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Recommended Citation

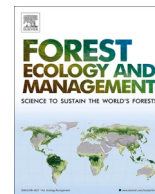
Palmroos, I., V. Norros, S. Keski-Saari, J. Mäyrä, T. Tanhuanpää, S. Kivinen, J. Pykälä, P. Kullberg, T. Kumpula, and P. Vihervaara. 2023. Remote sensing in mapping biodiversity – A case study of epiphytic lichen communities. *Forest Ecology and Management* 538:120993.

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Remote sensing in mapping biodiversity – A case study of epiphytic lichen communities

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ARTICLE INFO

Keywords:

Epiphytic lichen
Hierarchical model of species communities
Remote sensing
Light detection and ranging
Hyperspectral imaging

ABSTRACT

In boreal forests, European aspen (*Populus tremula* L.) is a keystone species that hosts a variety of accompanying species including epiphytic lichens. Forest management actions have led to a decrease in aspen abundance and subsequent loss of suitable habitats of epiphytic lichens. In this study, we evaluate the environmental responses of epiphytic lichen species richness and community composition on aspen, focusing on the potential of remote sensing by combined hyperspectral imaging and airborne laser scanning to identify suitable habitats for epiphytic lichens. We measured different substrate and habitat parameters in the field (e.g., aspen diameter and bark pH) and by remote sensing (e.g., mean canopy height and tree species composition of the surrounding forest) in the study area in Southern Finland that includes protected and non-protected forest. We used linear regression and the Hierarchical Model of Species Communities (HMSC) to compare how the different parameters explain and predict lichen species richness and community composition, respectively. We show that coarse predictions of epiphytic lichen community composition can be made using parameters extracted from remote sensing data. Estimated mean canopy height, tree density, dominant tree species and tree species diversity of the stand predicted the species community on aspens slightly better than field parameters. Remote sensing variables calculated over a larger area (30 m radius) always outperformed the same variables calculated over a smaller area (10 m radius) in predicting community composition, highlighting the cost-efficiency of remote sensing compared to covering a similar area with on-ground measurements. These results are encouraging for the prospects of using remote sensing data to direct field inventories and to map potential high-biodiversity habitats. Aspen bark pH was the only parameter affecting species richness regardless of whether the forest was protected or not, whereas, interestingly, the effects of tree diameter, height and furrow depth were only significant in protected areas. Our results also underline the importance of protected areas, since they hosted a higher tree-specific number of epiphytic lichen species, and red listed species, than non-protected areas.

1. Introduction

Standardized measures of biodiversity are needed to reliably detect patterns and trends in biodiversity to form a knowledge base for its protection from major disturbances. Using remote sensing methods in biodiversity monitoring is an increasing trend due to its efficiency (Luque et al., 2018). Remote sensing of biodiversity includes implementation of hyperspectral imaging to search for diversity in habitats, plant functional types and plant species (Wang & Gamon, 2019). For

example, habitats for rare bryophytes, good indicators of high biodiversity in Canadian boreal forests, were predicted by using indices extracted from satellite-based hyperspectral data (Correjon et al., 2022). For tree species detection, a combination of airborne light detection and ranging (LiDAR) and hyperspectral imaging has been shown to be efficient (Jones et al., 2010; Roth et al., 2015) and it applies also for scarce species such as European aspen (*Populus tremula* L.) (Viinikka et al., 2020; Mäyrä et al., 2021; Kuzmin et al., 2021).

European aspen is a keystone species in boreal forests (Kivinen et al.,

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<https://doi.org/10.1016/j.foreco.2023.120993>

Received 2 December 2022; Received in revised form 22 March 2023; Accepted 5 April 2023

Available online 13 April 2023

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2020, Rogers et al., 2020). The presence of aspen enriches the biodiversity of the forest areas since it hosts many accompanying species, such as polypores and other wood-inhabiting fungi, herbivorous and saproxylic invertebrates, woodpeckers, and Siberian flying squirrels (reviewed in Kivinen et al., 2020). Aspen trunks host many epiphytic lichen and moss species (Kuusinen, 1994) and many of them occur exclusively on aspen (Hedenäs and Ericson, 2000, Jüriado et al., 2003; Ranlund et al., 2018). Aspen's relatively high bark pH compared to other tree species in boreal forests gives an unique substrate for epiphytes (Kuusinen, 1996). Thus, aspens add additional diversity to the boreal forest with a limited total number of tree species, since they host different epiphyte species compared to the conifers and birches (*Betula*) (Jüriado et al., 2003). The presence and abundance of aspen is a useful indicator of boreal forest biodiversity.

Lichens are a diverse group of symbiotic associations between fungal and algal or cyanobacterial partners. Epiphytic lichens grow on tree bark or branches and several species are indicators of forest age and conservation values (Hedenäs & Ericson, 2000; Ellis, 2012). Epiphytic lichens have a great impact on forest ecosystem dynamics by affecting the water and nutrient cycles (Knops et al., 1996; Ellis, 2012) and their presence has a positive association to many invertebrate species abundances (Stubbs, 1989). The suitable habitats for epiphytic lichens are declining due to intensive forestry practices.

The richness and community composition of epiphytic lichens are affected by many environmental factors both at stand and at tree level, such as air humidity, light availability, tree density, tree species composition, stand and tree age, host tree species and bark pH (e.g., Bates, 1992; Hedenäs & Ericson, 2000; Fritz et al., 2009; Johansson et al., 2007; Jüriado et al., 2009; Ellis, 2012; Ódor et al., 2013). The epiphytic lichen species richness usually increases with tree age (Hedenäs & Ericson, 2000; Fritz et al., 2009; Johansson et al., 2007) with a co-occurring change in species composition (Hedenäs & Ericson, 2000, Ellis & Coppins, 2006). Bark pH affects the species richness and community structure of epiphytic lichens on aspen (Kuusinen, 1994; Nirhamo et al., 2021). Some epiphytic lichen species prefer more acidic bark pH and others more neutral, which can be dependent on host tree species or species-specific traits such as symbiont partner (Kuusinen, 1994; Ellis & Coppins, 2007; Jüriado et al., 2009). Species traits of epiphytic lichens have been shown to explain contrasting spatial aggregation patterns (Löbel et al. 2006). For conservation and management efforts, it is important to understand how traits determine species' responses to their environment since certain traits can predispose species to anthropogenic threats, leading to eroding functional diversity in nature (Chichorro et al., 2019, Carmona et al., 2021, Chichorro et al., 2022).

The aim of this study was to test the suitability of the remote sensing-based parameters to map and predict the species richness and community composition by using epiphytic lichens on aspen as an example group. Capturing the relevant parameters for large areas with field surveys is laborious. Large landscapes can only be covered through a network of sampled field plots, which means that the majority of the landscape is left unmeasured. The characteristics of the landscape can only be estimated through modelling. Therefore, we compared traditional field surveys with remote sensing-based variables that offer wall-to-wall coverage over the whole study area. We used airborne LiDAR and hyperspectral imaging for extracting tree-level and area-based parameters and tested their usability in surveying the importance of environmental parameters for the epiphytic lichen community composition. Protected and non-protected areas were included to get a perspective on whether the environmental parameters affecting lichen species richness are the same regardless of the conservation status. We wanted to answer the following questions: 1) Can remote sensing be utilized to identify important environmental parameters for epiphytic lichen community composition on aspen trees? 2) Which environmental parameters affect the species richness of epiphytic lichens on European aspen? 3) Do aspens in protected and non-protected forests host

different numbers of lichen species? 4) How environmental parameters affect epiphytic lichen community composition, and do species traits explain species-specific differences in environmental responses?

2. Materials and methods

2.1. Study area and field measurements

The 83 km² study area is in Evo, the municipality of Hämeenlinna in southern Finland (Fig. 1), which includes both protected and non-protected forests as well as several lakes. There are two major protected areas Kotinen and Sudenpesänkangas and a smaller one in the North-East corner of the area. The main tree species are Scots pine (*Pinus Sylvestris* L.), Norway spruce (*Picea abies* (L.) Karst), silver birch (*Betula pendula*, Roth) and downy birch (*Betula pubescens* Ehrh.), whereas European aspen is rather scarce and patchily distributed. Only a little topographic gradient is present with terrain elevation between 125 m and 195 m. The soil consists mainly of moraine.

In total, we measured 230 aspens in the field, 140 in non-protected and 70 in protected areas. The epiphytic lichens were surveyed from each study tree up to two meters from the ground in summer 2019. The lichen inventory was done by one person (author JP). Specimens were collected when lichens could not be identified with certainty during the field study. Specimens were identified using standard microscopic techniques and spot tests when necessary. *Lepraria* spp. includes *L. eburnea* and *L. finkii* which often cannot be identified by morphology and spot tests. Lichen nomenclature follows Pykälä et al. (2023). Trunk diameter at breast height (DBH) was measured at the height of 1.3 m and tree height by Vertex hypsometer (Haglöl) in summer 2018. Only aspen trees with a DBH exceeding 10 cm were chosen for the study. The coordinates of the aspens were recorded for the later geospatial analyses using Real-Time Kinematic Global Navigation Satellite System (RTK-GNSS).

pH and bark roughness were measured for 140 aspens in summer 2021, 90 in non-protected and 50 in protected areas. The pH was measured directly on aspen trunks (Krickle 2002) by a flat-headed electrode (pH-HALO, HI-14142, Hanna instruments) after watering the trunk with 0.1 M KCL solutions. The pH-electrode was calibrated twice a day, in the morning and at noon. Three separate pH measurements were executed on every tree and the average was used in the analyses. Bark roughness was measured by using furrow depth and width at a horizontal transect (Ellis & Coppins, 2007; Lewis & Ellis, 2010) at breast height for 25% of the perimeter on each tree trunk. Furrow depth correlated strongly with the furrow width (Fig. S1) and had a stronger effect on lichen species richness, so only furrow depth was used in the later analysis.

2.2. Remote sensing parameters

All remote sensing data were collected on July 16th, 2018. Airborne LiDAR data were collected using Leica ALS70-HP (Leica Geosystems AG, Heerbrugg, Switzerland) laser scanner from 1500 m altitude. Average point density was 10 pts/m². Hyperspectral data were collected with HySpex VNIR-1800 for spectral range of 405 nm – 995 nm and SWIR-384 for spectral range of 956 nm – 2500 nm (Norsk Elektro Optikk, Oslo Norway). With VNIR the ground resolution was 0.5 m and for SWIR 1.0 m. Data processing is explained in detail in Viinikka et al., (2020). We used the LiDAR data directly in the analysis, whereas for hyperspectral data derived features were acquired from the tree maps generated by Mäyrä et al., (2021). For calculating the remote sensing parameters for the analysis, we placed circular plots with radii of 10 m and 30 m around all field measured aspens. We used tree maps from Mäyrä et al., (2021) for determining the tree species composition within the plots. Within the maps, the species classification was done at tree level by using a fusion of LiDAR and hyperspectral data (for details see Mäyrä et al., 2021). In addition to the tree maps, we conducted a

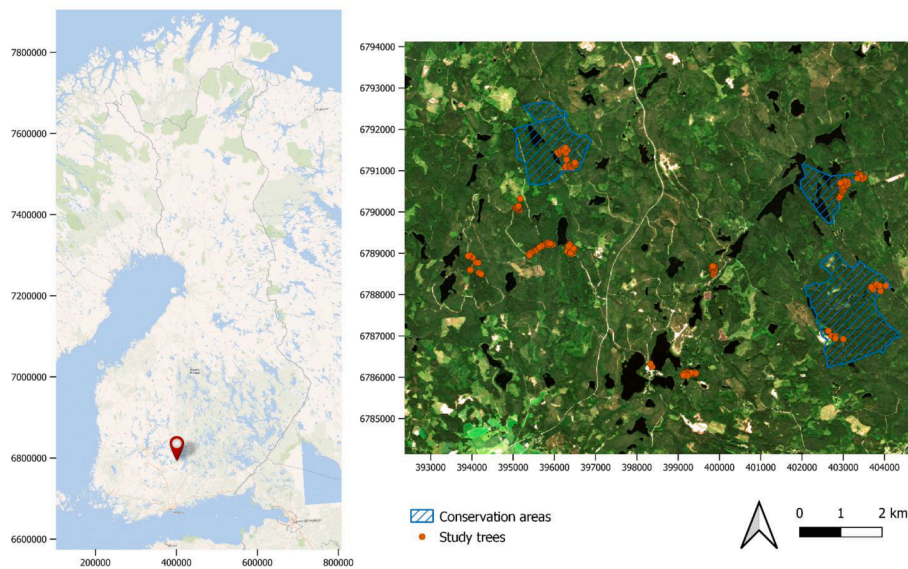


Fig. 1. Locations of study trees and conservation areas. Map produced from ESA remote sensing data (Sentinel-2 imagery, bands B04, B03 and B02) captured on July 19th, 2018.

separate individual tree detection (ITD) for the plots to acquire more precise estimates of tree count (n), canopy cover (m^2), and heights of individual aspens (m). Here, we processed the LiDAR data with R software version 4.0.2 using `lidR` package version 3.1.4 (Roussel et al., 2020). We detected the individual treetops using the `dalponte2016` function (Dalponte & Coomes, 2016) with minimum height of 5 m and circular window with size of 5 m. We then generalized the tree-level features from tree maps and ITD to the 10 m and 30 m circular plots. In addition to the tree-level features, we calculated mean heights of the LiDAR points (z_{mean}) within the plots as an area-based feature, using the `stdmetrics` function with minimum height threshold of vegetation set to 2 m. The threshold on 2 m is commonly used when computing LiDAR-based forest features (Næsset, 2002, Yu et al., 2011, Kankare et al., 2015). We used the features as parameters in the later models and in the calculation of the Shannon index and Pielou’s evenness (see abbreviations and descriptions of model parameters in table 1).

2.3. Data analysis

The comparison between the protected and non-protected areas and the effects of environmental parameters on epiphytic lichen species richness of aspen trees were analyzed in SAS Enterprise Guide 8.2. by using linear regression analyses with 95% confidence limits. With linear regression, we tested the effect of pH, furrow depth, DBH and height to the number of epiphytic lichen species on aspen trees in protected and non-protected areas. With regression analyses we also tested the correlation of the species richness with the mean height and the number of trees in a 30 m radius plot around the measured aspen. With t-tests we tested for a difference between the protected and non-protected areas in aspen-specific epiphytic lichen species richness and aspen bark pH values.

To test the community responses of epiphytic lichens on aspen to environmental parameters we used a joint species distribution model, the Hierarchical Model of Species Communities (HMSC; Ovaskainen et al., 2017, Ovaskainen & Abrego, 2020). In our application, the HMSC modelled the occurrence probability of each lichen species as a linear

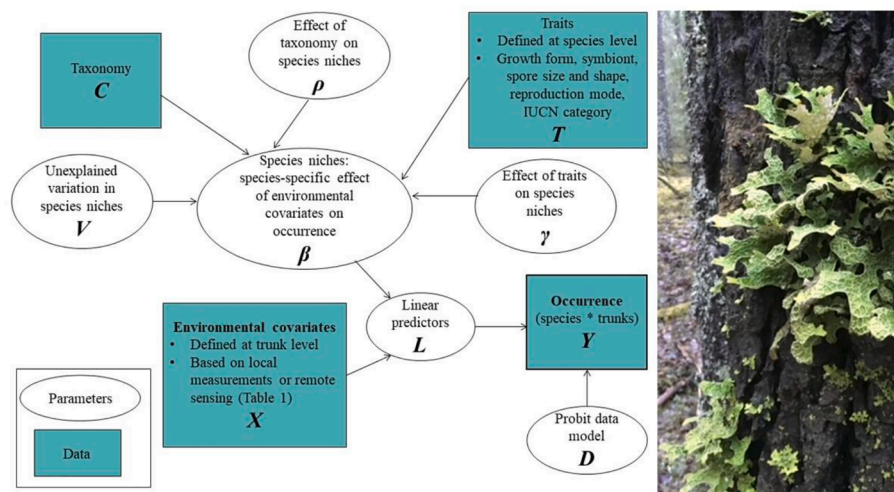


Fig. 2. Structure of the hierarchical community model (HMSC, Ovaskainen et al. 2017) that was applied to reveal and explain species- and community-level responses of lichens to environmental factors and to assess the power of remote sensing vs. locally measure.

combination of fixed environmental effects (Fig. 2). The method also allows random effects corresponding to the hierarchical and/or spatio-temporal structure of the data set, but we chose not to include these as we were primarily interested in the predictive ability of the environmental factors alone. The species-specific regression coefficients corresponding to environmental factors were further modelled as a linear combination of trait effects, considering taxonomic relationships by allowing for higher covariance in the environmental responses of species closer in the taxonomic tree. We used different combinations of the parameters shown in Table 1 as environmental factors in the model. Occurrence was defined on the tree level, resulting in 230 “sampling units” (aspen trees), except for 140 for pH and furrow depth. We included both 10 m and 30 m versions of remote sensing parameters based on circular plots to compare their predictive power.

To test whether species-specific responses to environmental parameters can be explained by species traits, all model versions included five species traits: symbiont type (cyanobacterial, green algal or tripartite), growth form (crustose, foliose or fruticose), the commonness of sexual reproduction (numerical scale from 0/never to 4/common), spore shape (length divided by width) and log-transformed spore size (spore volume calculated from length and width assuming a prolate ellipsoid shape). In addition, we included the current IUCN category on a numerical scale from 0 (LC) to 4 (CR) (Hyvärinen et al., 2019) as an additional predictor in the model to evaluate whether species of higher threat status respond to their environment differently from species with lower threat status. While IUCN category is not fundamentally a “trait”, it is treated similarly to true traits in the model and, for brevity, below we refer to all these predictors simply as “traits”. All numerical environmental variables and traits were z-transformed for the analyses. As the data set included many species with few observations, we included in the baseline HMSC analysis the 48 most common species for which all trait variables were available. However, to assess the robustness of our results when changing this arbitrary cut-off, we also repeated the analysis including all 99 taxa identified to species level and with complete trait data. The list of species and their traits are provided in Table S1. As an additional variation to the baseline version, we also fitted the HMSC models for 48 species separately for the protected and non-protected areas to test whether the same environmental factors best predict community composition in both areas. Thus, our analysis included four versions: 1) 48 species, all aspen trees (baseline); 2) 99 species, all aspen trees; 3) 48 species, protected areas only; 4) 48 species, non-protected areas only.

For all analysis versions, each candidate model with different environmental predictor(s) was fitted to the data using the Bayesian MCMC algorithm implemented in the Hmsc R package (Tikhonov et al., 2020), with four parallel chains run for 30 000 iterations. The first 5000 iterations were discarded as burn-in, and every 100th value of the last 25 000 iterations was retained as a sample of the posterior distribution. Convergence of the chains was confirmed visually and based on the potential scale reduction factor (Gelman & Rubin, 1992).

All fitted candidate models (158 in total) and their predictive performance metrics are listed in Table S2. For the 48 and 99 species analyses (versions 1–2), we started the model comparison by fitting 20 models with each of the parameters in Table 1 as the sole explanatory environmental factor. For the protected/non-protected area analyses (versions 3–4), we omitted the remote sensing variables calculated for 10 m radius, as in analyses 1–2 these always performed worse than the corresponding 30 m variables. To assess the predictive power of each model, we performed a cross-validation with the data split into four folds, one being the test data and the other three the training data. Sampling units (trees) were randomly assigned to the four folds. As a measure of model performance, we used the Area Under the Curve (AUC, Pearce & Ferrier, 2000), which measures how well the model discriminates between species’ presence and absence. The folding and cross-validation were repeated 10 times for each model to account for the variability in AUC due to the random splitting of the data. The one-predictor models were ranked by their mean AUC and for all 48 species

Table 1

The descriptions of the field and remote sensing parameters that were measured from the study aspens and used in the HMSC models.

	Abbreviation	Type	Unit	Description
Field parameters				
furrow depth	fur_depth	continuous	mm	Depth of bark furrows measured for each tree along a transect of 25 % of tree DBH
pH	pH	continuous		pH measured directly from the bark surface of tree trunk. Average of three measurements for each tree.
diameter	DBH	continuous	cm	Trunk diameter measured at breast height (1,3 m)
height	H	continuous	m	Tree height measured in the field with Vertex hypsometer
Laser scanning				
height	las_height	continuous	m	The height of the focal tree derived from the LiDAR point cloud.
mean canopy height	zmean	continuous	m	Mean height of the LiDAR point cloud within the circular focal area (10/30 m radius)
number of trees	ntrees	continuous		Number of trees detected from the circular focal area (10/30 m radius) by dalponte2016 algorithm with parameters min_h = 5 and window size = 5
canopy area	ca	continuous	m ²	Total canopy area (m ²) delineated by dalponte2016 algorithm within the circular focal area (10/30 m radius)
Hyperspectral				
dominant tree species	dom_sp	categorical		Tree species represented by the highest number of individuals within the circular focal area (10/30 m radius)
tree species diversity	shannon	continuous		Shannon-Weiner diversity of tree species based on the number of individuals within the circular focal area (10/30 m radius)
tree species evenness	pielou	continuous [0,1]		Pielou’s evenness of tree species based on the number of individuals within the circular focal area (10/30 m radius)
Other				
distance to water	dist_water	continuous	m	Distance from the focal tree to the nearest water body calculated in ArcMap (using near tool), based on the National Land Survey of Finland dataset “Ranta10” of waterbodies

(continued on next page)

Table 1 (continued)

	Abbreviation	Type	Unit	Description
slope aspect	aspect	categorical		Aspect of the slope at the point of the focal tree, calculated to each cardinal direction from 10 m elevation model (National Land Survey of Finland dataset "Korkeusmalli 10 m")

analyses (versions 1, 3 and 4), those variables that at least sometimes performed better than chance (maximum AUC > 0.5) were retained for the second step. For the 99 species analysis, the ranking of the one-predictor models was almost identical to the 48 species baseline, but AUC values were clearly lower due to the difficulty of predicting rare species. Here, we retained the same variables as in the 48 baseline although for some of these maximum AUC < 0.5, to obtain a directly comparable model ranking for the 48 and 99 species versions.

Second, we compared the predictive power of different combinations of the variables retained in the first step. As our primary goal was to assess the feasibility of remote sensing in predicting community composition, we assembled models with different combinations of either field parameters or remote sensing parameters. For each circular plot-based remote sensing variable, we retained only the better performing version (30 or 10 m radius). In both categories, all combinations of the retained variables were tested except for those including strongly correlated variables: DBH and tree height or DBH and furrow depth for field variables, mean canopy height (zmean) and tree height (las_height) for remote sensing variables (Fig. S1). As in the first step, the models in the second step were ranked by AUC based on cross-validation.

As HMSC does not allow gaps in explanatory variables, we included only data from trees which all environmental variables were available (140 trees for pH and furrow depth, 50 in protected areas and 90 in nonprotected areas; 230 trees otherwise, 70 in protected areas and 160 in non-protected areas). To exclude the possibility that the obtained model ranking was driven by data availability, we repeated the fitting of a subset of the 48 species models using only the 140 trees for which all variables were available. As this resulted only in minor differences that did not affect the ranking of the best-performing models nor the conclusions, we report only the results obtained using all available data.

For each fitted HMSC model, the significance of each environmental and trait effect can be quantified as the posterior probability (PP) that the corresponding coefficient in the model is different from zero (positive or negative). To assess epiphytic lichen species' and community responses to the environmental variables and the significance of species traits, we summarized results across all fitted models of the baseline analysis (48 species, all trees) with mean AUC > 0.5. We classified each response as follows: 1) uniform positive or negative response (supported by > 90% PP in all model versions), 2) occasional positive or negative response (supported by > 90% PP in at least two model versions; no opposite responses at > 90% PP in other model versions), 3) inconsistent response (at least one negative and one positive response with > 90% PP in different model versions), 4) no response (positive or negative response at > 90% PP in 0–1 model versions). To test the robustness of the environmental and trait effects to the number of species included, we repeated this classification also for the 99-species models, including the same models as in the 48 baseline version to ensure comparability although for some of these mean AUC < 0.5.

3. Results

We sampled a total of 230 aspens and found 106 different epiphytic lichen species (Table S3) and 8 samples that could be identified only at the genus level. A total of 22 species were red-listed, out of which 12

were near threatened (NT) and seven vulnerable (VU) species. The two endangered (EN) and one critically endangered (CR) species were only found in protected areas. The most common lichen was *Lecanora allophana* (Ach) which was found on 158 aspens. The conservation status of the forest area affected the number of lichen species per aspen ($P < 0.0001$), with an average of 12 species per tree in protected areas and 7 species per tree in non-protected areas.

Protected and non-protected areas also differed in the effect of DBH and height on epiphytic lichen species richness. In protected areas, aspens with a greater DBH and height had a higher number of epiphytic lichens than smaller aspens (DBH: $P < 0.0001$, R-square 0.4268, height: $P < 0.0001$, R-square 0.2828, Fig. 3). Furrow depth had a positive correlation with the number of species per tree in protected areas ($P < 0.0001$, R-Square = 0.4865, Fig. 3). Instead, in the non-protected areas DBH, height or furrow depth did not affect the number of lichen species. The aspens sampled in protected areas were significantly larger in DBH and height than those in non-protected areas (DBH: $P = 0.0004$, H: $P = 0.0011$).

pH significantly affected the number of species in both protected and non-protected areas even though the explanatory power in non-protected area was low (protected: $P < 0.0001$, $R^2 = 0.3318$, non-protected: $P = 0.0148$, $R^2 = 0.0656$ Fig. 3). The more acidic the bark was, the more species grew on the aspen trunks. Aspen trunks were more acidic in protected areas than in non-protected ones ($P < 0.0001$, Fig. 3) and the pH also showed high variation, especially in protected areas (range 3.93–6.89, vs. 5.64–7.01 in non-protected areas).

HMSC analysis revealed clear differences in the ability of different environmental parameters to predict lichen communities (Fig. 4). In general, the predictive power of individual variables was relatively low, with only 13 out of 20 variables resulting in better predictions of species' occurrence than chance in at least one out of ten cross-validation foldings in the baseline analysis (Fig. 4A; 48 species, all trees). The best individual variable to predict community composition in the baseline analysis was furrow depth (fur_depth, AUC = 0.67), followed by the LiDAR-based mean canopy height (zmean_30, AUC = 0.66). In every case, circular plot-based variables performed better when calculated using a larger radius (30 m rather than 10 m).

The top eight models in the baseline HSMC analysis were based on remote sensing variables (Fig. 4B), with the three best performing models (AUC = 0.71–0.72) including mean canopy height (zmean_30), dominant tree species (dom_sp_30), tree density (ntrees_30) and either tree species diversity (shannon_30), evenness (pielou_30) or both. The best model based on field parameters had slightly lower predictive performance (fur_depth, H, pH; AUC = 0.70) in the baseline analysis. The model ranking obtained for the 99-species analysis was even more in favor of remote sensing variables, but with clearly lower AUC scores (AUC ≤ 0.64; Fig. 4D), reflecting the difficulty of predicting the occurrences of rare species based on the limited data. By contrast, the obtained model ranking changed markedly when only protected or non-protected areas were included (Fig. 4E–F). Field parameters performed better for the protected areas (AUC = 0.71 for the best combination of field variables vs. AUC = 0.65 for remote sensing variables; Fig. 4E). As in the regression analyses for species number, the variation among aspen trees in non-protected areas remained largely unexplained, with only two remote sensing variables (dominant tree species and the slope aspect) reaching max. AUC > 0.5 and their combination predicting community composition on average only slightly better than chance (AUC = 0.55).

The summarized results of the fitted community models allow a closer look at species' and community responses to the environmental parameters. The occurrence of lichen species was generally more likely within forest areas with mature aspens: deeper bark furrows, larger DBH or higher trees or canopy (Fig. 5). This result was consistent in both 48 and 99 species analyses (Fig. 5A vs. B) and reflected also in the species-specific responses, with the majority of the species showing a uniformly positive response to these variables (Table S1). However, there were also

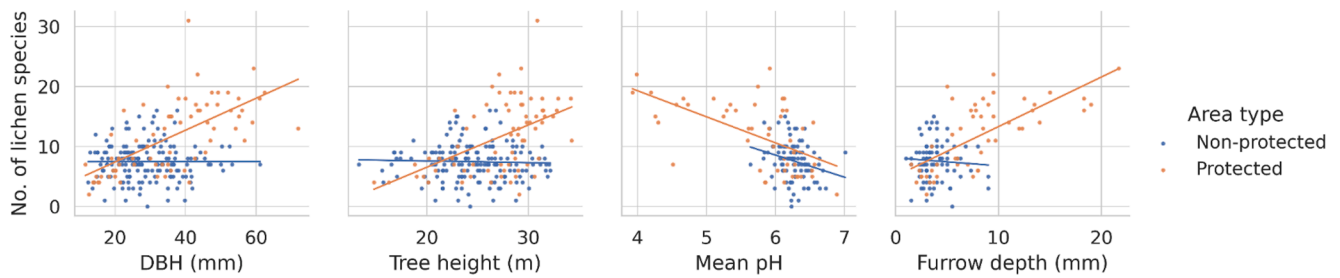


Fig. 3. The regression analysis results showed separately to protected and non-protected areas. The age-related parameters did not show any effect in non-protected areas even when they were significant in protected areas. The pH was the only parameter in regression analysis which was significant in both areas and had negative correlation with species richness. The number of aspens was 140 in non-protected and 70 in protected area for DBH and height measurements. For pH and furrow depth measurements the N was 90 in non-protected and 50 in protected area.

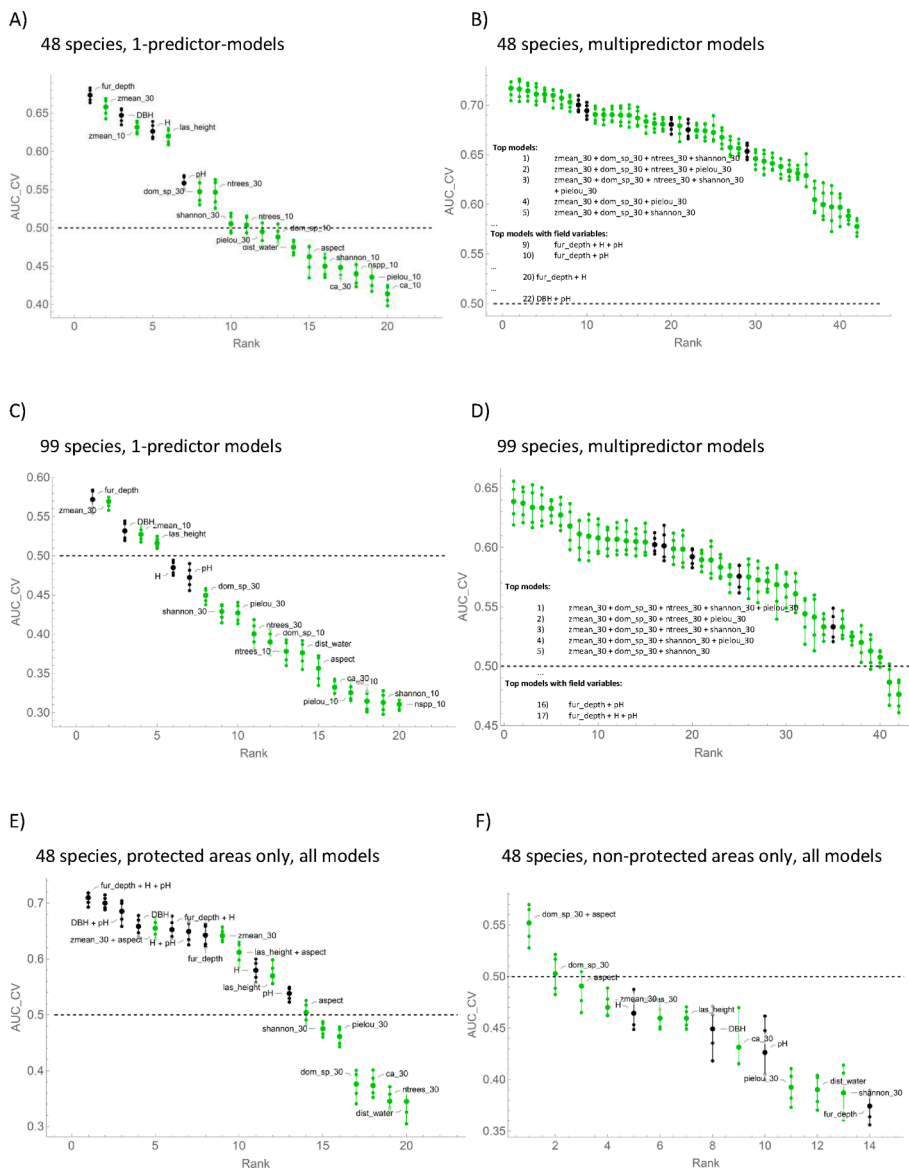


Fig. 4. Comparison of the power of different individual variables in predicting epiphytic lichen community composition using the Hierarchical Model of Species Communities (HMSC). Different model versions consist of either field (in black) or remote sensing (in green) variables and were ranked by the AUC measure based on 4-fold cross validation repeated 10 times. The symbols show the mean, +/- one standard deviation and range over the 10 different foldings. The explanations of the variable abbreviations can be found in Table 1. Panels A-B present the results of the baseline analysis with the 48 most common species, panels C-D the results of the 99-species analysis, both including data from both protected and non-protected areas. Panels E-F show the respective results of the 48-species analyses including only protected/non-protected areas, with both one-predictor and multipredictor models shown in the same figure. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

several lichen species showing the opposite response, indicating a preference for less mature forest characteristics (Table S1). The responses of a given lichen species to the forest maturity-related parameters were consistent, supporting the interpretation that these parameters represent a combination of general habitat features. By contrast, the other parameters (pH, dominant tree species and tree

density) clearly captured different characteristics of the habitat, as shown by the contrasting and less uniform responses (Fig. 5, Table S1). Traits were significant in explaining the species-specific responses of epiphytic lichens on aspen (Fig. 5). Commonness of sexual reproduction was the most relevant trait, with sexually reproducing species preferring less mature trees and forest habitats, higher pH and aspen-dominated

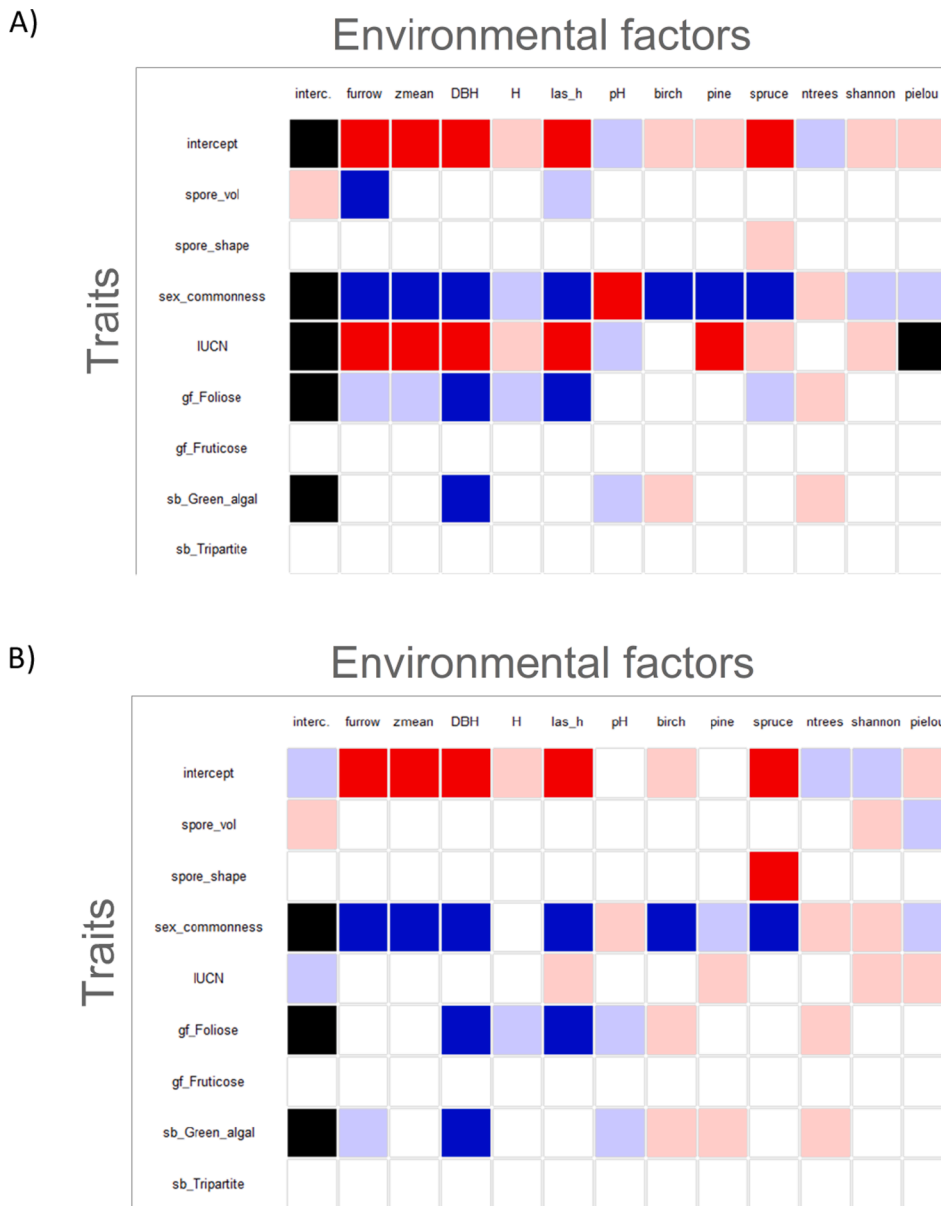


Fig. 5. Summary of the community level results of the 48-species (A) and 99-species (B) HMSC analyses including both protected and non-protected areas. Both summaries are based on those 52 variable combinations which had predictive power greater than chance (AUC > 0.5) in the 48-species analysis. Each grid cell shows the effect of the given trait (rows) on the given environmental response (columns). Red color indicates a positive effect, i.e. that looking across species, a higher value of the trait or the presence of a categorical trait was associated with a more positive response to the environmental factor. Similarly, blue color indicates a negative effect of the trait on the environmental response. The intercept row and column show the average effect of each environmental variable and trait on species' occurrence. Bright red/blue: effects supported by > 90% posterior probability (PP) in all model versions. Pale red/blue: effects supported by > 90% PP in at least two but not all model versions. White: effects supported by > 90% PP in no or only a single model version. Black: inconsistent effects (positive effect at > 90% PP in one model version, negative effect in another). Gf = growth form, sb = symbiont; see text and Table 1 for variable definitions. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

habitats more than species with rare sexual reproduction. Species' Red List status was related to their responses to environmental factors; however, the highlighted environmental factors were not consistent for the 48 and 99 species analyses. In the 48-species analysis, the seven red-listed species were distinguished primarily by a more positive response to variables related to forest maturity: DBH, tree height, forest canopy height and bark furrow depth. By contrast, the 22 red-listed species included in the 99-species analysis were in some candidate models distinguished by different responses, including a more positive response to tree species diversity and evenness in their surroundings. However, none of the effects of Red List status was consistent over all candidate models in the 99-species analysis.

4. Discussion

In this study, we show that the combination of LiDAR and hyperspectral data has potential in predicting the aspen epiphytic lichen communities in boreal forests. The average canopy height, the number of trees, the dominant tree species, tree species diversity and evenness within a 30 m radius circular plot predicted the species community

slightly better than the best-performing field variables when both protected and non-protected areas were included in the analysis. Including also rare species in the analysis decreased the predictive performance of the models but increased the dominance of remote sensing variables among the top models. Considering the efficiency and wide range of remote sensing compared to field measurements, this result is encouraging in terms of using new methods of aspen epiphytic lichen monitoring and also for finding high-biodiversity areas. It is also noteworthy that habitat parameters calculated with 30 m radius predicted community composition better than the same parameters calculated with a 10 m radius. The relevance of the surrounding habitat beyond the very local conditions at and around the focal tree further supports the benefits of remote sensing, as traditional mapping of forest parameters across wide areas is highly labour intensive. However, the predictive performance of the community models was moderate (AUC > 0.7) at best and a large proportion of the variation in community composition remained unexplained by either field or remote sensing parameters. Predicting community composition became more challenging when also the rare species were included in the analysis. Based on this study, remote sensing can be useful for cost-efficient mapping of potential

high-biodiversity areas in forest landscapes. A field inventory is always required to confirm actual species occurrences. Moreover, the size and geographic scope of our test data set was limited, and the next step in method development would be to demonstrate the performance of remote sensing variables at larger spatial scales.

The most important individual parameters affecting community composition were those indicating tree and forest maturity: DBH, tree height, forest canopy height and bark furrow depth. This is consistent with earlier results showing increasing species richness (Hedenås & Ericson, 2000; Fritz et al., 2009; Johansson et al., 2007; Schei et al., 2013; Tullus et al., 2022) and a change in species composition (Hedenås & Ericson, 2000; Ellis & Coppins, 2006; Tullus et al., 2022) with increasing tree and forest age. The higher accuracy of community prediction achieved by the average canopy height in a 30 m radius plot instead of the host tree height implies that not only the host tree properties alone define the environment for the lichens but rather the average stand properties created by the surrounding trees. DBH, height and furrow depth were also positively correlated with species richness in the regression analyses; however, unexpectedly, this pattern was significant only in protected areas. In the community analyses, too, these variables predicted community composition in protected areas but not in non-protected areas. It is possible that the best tree-level predictor of lichen richness and composition would be the age of the tree, and the size-related variables reflected tree age better in protected than in non-protected areas which include few or no very old trees. The better performance of remote sensing variables in predicting community composition in the whole data can be understood as a combination of their ability to distinguish between protected (high-biodiversity) and non-protected (lower biodiversity) areas, their ability to explain at least a small fraction of the variation between non-predicted areas and their ability to also capture some of the maturity-related variation relevant in protected areas (even though less well than the field variables). The generally good performance of remote sensing variables is in line with the success of LiDAR-based search of forest habitats for hazel grouse (*Tetrastes bonasia*) where vegetation height, shrub density and variation in canopy height defined suitability (Rechsteiner et al., 2017).

The results of our community analyses are based on comparisons of the performance of 158 different candidate models, each of which required 5–45 h for model fitting and cross-validation. While we believe that this effort was sufficient for robust main conclusions, we note that the ideal model selection process would be to compare all variable combinations without the pre-selection based on one-predictor models. With a higher degree of automatization and more efficient use of high-performance computing resources, including all combinations could be attainable in future studies performing model selection of community models.

Our results demonstrate the value of protected areas for epiphytic lichen diversity. The higher species richness and occurrence of the most threatened species in protected areas may be due to the older age of the host trees there. The DBH and the age of aspen are positively correlated (Schei et al., 2013), so we can say that trees in protected areas were older than those in non-protected areas. For example, in Scotland, old aspens have had a higher species richness of epiphytic lichens than young ones (Ellis & Coppins, 2006). Generally, the effects of tree size, age and bark roughness coincide so that they are difficult to separate from each other. Moreover, the trees in the protected areas have been allowed to grow without any disturbance such as logging, so that a higher number of epiphytic lichen species has had time to colonize them and adapt to the prevailing conditions. For beech (*Fagus sylvatica*) stands, it has been shown that sites that had a long undisturbed history had clearly more lichen species than those having a shorter one (Fritz et al., 2008).

Our results suggest that bark pH of aspen is largely defined by other factors than age, as implied by the weak association between pH and the maturity-related factors in the responses of both species richness and community composition. One such defining factor could be mineral nutrition of the soil (Gustafsson & Eriksson, 1995). However, a negative

correlation between age and pH has also been noted (Ellis & Coppins, 2007). In protected areas, the bark pH range was wide, as typical for aspen (Kuusinen, 1994; Lewis & Ellis, 2010). The narrower range of pH in non-protected areas cannot be explained with our parameters. However, our trees were sampled mostly beside small forest roads and the possible effect of sand dust on the bark pH cannot be excluded. Many studies have shown the effect of dust on bark pH and lichen species richness, but those studies were mainly made along roads with heavy traffic (e.g., Farmer, 1993; Marmor & Randlane, 2007).

pH affected the species richness in both areas, being the only parameter that explained the number of species in non-protected areas. The negative correlation was in accordance with the knowledge of aspens with more acidic bark pH having a higher richness of epiphytic lichens (Ellis & Coppins, 2007; Löbel et al., 2006; Nirhamo et al., 2021). However, it is also known that the trend is opposite for cyanogenic epiphytic lichens so that aspens with acidic bark host fewer lichen species (Kuusinen, 1994). The response to pH was also species specific in the community analyses, with particularly species with rare sexual reproduction preferring low pH. A similar result has been found in Lithuania in a study of epiphytic lichen functional traits and host tree characteristics (Mežaka & Kirillova 2019). The significance of the association between pH and species richness in non-protected areas despite the lower range variation implies the importance of pH as a habitat defining factor for epiphytic lichens. However, it is not known whether pH variation is the cause or the effect of epiphytic species community composition (Kovářová et al., 2022) and thus the relationship between epiphytic lichen diversity and pH would merit further study.

Dominant tree species and tree density in the surrounding forest affected community composition in additional aspects to those determined by maturity-related factors. The positive response of several lichen species to tree species diversity and evenness can be interpreted as a positive response of forest variability on epiphytic lichen communities. Increased environmental heterogeneity on a stand scale can have a positive effect on lichen communities and species richness (Ellis, 2012). In Estonia, tree species diversity also affected the stand-scale lichen diversity when lichen species on all tree species were explored (Jüriado et al., 2003). In some of our 99-species models, particularly red-listed species were found to benefit from tree diversity; however, this pattern was not found in the 48-species analysis which included fewer red-listed species. As the predictive performance of the 99-species models was limited, this result may also be driven by chance or by the specific features of our study areas and should thus be confirmed with more extensive data.

Forest canopy cover or closeness of the water source did not show clear effects on epiphytic lichen species richness nor community composition in our analyses. This was unexpected, as light availability and air humidity are important factors for epiphytic lichens (Ellis, 2012). However, it is also conceivable that the density of the stand i.e., the proximity of adjacent trees may better indicate the amount of shading than the canopy cover, for the lichens growing on the lower part of the trunk. Similarly, in our study landscape characterized by numerous small lakes, variation in air humidity may be more related to the structural features of the forest than the distance to the nearest water body.

Species traits were relevant in explaining lichen species' responses to host tree and forest features. This supports the premise of trait-based approaches that species are not black boxes but behave in a predictable manner depending on their traits (Violle et al., 2007; Webb et al., 2010), allowing generalizations e.g., on traits predisposing species to anthropogenic threats. Apart from range size, rarity and niche width, traits that appear to be the most universal predictors of extinction risk are related to size and reproduction (Chichorro et al., 2019; Carmona et al., 2021; Chichorro et al., 2022). For lichens and fungi, a comprehensive analysis has not yet been possible, but e.g. Nordén et al., (2013) reported a higher vulnerability to habitat fragmentation in rare,

specialist and small-spored wood-inhabiting fungi. Our results contribute to this discourse, highlighting the commonness of sexual reproduction as a trait that distinguishes between species requiring mature trees at forest sites and those preferring earlier successional stages. A similar pattern was reported by Ellis and Coppins (2007), who found that lichen communities shift towards dominance of asexual species with increasing tree and stand maturity. Moreover, Löbel et al., (2006) reported a stronger spatial aggregation in asexually than sexually dispersing epiphytic bryophytes and lichens, suggesting a stronger dispersal limitation in asexual species.

Tree species detection of European aspen with remote sensing methods in boreal forests has achieved reasonably accurate levels (Viinikka et al., 2020; Kuzmin et al., 2021; Mäyrä et al., 2021). In this study, we showed that aspen detection combined with tree height and density estimation by airborne LiDAR can be used as a tool for finding suitable habitats for aspen epiphytic lichens. These represent potential biodiversity hotspots due to the importance of aspen for forest biodiversity and the role of epiphytic lichens as indicator species in boreal forests. With remote sensing-based parameters in the community analyses, we can cost-efficiently include the effect of habitat features beyond the focal tree on species composition and the occurrence of individual species. In this study, we showed that this approach can be more effective than traditional field methods as the remote sensing parameters predicted community composition slightly better than field parameters when the studied landscape included both protected (high-biodiversity) and non-protected (lower biodiversity) areas. With the accelerating biodiversity loss, such efficient methods of surveying potential biodiversity hotspots have become increasingly important and valuable.

Authors' Contributions

Authors: Ida Palmroos, Veera Norros, Sarita Keski-Saari, Janne Mäyrä, Juha Pykälä, Topi Tanhuanpää, Sonja Kivinen, Peter Kullberg, Timo Kumpula & Petteri Vihervaara.

IP, PK, TK and PV developed the study idea; IP, SKS, JM, TT, SK, JP, PK, TK and PV collected the data; IP, VN and JM made the analyses; IP, SKS and VN lead the writing process. All authors contributed critically to the drafts and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

Acknowledgements

This study was supported by the Strategic Research Council under the Academy of Finland (IBC-Carbon, project numbers 312636, 335959), and the Academy of Finland (C-NEUT, project number 347862) and the Finnish Ministry of the Environment (Finnish Ecosystem Observatory project number VN/12351/2021-YM-2). We thank everyone who helped in collecting field data, especially Max Strandén and Aleksii Ritakallio, as well as Anniina Kantelinen for identifying the specimens of *Micraea*. We also wish to acknowledge CSC – IT Center for Science, Finland, for computational resources. And we also like to thank the two anonymous reviewers who helped us to improve our manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2023.120993>.

[org/10.1016/j.foreco.2023.120993](https://doi.org/10.1016/j.foreco.2023.120993).

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