

# Verifying an Extinction Debt among Lichens and Fungi in Northern Swedish Boreal Forests

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**Abstract:** Destruction and fragmentation of natural habitats results in small species populations that face increased risk of extinction. A time delay may be involved in the regional extinction of species, and the number of species that eventually may go extinct in the future is called the "extinction debt." In boreal Sweden, we examined whether the number of epiphytic crustose lichens and wood-inhabiting fungi in old-growth forest remnants diverges from species richness levels in forest patches that have been naturally isolated for millennia. An excess of species in forest remnants could indicate the presence of an extinction debt. Observed species richness in 32 old-growth forest remnants (also called woodland key habitats [WKHs]) was compared with predicted species richness. To predict species richness we used regression models based on data from 46 isolated old-growth forest patches in a forest-wetland matrix. The reference landscape is ancient and assumed to reflect the conditions of insular floras in dynamic equilibrium. Stand factors constituted predictive variables in the models. The observed number of lichen species was higher than expected (i.e., an extinction debt among lichens may exist). By contrast, there was no significant difference between observed and expected species richness among wood-inhabiting fungi. The species richness of wood-inhabiting fungi has adjusted to the changes in forest and landscape structure more rapidly than the species richness of lichens. Differences in substrate dynamics between epiphytes on living trees and species growing on decaying logs might explain the difference between species groups. The results also indicate that population densities of red-listed species were low, which may result in continuing extinctions of red-listed species. The importance of WKHs might be overvalued because species may be lost if conservation efforts consider only protection and preservation of WKHs.

**Key Words:** isolation, partial least squares, *Picea abies*, polyporaceae, polypores, woodland key habitats

Verificación de una Deuda de Extinción entre Líquenes y Hongos en Bosques Boreales del Norte de Suecia

**Resumen:** La destrucción y fragmentación de hábitats naturales provoca que poblaciones de especies pequeñas enfrenten mayores riesgos de extinción. Puede haber retraso en la extinción regional de especies, y el número de especies que eventualmente podrán extinguirse en el futuro es denominado la "deuda de extinción." Examinamos, en Suecia Boreal, si el número de líquenes epifitos y de hongos de la madera en remanentes de bosques maduros difiere de los niveles de riqueza de especies en parches de bosque que han estado naturalmente aislados por milenios. Un exceso de especies en los remanentes de bosque podría indicar la presencia de una deuda de extinción. La riqueza de especies observada en 32 remanentes de bosque maduro (también denominados hábitats boscosos clave [HBC]) fue comparada con la riqueza de especies predicha. Para predecir la riqueza de especies utilizamos modelos de regresión basados en datos de 46 parches aislados de bosque maduro en una matriz de bosques-humedales. El paisaje de referencia es antiguo y se asume que refleja las condiciones de floras insulares en equilibrio dinámico. Atributos de los bosques fueron las variables predictivas en los modelos. El número observado de especies de líquenes fue más alto que el esperado (i. e. puede existir una deuda de extinción). En contraste, no hubo diferencia significativa entre la riqueza de especies de hongos de la madera observada y esperada. La riqueza de especies de hongos de la madera se ha ajustado más rápidamente a los cambios en la estructura del bosque y del paisaje que la riqueza de especies de líquenes. La

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*diferencia entre grupos de especies se puede explicar por diferencias en la dinámica del sustrato entre epífitas sobre árboles vivos y especies que crecen en troncos en descomposición. Los resultados también indican que las densidades poblacionales de especies enlistadas fueron bajas, lo que puede resultar en extinciones de estas especies. La importancia de HBC se puede sobrevalorar porque se pueden perder especies si los esfuerzos de conservación sólo consideran la protección y preservación de los HBC.*

**Palabras Clave:** aislamiento, cuadrados mínimos parciales, hábitats boscosos clave, *Picea abies*, políporos, polyporaceae

## Introduction

Old-growth forest (i.e., forest in a late successional stage with internal tree fall dynamics) is an important constituent of the natural forest of the boreal region (Esseen et al. 1997; Engelmark & Hytteborn 1999). The reduction of old-growth forests in Fennoscandia (i.e., the Scandinavian peninsula and Finland) by modern forestry, however, has been dramatic (Esseen et al. 1997; Kouki et al. 2001). The overall proportion of the forest land in Sweden currently covered by old-growth forest is at <5% (Bernes 1994), but it is even smaller in many regions of Sweden (see discussion that follows). The managed forests are dominated by young stands characterized by single-aged and even-sized monocultures (Östlund 1993). The old-growth forest habitat is decreasing and becoming more isolated. Today the majority of the remnant old-growth forest is only a few hectares in size (Anonymous 1999). In Sweden old-growth forest remnants have been identified through a nationwide survey named the woodland key habitat (WKH) inventory. Woodland key habitats are defined as “sites with a high conservational value in which red-listed species occur or are likely to occur” (Nitare & Norén 1992). The estimated total number of WKHs in Sweden is 70,000–80,000, corresponding to about 1% of the productive forest land (Anonymous 1999).

The fragmentation and degradation of old-growth forests constitute threats to the long-term persistence of many forest-dwelling species (Berg et al. 1994; Cederberg 2001). The risk of stochastic species extinctions increases because of the decreasing size and quality of habitat patches, and species dispersal and colonization are impeded by an increasing degree of isolation between fragments (Hanski et al. 1996; Hanski 1999). The relative amount of edge habitat increases with fragmentation, and edge effects may limit sensitive species to unaffected core areas of large forest remnants (Murcia 1995; Moen & Jonsson 2003). Selective logging of many old-growth forest remnants deteriorates habitat quality (Sippola et al. 2001; Svedrup-Thygeson & Lindenmayer 2003). The threats imposed by forestry on biodiversity are indicated by the number of extinct and red-listed forest-dwelling species. The Red List System of the World Conservation Union (IUCN) provides a threat status of species on a national scale. The species are grouped according to a

system of six categories reflecting the risk of extinction at a national level. Taking all taxa into account, some 115 forest-inhabiting species have gone extinct in Sweden and 1986 forest species are currently listed on the Red List of Swedish species (Gärdenfors 2000).

The extent to which species may survive and reproduce in small-sized old-growth forest remnants is unclear (Hanski 2000; Hansson 2001). It is likely that the populations of many species have not reached a stochastic equilibrium with respect to the current structure of the forest landscape. Many forest-dwelling species may currently occur in populations that are too small and too isolated from other sites for long-term persistence. If extinction risk increases in small old-growth forest remnants, it may also increase at the landscape scale. There may be a time delay involved, however, in the extinction of species. A substantial future cost in terms of species extinctions, or an “extinction debt” (sensu Tilman et al. 1994), is therefore likely to exist in fragmented landscapes (Hanski 2000). Thus, transient dynamics (i.e., the successive reduction of species richness and population sizes) resulting from fragmentation may complicate examinations of species distributions in recently isolated old-growth forest remnants.

Explorations of the extinction debt in landscapes where the fragmentation process has already occurred are challenging. In Fennoscandia, for example, we have limited knowledge about the distribution of many forest-dwelling species before large-scale modern forestry operations began. Changes in forest biodiversity have not been monitored through time. One potential way of approaching the questions about the long-term effects of forest fragmentation and extinction debt is to examine natural heterogeneous landscapes where discrete forest stands have been naturally isolated for a long time. Such landscapes are potential “reference landscapes” that can be used to evaluate species occurrences in recently fragmented landscapes.

We examined whether the richness of epiphytic lichens and wood-inhabiting fungi growing on dead trees in recently isolated WKHs diverges from species richness levels in forest patches that have been naturally isolated for millennia. The observed species richness in WKHs was compared with expected (or predicted) species richness values. Expected values were assumed to reflect

species richness when WKHs had reached a “stochastic equilibrium” with respect to the surrounding landscape. To predict the expected species richness, we used models extracted from data on species occurrences and stand variables recorded in a reference landscape, composed of naturally isolated old-growth forest stands. Thus, we assumed that species populations in WKHs are not at stochastic equilibrium and that an extinction debt may exist when the observed species richness exceeds the reference level (i.e., the expected species richness).

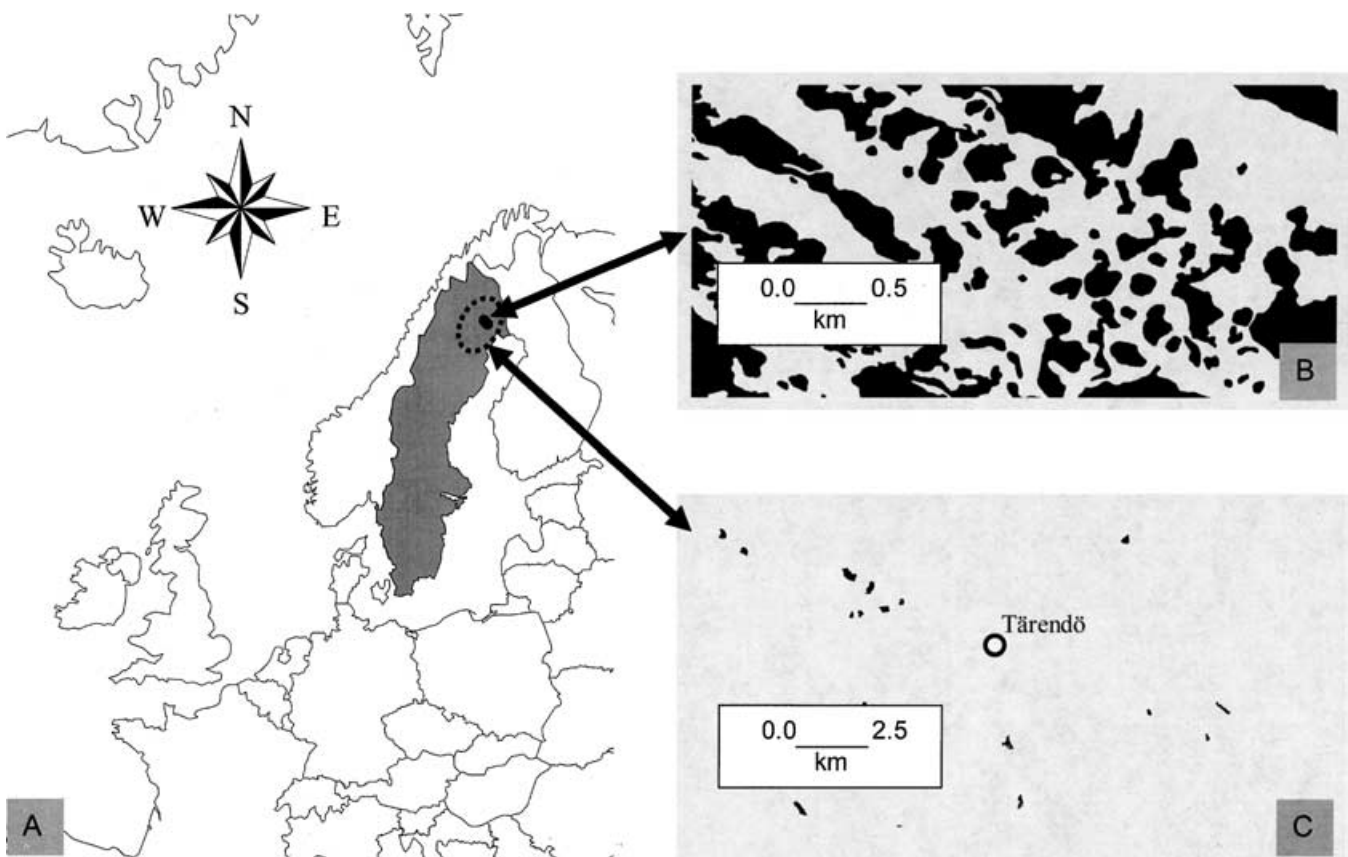
## Methods

### Area Description and Site Selection

We examined sites in Norrbotten County, within the north-boreal zone of Sweden (sensu Ahti et al. 1968). We recorded data for (1) naturally isolated old-growth forest stands within a reference landscape (Granlandet

Nature Reserve) and (2) recently isolated old-growth forest remnants within the managed forest landscape surrounding the reference landscape (Fig. 1). All forest stands represented the same forest vegetation type, one of the most common in the region, namely *Vaccinium myrtillus* (sensu Ebeling 1978). Norway spruce (*Picea abies* L. [Karst.]) dominates in the tree layer and mainly bilberry (*Vaccinium myrtillus* L.) dominates the field layer. The ground conditions in the forest stands we examined were moist to mesic (according to definitions by Hägglund & Lundmark [1987]), and the soil type was morain. The inclination was low and the productivity in the different stands was estimated to range from 2.3 to 3.3 m<sup>3</sup>/ha/year. The forests exhibited no traces of fire. The vascular plant flora was generally species poor. The flora of cryptogams was often diverse, however, with a large number of rare and threatened species (Berglund & Jonsson 2001).

Granlandet, located at 66° 35′ N, 21° 38′ E at an elevation of 250–400 m, is one of the largest forest reserves in Sweden with an area of 25,600 ha. It is composed of



**Figure 1.** Map of (a) Northern Europe, showing the position of the study area in Sweden; (b) section of the reference landscape, Granlandet nature reserve, showing tree-covered moraine hills (black) surrounded by a sphagnum-dominated wetland matrix (lightly shaded); and (c) section (i.e., the landscape close to the village Tärendö in Pajala Commune) of the managed forest landscape in Norrbotten County, where some of the studied woodland key habitats (WKHs) were sampled (WKHs in black and surrounding managed forests lightly shaded). Scales in (b) and (c) are different.

almost 1000 tree-covered moraine hills surrounded by a sphagnum wetland (Fig. 1). The hills are mostly covered by spruce, forming naturally isolated forest patches of varying size (from 200 m<sup>2</sup> to >20 ha) and shape. The basal area ranges from 7 to 26 m<sup>2</sup>/ha and is composed of 81% spruce and 18% deciduous trees (mainly *Betula* spp.). Scattered Scots pine trees (*Pinus sylvestris* L.) also occur. In 1997 and 1998 we randomly selected and examined 46 forested patches, distinctly separated from the wetland, within the reference landscape Granlandet. The studied patches ranged in size from 0.17 to 12 ha and together comprised 100 ha. No systematic investigation has been made of the forest history of Granlandet. The forests in the studied patches, however, represent late successional stages with internal gap phase dynamics. Dead spruces in different stages of decay occur abundantly (Jonsson 2000). The multilayered tree canopy is dominated by spruces ranging from about 150 to 200 years in age, with some spruces attaining an age of 300 years (Lövgren 1986). The studied forest patches show no signs of forestry or recent forest fires. The studied forests, then, were considered to have been in a natural old-growth state for a long period of time. Spruce probably colonized the area approximately 3000 years ago (cf. Tallantire 1972). Thus, extinction and colonization should have reached a dynamic equilibrium, and major changes in species distributions (i.e., transient dynamic phases) are unlikely. Accordingly, potential long-term effect of stand size and forest structure should be detectable in the species distribution.

The sampled WKHs were located within the managed forest landscape surrounding the model landscape between 65° 42' and 67° 15' N and between 19° 24' E and 23° 33' E at an elevation of 20–470 m (Fig. 1). The basal area varied from 6 to 36 m<sup>2</sup>/ha and was composed of 72% spruce and 20% deciduous trees. Scots pine occurred as subdominant. During 2000 we surveyed 32 WKHs, which comprised together 55 ha and ranged in size from 0.10 to 6.5 ha. The majority of these WKHs was randomly selected from a database compiled by the Swedish National Board of Forestry (Anonymous 1999). Studied WKHs were also selected from inventory data compiled for Jokkmokk Commune (Karström 1997). Personal communications with M. Karström provided us with information on areas where fragments of old-growth spruce forests had been left after clearcutting. Finally, studied WKHs were also randomly selected from inventory data compiled for the forest land owned by the forest company SCA (Svenska Cellulosa Aktiebolaget). As for the studied patches within the reference landscape, the studied WKHs exhibited no traces of fire. The isolation of most WKHs, however, has occurred gradually and fairly recently (i.e., during the last 100 years), with the extensive fragmentation of northern Swedish boreal forests by modern forestry practices (Östlund 1993; Esseen et al. 1997). In addition, the degree of isolation of studied

WKHs is likely to be an order of magnitude greater than for forest stands in the reference landscape (cf. Fig. 1). Further, the majority of the studied WKHs have been affected by different degrees of selective logging. Eight of the studied WKHs represented a subgroup of WKHs that had undergone an isolation process clearly defined in time and space. They were all isolated from natural forests during 1978 to 1989. This subgroup of WKHs ( $n = 8$ ) was defined as recent isolates. The isolation process of the other studied WKHs was not possible to determine as precisely as for the subgroup of recently isolated WKHs, but it was likely that the isolation of the other WKHs occurred much more gradually and over a longer time period (i.e., the last century). Thus, the rest of the WKHs ( $n = 24$ ) were defined as old isolates. All fieldwork was performed during August and September, when most annual wood-inhabiting fungi produce fruiting bodies.

### Stand Variables

Stand variables were recorded in the same manner in all the studied stands in both landscapes. Surveys occurred in a 0.1-ha circular plot in the center of each forest stand. We measured the number and diameter at breast height (dbh) of large spruces ( $\geq 25$  cm dbh), basal area (dead and living spruce and deciduous trees separately measured by a relascope), and maximum tree height of all spruces. The degree of cutting within each plot was estimated by counting the number of cut stumps. For downed spruce logs that originated within the sample plot and had a maximum diameter of  $\geq 10$  cm and a length of  $\geq 1$  m, we measured the maximum and minimum diameter and the length of the trunk. From these measurements we calculated the volume of the trunk, assuming downed logs were truncated cones. The stage of downed log decay was classified in 6 categories according to McCullough (1948) and Söderström (1988): (1) wood hard, bark intact; (2) wood hard, 50% of bark remaining; (3) wood hard, <50% of bark remaining; (4) wood starting to soften; (5) wood soft, small pieces missing; and (6) downed log deformed, loss of large pieces of wood.

In forest stands <1 ha, the circular plot corresponded to >10% of the total area of the stand. To ensure a representative sample of the forest variables at stand level in stands >1 ha, we sampled for additional forest variables in a number of transects (10 × 100 m). This sampling made certain that  $\geq 10\%$  of the total area of stands  $\geq 1$  ha was sampled. The transects were placed in a regular grid and spaced 50 m apart. At three points—start, middle, and end of each transect—the basal area and the maximum tree height were noted. We recorded the number of large (dbh  $\geq 25$  cm) spruces, downed spruce logs, and cut stumps along the entire transect. The characteristics of each log were recorded in the same manner as in the

circular plot. The data from transects were pooled to yield stand-level descriptions.

### Species Occurrences

We surveyed epiphytic crustose lichens and wood-inhabiting fungi. Red-listed species (according to Gärdenfors 2000) in the two species groups were recorded and treated as a subgroup of species. The crustose lichens occur as epiphytes on spruce trees and the wood-inhabiting fungi live on downed spruce logs. The presence of old spruces with rough bark and humid microclimate are important factors for crustose lichens (Thor 1998). The habitat quality (e.g., downed-log availability) and properties of downed logs (e.g., diameter and stage of decay) affect species composition among wood-inhabiting fungi (Niemelä et al. 1995; Renvall 1995).

Separate recording of species occurrences were done in the 0.1-ha circular plot (plot level) and over the entire stand (stand level). Thus, the species richness at stand level represented an estimate of the total species richness of the forest stand. The species richness at plot level was a measure of the density of species within forest stand interior.

For each large spruce ( $\geq 25$  cm dbh) in the plot, we noted the occurrence of epiphytic crustose lichen species. At the stand level, we surveyed lichens on all living spruces, irrespective of dimension. All species except for the genus *Mycoblastus* were recorded on the species level. *Japewia tornoenensis* and *Lecanora hypoptella* were treated as one taxon. We excluded 14 species and all *Leparia* spp. and *Micarea* spp. from the analysis because it was difficult to efficiently identify them in the field. Among wood-inhabiting fungi, we focused on the Polyporaceae and poroid Hymenochaetaeaceae (i.e., polyporous wood-inhabiting fungi). Nine corticoid wood-inhabiting fungi species were also included: *Amylostereum chailletii*, *Asterodon ferruginosus*, *Cystostereum murrayi*, *Laurilia sulcata*, *Peniophora pithya*, *Plebia centrifuga*, *Plebiopsis gigantea*, *Stereum sanguinolentum*, and *Veluticeps abietina*. The wood-inhabiting fungi we surveyed for are important wood decomposers and are mainly confined to conifer forests. All species were noted on the species level. Hereafter, all wood-inhabiting fungi are referred to as polypores.

At both spatial levels of inventory, we noted the presence of polypores on downed spruce logs (maximum diameter  $\geq 10$  cm and length  $\geq 1$  m) and their stumps. The presence of fungi basidiocarps (i.e., presence of sexually reproducing wood-inhabiting fungi) was used to detect species occurrences. Thus, nonfruiting mycelia were not recorded. To assess the size of between-year variations in species number among polypores, seven 0.1-ha plots in the reference landscape were reinventoried from 1997 through 2003. The mean difference in polypore species richness per plot (i.e., species richness in the original

year of inventory subtracted from that of a particular year) was  $-0.6 - 1.6$ . Thus, no major between-year differences were found. For further details on the sampling procedure, see Berglund (2004).

### Data Analysis

We extracted models predicting species richness from data on species occurrences and stand variables recorded in Granlandet. The impact of stand variables on the species richness was analyzed by partial least squares (PLS) regression. A PLS combines ordination and regression for relating two data matrices,  $\mathbf{X}$  and  $\mathbf{Y}$ , to each other through a linear multivariate model (Eriksson et al. 1999). The information in the  $\mathbf{Y}$  matrix (i.e., response variables) is used directly as a guide for optimal decomposition of the  $\mathbf{X}$  matrix (i.e., predictor variables). The number of predictor variables is reduced to one or several latent components. For prediction purposes, PLS yields a model for predicting  $\mathbf{Y}$  from an  $\mathbf{X}$  data table. The PLS modeling requires only that data are distributed fairly symmetrically. A general description of PLS can be found in Eriksson et al. (1999). The PLS models were made using SIMCA-P 10.0 (Umetrics AB, Umeå, Sweden).

The cross-validation (CV) procedure during the extraction of PLS components (cf. Eriksson et al. 1999) generates three measures of model validity: (1)  $R^2\mathbf{X}$ , the proportion of the variance in the  $\mathbf{X}$  matrix that is used in the models; (2)  $R^2\mathbf{Y}$ , the proportion of variation in the  $\mathbf{Y}$  data explained by the extracted PLS components (corresponds to the multiple correlation coefficient,  $R^2$ ); and (3)  $Q^2$ , the fraction of the variation in the  $\mathbf{Y}$  data that can be predicted by the extracted components (i.e., a cross-validated  $R^2\mathbf{Y}$ ). During PLS modeling, all variables were standardized to unit variance (i.e.,  $\mathbf{X} = 0$  and  $SD = 1$ ) before the analysis. This procedure yielded variables of the same weight in analysis. Area (i.e., stand size) and species richness at stand level were  $\log_{10}$  transformed in all analyses.

The PLS models predicting species richness were extracted from the Granlandet data set for both spatial levels of inventory (i.e., stand and plot). Models were based solely on the area and stand structure characteristics.

Elevation, north-south and east-west geographical position in Sweden, and cut stumps per hectare were not used as explanatory variables in models. The range and variation of these variables within Granlandet was short or almost nonexistent. For example, only a few cut stumps were found in one of the studied forest patches within Granlandet. These variables were, however, considered during the explorations of the differences between observed and predicted species richness within the WKHs. We defined the differences between species richness values observed within the WKHs and those predicted from the models as WKH differences. We analyzed the correlation between the WKH differences and variables not

**Table 1.** Species richness estimates<sup>a</sup> from inventories of sample plots and whole stands (i.e., plot and stand level) in woodland key habitats (WKHs) in northern Sweden as well as forest patches within the reference landscape (Granlandet; GL) in northern Sweden.

Spatial level	Species group	Total species richness <sup>b</sup>			Unique species <sup>c</sup>	
		WKHs	GL	WKHs & GL	WKHs	GL
Stand	crustose lichens	57 (7)	41 (4)	63 (7)	22 (3)	6 (0)
	polypores	56 (22)	53 (23)	59 (24)	6 (1)	3 (2)
	red listed	29	27	31	4	2
	all species					
	sum	113	94	122	28	9
	range	21–61	25–63			
	mean (SD)	43.1 (9.6)	40.7 (11.5)			
Plot	crustose lichens	45 (4)	35 (4)	49 (5)	14 (1)	4 (1)
	polypores	37 (15)	40 (16)	46 (19)	6 (3)	9 (4)
	red listed	19	20	24	4	5
	all species					
	sum	82	75	95	20	13
	range	0–35	6–42			
	mean (SD)	24.8 (7.1)	29.2 (7.1)			

<sup>a</sup>Species richness estimates are presented for each species group and for all species together. Number of red-listed species (according to Gärdenfors 2000) in different species groups is given in parentheses.

<sup>b</sup>The cumulative number of species recorded in (1) WKHs ( $n = 32$ ), (2) forest patches in GL ( $n = 46$ ), and (3) all forest stands (i.e., both the WKHs and the forest patches in GL together [WKHs & GL;  $n = 78$ ]).

<sup>c</sup>The number of species found only within the WKHs or the forest patches of GL.

included in the models: (1) the number of cut stumps per hectare, (2) elevation, and (3) the north–south and (4) east–west geographical location in Sweden.

Some WKHs exhibited variable values that were outside the variable ranges of the model data set. To evaluate the PLS model predictions in these stands, multiple factors (e.g., number and degree of deviations and variable importance) must be considered. Consequently, it is a multivariate problem. The probability that predictions of new observations are made within the model multi-dimensional tolerance volume can be calculated. In the current study four to five WKHs at stand level and six to seven WKHs at plot level had membership probabilities of  $<0.01$ . The major results of the comparisons between predicted and observed species richness in WKHs did not change when these sites were excluded from analyses. Thus, we chose to retain those WKHs where the prediction was based on an extrapolation slightly outside the model tolerance volume. Ecologically all the WKHs represent the same old-growth forest habitat (i.e., the same vegetation type and soil and water characteristics) as in the reference landscape, and we considered the extrapolations minor.

## Results

### Stand Variables and Species Richness

The ranges of stand variables and species richness in the two landscapes overlapped and were comparable. In all,

we observed 122 species in the 78 studied forest stands. The total number of observed species was about the same in both studied species groups (Table 1). About 25% ( $n = 31$ ) of the species were red-listed species. The number of species recorded in all the WKHs was generally higher than the number of species recorded in all the forest patches of Granlandet (Table 1). The number of crustose lichens found only in WKHs was higher than the number of crustose lichens found only in the forest patches of Granlandet. The number of polypores and red-listed species recorded at plot level was, however, lower in the WKHs compared with the forest patches in Granlandet (Table 1). Straightforward comparison of the species richness estimates of WKHs with that of forest patches within Granlandet was biased, though, because no control of differences in important forest-stand parameters was done.

### PLS Models and Observed and Predicted Species Richness

The extracted PLS models contained one or two significant PLS components. The proportion of explained variation in species richness ( $R^2\mathbf{Y}$ ) was 47–86% at stand level and 44–71% at plot level. The proportion of the variance in the predictor stand variables ( $R^2\mathbf{X}$ ) that was used in the models was 26–40%. The predictive ability of the models ( $Q^2$ ) varied between 0.31 and 0.70 and corresponded well to the explained variation ( $R^2\mathbf{Y}$ ).

The area, maximum tree height, and number of large spruces ( $\geq 25$  cm dbh) per hectare were important variables in all predictive models at stand level. The composition of predictor variables in models at plot level varied

between the different species groups. Different tree variables were important predictors in the model for crustose lichens. The downed spruce log volume per hectare was an important predictor in the models for polypores and red-listed species.

The observed species richness among crustose lichens at stand level was higher than expected from predictions, but there was no difference between observed and predicted species richness at plot level (Fig. 2). Observed and predicted species richness among polypores and red-listed species at stand level did not differ, whereas at plot level the observed species richness (i.e., species density in forest stand interior) among these species groups was lower than predicted (Fig. 2). The major results of the comparisons between predicted and observed species richness stayed the same even when predictions based on extrapolations outside the model tolerance volume were excluded. The unexpectedly low densities of red-

listed species, however, became marginally significant ( $p = 0.10$ , one-sample  $t$  test).

#### Distribution of WKH Differences

The degree of cutting and the geographical position of WKHs were related to the WKH differences (see Methods for definition). The number of cut stumps per hectare and elevation exhibited more and stronger correlations to the WKH differences than the east-west and north-south positions. The WKH differences among polypores and red-listed species were significantly negatively correlated with the number of cut stumps per hectare at both sampling scales ( $r = -0.51$  to  $-0.37$ ,  $p < 0.05$ , Pearson correlation). Elevation was significantly positively correlated with the WKH differences in most cases ( $r = 0.32$ – $0.67$ ,  $p < 0.05$ , Pearson correlation), except among crustose lichens at the stand level ( $r = 0.26$ ,  $p = 0.145$ ,

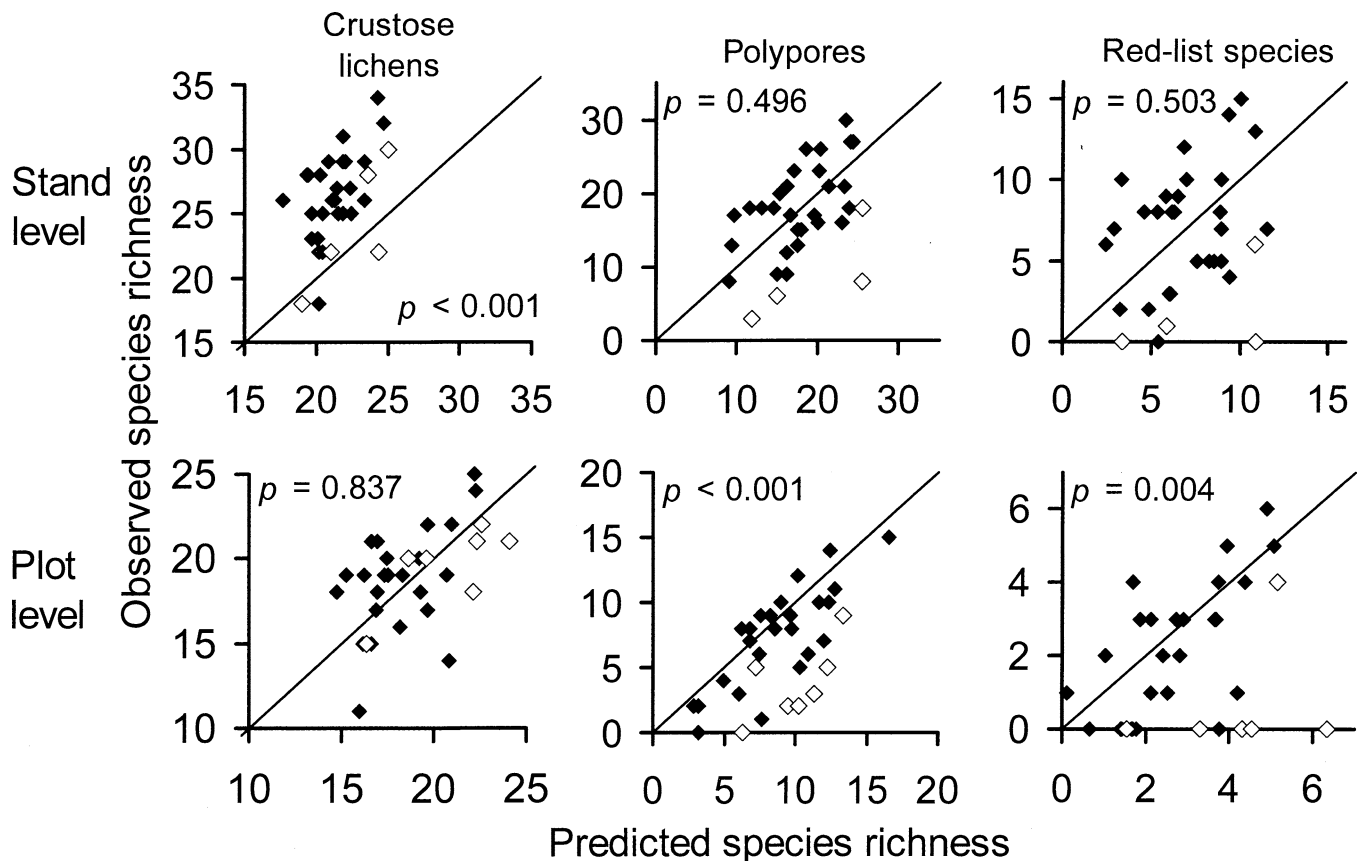


Figure 2. Observed species richness plotted against predicted species richness in 32 woodland key habitats (WKHs) in northern Sweden. The solid line illustrates the one-to-one relationship (the normal regression line; i.e., slope = 1) between predicted and observed species richness ( $n = 31$  for crustose lichens at plot level because of a missing value). Open diamonds are WKHs outside the partial least square regression model multidimensional tolerance volume (see Methods). The two-tailed probability ( $p$ ) of the differences between observed and predicted species richness with a mean value equal to 0 (one-sample  $t$  test) is given. Observed and predicted species richness are significantly correlated ( $p < 0.05$ , Pearson correlation) in all cases except among red-listed species at stand level ( $p = 0.132$ , Pearson correlation).

Pearson correlation). There was generally a positive trend between WKH differences and the north-south position of the WKHs in Sweden, but only correlations at stand level were significant ( $r = 0.44-0.56$ ,  $p < 0.05$ , Pearson correlation). The east-west position of WKHs in Sweden was negatively related to the WKH differences, but only one correlation (i.e., red-listed species at plot level) was significant ( $r = -0.36$ ,  $p = 0.044$ , Pearson correlation). The observed number of species was generally high compared with the predicted species richness level in WKHs with low degrees of cutting. These sites were generally located at high elevations in the northwest part of the study area (i.e., close to the Swedish mountains). Four of five correlations between elevation and the WKH differences remained significant when controlling for number of cut stumps per hectare ( $r = 0.41-0.60$ ,  $p < 0.001-0.023$ , partial Pearson correlation). However, only the correlation between number of cut stumps per hectare and the WKH differences among red-listed species at plot level remained significant when controlling for elevation ( $r = -0.38$ ,  $p = 0.036$ , partial Pearson correlation).

#### WKH Differences in Recent and Old Isolates

We tested whether the mean of the WKH difference of recently isolated WKHs deviated from the mean of the WKH differences in the old isolates. Most mean values for recently isolated WKHs were positive or close to 0, whereas the mean values for old isolates were negative. Thus, the mean WKH difference for the recently isolated WKHs was generally higher than the mean value found

for the old isolates ( $p < 0.05$ , two-sample  $t$  test; Table 2). The recently isolated WKHs also exhibited a lower mean number of cut stumps per hectare and they were located at a higher mean elevation than the old isolates ( $p < 0.05$ , two-sample  $t$  test; Table 2).

The WKH differences generally exhibited a negative relation with time since clearcutting of the forest surrounding the recently isolated WKHs (i.e., time since isolation; Fig. 3). Elevation also exhibited a negative relation with time since clearcutting, whereas the number of cut stumps per hectare did not. No correlations with time, however, were significant ( $p > 0.05$ , Spearman rank correlation).

#### Discussion

Our results indicate that WKHs in north boreal Sweden may host an excess of crustose lichen species. The observed numbers of crustose lichens in studied WKHs exceeded a reference species richness level predicted by models that reflect the conditions of insular old-growth stands in dynamic equilibrium. When controlling for stand size and forest structure characteristics, the observed species richness levels among crustose lichens were higher than could be expected. The results suggest that species populations among crustose lichens are not at a dynamic equilibrium with respect to the prevailing structure of the forest landscape of north boreal Sweden. An extinction debt (sensu Tilman et al. 1994) might thus exist among

**Table 2.** Mean values of WKH differences<sup>a</sup> and environmental variables for the two categories of studied woodland key habitats (WKHs) (recent isolates [ $n_1 = 8$ ] and old isolates [ $n_2 = 24$ ]) in northern boreal Sweden.

Variable	Spatial scale	Recent isolates		Old isolates		t test <sup>b</sup> p
		mean	SD	mean	SD	
WKH differences	stand					
	crustose lichens	5.3	2.2	4.3	3.5	0.334
	polypores	2.8	5.2	-1.9	5.9	0.050*
	red listed	2.3	3.7	-1.4	3.9	0.030*
	plot					
	crustose lichens <sup>c</sup>	1.6	2.0	-1.0	3.9	0.021*
	polypores	-1.5	1.9	-2.7	3.4	0.194
	red listed	-0.1	1.1	-1.3	2.1	0.045*
Environmental <sup>d</sup>	landscape					
	north-south	7.40	0.01	7.38	0.05	0.093
	east-west	1.74	0.03	1.77	0.05	0.043*
	elevation	387.5	57.8	173.8	134.4	<0.001*
cut stumps	stand					
	cut stumps	13.1	24.6	69.2	54.2	<0.001*
	plot					
	cut stumps	12.5	24.3	69.6	62.5	<0.001*

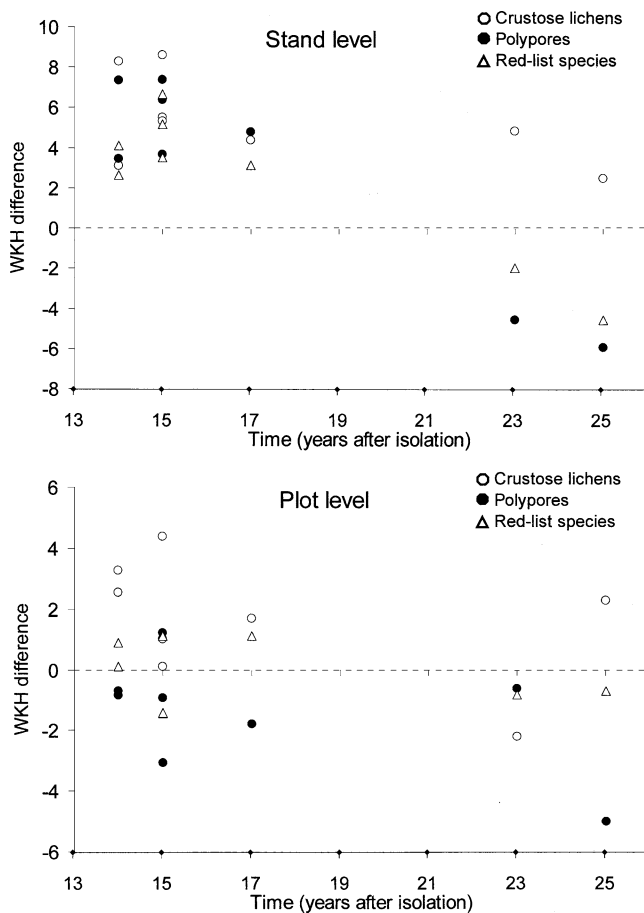
<sup>a</sup>The differences between species richness values observed within the WKHs and those predicted from the models.

<sup>b</sup>The two-sample  $t$  test (assuming unequal variance) gives the two-tailed probability (p) that WKHs that were considered recent isolates have the same variable mean value as do old isolates. Significant differences ( $p < 0.05$ ) marked with an asterisk (\*).

<sup>c</sup>The  $n_2$  is 23 for crustose lichens at plot level because of a missing value.

<sup>d</sup>Results on four environmental variables; the number of cut stumps per hectare (measured at plot and stand level, respectively), elevation (m above sea level) and the east-west and north-south geographical location in Sweden (m; according to the Swedish grid RT90) are presented on different spatial scales.





**Figure 3.** The woodland key habitat (WKH) difference (i.e., between observed and predicted species richness; see Methods for definition) plotted against time since clearcutting of the forests surrounding eight WKHs in northern Sweden defined as recent isolates (see Methods). The WKH differences are plotted for two species groups and the subgroup of red-listed species at two spatial scales (stand and plot level).

the crustose lichens because there is a risk that species will go extinct at a landscape scale in the future. The density of lichens in the interior of WKHs did not exceed expected levels, which indicates that the population sizes of crustose lichens have decreased but are still present at stand level.

By contrast, data for polypores or red-listed species showed that the observed total species richness did not exceed expected values in studied WKHs. Thus, both groups, at stand level, seem to have adjusted to the environmental changes caused by forestry more rapidly than the crustose lichens. In fact, their density was even lower than expected (i.e., the reference levels that were assumed to reflect the situation at a stochastic equilibrium). This indicates that predicted reference levels were high and provided a conservative test of observed species richness. The interpretation of the observed patterns is

complicated because some differences exist between the WKHs in the managed forest landscape and the forest patches in Granlandet: (1) the isolation of the WKHs are likely to be an order of magnitude greater than for forest patches within Granlandet, which may negatively affect species colonization probabilities (cf. Hanski 1999, 2000) and (2) potential gaps in supply of downed logs as an effect of earlier logging in the WKHs may have negatively affected the occurrence of wood-inhabiting fungi (Bader et al. 1995; Sippola et al. 2001). It could be argued that the unexpectedly low densities of polypores and red-listed species indicate that species populations are so small that this will increase the risk of further species extinctions at a stand level. Thus, the richness of polypores and red-listed species could be depleted further, even below the current and predicted levels.

Differences in substrate preferences among studied species groups may partly explain why polypores and red-listed species seem to have adjusted species richness to the environmental changes faster than the crustose lichens (cf. Fig. 2). For the two former groups, the combination of decreased formation of dead wood (as an effect of logging) and its relative fast turnover (e.g., Jonsson 2000) may have caused gaps in the continuity of dead wood supply, negatively affecting their maintenance (Bader et al. 1995; Lindgren 2001). Polypores with preferences for coarse downed logs and downed logs at the mid to late stages of decay especially tend to suffer negatively when downed-log densities are decreased (Niemelä et al. 1995; Sippola et al. 2001). In fact, some WKHs exhibited low densities and small diameters of downed logs. Thus, logging seems to have sped up the process of species extinctions in many WKHs, especially among polypores and red-listed species. The negative effects of logging were further supported by the results from the analyses of the WKH differences. The WKH differences exhibited correlations with the level of cutting (i.e., densities of cut stumps) and recently isolated WKHs had higher WKH differences compared with old isolates (Table 2). For crustose lichens, unexpectedly high species richness may have remained over time because of the long-lived nature of living trees. Basal area of spruce and density of large spruces in WKHs was comparable to that observed in the reference landscape. Thus, despite former logging operations in WKHs, it is likely that habitat conditions important for lichens (e.g., presence of trees with rough bark and humid microclimate) have been fairly good over time.

Our overall results suggest a trend in the impoverishment of species diversity. The density of species decreases before species are lost at the stand level. The density of crustose lichen species had reached the expected species density level, but there was still an excess of species at the stand level (cf. Fig. 2). In accordance, the densities of polypores and red-listed species were unexpectedly low when the species richness was at expected levels (cf. Fig. 2). Hence, the loss of species at the stand level

seems to have a longer time lag compared with the decrease of species densities. The trend of impoverishment is also revealed in Fig. 3: the six youngest WKHs among the recently isolated WKHs ( $n = 8$ ) all exhibited WKH differences above 0 at the stand level. At the plot level, only a few WKHs exhibited WKH differences above 0. The observed patterns in species diversity could therefore have arisen from the fact that the sizes of species populations were decreasing and this decrease was manifested at the plot level as decreasing species densities. This may eventually result in extinctions at the stand level and later at a landscape scale.

## Conclusions

We investigated the existence of an extinction debt in fragmented landscapes with empirical data. By extracting strong predictive models from a reference landscape, species diversity patterns of remnant old-growth forests in the managed forest landscape may be evaluated.

The importance of small, old-growth forest habitats, such as the WKHs, for the maintenance of the biodiversity in Fennoscandian managed boreal forests is unclear (Hanski 2000; Sverdrup-Thygeson 2002). There is generally a lack of understanding of the future functioning of WKHs and whether their native species will persist or go extinct (Hansson 2001). Our results indicate that species populations in WKHs are not at stochastic equilibrium with respect to the prevailing environmental conditions. Thus, species richness in WKHs will most likely decrease in the future because of transient dynamics (i.e., an extinction debt probably does exist). In other words, there is a possibility that we have overvalued the importance of the WKHs because species may be lost if conservation efforts consider protection and preservation of WKHs only. The species that still exist, however, represent a base for future restorations.

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