaining 30–50 % of the differences of species assemblages (Fig. 7). For lichens, there was a decrease in species richness from 2018 to 2021 for pine snags (Fig. 4, Appendix 4) and fewer species contributed to the differences in total assemblage composition (Fig. 7). Calcioid

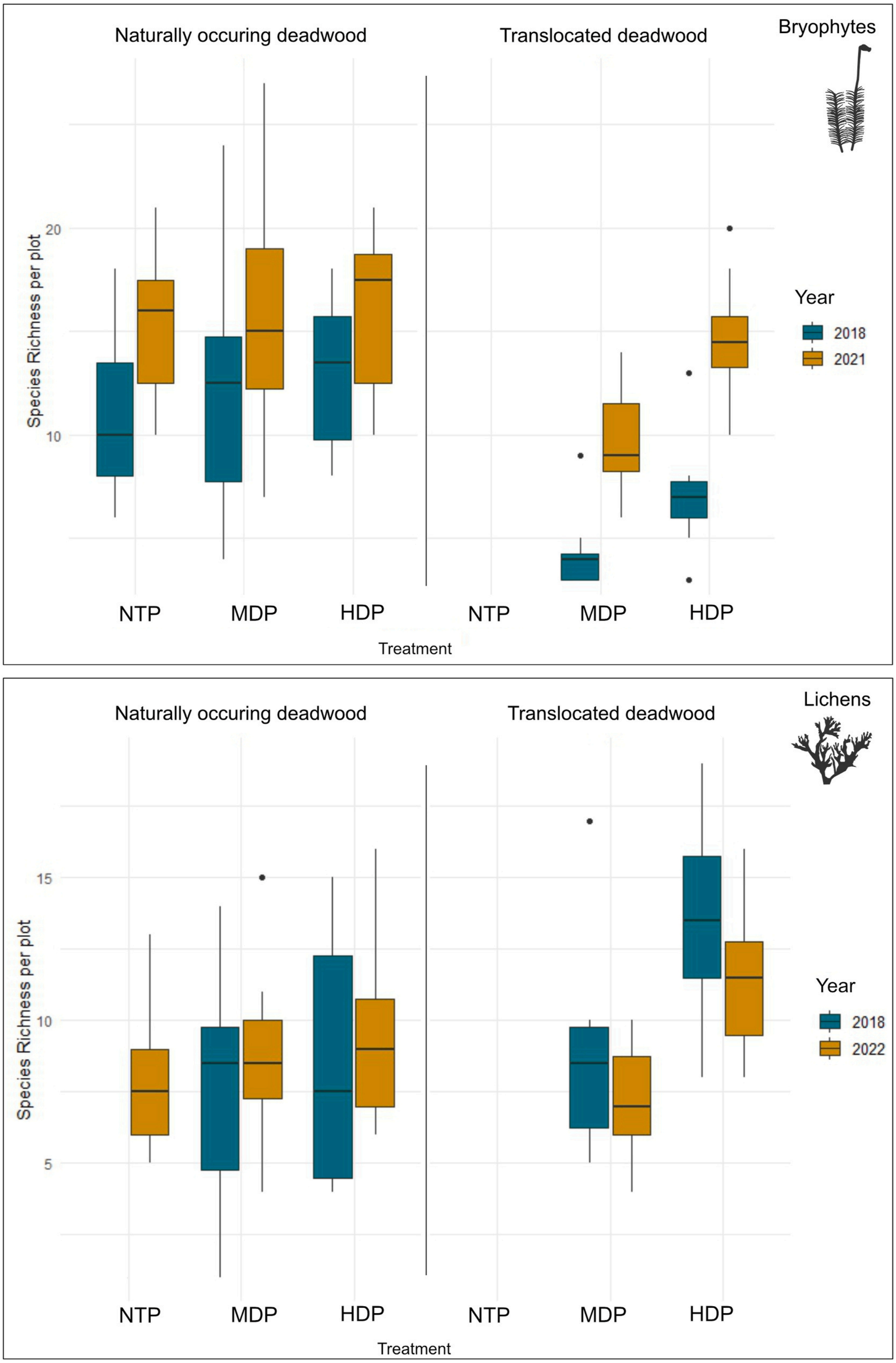

Fig. 2. Species richness on translocated and naturally occurring deadwood for bryophytes and lichens on plot level. Treatments are: no translocation plots (NTP, no deadwood addition), medium-density plots (MDP, addition of 16 substrates/plot), and high-density plots (HDP, addition of 48 substrates/plot). Note that naturally occurring deadwood for lichens in no translocation plots were not surveyed in 2018, hence missing in graph.

Table 2

Results from analysis of assemblage composition (PERMANOVA) and species richness (GLM) for bryophytes and lichens on plot level. Number of observations was 89 in both PERMANOVA and GLM.

Organism	Term	*PERMANOVA*			*GLM*		
		F	SS	p	χ2	p	Significant contrasts GLM
Bryophytes	Translocated	15.5	15,569	0.001*	1310.69	<0.001*	Nat.dw > Trans.dw
	Treatment	3.54	3558	0.001*	6.37	0.041*	NTP < HDP, MDP < HDP
	Year	22.9	23,063	0.001*	999.86	<0.001*	2018 < 2021
	Translocated x Treatment	5.93	5959	0.001*	1.00	0.317	
	Translocated x Year	12.7	12,815	0.001*	465.17	<0.001*	Appendix 2
	Treatment x Year	2.92	5873	0.003*	0.50	0.780	
	Translocated x Treatment x Year	5.66	5687	0.001*	1.10	0.293	
Lichens	Translocated	13.893	20,115	0.001*	512.13	<0.001*	Nat.dw > Trans.dw
	Treatment	2.2421	6493	0.005*	11.16	0.004*	NTP < HDP
	Year	5.1253	7421	0.001*	0.19	0.660	
	Translocated x Treatment	7.5681	10,958	0.001*	0.50	0.477	
	Translocated x Year	2.4499	3547	0.007	3.44	0.063	
	Treatment x Year	0.85504	1238	0.562	0.00	0.975	
	Translocated x Treatment x Year	0.32746	474	0.971	0.25	0.617	

Asterisks mark significant terms (p ≤ 0.05). Significant contrasts for terms in the GLM (interactions in Appendix 2) include Naturally occurring (Nat.dw) vs Translocated deadwood (Trans.dw), no translocation plots (NTP, no deadwood addition), medium-density plots (MDP, addition of 16 substrates/plot), and high-density plots (HDP, addition of 48 substrates/plot). 2018 < 2021 indicate that the richness was significantly greater in 2021 compared to 2018. Pairwise comparisons of interacting variables for assemblage composition (PERMANOVA) are shown in Appendix 3.

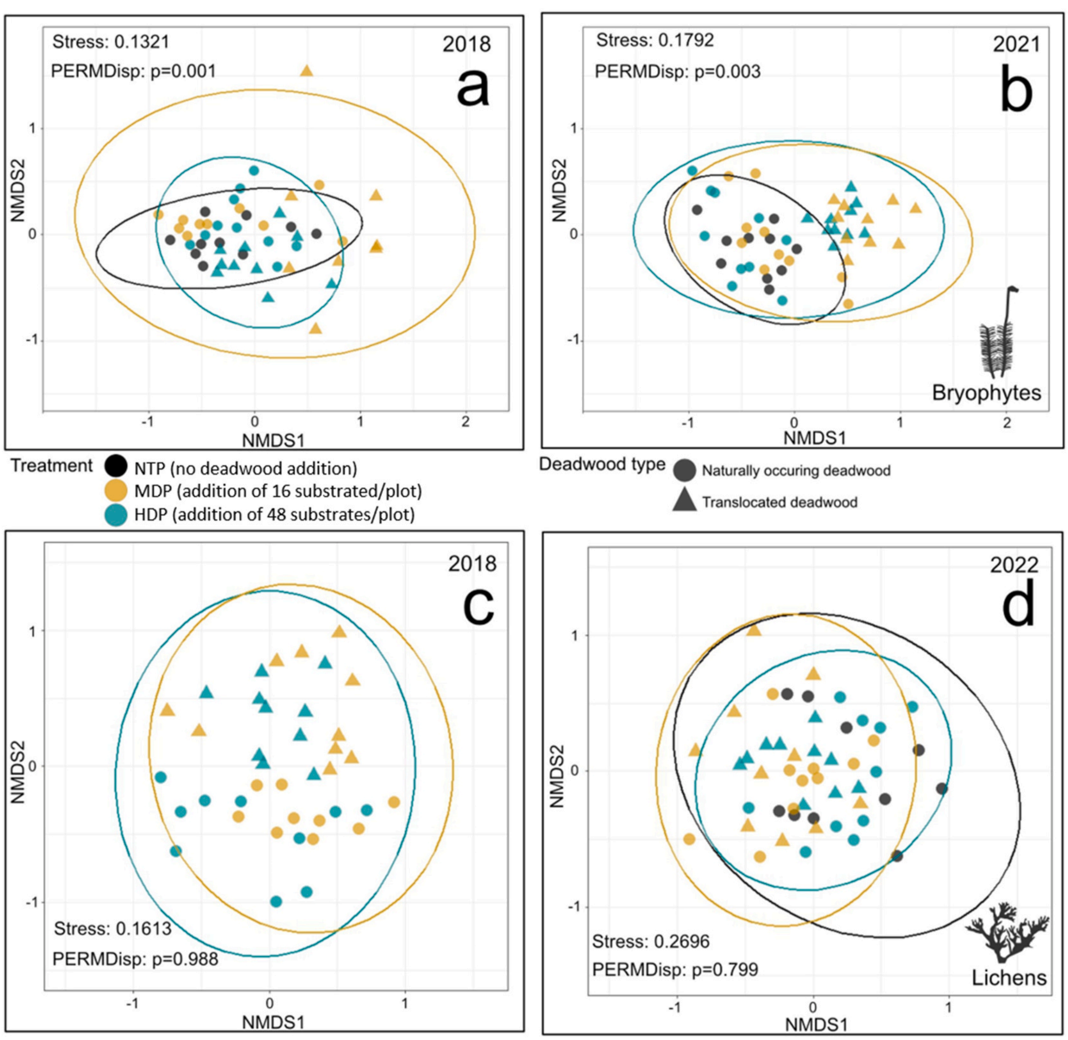

Fig. 3. NMDS ordination for assemblage composition for bryophytes on plot level in 2018 (a) and 2021 (b), and for lichens in 2018 (c) and 2022 (d). Treatment (NTP/MDP/HDP) marked by colour and deadwood type by different symbols; Naturally occurring (Natural dw) vs Translocated deadwood (Translocated dw). Treatments are: no translocation plots (NTP, no deadwood addition), medium-density plots (MDP, addition of 16 substrates/plot), and high-density plots (HDP, addition of 48 substrates/plot). Note that naturally occurring deadwood for lichens in no translocation plots were not surveyed in 2018, hence missing in graph c).

Table 3
Results from analysis of assemblage composition (PERMANOVA) and species richness (GLM) for bryophytes and lichens on substrate level. Number of observations was 1274 in both PERMANOVA and GLM.

Organism	Term	*PERMANOVA*			*GLM*		
		F	SS	p	χ2	p	Significant contrasts GLM
Bryophytes	Treatment	2.03	806	0.104	0.000	0.998	
	Type	15.7	43,503	0.001*	75.432	<0.001*	P_NV < P_int, Sp_early < Sp_int
	Year	1192.8	472,160	0.001*	0.002	0.964	
	Treatment x Type	1.77	4913	0.019*	13.019	0.072	
	Treatment x Year	1.83	724	0.130	0.000	0.999	
	Type x Year	2.83	7892	0.001*	46.335	<0.001*	Appendix 4
	Treatment x Type x Year	0.69	1931	0.834	6.953	0.434	
Lichens	Treatment	3.5435	1705	0.001*	1.123	0.289	
	Type	60.569	204,040	0.001*	118.458	<0.001*	P_early < P_NV < P_int, P_NV < P_snag < P_int, Sp_early < Sp_int, Sp_NV < Sp_int, Sp_snag < Sp_int
	Year	18.461	8884	0.013*	1.664	0.197	
	Treatment x Type	4.3827	4502	0.001*	2.837	0.899	
	Treatment x Year	0.51565	248	0.729	1.062	0.303	
	Type x Year	1.3366	14,764	0.130	14.296	0.046*	Appendix 4
	Treatment x Type x Year	0.848	2857	0.693	2.225	0.946	

Asterisks mark significant terms ($p \leq 0.05$). Substrate types in contrasts are pine early (P_early), pine cut nature value trees (P_NV), pine snags (P_snag), pine intermediate (P_int), spruce early (Sp_early), spruce cut nature value trees (Sp_NV), spruce snags (Sp_snag), spruce intermediate (Sp_int).

lichens, like *Calicium dengratum* and *C. trabinellum*, that are associated with standing pines decreased or disappeared and generalist species as *Xylographa vitiligo* increased on several different deadwood types.

Habitat amount (plot density treatment) had no significant effect neither on bryophyte nor lichen species richness on individual substrates, but assemblage composition differed significantly on substrates located in medium- and high-density-plots (Table 3).

4. Discussion

We examined the direct effects on bryophyte and lichen assemblage composition and species richness resulting from the translocation of deadwood one and three or four years post-translocation. The concept of "whole-of-community" (multi-taxon) conservation translocation of entire deadwood communities has been suggested (Rudolphi, 2007) but has not been tested before, particularly at such a large scale. In agreement with our predictions, the results reveal that translocated deadwood significantly alters the assemblage composition and species richness of bryophyte and lichen deadwood communities as compared to naturally occurring deadwood in the compensation area. Specifically, while naturally occurring deadwood maintained stable species assemblages and richness over time, translocated deadwood demonstrated increasing bryophyte richness with generalist species colonising the wood but unchanged richness of lignicolous lichens.

The observed differences in richness and assemblage composition between naturally occurring deadwood and translocated deadwood align with our predictions. The differences are most likely due to the translocated wood consists of different qualities or substrate types compared with naturally occurring deadwood. The translocated wood consisted of several substrate types that were missing or rare in the compensation area including large diameter pine and spruce logs in intermediate decay stages, kelo wood and fresh cut wood from nature value trees (Tranberg et al., 2024). Naturally occurring deadwood contained fewer substrate types and was dominated by wood in later decay stages and birch deadwood and included whole trees including root ends, tops and branches (Tranberg et al., 2024). Thus, the translocated wood provided substrates that were lacking in the compensation area and could potentially fill a gap in deadwood continuity.

The changes in species richness and assemblage composition over time on the translocated deadwood is likely driven by alterations in microhabitat conditions, as a result of the translocation, combined with colonisations of new species on the fresh wood. The main microhabitat impact affected standing deadwood that were placed laying in the compensation area. Such changes in microhabitat generally seem to have less negative effect on bryophytes (potentially even favouring colonization of many species), while disadvantaging certain lichen species that are more substrate-specific and sensitive to environmental changes (Ellis, 2013; Lõhmus and Lõhmus, 2001). Although substrate type is an important factor for bryophyte communities (Stokland et al., 2012), microhabitat conditions, indirectly influenced by external factors such as canopy openness affecting level of light and moisture, seem to play a more significant role than substrate type for moss growth (Barbé et al., 2020; Haughian and Frego, 2017). Generalist ground-covering forest mosses have been shown to be particularly efficient in colonising downed deadwood (Dittrich et al., 2014), which is consistent with our results. However, true deadwood specialist bryophytes are likely more sensitive to changes in both substrate and microclimate (Barbé et al., 2020; Spitale, 2016). For instance, we observed a decline in the deadwood specialist *Neoorthocaulis attenuatus* on intermediate decay pine logs after translocation.

The decline in lichen species richness, for example calicoid lichens *Calicium denigratum* and *C. trabinellum* on translocated kelo wood, is likely a result of changes in microclimate and posture, from standing to downed deadwood. Previous studies have shown greater species richness and occurrence of red-listed lichens on standing kelo wood compared to pine logs (Larsson Ekström et al., 2023). Downed kelo wood may provide a less favourable microclimate for translocated lichens due to reduced sun exposure and the change in moisture regime resulting from increased ground contact, as demonstrated for downed versus standing deadwood by Svensson et al. (2016) and Larsson Ekström et al. (2023). The role of microclimatic changes, accompanying changes in deadwood positioning as well as surrounding forest stand structure, warrants further research to better understand its impact on translocation success. Even in single-species translocations, it can be challenging to account for the complexities of the translocation environment (Smith, 2014). The habitat can be viewed as a community of organisms rather than solely focusing on the niche requirements of a single target species (Smith, 2014). Moving habitat together with entire communities can overcome some of these uncertainties. However, the diverse and complex responses within and between species and taxonomic groups detected in our study underscore the complexities involved in whole-of-community translocations. In comparison to single-species translocations, we show that translocation of entire species communities of taxonomic groups along with their habitat pose an

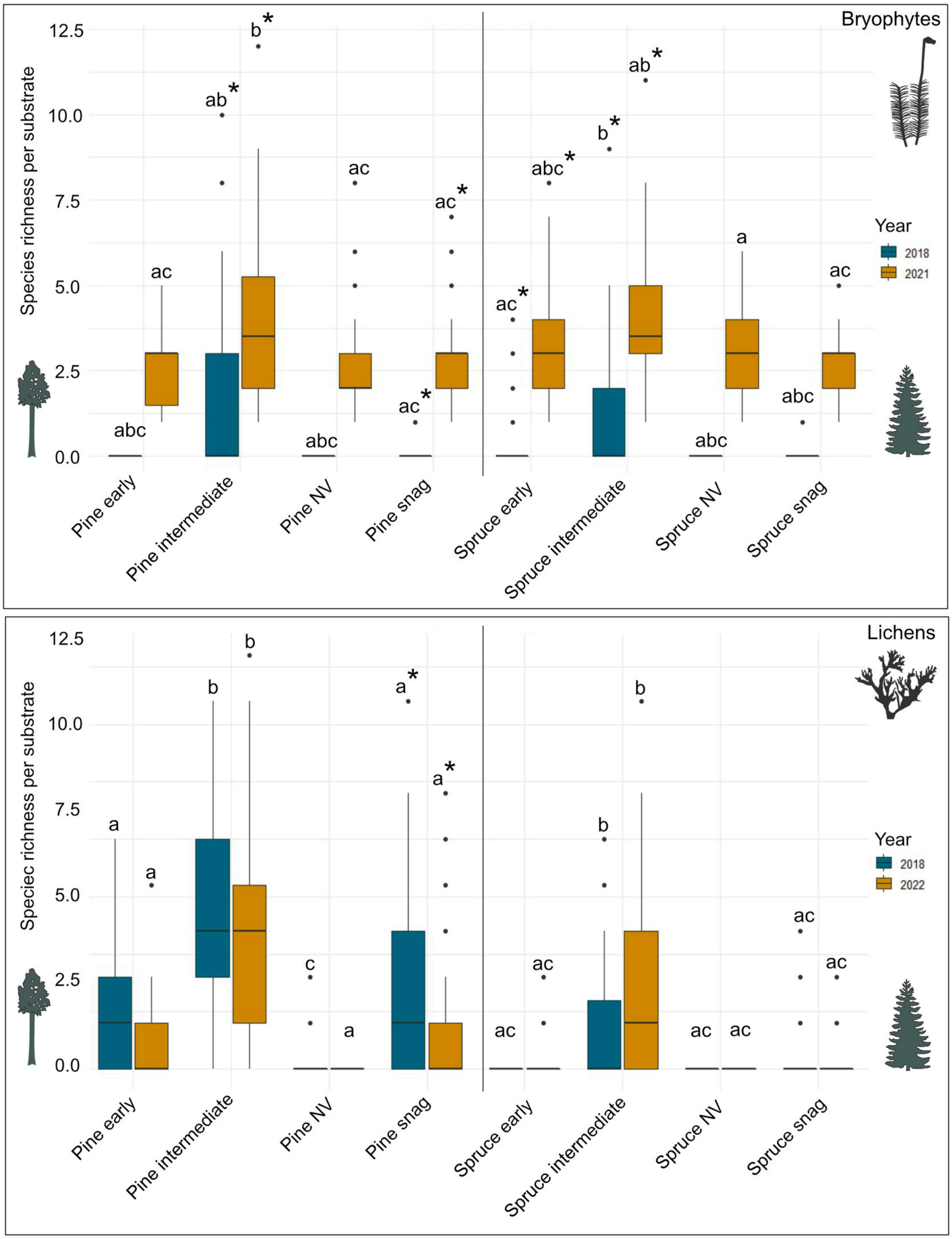

Fig. 4. Bryophyte and lichen species richness on translocated deadwood at the substrate level, grouped by substrate type. Pairwise comparisons for lichen species richness on substrate level for significant interactions of GLM for each tree species; significance for 'Type within Year' marked with letters for each year group and 'Year within Type' marked with asterisk (*) for significant different substrate richness. Pine NV = pine cut nature value trees; Spruce NV = spruce cut nature value trees.

even greater challenge in fulfilling the diverse conditions needed in terms of microhabitat conditions of the receptor site (i.e., compensation area).

We assessed how habitat amount and substrate diversity affected the success of translocation for bryophytes and lichens. In agreement with our hypothesis, high-density plots exhibited greater bryophyte richness than medium-density plots. This suggest that a greater volume and diversity of translocated deadwood can enhance the habitat's capacity to support bryophyte diversity (Haeler et al., 2021; Hylander, 2009). In contrast to our predictions, density of deadwood did not significantly impact lichen richness on substrate level, aligning with the observation that lichens may rather require more specific substrate types or microhabitats that are not sufficiently provided by increasing downed deadwood volume alone.

The different translocated deadwood substrates supported significantly different species assemblages for both bryophytes and lichens. This confirms the importance of translocating a variety of substrates to maintain high species diversity, as pointed out in Tranberg et al. (2024). This result is consistent with previous studies showing that a diversity of substrate types provides habitat for a range of different species Mežaka

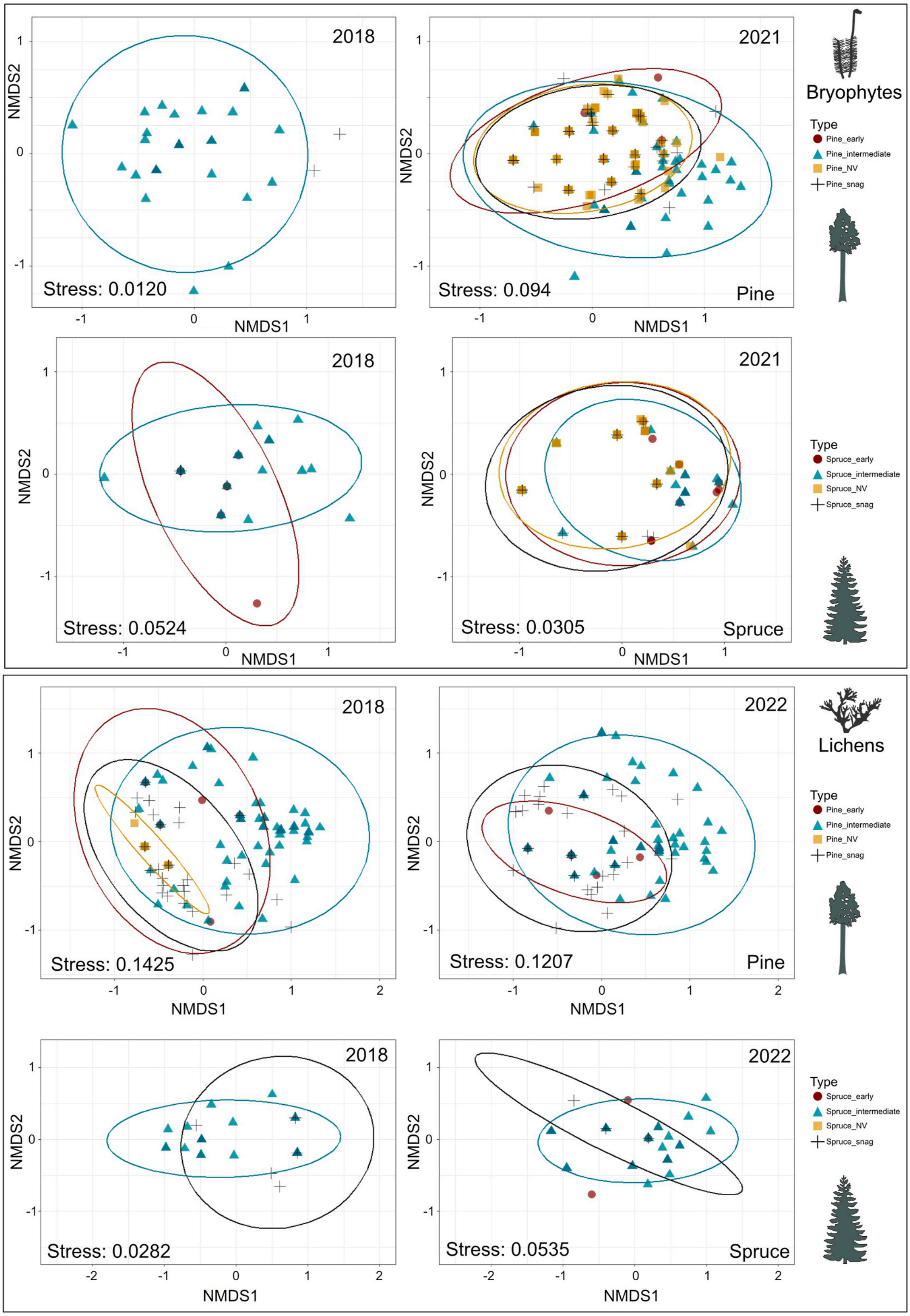

Fig. 5. NMDS ordination for assemblage composition for bryophytes and lichens for substrates, divided for Year and Type (Pine and Spruce), deadwood type marked by colour (including types; early, intermediate, NV (cut nature value trees) and snags). Note that early logs of spruce in 2018 and nature value trees of both spruce and pine in 2022 were surveyed but contained few or no lichens, hence not visible in graphs due to few observation points.

(2023) and Santaniello et al. (2017), thereby supporting a broader range of bryophyte and lichen communities. For instance, later stages of deadwood such as intermediate decay and snag substrates harboured greater species richness and hosted distinct communities compared to earlier decay stages. Given the highly diverse communities across different and specific substrates, it is crucial in conservation translocations to incorporate a wide range of substrate types, including more challenging ones like deadwood in more advanced stages of decay. A greater abundance of a particular substrate cannot make up for the loss of species associated with another substrate type.

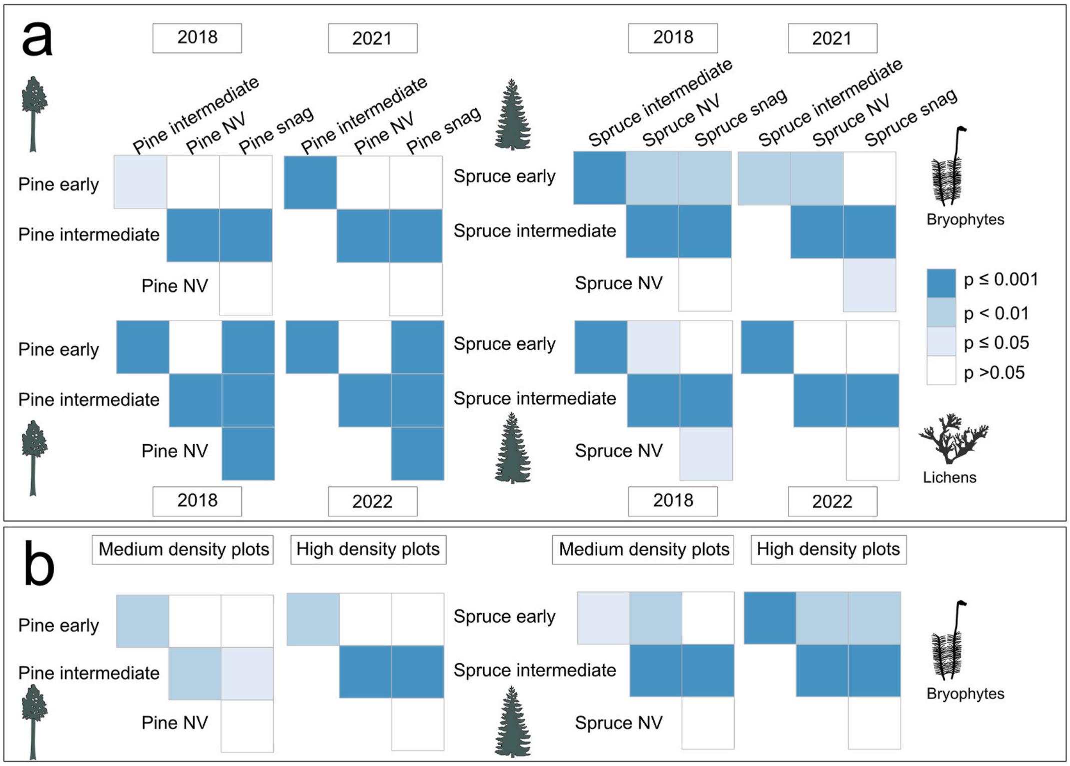

Fig. 6. Pairwise comparisons of PERMANOVA for bryophyte and lichen assemblages for a) 'Type within Year' and b) 'Type within Treatment'. Colour intensity indicates level of significance. Types of deadwood include both pine and spruce in the following categories: early decay, intermediate decay, cut nature value trees (NV), and snags.

Generalist bryophytes, such as *Pleurozium schreberi* and *Hylocomium splendens*, rather than wood dependent species or species of conservation concern showed clear colonization across all translocated substrate types, which explained much of the differences in bryophyte assemblage composition. If we would only include lignicolous bryophytes the patterns would have been more similar to those observed for lichens, with only a few colonisations. A significant difference between the two organism groups was the number of species surviving the translocation. While several lichen species failed to persist on translocated substrates, this was rarely the case for bryophytes (Appendix 1). Among the bryophytes that that did not survive the translocation, only one species is strictly associated with dead wood: *Lophozia guttulata*. This red-listed species (NT) was found on only one translocated log in 2018 (an intermediately decayed pine log) but was not found again in 2022. However, it remained present on naturally occurring dead wood in both survey years. Even if a number of colonizing events occurred on the translocated as well as on naturally occurring deadwood, the study period is too short to fully answer if translocated deadwood can serve as a "life-boating" method for threatened bryophytes and lichen species. The first criteria for a successful life-boating through translocation is the survival of target species. In theory, translocation could support species aid in their dispersion and establishment in new habitats. Our results show that most of the new species on both translocated and naturally occurring deadwood were generalist species. This can potentially obstruct colonization of species of conservation concern, or even out-compete them. Further, the life-boating concept through translocation of deadwood appears less effective for conserving certain lichen species with the methodology used in this study. This is particularly true for species with specific habitat requirements, since some of the translocated substrates may not be adequately re-established in the new environment. For example, when snags were placed lying on the ground after translocation, it resulted in a significant change in microclimate conditions for these habitat types. Previous studies on translocations of single lichen species have demonstrated that, while the target species can be relocated, "life-boated", and survive in new environments, they often struggle to colonize new substrates at the new site (Hilmo and Såstad, 2001).

A number of extinction events of species on translocated deadwood were observed and additional declines of single species were most prevalent for lichens, whereas for bryophytes only a few species clearly declined. For lichens, *Chaenothecopsis fennica* (red-listed as near threatened, NT), *Xylopsora friesii*, *Lecidea apochroeella* and *Micarea eximia* disappeared from the translocated deadwood, and among the bryophytes *Harpanthus flotovianus* disappeared. Species groups that experienced a more pronounced decrease in occurrence and thereby can be considered extra vulnerable to this type of translocations are many calicioid lichens species such as *Calicium denigratum* (NT), *C. trabinellum*, *Mycocalicium subtile* and *Chaenothecopsis fennica* (NT). All of these species are restricted to sun exposed snags of Scots pine and appear to struggle with survival following the transition from a standing to a lying position.

5. Conclusions and implications for management

The overall aim of conservation translocations and assisted dispersals is to enhance the survival prospects of species or organisms (Seddon et al., 2014), especially in fragmented landscapes and species in habitat exposed to exploitation. Ecological compensation strategies, and conservation translocations, are crucial in maintaining biodiversity and ecosystem functions in the face of habitat loss. However, a clear goal for ecological compensation efforts must be set, such as providing a "life--boat" for specific target species or groups. Our experiment shows that several common generalist species become more abundant after translocation. Given their relative abundance, we suggest that it is more effective to shift the conservation focus away from these species. Instead, it might be more beneficial to prioritize on species that are rare,

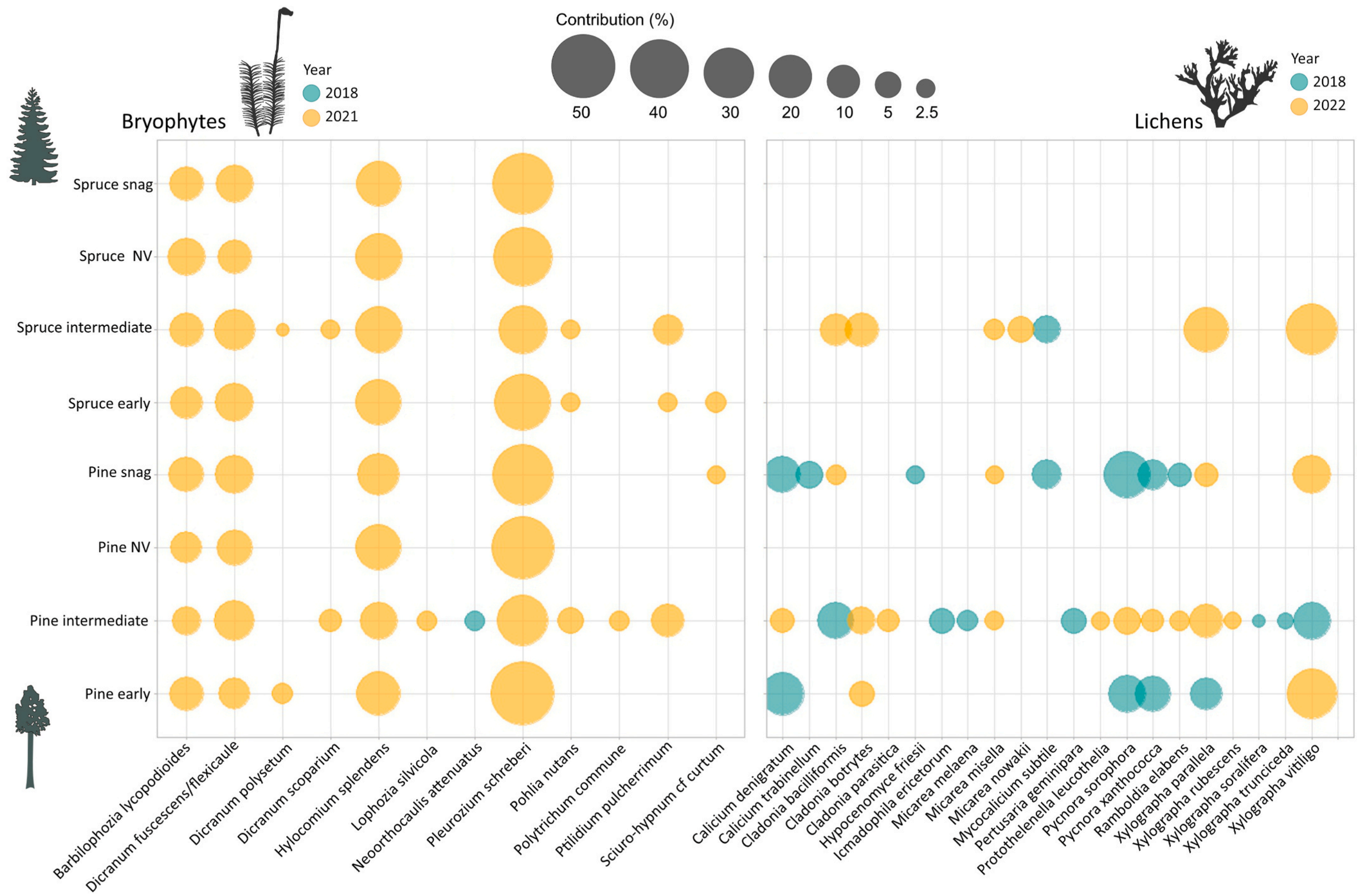

Fig. 7. Bubble graph illustrating the results of the SIMPER analysis. Each bubble represents a species, with bubble size proportional to the species' average contribution to dissimilarity between the two years for different substrate types. The colours of the bubbles highlight if the species contribute most to dissimilarities by its presence in 2018 (blue) or 2021–22 (yellow).

specialized, have low dispersal abilities, and exist in small fragmented populations when selecting targets for translocation. These species are often at a higher risk of extinction and can potentially benefit from translocation efforts, if they face unavoidable exploitation. For instance, maximizing the source populations of certain lichens or bryophytes can be achieved through the translocation of substantial amounts of deadwood, as shown in our study where the plots with highest addition of translocated deadwood also had the clearest effects on species richness and assemblage composition. A high addition of deadwood is likely to reduce the risk of local species extinctions, as the number of local extinctions, at least initially, likely decreases in proportion to the amount of translocated substrates.

To safeguard unique biological values of each deadwood type, we recommend managing them according to their specific qualities. Snags should remain standing after translocation, for example by leaning them against other standing trees and securing them with ties for stability. Similarly, shaded intermediate logs should maintain similar microclimatic conditions as pre-translocation, to support the survival of target species. This can help in reducing stress on the translocated organisms and increasing their chances of successful establishment.

While translocation of deadwood on plot level significantly alters the assemblage composition, leads to an increased bryophyte richness, yet unchanged lichen richness, incorporating a variety of deadwood types are important to benefit a variety of bryophyte and lichen communities. Different deadwood types comprise habitat for significantly different bryophyte and lichen assemblages, and several threatened species were only found on specific substrate types, for example *Chaenothecopsis fennica*, almost only found on kelo wood or *Cladonia parasitica* on intermediately decayed pines. It is therefore crucial to include a variety of deadwood substrates in translocation efforts. In addition, it is important to closely monitor microhabitat conditions of each substrate type both before and after translocation. Snags in particular, which support a distinct assemblage of species, would ideally remain standing to preserve their ecological value.

The results of this study emphasize the need for careful planning and implementation of deadwood translocation if used as a conservation strategy. For effective conservation, it is essential to consider the specific ecological requirements of target species groups, particularly those sensitive to microhabitat changes such as many lichen species. The negative trend for lichen species richness on translocated deadwood highlights the potential risks of disrupting established communities, which may lead to the loss of species and net-loss of species in biodiversity offsetting.

CRediT authorship contribution statement

Olov Tranberg: Writing – original draft, Visualization, Formal analysis, Data curation, Conceptualization. **Therese Löfroth:** Writing – review & editing, Supervision, Conceptualization. **Mari Jönsson:** Writing – review & editing, Supervision. **Jörgen Sjögren:** Writing – review & editing, Supervision, Methodology, Data curation, Conceptualization. **Anne-Maarit Hekkala:** Writing – review & editing, Supervision. **Joakim Hjältén:** Writing – review & editing, Supervision, Project administration, Methodology, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known financial or personal interests that could affect the work reported in this paper.

Acknowledgments

We thank Boliden AB and Sveaskog AB for cofunding the research project and conducting the translocations, Nordlund Konsult for planning and organizing the translocations, species identifiers Fredrik Jonsson, Ulrika Nordin and Henrik Weibull, and all field assistants for help with inventory. This work was funded by the Swedish Research Council Formas [grant no 2019-00923, to Joakim Hjältén], Göran Gustafssons Stiftelse [grant to Joakim Hjältén], SLU and Boliden AB.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2025.125161.

Data availability

Data will be made available on request.

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