Examensarbeten **2010:24**

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Utvärdering av en ektomykorrhizabildande storsvamp som indikatorart av skyddsvärda tallhedsbiotoper i norra Sverige

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Abstract

Since the 1950s, the development of modern rotation forestry in boreal Fennoscandia has resulted in a severe reduction of older forests, and a high degree of fragmentation among the small patches that remains of old forest. In Sweden, when performing conservation value assessments in order to identify and preserve the remaining forest habitats, the government authorities use to a significant extent a set of indicator species that indicate habitats of high biological conservation value. One species considered to indicate high conservation values in pine-heath forests is the red-listed ectomycorrhizal (EM) macrofungi *Sarcodon scabrosus* (Fr.) P. Karst. In the present study, the validity of using *S. scabrosus* as an indicator species was evaluated by performing a survey including 41 pine-heath habitats in northern Sweden. In each stand, the occurrence and abundance of *S. scabrosus* was quantified together with occurrence of other red-listed macrofungi and different structural variables related to stand and tree continuity, historical disturbances, ground vegetation and soil type. Results were analysed by performing single and multiple regressions based on the maximum number of observed *S. scabrosus* sporocarps, and using 2-sample T-tests comparing stands with and without occurrences of the species. Results revealed that the occurrence of *S. scabrosus* neither is correlated with the presence of other red-listed macrofungi, nor with none of the studied parameters indicating long stand and tree continuity. In fact, occurrence of the species was negatively correlated to increasing tree age, but positively correlated to variables related to an open stand structure (low basal area, abundance of pine seedlings, a wide tree diameter range) and a proportionally high amount of needle dominated litter on the ground. The negative correspondence with tree age may be related to a reduced production of needle biomass in older trees, which may reduce nutrient availability for *S. scabrosus*. To analyse the distribution of *S. scabrosus* and other red-listed ectomycorrhizal species in relation to chemical soil properties would therefore be an interesting topic for further studies. In line with previous studies with other species groups, the present study clearly reveals the hazards of relying on presumed indicator species where an actual relationship with the variables considered to be of high biological value has not been confirmed in scientific studies.

Keywords: continuity, disturbance, ectomycorrhizal (EM) fungi, habitat requirements, indicator species, microclimate, pine-heath forest, *Sarcodon scabrosus*

Sammanfattning

Sedan 1950-talet har utvecklingen av det moderna rotationsskogsbruket i boreala Fennoskandien resulterat i kraftig minskning av andelen gammal skog och en hög grad av fragmentering av de små områden som finns kvar. I arbetet med att identifiera och bevara kvarvarande habitat i Sverige används ofta signalarter, som är en uppsättning av indikatorarter som indikerar habitat med höga bevarandevärden. En art som anses indikera höga bevarandevärden på tallhedar är den rödlistade ektomykorrhizabildande storsvampen *Sarcodon scabrosus* (Fr.) P. Karst. I denna studie utvärderas användandet av *S. scabrosus* som indikatorart genom inventeringar av 41 tallhedshabitat i norra Sverige. I varje skogsbestånd kvantifierades förekomsten och mängden av *S. scabrosus* tillsammans med förekomsten av andra rödlistade storsvampar samt olika strukturella variabler relaterade till bestånds- och trädkontinuitet, historiska störningar, markvegetation och jordartstyp. Data analyserades genom enkla och multipla regressioner baserade på det maximala antalet observerade fruktkroppar av *S. scabrosus,* och genom 2-sidiga T-test av områden med respektive utan förekomst av arten. Resultaten visar att förekomsten av *S. scabrosus* varken är korrelerad med andra rödlistade storsvampar eller med någon av de studerade parametrar som indikerar lång bestånds- och trädkontinuitet. I själva verket var arten negativt korrelerad med ökande trädålder, men positivt korrelerad med variabler relaterade till en öppen beståndsstruktur (låg grundyta, förekomst av tallplantor, vid diameterspridning) och en stor täckningsgrad av barrdominerad förna på marken. Det negativa sambandet med trädålder kan därför möjligen bero på en reducerad produktion av barrbiomassa hos äldre träd, vilket kan reducera näringstillgången för *S. scabrosus*. Att analysera förekomsten av *S. scabrosus* och andra rödlistade ektomykorrhizasvampars relation till kemiska markegenskaper skulle därför vara ett intressant ämne för vidare studier. I linje med tidigare studier med andra artgrupper visar denna studie tydligt riskerna med att förlita sig på förmodade indikatorarter, innan det faktiska sambandet med de variabler som anses vara av högt biologiskt värde har bekräftats genom vetenskapliga studier.

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Introduction

Since the 1950s the development of modern rotation forestry in boreal Fennoscandia has resulted in a severe reduction of older forests, and a high degree of fragmentation among the small patches that remain. In order to identify and select valuable habitats for protection, the Swedish Forestry Agency has identified a set of indicator species that indicate habitats of high biological conservation value, referred to as signal species (Nitare 2005). In doing this, a few central requirements was a presumed strong association to high value forest habitats, and that the species rarely occurs where biodiversity values are low. In Sweden, the use of the listed signal species has become widely applied in surveys of high conservation value habitats performed both by the Forestry Agency and the Swedish Environmental Protection Agency (EPA) (Norén et al. 2002). One of the biotope types currently in focus for conservation efforts in Sweden is an ecosystem dominated by Scots pine (*Pinus sylvestris* L.) on predominantly glaciofluvial sand or gravel soils with a thin humus layer, hereafter referred to as pine-heath forests (Arnborg 1990; Anon 2005).

At first sight, these biotopes can appear rather species-poor, but a large proportion of the biodiversity in pine-heath forest consists of ectomycorrhizal (EM) soil fungi (Tedebrand 2002). The dispersal mechanisms of EM fungi are not entirely understood (Newton 1992; Dahlberg et al. 2001). While dispersal by mycelia generally is very slow compared to spore dispersal in terms of covering larger distances, the mycelial network provides the advantage of carbohydrate supply from the tree roots (Jumpponen & Egerton-Warburton 2005). This may have resulted in the evolution of primarily vegetative dispersed species that are able to colonize already established forests where spore establishment may be less successful, but on the other hand have become dependent on unbroken tree continuity (Newton 1992; Dahlberg 1997; Jonsson et al. 1999a; Jonsson et al. 1999b). Since threatened EM fungi mainly are found in mature or old growth forest, a continuity of living trees is believed to be essential for their occurrence (Nitare 2006). This assumption has consequently also resulted in that most of the red-listed EM species are considered to be threatened by modern even-aged rotation forestry (Nitare 2005; Gärdenfors 2005; Nitare 2006). The importance of long tree continuity for threatened forest biodiversity is also emphasized in the Swedish national strategy for the formal set-aside protection of forest (Anon 2005).

In Sweden, the EPA and the Swedish Forest Agency use twelve species from the genus *Sarcodon* as indicator species for high conservation value forests (Nitare 2005). The genus *Sarcodon* consists of stipitate hydnoid macrofungi, which form EM symbiosis with Scots pine. According to the Swedish Forest Agency, they are associated with habitats “with mature trees where both the forest- and the vegetation type are characterized with continuity and cannot withstand clear felling” (Nitare 2005). *Sarcodon scabrosus* (Fr.) P. Karst. is considered as a valuable indicator species since it is relatively common, which reduces the risk for occurrences remaining undetected.

The functionality of indicator species is often not verified empirically (Landres et al. 1988; Nordén & Appelqvist 2001; Rolstad et al. 2002; Roberge & Angelstam 2004), which is the case also for the *Sarcodon* species. Although the *Sarcodon* indicator species are used to indicate high conservation values e.g. in pine-heath forests and abundance and/or diversity of other red-listed species, it is unclear what the underlying functional relationship in that case would be. A few such plausible relationships could be that both the *Sarcodon* indicator species and the rest of the red-listed biodiversity in these biotopes are associated with 1) long continuity of Scots pine trees or old growth forest, 2) conditions related to the forest microclimate, or 3) chemical soil properties, which in turn may be affected by e.g. historical fire regimes, characteristics of the soil sediments, or allelopatic species in the field layer.

The use of any macrofungi as indicator species is problematic also from a practical perspective. In Sweden, the main production of sporocarps is concentrated to a few autumn weeks (Larsson 1997; Nylén 2000). Further, as for many other macrofungi, the exact timing of the annual sporocarp production is driven by local weather conditions (temperature and soil humidity) and can hence vary to a large extent between years (Dahlberg 1991; Vogt et al. 1992; Lodge et al. 2004). This complicates the performance of surveys targeting these species, especially since the survey personnel need to distribute their work throughout the whole vegetation period. From a biodiversity management perspective it would therefore be most practical if structural variables could be identified that with a high degree of accuracy may predict the occurrence of red-listed biodiversity in pine-heath forests. However, irrespective of whether EM species or structural variables are to be used as indicators for biodiversity in the pine-heath forest habitats, it is essential to verify that the variables surveyed indeed have a correlation to the variable they are thought to indicate. Currently, we observe that this kind of knowledge is far from satisfactory for the pine-heath forest habitats, which makes the task of making conservation priorities arbitrary and unnecessarily difficult.

Objectives

The main objective of this study was to evaluate the validity of the use of *Sarcodon scabrosus* as an indicator species for different kinds of conservation values in pine-heath forests in northern Sweden. To achieve this, the more specific aims were to investigate the association between *S. scabrosus* and (1) diversity of other red-listed macro fungi; (2) structural variables related to long forest continuity; (3) a high stand age; (4) variables that may affect the forest microclimate; and (5) variables related to soil and ground vegetation, in pine-heath habitats previously identified by the Swedish Environmental Protection Agency as potential habitats for *S. scabrosus*. Finally, (6) the association between other red-listed macrofungi observed in pine-heath forest and old growth forest were investigated.

Material and methods

Study species

Sarcodon scabrosus (Fr.) P. Karst. is a stipitate hydnoid species (tooth fungi) with large pale red-brown ephemeral sporocarps. The dark blue colored cross-section of the foot tip is a characteristic used for identification of the species (Maas & Nannfeldt 1969). *S. scabrosus* is red-listed as NT (Near Threatened) in the Swedish red-list (Gärdenfors 2010). The species grows in boreal forests, preferably in dryer pine-heath forests on sand and gravel with thin humus layers and sparse field vegetation cover (Maas & Nannfeldt 1969; Nitare 2006).

Study sites

In the present study, the selection of survey sites was based on sites previously surveyed for the species in order to establish an action plan for EM fungi of the genus *Sarcodon* (Nitare 2006). In the previous survey, which was conducted by the County Administrative Board (CAB) of Norrbotten on behalf of the Swedish EPA between the years 2005 – 2007, *S. scabrosus* sporocarps were marked with a coordinate with a 10-meter accuracy, and other signal- and red-listed species were noted. In the present study, all sites within the County of Norrbotten that were not recently clear-cut, or considered too inaccessible were revisited and surveyed with the methodology specified below. In total, this resulted in 41 stands being surveyed in the present study, including seven stands that had no observations of *S. scabrosus* sporocarps in the first EPA survey. The size of the stands varied from approximately 5-30 ha. All surveyed sites are located in the northern and middle boreal zone of Sweden (Ahti et al. 1968) in an area extending from 65,33° to 67,53° North and 19,28° to 23,37° East (Figure 1). The study was performed between 18th of September and 8th of October 2009.

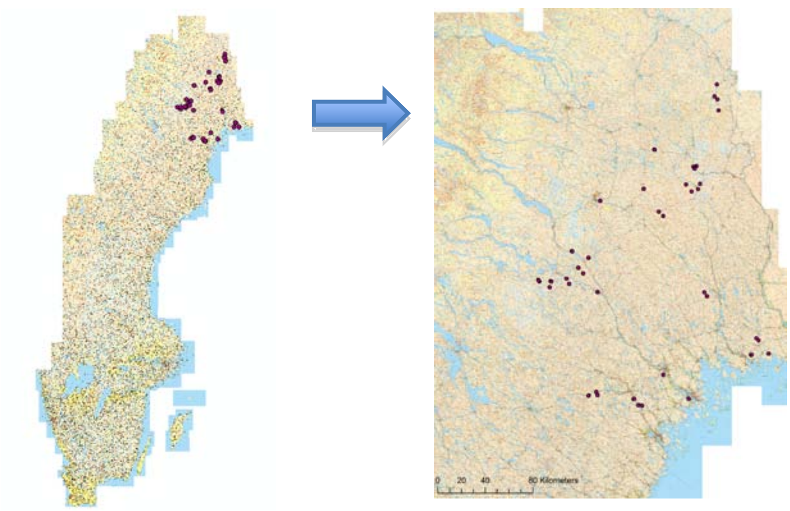

Figure 1. The location of the study sites in northern Sweden

Experimental design

In all stands, the outer boundaries of the biotope were first delimited. After this, the entire biotope was thoroughly searched for *S. scabrosus* and the number of found sporocarps was noted, as well as occurrences (present/undetected) other red listed macrofungi. This was done by thoroughly walking through each stand. Then, variables related to stand and tree continuity, historical disturbances, ground vegetation, topography and soil type were assessed. In all stands, the different variables were measured at one or more of three different surveys levels; stand, plot-, and frame level (Table 1). Plot level: In each stand, three circular survey plots with a radius of 15 meters were distributed. The plots were primarily placed at microsites with either current occurrences, or previously registered occurrences of *S. scabrosus* sporocarps, with the *S. scabrosus* sporocarp cluster or coordinate in the center of the plot. At sites where there were fewer or none at all, present or previously registered *S. scabrosus* sporocarp clusters, complementary plots were randomly distributed. Frame level: In each circular survey plot two frames (50x50 cm) were placed. The frame was primarily placed with a sporocarp of *S. scabrosus* in the middle of frame. When no (or too few) sporocarps were found, the frames were placed parallel to each other in the center of each surface.

Table 1.Variables that were assessed in the present survey and at which level they were measured.

Variable:	**Measured at level:**
Red-listed macrofungi (present/not detected: no./stand)	STAND
Dead wood (sum. of logs, snags and high stumps) (no./ha)	STAND & PLOT
High conservation value trees (no./ha)	STAND & PLOT
Maximum tree age (at breast height)	STAND
Felling stumps (young and old) (no./ha)*	PLOT
Average tree age (at breast height)*	PLOT
Average tree diameter (at breast height)*	PLOT
Diameter range (cm)*	PLOT
Basal area (m^2/ha, for each tree species)*	PLOT
Small-scale disturbances (trail, tracks or road cuts, signs of forest fire, reindeer pen, newly thinned) (present/not detected)	STAND & PLOT
Field layer coverage (%) (total field layer, *Caluna vulgaris*, *Empetrum nigrum*, *Lycopodium complanatum*, *Rhododendron tomentosum*, *Vaccinium myrtillus*, *Vaccinium vitis-idaea* and seedlings of *Pinus sylvestris*)**	FRAME
Bottom layer coverage (%) (*Cladonia* spp., other lichens, *Pleurozium schreberi*, *Dicranum* spp., ground components (bare soil, rock and litter))**	FRAME
The thickness of the organic layer (mm; humus and litter)**	FRAME
The thickness of the bottom layer vegetation (mm; mosses/lichen)**	FRAME
Soil type (morain or sediment)	STAND
Topography (three classes; 1) hilly, 2) slightly hilly, 3) flat terrain	STAND

* Mean values from these variables were calculated per stand
** Mean values from these variables were calculated per stand and per plot

To estimate the degree of tree and stand continuity at the studied sites, variables were surveyed that are considered to indicate long forest continuity, including the amount of dead wood in different degradation rates and different size (Linder et al. 1997; Rouvinen et al. 2002; Jönsson et al. 2009); the number of high conservation value trees (for example large or old trees, or trees with fire scars) (Anon 2000; Gray & Blackwell 2008); the number of felling stumps (Rouvinen et al. 2002; Uotila et al. 2002); and maximum tree age cored at breast height (Nilsson et al. 2001; Bond &

Franklin 2002; Andersson & Östlund 2004). The oldest pine tree in the stand, estimated by appearance, was cored at breast-height to estimate the maximum tree age. In each stand, dead wood (the sum of snags, high stumps and logs) and high conservation value trees of pine were counted to obtain an average value (no/ha) for the stand. Depending on the size of the habitat/stand, three to five circles with the diameter of 25 meters (=1/5 ha) was used. The logs (over 1 meter in length), high stumps (over 1,5 meter in height) and snags were only noted if they had a diameter over 15 cm at breast height. Felling stumps were counted within each survey plot and categorized into young stumps and old stumps and values per ha were calculated. Young stumps are cut by a chainsaw at the base of the tree, and thus younger than approximately 60 years, (Carpelan 1948; Ekelund & Hamilton 2001). Old stumps are cut with an ax or saw, typically being relatively tall with uneven surfaces, practices which in Sweden have not been widely applied since around the 1950s.

Further, to estimate *S. scabrosus* association with stand age, the average tree age was determined in each stand. The average tree age were calculated from three trees (one per survey plot) in the dominant canopy layer that were randomly selected and cored at breast-height.

To assess the importance of variables linked to historic disturbance dynamics, which may affect forest microclimate and/or chemical soil and ground vegetation properties, the following variables were used: average diameter; diameter range; basal area; the cover of Scots pine seedlings in the field layer; small-scale forest floor disturbances; field and bottom layer coverage; the organic layer depth (mm); and the thickness of the bottom layer (mm). Further, a brief classification of soil type and topography was made in each stand. Average diameter at breast height (dbh) was measured for three randomly selected trees (one per survey plot) in the dominant canopy layer. A value for diameter range was obtained by subtracting the dbh of the coarsest tree with the dbh of the thinnest tree in each survey plot. Using these data, mean values per stand were finally calculated. Basal area for Scots pine, Norway spruce (*Picea abies* (L.) Karst.) and Downy birch (*Betula pubescens* Ehrh.) was estimated within each plot using a relascope from the middle point of each survey plot. Using these data, mean values were calculated per stand. For assessment of small-scale disturbances, the following categories were used: no noticeable disturbance, trail, tracks or road cuts, signs of forest fire, reindeer pen, newly thinned and other. These variables were noted within each stand and within each survey plot. The percentage cover of both the total field layer, and each individual field layer species (*Calluna vulgaris* (L.) Hull, *Empetrum nigrum* L., *Lycopodium complanatum* L., *Rhododendron tomentosum* Harmaja, *Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L. and seedlings of *P. sylvestris*) occurring in the frames was assessed. Also, the percentage cover was assessed for the bottom layer vegetation (*Cladonia* spp., other lichens, *Pleurozium schreberi* (Brid.) Mitt. and *Dicranum* spp.) and ground components (bare soil, rock and litter). Thickness of the bottom layer (mm; from bottom to top of mosses/lichens), litter in the organic layer (mm), and humus in the organic layer (mm) was measured twice per frame following Green et al. (1993). Measurements were performed immediately adjacent to the sporocarps in frames with occurrences of *S. scabrosus*, and otherwise at the side of the frame. The lower limit of the litter layer was set where decomposition had reached a stage where the original material could not be visually distinguished, and the lower limit of the humus layer was set at the surface of the mineral soil. As the frames within each survey plot were placed adjacent to each other, a mean of the variables estimated in the two frames were calculated for all variables that represented the value for the plot (n=123). Finally, mean values were also calculated per stand. Further, the soils in each stand were classified as consisting of either sediments or moraine. The topography of the landscape in each stand was classified into one of the following three classes: 1) hilly - the ground being uneven with a distinct undulating nature; 2) slightly hilly - the ground being fairly undulating; and 3) flat terrain.

Statistical analysis

For estimation of the abundance of *S. scabrosus,* the highest number of sporocarps registered in one specific season, i.e. in either the present survey or the CAB survey (2005-2007), was used. For estimation of occurrence (present/not detected) of other red-listed macrofungi, data from the present and CAB (2005-2007) surveys were summed for each site. These approaches were adopted to minimize the risk for unrepresentative figures and/or or undetected occurrences due to the briefness, seasonality and annual variation in sporocarp production.

Linear and multiple regression analysis (MINITAB 15 software) were used to relate the number of found sporocarps to independent forest stand variables. This was done at stand-, survey plot- and frame level. At stand level (n= 41), the maximum number of sporocarps of *S. scabrosus* found during one year in each stand was used as the dependent variable. The independent variables at stand level were those measured at stand level and mean values of the variables measured at plot and frame level (Table 1). Further, the number of identified red-listed macrofungi was used as an additional dependent variable at the stand level, and was tested against maximum and average tree age at stand level using linear regression analysis. As the plots primarily were placed at found clusters of sporocarps, which were located more that 100-meter apart from each other, each plot represented a separate independent microsite (n=123). For the plot level, the maximum number of sporocarps found during one year in each plot was used as a dependent variable. The independent variables at plot level were those measured at plot level and mean values of the variables measured at frame level (Table 1). Further, the number of high conservation value trees, the amount of dead wood, the maximum tree age, the classification of the topography and the soil type were also used as independent variables at plot level, using the mean values obtained at the stand level. In contrast to the plot level regression, the dependent variable at the frame level was the mean value number of sporocarps for the two frames surveyed in each plot in the present study. Further, the selection of independent variables only included those related the composition of the field and bottom vegetation layers, and the thickness of the bottom layer vegetation and the organic layers (Table 1). A 2-sample T-test was performed to see how the means of the estimated variables differed between sites with occurrences of *S. scabrosus* and sites with no sporocarps; this was done at stand-, plot- and frame level. Prior to running the test, an F-test was performed to determine whether the samples had equal or unequal variances.

Results

General stand structures at the study sites

The studied habitats were exceedingly dominated by Scots pine trees, characterized by a relatively open stand structure, and represented a wide span considering the variables maximum tree age, average tree age and diameter range (Table 2). Some form of logging in various degrees of intensity had previously been performed in all surveyed stands.

Table 2. Mean and range values for general stand characteristics, the field and bottom layer coverage and the thickness of the organic- (humus and litter) and bottom layer (mosses and lichen) in stands with (n=34) and without (n=7) observed sporocarps. The numbers within brackets display the number of stands with no occurrence of the estimated variable.

Variables	With sporocarps			With no observed sporocarps		
	Mean	Range	Stands	Mean	Range	Stands
General characteristics						
Maximum tree age (at breast height)	171	70-320		169	66-260	
Average tree age (age at breast height)	108	49-242		120	62-202	
Tree diameter (cm)	26	16-34		29	21-38	
Diameter range (cm)	14	3-29		15	6-26	
Total tree basal area (m^2/ha)	17,7	12-23		16,6	14-21	
Scots pine basal area (m^2/ha)	17,6	12-23		16,4	13,7-21	
Old stumps (no./ha)	34	0-146	(5)	23	0-66	(1)
Young stumps (no./ha)	100	0-340	(1)	118	19-363	
Total stumps (no./ha)	134	28-372		141	85-377	
Red-listed macrofungi (no/stand)	3	1-7		2	1-5	
Trees with high biodiversity value (no/ha)	6	0-53	(21)	5	0-15	(4)
Dead wood (no/ha)	9	0-42	(7)	4	0-12	(1)
The field layer cover (%)						
Total field cover	18,1	8,5-33		18,2	14-29	
Vaccinium vitis-idaea	11,9	3,8-24		8,64	2,7-15	
Calluna vulgaris	3,93	0,0-12	(5)	3,75	0,0-14	(4)
Empetrum nigrum	2,76	0,0-17	(15)	5,38	0,0-10	(4)
Vaccinium myrtillus	1,53	0,0-12	(15)	1,79	0,0-4,7	(2)
Rhododendron tomentosum	0,19	0,0-2,5	(30)	0,00	0,0-0,0	
Lycopodium complanatum	0,03	0,0-0,7	(32)	0,00	0,0-0,0	
Scots pine seedlings	0,25	0,0-3,2	(30)	0,19	0,0-1,0	(5)
The bottom layer cover (%)						
Cladonia spp.	37,9	3,17-71,0		45,8	3,00-80,8	
Other lichens	1,78	0,00-17,3	(22)	3,02	0,00-15,0	(2)
Pleurozium schreberi	21,4	0,00-70,8	(1)	15,7	0,00-66,7	(1)
Dicranum spp.	8,26	0,00-43,7	(3)	8,48	1,33-25,7	
Rock	0,73	0,00-6,00	(30)	0,33	0,00-2,00	(5)
Litter	24,6	7,33-46,7		16,9	11,3-22,7	
Bare soil	5,53	0,00-25,0	(11)	9,76	2,00-22,7	
Thickness of the organic- & bottom layer (mm)						
Humus						
Litter	25,5	10,5-50,8		24,2	12,8-37,3	
Mosses and lichen	4,97	0,00-27,5	(1)	1,96	0,00-8,33	(1)
	28,3	16,7-60,0		21,6	13,3-28,3	

The stands typically had a field layer characterized by *V. vitis-idaea* and *Cladonia* spp. with minor occurrences of *C. vulgaris*, *E. nigrum*, *V. myrtillus*, *P. schreberi*, and *Dicranum* spp. All sites correspond well to what Arnborg (1990) identifies as the Xeric Dwarfshrub Type ('Skarp ristyp' in Swedish), and most of them correspond to what Jonsson et al. (1999a) refers to as the *Ericaceae-Cladina* forest type. Further, all stands had dry, sandy soils with a thin humus layer and were predominantly situated on moraine ground (Table 3).

Table 3. Frequency of soil type (sediment or moraine), the topography (flat, slightly hilly or hilly) and ecological field disturbances (trail, track, fire, newly thinned and reindeer pen) between stands with occurrences of *S. scabrosus* sporocarps (n: 34) and stands with no observed sporocarps (n: 7).

Variables Frequency: %	With sporocarps	With no observed sporocarps
Soil type:		
Sediment	33	14
Moraine	67	86
Topography:		
Flat	35	86
Slightly hilly	27	14
Hilly	38	0
Disturbance:		
Trail	50	29
Track or road cuts	76	71
Fire	74	86
Newly thinned	12	29
Reindeer pen	21	57

S. scabrosus as an indicator species

When examining the associaton between the maximum number of observed sporocarps of *S. scabrosus* and the variables considered to indicate long forest continuity (i.e. the numbers of pine trees with high biodiversity value; the amount of dead wood; or the maximum tree age), no statistically significant relationship was found (Figure 2a).

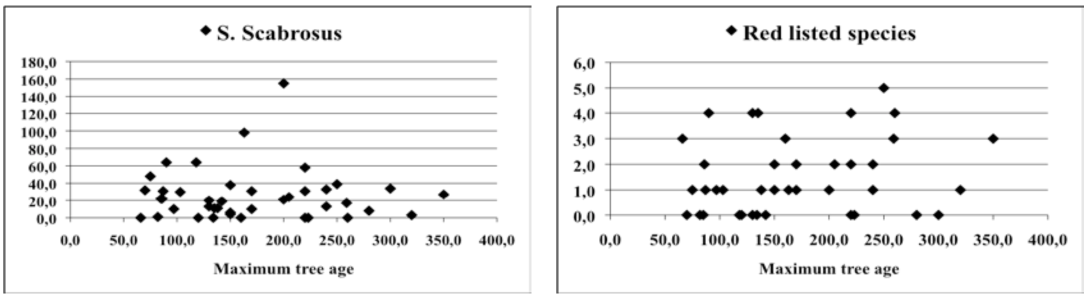

Figure 2. The relationship between the maximum tree age and a) the number of sporocarps of *S. scabrosus*, and b) the number of red-listed macrofungi in the surveyed stands.

In contrast, a significant negative relationship was found between the maximum number of observed sporocarps of *S. scabrosus* and average tree age in a multiple regression analysis (Table 4 and Figure 3a).

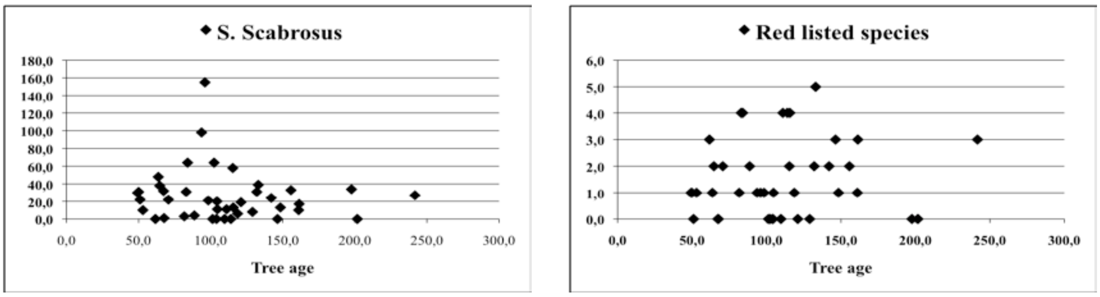

Figure 3. The relationship between the average tree age and a) the number of sporocarps of *S. scabrosus*, and b) the number of red-listed species in the surveyed stands.

The other red-listed species, registered either in the present study or in the previous study were; *Albatrellus subrubescens* (Murrill) (VU), *Boletopsis grisea* (Peck) (VU), *Hydnellum gracilipes* P. Karst (EN), *Hygrophoropsis olida* (Peck) H. Bigelow (VU), *Lactarius musteus* Fr. (NT), *Phellodon niger* (Fr.: Fr.) P. Karst. (NT), *Ramaria botrytis* (Pers.:Fr.) Ricken. (NT), *Ramaria magnipes* Marr & Stuntz, *Tricholoma colossus* (Fr.) Quél (NT) and *Tricholoma matsutake* (S. Ito & S. Imai) Singer (NT) (Gärdenfors 2005). No statistically significant relationship was found between observed sporocarps of *S. scabrosus* and the numbers of other red-listed macrofungi (Figure 4). Further, when examining the relationship between other red-listed macrofungi and average tree age or maximum tree age, no statistically significant relationship was found (Figures 2b and 3b).

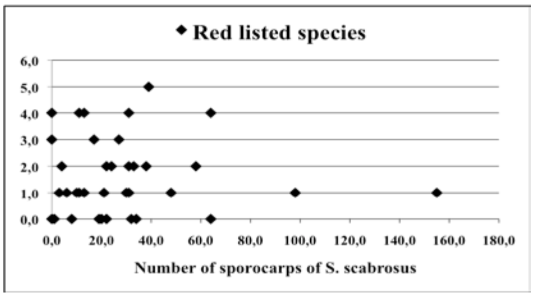

Figure 4. The relationship between the number of sporocarps of *S. scabrosus* and number of other red-listed macrofungi noted in the surveyed stands.

Disturbance dynamics and forest microclimate

When examined by regression, a significant positive relationship was found between the maximum number of observed *S. scabrosus* sporocarps and pine diameter range (Table 4). In contrast, significant negative relationships were found with total basal area, Spruce basal area, and fire (Table 4).

Table 4. Results of multiple linear regression test between maximum number of observed sporocarps of *S. scabrosus* and different stand variables at the study sites at stand-, plot-, and frame level. Cross-validation was performed at all levels (see PRESS ratio).

Level	Predictor	Coef.	p
Stand	Average tree age (years)	-0,254	0,037
PRESS ratio = 1,50	Diameter range (cm)	2,701	0,003
R-Sq(adj) = 35,6%	Spruce basal area (m^2/ha)	-61,29	0,023
	Cover of Dicranum spp. (%)	-1,032	0,009
	Cover of bare soil (%)	-1,474	0,006
	Cover of litter (%)	0,807	0,038
Plot	Fire (%)	-4,654	0,008
PRESS ratio = 1,12	Diameter range (cm)	0,277	0,009
R-Sq(adj) = 18,8%	Total tree basal area (m^2/ha)	-0,501	0,031
	Cover of Dicranum spp. (%)	-0,165	0,023
	Cover of bare soil (%)	-0,105	0,219
	Cover of litter (%)	0,163	0,006
	Height of bottom layer (mm)	0,181	0,042
Frame	Total field cover (%)	-0,026	0,081
PRESS ratio = 1,11	Cover of Scots pine seedlings (%)	0,381	0,021
R-Sq(adj) = 12,4%	Cover of bare soil (%)	-0,031	0,017
	Cover of Dicranum spp. (%)	-0,027	0,019
	Depth of humus (mm)	0,022	0,091

Further, the disturbance-related variables “fire traces in stumps” and “reindeer pen” were significantly more common in stands without *S. scabrosus* sporocarps (Table 5). In contrast, presence of “tracks and road cuts” was significantly more common in stands with *S. scabrosus* sporocarps. When examining the correlation between pine tree diameter and the maximum number of *S. scabrosus* sporocarps, no significant relationship was found. The topography showed to be of importance for the occurrence of *S. scabrosus*, since significantly more stands with sporocarps were found on “hilly ground” (Table 5).

Table 5. 2-sample T-test values for differences between stands with found sporocarps and sites with no sporocarps (34 and 7, respectively), with respect to estimated variables and at different levels. Only the variables showing significantly difference ($p \leq 0,05$) between the stands are displayed. Mean values and standard deviation for each parameter is also shown. The number of studied plots were 74 (with sporocarps) and 49 (without sporocarps), and the number of frames were 44 and 79, respectively.

Level	Variable	With sporocarps		With no sporocarps		t-test	
		Mean	**S.D.**	**Mean**	**S.D.**	**t**	**p**
Stand	Topography (%)	1,029	0,870	0,143	0,378	4.290	0,000
	Reindeer pen (%)	0,206	0,410	0,571	0,530	-2,040	0,048
	Cover of litter (%)	24,60	10,70	16,88	4,490	3,080	0,005
Plot	Tracks or road cuts (%)	0,390	0,492	0,200	0,407	-2,220	0,030
	Fire traces in stumps (%)	0,350	0,481	0,550	0,503	2,210	0,030
	Cover of bare soil (%)	4,690	10,30	8,600	11,60	1,960	0,050
	Depth of litter (mm)	5,430	7,350	2,970	4,440	-2,310	0,020
	Height of bottom layer (mm)	29,10	2,500	24,10	9,030	-2,600	0,010
Frame	Cover of bare soil (%)	1,850	6,300	8,700	12,20	-4,090	0,000
	Depth of litter (mm)	6,550	8,970	3,290	4,090	2,290	0,030
	Height of bottom layer (mm)	31,00	13,40	25,00	9,690	2,650	0,010

Soil and ground vegetation

When examining the field layer vegetation, no significant relationships were found between the maximum number of *S. scabrosus* sporocarps and neither total field cover, nor the respective cover of *V. vitis-idaea*, *C. vulgaris*, *E. nigrum*, *V. myrtillus*, *R. tomentosum or L. complanatum*, *P. schreberi*, *Cladonia spp.*, other lichens, or cover of rocks in the bottom layer. In contrast, significant correlations were found in multiple and single regression analyses (Table 4 and 6) for the cover of Scots pine seedlings (positive), the cover of bare soil (negative), and the cover of *Dicranum* spp. (negative). Further, the 2-sample T-test revealed that the proportion of bare soil was higher at sites without *S. scabrosus* sporocarps (Table 5). Regression analysis revealed that that the cover of litter as well as the height of bottom layer vegetation had a significantly positively relationship with the maximum number of observed sporocarps at several levels (Table 4 and 6). The 2-sample T-test confirmed this relationship, as these variables differed significantly between the compared stands (Table 5). Further, the 2-sample T-test also revealed that the thickness of litter were significantly higher in stands with *S. scabrosus* sporocarps. However, no correspondence was found between the thickness of the humus layer and the maximum number of observed sporocarps in neither the regression analysis nor the 2-sample T-test. In addition, no significant relationship could be discerned that showed that the *S. scabrosus* prefer sediment- or moraine soils.

Table 6. Results of single linear regressions tests between maximum number of observed sporocarps of *S. scabrosus* and different stand variables at the study sites at stand-, plot-, and frame level. The result only shows variables with a significant difference ($p \leq 0,05$).

Level	**Predictors**	**R-Sq(adj)**	**Coef**	**p**
Stand	Cover of litter (%)	7,2%	0,892	0,050
Plot	Fire (%)	2,5%	-3,709	0,044
	Cover of Dicranum spp. (%)	3,3%	-0,168	0,025
	Cover of bare soil (%)	2,6%	-0,173	0,041
Frame	Cover of Scots pine seedlings (%)	2,8%	0,359	0,035
	Cover of bare soil (%)	4,1%	-0,033	0,014
	Height of bottom layer (mm)	2,6%	0,026	0,040

Discussion

Sarcodon scabrosus as an indicator species

Since no support could be found for any relationship between the studied continuity variables and the occurrence of *S. scabrosus*, the present study cannot provide support for further use of *S. scabrosus* as an indicator of continuity in pine-heath forests. These results are in accordance with Newton et al. (2002) observations, which found *S. scabrosus* in plantations during a survey in Scotland. Since the present surveyed sites included several stands consisting of homogenous 60-year-old pine plantations with no presence of older trees, these results suggest that *S. scabrosus* is compatible with a low degree of tree continuity, restricted at the most to a previous presence of seedling trees which typically would have been removed at a plant height of 0,5-2 meter (Risberg et al. 2004). Other possible scenarios would be that *S. scabrosus* is capable to sustain the mycelia through connections with trees in adjacent uncut stands, or that the species after 60 years has been able to recolonize the clear-felled area through mycelia spread from adjacent stands (Humphrey et al. 2000). Since the variables “felling stumps” or “newly thinned areas” in the present survey did not affect the occurrence of the species significantly at any level, we can also conclude that thinning does not seem to disfavour the species.

The lack of a correlation reappeared when testing the relationship between the occurrence of *S. scabrosus* and the number of red-listed fungi sporocarps (Figure 4). Even though this potentially may be due to species- specific differences in seasonality of fruiting bodies (Vogt et al. 1992), the primary conclusion must be that *S. scabrosus* does not indicate the occurrence of other red-listed macrofungi. This further underscores the inappropriateness of basing conservation decisions in pine-heath habitats on the occurrence or abundance of *S. scabrosus*.

Similar results have been obtained when evaluating the use of different vertebrate species (Landres et al.1988) and the wood decomposing fungi *Phellinus nigrolimitatus* (Romell) Bourdot and Galzin and *Cystostereum murraii* (Berk and Curtis) Pouzar (Sverdrup-Thygeson & Lindenmayer 2003) as indicator species, while Bader et al. (1995) found the wood inhabiting fungi *Fomitopsis rosea* (Fr.) Karst. and *Amylocystis lapponica* (Rom.) Sing. justifiable as indicator species. The absence of co-occurrence among *S. scabrosus* and the rest of the red-listed macrofungi in pine-heath forests initially leave the possibility that other red-listed macrofungi are more restricted to habitats with a high degree of tree continuity. However, the present study could not reveal any correspondence between the number of other red-listed macrofungi and neither maximum tree age nor average tree age (Figures 2b and 3b).

Relation to forest age

A negative relationship was found between the number of sporocarps and average tree age (age range: 49-242; Table 1), indicating that old-growth forest, contrary to previous beliefs, may be suboptimal for the species. Similar patterns have been obtained in sporocarps surveys on stipitate fungi growing in pine forest on sandy soil in Scotland (Newton et al. 2002) and in Finland (Hintikka 1988). Hintikka (1988) concluded that the result partly could be explained by physiological differences related to tree age, since younger stands have higher net photosynthesis and produce more needle biomass compared to over-aged trees, which favored the mycorrhizal species. In accordance with Hintikkas conclusion, the present study shows that *S. scabrosus* is associated with relatively large proportions of both litter in the vegetation cover and accumulated litter in the organic layer, which may increase nutrient availability.

Relations to variables affecting the forest microclimate

In the present study, all stand variables positively correlated with the occurrence of *S. scabrosus* ("tracks and road cuts", low total basal area, the cover of Scots pine seedlings and a wide diameter range) are associated with an open stand structure, which results in increased irradiation and temperature, and decreased humidity (Bonan & Shugart 1989). This suggests that *S. scabrosus* may be more restricted by factors affecting the forest microclimate, with respect to e.g. irradiation, soil temperature and/or soil humidity, than by continuity parameters. The positive correlation with "tracks or road cuts" is in line with observations made by Newton et al. (2002) and Arnolds (1989), which both observe that these microhabitats display high abundances of sporocarps of stipitate hydonid fungi growing with pine trees on sandy soils. The positive association between *S. scabrosus* and an open stand structure is further supported by negative correlations to both total basal area and basal area for *Picea abies*. Heterogeneity with respect to tree size, in the present study quanitified by "diameter range", could indicate an historic occurrence of disturbances such as fire or selective cuttings. These historic disturbances could in turn result in parts of the stand being more open, which may facilitate germination of pine seedlings (Vickers & Palmer 2000; Zhu et al. 2003). In addition, a slightly hilly topography was significantly overrepresented among the habitats with observations of *S. scabrosus* sporocarps. Originating from different geological processes, this pattern could possibly be due to differences in chemical composition among flat and hilly soils (Brady & Weil 2002). Another possible explanation may be that a varied topography could contribute to create suitable microhabitats with respect to abiotic variables such as temperature or humidity. The question of whether the occurrence of *S. scabrosus* is functionally linked to any of the mentioned abiotic variables cannot be resolved with the present study design, to reveal the functional relationship further studies would be required. Both a relatively open habitat and a slightly hilly topography may be used as survey criteria to indicate potential habitats for the species.

Relations to variables indicating historic fire disturbance

At plot level, the regression analysis and the 2-sample T-test indicates that the occurrence of variables indicating historic fire disturbance is negative for the observed abundance of sporocarps. The major part of EM fungi mycelia is concentrated in the top humus layer (Dahlberg et al. 2001), and research has shown that EM fungi colonizing this layer decrease after fire (Stendell et al. 1999; Dahlberg et al. 2001). A potentially negative effect of ground fire may therefore be due to toxic compounds leaking from the ashes (Kin et al. 2003), or to that mycelia may have died in burnt patches due to a strong heat development in the top humus layer (Dahlberg et al. 2001). However, although variables indicating historic fire disturbance seems to be negative at the specific patches where ground fire has resulted in ash traces, the effects of historic fire disturbance at the stand level could still on the whole be positive for *S. scabrosus*. Such compensatory effects could be that relatively intensive fires typically result in a more open stand structure, which the present study has identified as an important biotope characteristic for the species.

Relations to soil and ground vegetation

In the present study, both the cover and depth of litter was found to have positive significant impact on the species. This association could be explained by the species ability to use litter as a nutrient source. Research has shown that some mycorrhizal species have the abilities to utilize N and P from organic compounds (Nygren 2008) and weathered minerals through enzymes (Landweert et al. 2001), but the ability seems to be highly variable between species. Nygren (2008) found that the taxa *Sarcodon*, among others, have the ability to degrade organic proteins. Further, Hintikka (1988) speculated that accumulation of litter may lead to a protection against temperature differences in favor for the EM growth. The positive correlation between *S. scabrosus* and the height of the bottom layer, and the respective negative correlation to the proportion of bare soil found in the present study, indicate that *S. scabrosus* does not prefer completely bare surfaces.

When examining the relation between dominant soil type and *S. scabrosus*, no tendency was found indicating that the species favored either sediment or moraine soils. Neither was any negative correlation detected between occurrence of Ericaceae dwarf-shrubs and *S. scabrosus* in the present study. However, since *S. scabrosus* does not seem to have the same biotope requirements as other red-listed macrofungi in pine-heath forests, the build-up of Ericaceae dwarf-shrubs that is likely to be a long-term consequence of the unnatural absence of ground fires (Engelmark 1999; DeLuca et al. 2002) could still be a valid risk for other species (Termorshuizen 1991). Instead, the cover of *Dicranum* spp. showed a significant negative correlation with the number of sporocarps at many levels. This correlation is probably not due to any functional relationship, but may potentially be due to different soil chemical preferences.

Methodological considerations

Since sporocarps of EM species are ephemeral, and sporocarp production is affected by annual fluctuations in weather conditions, which can vary from year to year and geographically depending on local climatic factors (Vogt et al. 1992), sporocarp surveys always involve a risk of unbalanced frequencies of detection among different sites. Thus, while this study is based on observations in a wide geographic area, some areas may have had a less suitable year for production of sporocarps than others during the surveys (Vogt et al. 1992). To mitigate this risk, the regression analyses of *S. scabrosus* was based on the maximum number of observed sporocarps found at a site during one of the two surveyed seasons. To achieve an absolute certainty of whether the species is present in a habitat or not, extensive soil samples with DNA analysis of mycelia would be needed.

Conclusions

The present study clearly demonstrates that the validity of using *S. scabrosus* as an indicator species for either red-listed species or tree and/ or stand continuity in pine-heath forest habitats needs to be reconsidered. Instead, the present study indicates that the species seems to be associated with certain soil properties, and with biotope characteristics related to a present-day or historically relatively open stand structure. Further, it is shown that *S. scabrosus* in fact is negatively correlated to increasing tree age. One possible explanation may be that older trees have a lower net photosynthesis compared to younger trees, resulting in a lower accumulation of litter in stands with a higher average tree age (Yoder et a. 1994; Lehtonen et al. 2004). The observed pattern may be due to that litter may protect the species from extreme temperature shifts, or that litter may have beneficial effects on nutrient availability for the species. To analyse the distribution of *S. scabrosus* and other red-listed EM species in relation to chemical soil properties would therefore be an interesting topic for further studies. Finally, in line with previous studies, the present study clearly reveals the hazards of relying on presumed indicator species where an actual relationship with the variables considered to be of high biological value has not yet been confirmed.

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