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Indicators of biodiversity, what do they indicate? – Lessons for conservation of cryptogams in oak-rich forest

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ABSTRACT

In the Nordic countries, sets of Indicator (Signal) species, predominantly cryptogams, have been used as one measure to find forest stands which may harbour Red List species. Such data could potentially also be used to prioritise among stands for protection as nature reserves. We studied if the number of Signal species indicates the number of Red List species in oak-rich mixed forest in south Sweden. We also explored if species richness of the investigated groups is correlated with the number of Red List or Signal species. In 25 stands, we surveyed epiphytic and epixylic bryophytes and lichens, ground-floor bryophytes, and wood-living fungi. We studied correlations for two datasets; (1) all forest species and (2) deciduous forest specialists. When relating the number of Signal species to the number of Red List species for each taxon and in total, a significant correlation was found for temperate deciduous forest lichens. The number of Signal species was further significantly correlated to total species richness for lichens (all forest species) and for wood-living fungi (both datasets). The number of Red List lichens was correlated to total lichen richness (deciduous forest species). Signal species seem not to be unequivocal in prioritising potential reserves among valuable oak-rich woodlands and surveys by Red List species experts may be needed. Signal species may be more useful for finding relatively valuable sites in a matrix of production forest. Moreover, Signal species seem to be useful surrogates for total cryptogam species richness.

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1. Introduction

Indicators of biodiversity can be very useful tools in conservation surveys, but to identify relevant indicators has often proved a difficult task. A bewildering array of approaches exists and a general view of the literature can be hard to achieve. Two classical approaches involve using either structural or biological (species) aspects as indicators or surrogates (review in Lindenmayer et al., 2000). As a recent development, Faith et al. (2004) and others advocate the combined use of species and environmental diversity data in multivariate sta-

tistics to achieve the goal of finding useful surrogates of biodiversity. It remains to see how the outcomes of such sophisticated methods can be used in practice.

In the following we focus on species criteria which have lately met with a surge of interest in northern Europe, in particular those based on cryptogams (lichens and other fungi, and bryophytes; Gustafsson et al., 1999; Gustafsson, 2000; Nordén and Appelqvist, 2001; Rolstad et al., 2002). Cryptogams are widely used in conservation surveys, since many of the species can be surveyed throughout the year and since the species often occur on old trees and dead wood, essential components

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of old-growth forests (McComb and Lindenmayer, 1999). Sets of indicator species of biodiversity and conservation value in woodland have been developed repeatedly for different regions, usually on the basis of advice from expert panels. This initially predominantly Scandinavian approach has recently inspired other countries (Prieditis, 2002; Sverdrup-Thygeson, 2002; Andersson et al., 2003; Andersson et al., 2005), and the methods used need to be scientifically evaluated.

Indices based on species criteria can be subdivided in categories depending on the aspects of diversity that are emphasized, for instance species richness or presence of rare species. Species richness (or species density) is a common measure in community ecology, and can be used as an index of nature conservation value, although its estimation and interpretation are fraught with difficulties (Hambler, 2004; Magurran, 2004). Diversity (usually species richness) and the presence of rare species are the most frequently cited criteria for site selection by conservationists (Prendergast et al., 1993). Although other criteria may be more used in practical conservation due to lack of data, species surveys are increasing in number and importance, at least in Scandinavia. Total or near-total species richness (all taxa) is however very costly to measure, and this criterion is seldom if ever used in practice. Another reason why species richness is not always useful for conservation work is that a high value for an area may ensue from heterogeneity or various forms of disturbance (Hambler, 2004). A disturbed area may harbour a mixture of many species from several communities. Still, within relatively homogeneous patches of a habitat type, species richness (or species density) may be a useful surrogate index of high conservation value when sampling effort is considered sufficient (Magurran, 2004; Jiguet and Julliard, 2006).

It is often desirable to complement or replace measures of the number of species with aspects of species composition, e.g. presence of rare or threatened species. Of special conservation concern is the identification of areas containing species at risk of regional or global extinction (Red List species). However, Red List cryptogam species are often considered difficult to survey because of their large numbers and that some may be rare, cryptic, little known by surveyors, or detectable only for part of the year. The use of surrogate (Indicator) species has for these reasons been advocated as practical in mapping of sites for Red List species in forests (Peterken, 1996; NBF, 1999; Nilsson et al., 2001).

In northern Europe, sets of Indicator ('Signal') species, selected by expert panels, have been and are much used in woodland surveys. Signal species among bryophytes, lichens, wood-living fungi with perennial fruiting bodies, and vascular plants are used to locate so called Woodland Key Habitats (WKHs; Gustafsson et al., 1999, 2004; Andersson et al., 2003, 2005; Bermanis and Ek, 2003). Presence of structural elements such as springs, cliffs, large trees and dead wood are other important criteria used in site selection. A WKH is a small (usually 1–5 ha) forest stand, which potentially harbours Red List species (NBF, 1999). The number of identified stands now amounts to $\approx 60,000$ – $70,000$ in Sweden alone (NBF, 1999; Gustafsson et al., 2004).

The Signal species used in Nordic WKH inventories are assumed to indicate stands with Red List species but this assumption has rarely been tested and evaluation is urgently

needed (Nilsson et al., 2001). One evaluation study suggests that WKHs in Sweden contain a higher number of Signal and Red List bryophytes than the surrounding production forest (which we do not test here) and that there is a significant correlation between these two groups within WKHs (Gustafsson et al., 2004). For boreal forests in northern Scandinavia, Gjerde et al. (2004) found that WKHs covering approximately 5% of the landscape may contain around 20–25% of the occurrences of Red List species.

In Sweden, WKHs are only weakly protected, and there is a need to prioritise the richest sites for protection as Nature reserves or in other ways. One way of setting the priority for conservation of stands is to use data on the number of Red List species. If there is a clear positive relationship between the number of Signal species and the number of Red List species, the former can act as surrogates in a quantitative respect. In the present study, we will explore if Signal species could be useful in the prioritising process among stands of high conservation value. We are also interested in how the Red List and Signal species-indices are related to another common index of conservation value – the total number of species.

We here focus on Indicator species among cryptogams in temperate oak-rich forest in south Sweden (Signal species), evaluating their relation to Red List species and total species richness in WKHs. We posed the following research questions: (1) Can Signal species be used to identify areas with Red List species? (2) Is the number of Signal species correlated to the number of Red List species among stands? (3) What is the relationship between total species richness in a stand and the number of Red List and Signal species, respectively? Since the effectiveness of surrogate species is dependent on congruence between taxa, we also analyse separately; (4) Do local hotspots overlap between bryophytes, lichens and wood-living fungi? We examined these questions using two data sets: the total number of forest cryptogams recorded, and a subset of cryptogams typical for temperate oak-rich forest, excluding coniferous forest species.

2. Methods

2.1. Study area and stands

Temperate deciduous broadleaved forest has declined drastically during the last millennium in Sweden (Lindbladh et al., 2000) and worldwide (Hannah et al., 1995), due to logging and other land-use. At present 56% of the land in southern Sweden is covered with forest but this is mainly commercial coniferous forest dominated by Norway spruce *Picea abies* (L.) Karst. and only a small fraction is temperate broadleaved forest. For the area in southern Sweden studied by us (Göta-land) these trees currently amount to 4.2% of the volume of living trees (Götmark et al., 2005). Despite the small total area of temperate broadleaved forest, the highest richness of Red List forest species in the Nordic countries is found in remnants of temperate broadleaved, often oak-rich forest (Berg et al., 1994; Gärdenfors, 2005). Evaluation of conservation criteria is urgent for this forest type.

Our study sites in southern Sweden (Fig. 1) are located in the boreonemoral zone, a transition zone between the boreal forest in northern Europe and the temperate (nemoral) forest

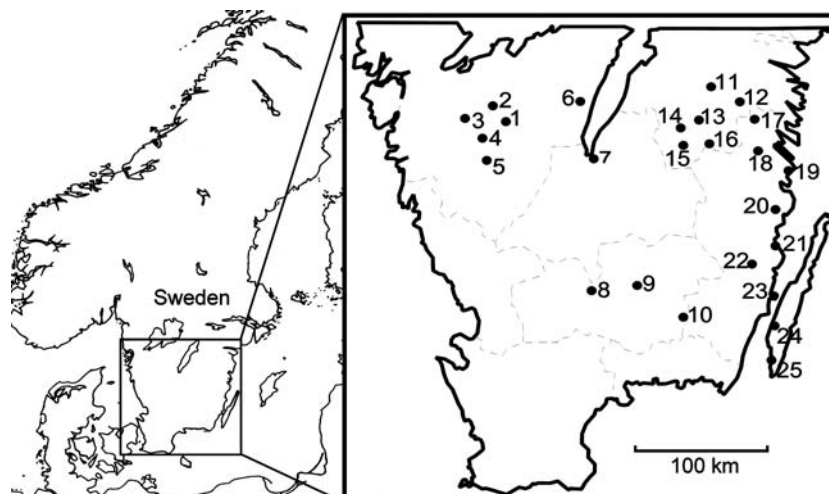


Fig. 1 – Location of the 25 study sites in South Sweden.

in the middle parts of Europe (Ahti et al., 1968; Esseen et al., 1997; Nilsson, 1997).

The sites are situated 5–230 m above sea level. The mean monthly precipitation (July) ranges from about 50 mm at the eastern coastal sites to about 90 mm at the western sites and the mean temperature in July varies from about 14 °C in the west to about 17 °C in the east (Raab and Vedin, 1995). The 25 sites/stands were identified as WKHs by the forestry boards prior to our study. Seven of them are now parts of Nature reserves; all stands are collectively referred to as WKHs below. Information about possible study sites was obtained through the Swedish forestry boards and their WKH database. Study sites were selected using many criteria: in particular, they should be ≥ 15 km apart, contain oaks (see below), be situated on mesic soils and rather level surface, have essentially closed canopies, and contain at least some dead wood. In each stand, we delimited two plots (each 1 ha), of approximately quadratic shape. The mean distance between the plots at a site was on average 50 m (range 10–250 m).

The stands are former oak woodland pastures or meadows abandoned about 50–70 years ago, characterized by remnant large oaks and many other broadleaved/coniferous trees of thinner dimensions, due to secondary succession. The forest communities were oligotrophic oak forests or mesotrophic mixed broadleaved forests following the classification by Diekmann (1994). The mean basal area of living trees (at 1.3 m) in the stands was 28.4 m² per ha ($n = 25$, data for individual sites in Nordén et al., 2004a). The most common tree species (in decreasing proportion of total basal area) are oaks (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.), Norway spruce (*Picea abies*), trembling aspen (*Populus tremula* L.), birches (*Betula pubescens* Ehrh. and *Betula pendula* Roth), ash (*Fraxinus excelsior* L.), small-leaved lime (*Tilia cordata* Mill.), hazel (*Corylus avellana* L.), maple (*Acer platanoides* L.), Scots Pine (*Pinus sylvestris* L.), beech (*Fagus sylvatica* L.), alder (*Alnus glutinosa* (L.) Gaertn.) and goat willow (*Salix caprea* L.). The proportion of oaks of the total basal area was 50% (range 13–86%). Corresponding figure for other broadleaved trees was 37% (0.0–72%) and for coniferous trees 12% (0–48%) (Nordén et al., 2004a).

The mean volume of coarse dead wood (>10 cm in diameter) was 12.0 m³ per ha ($n = 25$), and the mean volume of fine dead wood (1–10 cm) was 11.1 m³ per ha ($n = 25$); less than 10% of the deadwood came from conifers (data for sites in Nordén et al., 2004b).

2.2. Species surveys

Five surveys were conducted in each of the 25 study stands: (1) epiphytic Red List and Signal species (bryophytes and lichens); (2) ground-living bryophytes and lichens; (3) epixylic bryophytes and lichens; (4) epiphytic bryophytes and lichens on large oak trees; and (5) fungal fruit-bodies on dead wood.

We calculated the species number per study site for each species group. Sampling was designed to cover as large fraction of the diversity of each group as possible. ‘Red List species’ and ‘Signal species’ include species from all three organism groups. Organism group data (bryophytes, lichens, wood-living fungi) include Red List species, Signal species, or the sum of all species. The area sampled within plots differs among organism groups, but the surveyed area for each group was standardized as far as possible and any effects of remaining differences were tested for (see below), enabling comparison of species richness estimates among groups. We refer to the species number as species richness and the unit is ‘minimum number of species per 2 ha’.

The first inventory included Red List species (nationally listed according to the IUCN criteria; Gärdenfors, 2005) and Signal species (Swedish WKH Inventory lists by Larsson, 2002). Such species were also distinguished in the other four inventories. We surveyed Signal and Red List species of epiphytic lichens and bryophytes on tree trunks up to 1.7 m height along 10 m broad transects covering about 64% of the plot area (10 m along plot border excluded). All Red List species and the following selection of Signal species were recorded in this survey: the bryophytes *Anomodon* spp., *Antitrichia curticipendula*, *Frullania tamarisci*, *Neckera* spp., *Porella platyphylla*, and the lichens *Collema* spp., *Lobaria pulmonaria*, *Nephroma* spp., *Peltigera collina* and *Sphaerophorus globosus*. In the other surveys, all Signal species recorded were included.

Bryophytes and fruticose lichens (very few) living on the ground (but not on dead wood and living trees) were recorded in 16 subplots per study site, distributed along transects (83 or 100 m long) across plots. One subplot (1 × 5 m) was randomly selected in each 20–25 m transect section. Stones were included but we selected a new plot if it had $\geq 25\%$ stones. Species on ≥ 2 cm deep soil, decayed soft dead wood (class 5, Renvall, 1995) or on litter components (fallen bark, twigs, etc.) were defined as ground-living.

Epixylic (wood-living) lichens and bryophytes were recorded on 10 logs and 6 stumps at each study site. Species on any remaining bark on logs/stumps were included. The diameter of logs was 10–90 cm and of stumps 20–110 cm. Epiphytic lichens were investigated on 10 oaks per study site, randomly selected among the 20% largest oaks in each plot. We inventoried one 40 × 40-cm square mesh with 100 4 × 4 cm small squares, one on the south facing side, and one on the north facing side of each oak trunk, at a height of about 1.5 m. Later, we also analysed data on total circumference of different tree species at our sites, a measure proportional to the total bark area. The number of Signal/Red List species from the inventory of epiphytic Signal/Red List species was not correlated to the total bark area (all trees) or total bark area of deciduous trees (tested in two ways; for all trees, and for trees with a dbh of over 30 cm). Fruit-bodies of wood-living fungi were surveyed along the same transects as bryophytes and fruticose lichens on the ground, to a total length of 600 m per study site. We recorded all species within one meter on both sides of a measuring tape (i.e. in an area of 1200 m²) while walking slowly along each transect, recording all encountered species in sections of 20–25 m (for more information, see Nordén et al., 2004b).

Epiphytic Signal/Red List species were surveyed in March–June 2002. Ground-living bryophytes and lichens were surveyed in May–September 2002, epixyles in September–November 2000 and epiphytes of oaks in April–June 2001. Wood-living basidiomycetes were inventoried twice in autumn (September–November 2000 and September–October 2001) and ascomycetes were inventoried in April–May 2001.

2.3. Statistical analyses

Species were classified as belonging to one of two forest types, either occurring predominantly in temperate deciduous broadleaved forest, also called hardwood or nemoral forest ('noble forest' according to Swedish legislation; species often associated with *Quercus*, *Fraxinus*, *Tilia*, *Corylus*, *Acer*, *Fagus* or *Ulmus*), or occurring predominantly in coniferous, boreone-moral forest (species often associated with *Picea*, *Pinus*, *Betula*, *Populus* and *Salix*). The classifications of species are based on catalogues of ecological preferences of bryophytes and lichens (Hallingbäck, 1995, 1996), and fungi (Hallingbäck and Aronsson, 1998).

The species were for each correlation analysis classified as Red List, Signal or other species. Some species are Red-listed as well as Signal species (Table 1). We considered it as realistic and reasonable to test the sets of Signal and Red list species as they occur in nature, and not to permanently exclude all species that are classified as both Signal

and Red List species from all analyses. Individual species did in no case occur in both test variables, but were in case of membership in both tested groups, excluded from the more encompassing group in the following order: 'total' species number, Signal species and Red List species (the last category of species retained). This was considered necessary to create independent data sets. Thus, Red List species that are also used as Signal species are excluded from Signal species in the analysis (correlations Red List vs. Signal species), but Signal species that are also Red List species were not excluded from Signal species in correlations Signal vs. 'total' species.

Considering the correlation 'Red List species vs. Signal species' one may however carry out the analysis in different ways. Species belonging to both groups may be included in the Signal species group or in the Red-list species group, or excluded from both. To explore the effect of stringently avoiding the 'circularity' ensuing from inclusion of species belonging to both groups in either of the groups (see above), we choose the third option (exclude from both groups) as a complement to our initial analysis. However, this also means that much information is lost and that sample sizes are critically small (only lichens could be tested). The data presented below was obtained using the initial approach, unless otherwise stated. For the tests of overlap among local hotspots for bryophytes, lichens and wood-living fungi, the respective species group was tested against the sum of the two other organism groups. Below, the term 'total' is used without quotation marks, although 'nearly total' or 'total minus species belonging to both groups' (hotspot analysis) would strictly be more correct.

The tests for co-variation among groups were performed using Bootstrap technique, with the null hypothesis of no correlation. We applied a non-parametric Bootstrap following Efron and Tibshirani (1998, pp. 49–50), using a Bootstrap sample of 5000, each containing data from 25 sites. For each sample, a correlation coefficient was estimated without transformation of the original data.

3. Results

3.1. Deciduous forest species and coniferous forest species pooled

We found totally 179 bryophytes, 131 lichens and 404 wood-living fungi. The mean number of species recorded per site for the three groups is given in Table 2. The number of ground-living bryophytes was 99 (2 lichens). The number of bryophytes on dead wood was 67 (60 lichens) of which 40 species also occurred on the ground (1 lichen). Twenty bryophytes were epiphytic on oaks (116 lichens) and five were covered in the separate Signal/Red List species inventory (5 lichens).

All surveys pooled, the following number of species of special interest for nature conservation were found: Of the bryophytes, 20 were Signal species and one a Red List species. For lichens, 27 were Signal species and 17 were Red List species. For the wood-living fungi, six were Signal species and nine Red List species. Data about recorded Red List and Signal species are given in Table 1.

Table 1 – Red List and Signal species recorded at the 25 study sites

Species	Signal species	Red List category	Dominating forest type ^a	Number of sites	Number of records
Bryophytes					
<i>Anastrophyllum hellerianum</i>	Yes	NT	C	1	1
<i>Anomodon attenuatus</i>	Yes	–	D	1	2
<i>Anomodon longifolius</i>	Yes	–	D	2	2
<i>Anomodon viticulosus</i>	Yes	–	D	1	1
<i>Antitrichia curtipendula</i>	Yes	–	D	15	30
<i>Buxbaumia viridis</i>	Yes	–	C	3	3
<i>Eurhynchium striatum</i>	Yes	–	D	2	2
<i>Frullania tamarisci</i>	Yes	–	D	4	8
<i>Herzogiella seligeri</i>	Yes	–	D	11	20
<i>Homalia trichomanoides</i>	Yes	–	D	4	6
<i>Homalothecium sericeum</i>	Yes	–	D	6	20
<i>Lejeunea cavifolia</i>	Yes	–	D	4	7
<i>Leucobryum glaucum</i>	Yes	–	C	1	1
<i>Neckera complanata</i>	Yes	–	D	1	1
<i>Nowellia curvifolia</i>	Yes	–	D	13	45
<i>Plagiothecium undulatum</i>	Yes	–	C	1	3
<i>Porella cordaeana</i>	Yes	–	D	2	2
<i>Porella platyphylla</i>	Yes	–	D	2	2
<i>Rhytidiadelphus loreus</i>	Yes	–	D	5	14
<i>Ulota crispa</i>	Yes	–	D	4	5
Lichens					
<i>Absconditella delutula</i>	No	VU	C	1	1
<i>Acrocordia gemmata</i>	Yes	–	D	3	6
<i>Arthonia spadicea</i>	Yes	–	D	5	10
<i>Arthonia vinosa</i>	Yes	–	D	22	110
<i>Bacidia biatorina</i>	No	NT	D	4	10
<i>Bacidia rosella</i>	Yes	NT	D	1	2
<i>Bacidia rubella</i>	Yes	–	D	6	13
<i>Biatoridium monasteriense</i>	No	NT	D	1	1
<i>Buellia violaceofusca</i>	No	NT	D	3	7
<i>Calicium adspersum</i>	Yes	–	D	4	8
<i>Caloplaca lucifuga</i>	No	NT	D	1	2
<i>Chaenotheca chlorella</i>	Yes	–	D	2	2
<i>Chaenotheca hispidula</i>	No	NT	D	1	1
<i>Cladonia parasitica</i>	Yes	NT	C	5	8
<i>Cliostomum corrugatum</i>	Yes	NT	D	2	3
<i>Cyphelium inquinans</i>	Yes	–	D	4	6
<i>Gyalecta ulmi</i>	Yes	NT	D	2	2
<i>Hypogymnia farinacea</i>	Yes	–	C	1	1
<i>Lecanactis abietina</i>	Yes	–	C	6	18
<i>Lecanographa amylacea</i>	Yes	VU	D	1	1
<i>Lecidea botryosa</i>	Yes	–	C	1	1
<i>Lobarina pulmonaria</i>	Yes	NT	D	4	4
<i>Lopadium disciforme</i>	Yes	–	D	6	22
<i>Micarea adnata</i>	No	VU	D	4	4
<i>Nephroma bellum</i>	Yes	–	D	1	2
<i>Nephroma parile</i>	Yes	–	D	2	2
<i>Normandina pulchella</i>	Yes	NT	D	1	1
<i>Opegrapha vermicellifera</i>	Yes	VU	D	1	4
<i>Peltigera collina</i>	Yes	–	D	2	2
<i>Schismatomma decolorans</i>	Yes	NT	D	3	7
<i>Schismatomma pericleum</i>	Yes	NT	D	4	10
<i>Sclerophora nivea</i>	Yes	–	D	2	2
<i>Sphaerophorus globosus</i>	Yes	–	C	3	4
<i>Thelotrema lepadinum</i>	Yes	–	D	1	2
Wood-living fungi					
<i>Amylocorticium subincarnatum</i>	No	NT	C	1	1
<i>Antrodia pulvinascens</i>	Yes	NT	D	2	3
<i>Ceriporia excelsa</i>	No	NT	D	2	2
<i>Dichomitus campestris</i>	Yes	–	D	5	12

(continued on next page)

Table 1 – continued

Species	Signal species	Red List category	Dominating forest type ^a	Number of sites	Number of records
<i>Hyphodontia spathulata</i>	No	DD	C	1	1
<i>Kavinia alboviridis</i>	Yes	NT	C	1	1
<i>Metulodontia nivea</i>	No	NT	C	1	1
<i>Perenniporia medulla-panis</i>	No	NT	D	1	1
<i>Phlebia fensioeensis</i>	No	DD	C	1	1
<i>Plicatura crispa</i>	Yes	–	D	4	10
<i>Skeletocutis nivea</i>	Yes	–	D	16	63
<i>Xylobolus frustulatus</i>	Yes	NT	D	1	1

Note that some species are at the same time both Red List species and Signal species.

^a Dominating forest type refers to the ecological habitat preference of each species, either occurring predominantly in temperate deciduous forest (D) or coniferous forest (C). Nomenclature follows Gärdenfors (2005) for Red List species and Larsson (2002) for Signal species.

Table 2 – Mean and standard deviation of number of species per site (n = 25)

Number of species	Total ^a	Red List species	Signal species
Bryophytes	45.7 ± 9.7	0.0 ± 0.2	3.3 ± 2.1
Lichens	39.6 ± 7.9	1.5 ± 1.5	2.9 ± 1.6
Wood-living fungi	115.8 ± 17.4	0.9 ± 0.8	2.0 ± 1.6
All groups ^a	201.1 ± 25.6	2.4 ± 2.0	8.2 ± 3.3

At each site, the following areas were covered in the different inventories: Epigeic bryophytes 80 m²; epiphytic lichens on oaks: 3.2 m²; epixylic bryophytes and lichens (on 10 logs and 6 stumps) 24.6 ± 14.3 m² (depending of the varying sizes of dead wood objects); wood-living fungi 1200 m². The complementary inventory of Red List and Signal bryophytes and lichens covered 12,800 m². Red List species that are also used as Signal species are excluded from Signal species.

^a Figures include Signal and Red List species.

Table 3 – Correlations between species richness of Signal species, Red List species and total species richness for each organism group separately as well as pooled

Species groups	Organism group	r-value	P-value
Total vs. Signal	Bryophytes	0.252	0.185
Red-Listed vs. Signal	Lichens	0.372	0.067 ^c
Red-Listed vs. Signal	Lichens	0.209	0.284
Total vs. Red-Listed	Lichens	0.183	0.348
Total vs. Signal	Lichens	0.304	0.027 ^a
Red-Listed vs. Signal	Wood-living fungi	–0.190	0.296
Total vs. Red-Listed	Wood-living fungi	0.048	0.830
Total vs. Signal	Wood-living fungi	0.461	0.001 ^b
Red-Listed vs. Signal	All	0.130	0.626
Total vs. Red-Listed	All	–0.126	0.596
Total vs. Signal	All	0.140	0.439

The sample size is n = 25, in all tests. Red-listed bryophytes were too few to allow testing. Correlation coefficients were acquired through non-parametric bootstrapping.

^a Significant at the 0.05 level.

^b Significant at the 0.001 level.

^c Red List species that are also used as Signal species are excluded from Signal species in the analyses except for this row for which species belonging to both categories were totally excluded. Red-listed wood-living fungi were too few to allow testing when pruning the data set from overlapping species.

The number of Signal species indicated the number of Red List species for lichens with main distribution in temperate deciduous forest, and the analogous correlation was nearly significant also when all species were considered (Tables 3 and 5). These results were only obtained in the case when species belonging to both groups were totally excluded. We found significant correlations between species richness of lichens and lichen Signal species richness (Table 3), and between total species richness of wood-living fungi and fungal Signal species richness (Table 3, Fig. 2(a)). The remaining tests (correlations) were all non-significant and showed little indication of positive (or negative) relationships as judged by graphs (not shown).

Fig. 3(a) shows the relationship between total Red List and total Signal species richness. Red List species that are also used as Signal species are excluded from Signal species in the analysis. The 25 sites contained between 3 and 15 Signal species, while four sites lacked Red List species, but contained 4–12 Signal species. The total number of Red List species varied from 0 to 7 per site.

Local hotspots did not overlap between bryophytes and lichens, or between lichens and wood-living fungi, but species richness of bryophyte and wood-living fungi were significantly correlated (Table 4). Total species richness of bryophytes and of wood-living fungi, respectively, was significantly correlated to the sum of all species in the other two organism groups; this relationship was strongest for the fungi (Table 4).

3.2. Considering only deciduous forest species

The total number of recorded Red List species was reduced by 8 (29.6%) and the number of Signal species was reduced by 7 (17.9%) in this analysis compared to the one using all species pooled. For other species the corresponding figure was 163 excluded coniferous forest species, or 40.3% of all other species. Most, and the largest proportion of coniferous species at our sites thus belonged to the category of species of lower conservation importance.

For this reduced dataset, we found a strongly significant correlation between total wood-living fungi species richness and the number of Signal species of wood-living fungi (Table 5, Fig. 2(b)). The relationship between total lichen species richness in a stand and the number of Red List lichen

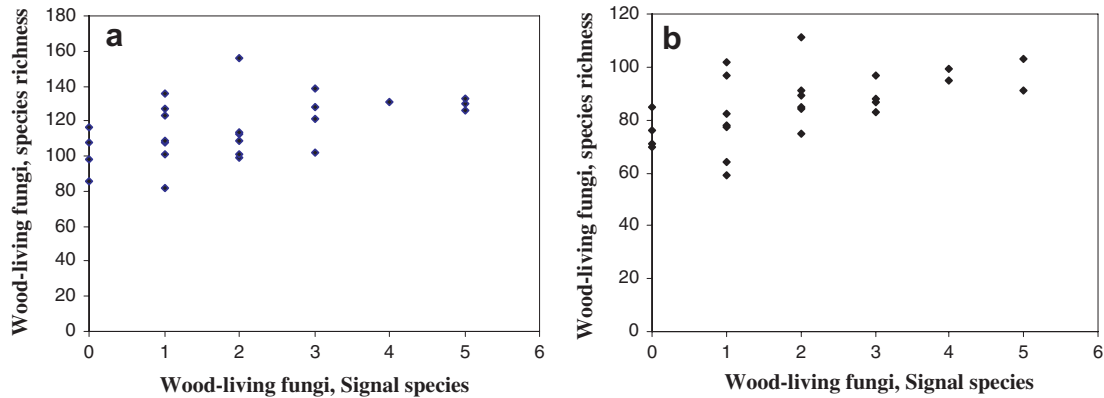


Fig. 2 – Relationship between the number of Signal species and total species richness of wood-living fungi. (a) For the whole dataset. (b) For the subset of species typical of temperate deciduous (hardwood) forest.

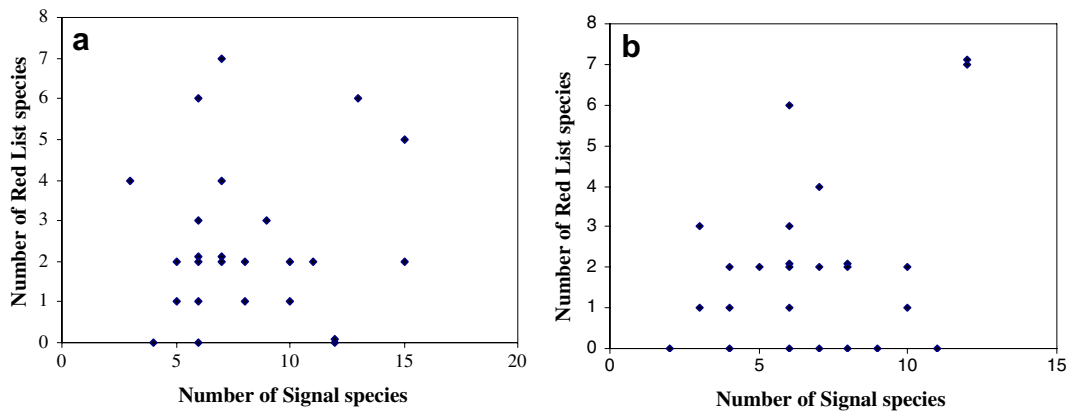


Fig. 3 – Relationship between the number of Signal species and Red List species of cryptogams in temperate deciduous forest stands in southern Sweden (n = 25). (a) For the whole dataset. (b) For the subset of species typical of temperate deciduous (hardwood) forest. Red List species that are also used as Signal species are excluded from Signal species in the analyses.

Table 4 – Correlations between total species richness of the three organism groups

Species groups	r-value	P-value
Lichens vs. bryophytes	0.000	1.00
Lichens vs. wood-living fungi	0.258	0.188
Bryophytes vs. wood-living fungi	0.371	0.021 ^a
Lichens vs. total other species	0.196	0.308
Bryophytes vs. total other species	0.309	0.046 ^a
Wood-living fungi vs. total other species	0.451	0.015 ^a

Correlation coefficients were acquired through non-parametric bootstrapping.
^a Significant at the 0.05 level.

species was significant, and the number of Signal lichen species did indicate the number of Red List lichen species (Table 5).

When considering the dataset restricted to typical deciduous temperate forest cryptogams and all three organism groups, stands with several Signal species did not invariably contain Red List species (Fig. 3(b), Table 5). Seven sites had

no Red List species but several (2–11) Signal species. The plot shape was similar to the plot in Fig. 3(a). Red List species that are also used as Signal species are excluded from Signal species in the analysis.

Local hotspots did not overlap significantly between bryophytes and lichens or between bryophytes and wood-living fungi, but richness of lichen and wood-living fungi richness was correlated (Table 6). Total species richness of either group did not indicate the sum of all species in the other groups, though the correlation was close to significance for wood-living fungi (Table 6).

4. Discussion

The Signal species set evaluated here was designed by a panel of experts nominated by the Swedish National forestry board. Expert judgements in conservation are often called upon to solve problems when time or funding for research is limited and the best available knowledge needs to be compiled quickly (Groom et al., 2005). Wamelink et al. (2005) cautioned that expert judgement regarding Indicator species contains bias and may introduce uncertainty in analyses. It is therefore reasonable that any major decisions and programs based on

Table 5 – Correlations between Signal species, Red List species and total species richness for each organism group separately as well as pooled. Only species with main distribution in temperate deciduous forest considered

Species groups	Organism group	r-value	P-value
Total vs. Signal	Bryophytes	0.222	0.241
Red-Listed vs. Signal	Lichens	0.415	0.039 ^{a,c}
Red-Listed vs. Signal	Lichens	0.266	0.161
Total vs. Red-Listed	Lichens	0.427	0.038 ^a
Total vs. Signal	Lichens	0.248	0.114
Red-Listed vs. Signal	Wood-living fungi	−0.095	0.558
Total vs. Red-Listed	Wood-living fungi	0.174	0.288
Total vs. Signal	Wood-living fungi	0.502	0.001 ^b
Red-Listed vs. Signal	All	0.304	0.293
Total vs. Red-Listed	All	0.185	0.235
Total vs. Signal	All	0.272	0.128

Red-listed bryophytes were too few to allow testing. $n = 25$, all cases. Correlation coefficients were acquired through non-parametric bootstrapping.

a Significant at the 0.05 level.

b Significant at the 0.001 level.

c Red List species that are also used as Signal species are excluded from Signal species in the analyses except for this row for which species belonging to both categories were totally excluded. Red-listed wood-living fungi were too few to allow testing when pruning the data set from overlapping species.

Table 6 – Correlations between total species richness of the three organism groups, considering only species with main distribution in temperate deciduous forest

Species groups	r-value	P-value
Lichens vs. Bryophytes	0.183	0.452
Lichens vs. wood-living fungi	0.408	0.032 ^a
Bryophytes vs. wood-living fungi	0.248	0.216
Lichens vs. total	0.405	0.069
Bryophytes vs. total	0.263	0.219
Wood-living fungi vs. total	0.427	0.052 ^a

Correlation coefficients were acquired through non-parametric bootstrapping.

a Significant at the 0.05 level.

expert judgements strategies be evaluated by research, as done here for WKH surveys that rely much on cryptogams as indicators.

The number of sites covered in this study was limited by time and funding for surveys and by the availability of taxonomic experts. On the other hand, we consider the quality of data from individual sites as good, and few thorough cryptogam inventories have been analyzed in the context of biodiversity indicators. The investigated set of sites is not representative for the whole forest landscape, but for the many small oak-rich WKHs in southern Sweden. Within the population of WKHs, the number of Red List species may vary considerably. The richest sites are often considered for protection as forest reserves. Not only species data is considered when WKHs are assigned, but also structural variables such as presence of springs, cliffs, old trees and dead wood are equally important. At our sites the total number of Red List species varied from 0 to 7 per site (four sites lacked Red List species) and the range for Signal species was from 3 to 15

per site. Thus, our sites cover a relatively broad spectrum of conservation values, in terms of species content.

The current list of Signal species seems not to be useful as surrogate in a prioritization process among this type of forests of high conservation value, a possible exception being the temperate deciduous forest lichens. Signal species may be more useful in surveys of a broader range of forest types (including both production and semi-natural stands), a correlation between Signal and Red List species richness may then be likely and could be of interest. However, conservation surveys rarely sample all types of forests, but need to select and study particular stand types that are of more immediate interest.

Signal species are selected to be common enough to occur in most, or even all, suitable habitat patches, while Red List species are declining or rare species, most of which will appear only at a fraction of all suitable habitat patches. The IUCN criteria for Red Listing (criterion A, severe population reduction; criteria B, small geographic range and subjected to reduction and fragmentation; criteria C, small population and reduction and criteria; D, very small or restricted population), apply to varying degrees to Red List cryptogams. Some Red List species, e.g. forest vascular plants, may occur mainly in remnant populations and have little dynamics in the landscape while other taxa are more easily dispersed with metapopulation dynamics. The distribution patterns of many cryptogamic species, such as those investigated here may be governed by metapopulation dynamics and dispersal at the landscape level rather than mainly by local habitat factors (Nordén and Appelqvist, 2001).

Using 22 of the same study sites, Paltto et al. (2006) investigated the relative impact of local and regional factors on local richness of Red List and Signal species (cryptogams and phanerogams pooled). The results indicate that habitat loss in the surrounding landscape and isolation are detrimental for Red List species, but not for Signal species. The latter

may be more easily dispersed and/or have wider ecological amplitudes than Red List species and therefore be less affected by habitat fragmentation. The scarcity of correlation in richness between these groups in the present study might be connected to a discrepancy between their respective responses to local and landscape factors. We hypothesize that Signal species are more of 'indicators of local habitat quality' while Red List species are more of 'indicators of landscapes rich in suitable habitat'. More work is needed to test this idea. If true, landscape indicators could complement habitat quality indicators in areas where the configuration of valuable stands and the species' landscape habitat thresholds are not known.

For temperate deciduous forest lichens, the number of Signal species did indicate the number of Red List species when pruning the data set from overlapping species (nearly significant also when deciduous forest species and coniferous forest species pooled), which is encouraging. A reason for the correlation may be that the lichens are relatively more narrow in their ecological requirements (e.g. many species, both Red List and Signal species, require old trees) than bryophytes that to a larger extent may grow also on other substrates. Further, the number of Signal species was correlated to the total number of species for lichens (deciduous forest species and coniferous forest species pooled) and for wood-living fungi (both datasets). For wood-living fungi, the correlation between the number of Signal species and the total number of species was stronger than for lichens, possibly because varying amounts of dead wood was sampled along transects (this inventory not standardized according to substrate amount). The amount and quality of dead wood varied considerably between sites (Nordén et al., 2004a).

For deciduous forest lichens, we found a significant correlation between the number of Red List species and total species richness. This agrees with Lawler et al. (2003) who found that at-risk species themselves performed well as an indicator group, covering an average of 84% of all other species. Some communities have been shown to exhibit nestedness, i.e. species in species-poor sites comprise a subset of richer ones. Thus, rare species are confined to species-rich sites (Wright et al., 1998; Jonsson and Jonsell, 1999; Berglund and Jonsson, 2004). In order for Signal species to be suitable surrogates of Red List species the former should be found relatively close to the top of a hierarchical community structure according to Gustafsson (2000). An analysis of the abundance of a subset of individual cryptogam species as potential indicators of biodiversity should be of interest. Hierarchical structure has been tested for a few cryptogam communities, but nestedness seems to be relatively weak, and indicator species for biodiversity reliable over varying situations and regions have been hard to assign (Ehrlich, 1996; Niemi et al., 1997; Sætersdal et al., 2005). A nested pattern for our data is less likely due to the influence of habitat heterogeneity and spatial scale. For example, sites vary in tree composition and soil pH. Further, our sites span a wide geographical area, which makes it less likely to detect nestedness (Sætersdal et al., 2005). The Indicator species and Red List species found are often not the same over these geographical distances, but the quantitative correlation between numbers of species may be robust.

Prendergast et al. (1993, plants and birds), Prendergast (1997, different taxa of butterflies) as well as Jonsson and Jonsell (1999, vascular plants, bryophytes, epiphytic lichens and wood-inhabiting fungi) all found poor correlations between the richness of taxa at geographical scales relevant for conservation. Therefore, it was interesting to note that hotspots overlapped between bryophytes and wood-living fungi. Bryophyte number further indicated high species richness of the other groups, although this correlation was not strong. Wood-living fungi indicated richness in the other groups best, as judged by size of correlation coefficient (though barely significant in the case of deciduous species). This is promising and suggests that dead wood or some factor related to it (e.g. forest succession, shade, moisture) favors high species richness in cryptogams. For deciduous forest species, the number of lichens was also correlated to the number of wood-living fungi.

The largest proportion of conifer-associated species at our sites was species of no special conservation interest and the total number of species in this group decreased by 40% when cryptogams chiefly associated with coniferous forest were omitted from the data set. This probably explains some of the differences in results for the data sets. Nevertheless, coniferous trees and dead wood increased the species richness of our stands; since wood-living fungi were relatively strong indicators of overall cryptogam species richness, they merit more research and should be considered in conservation surveys of mixed stands in the future. For usefulness of wood-living fungi as predictors of beetle species richness see Franc et al. (2006).

Even if there is a high correlation between species numbers of two groups, species composition between hotspots may change differently for each taxon considered because of different beta diversities, i.e. different spatial species turnover rates (Sætersdal et al., 2004). This has implications for nature conservation if not every hotspot is protected and if for selection a taxon with low beta diversity is chosen. More studies of this problem are needed for cryptogams.

There is a theoretical possibility that the correlation between bryophytes and wood-living-fungi hotspots was driven by the amount of dead wood at the sites. The fungi are sampled along transects with varying amount of dead wood, but the epixylic bryophytes on standardized amount of dead wood (which may vary in quality). Although the girth of the logs surveyed for epixylic bryophytes varies somewhat between sites (stump girth is more similar), more variation occurs in the total amount of dead wood per site (see Nordén et al., 2004). This might influence the total number of wood fungi, but the amount of coarse dead wood in the surrounding landscape seems to be a more important factor for local diversity (Björn Nordén, unpublished data). Epixylic species did not dominate the species richness of bryophytes. There was no correlation (regression analysis) between local amount of dead wood and the number of epixylic bryophytes (Tönnberg, 2001). This number also seems to be more determined by the regional amount of dead wood (Björn Nordén, unpublished data).

Although lichen Signal species performed better, the weak correlation between Red List and Signal species for valuable stands for the other organism groups may be seen as problematical. An alternative to Signal species inventories may be to focus on Red List species more directly (see also Lawler et al., 2003), which deserves further study. MacNally and Fle-

ishman (2004) stated that ‘...an experienced observer would not need to spend considerably more time and money to conduct a comprehensive inventory of the focal taxonomic group than on a search aimed at just the indicator species’. Red List or threatened species might be suitable focal groups for surveys since the number of experts on Red List species and national databases of red-listed species are growing rapidly (see e.g. regional maps in Gärdenfors, 2005). Such studies should consider that: (1) certain Red List species, which are easy to find and identify, may be added to surveying protocols, and (2) since Red List species are more commonly encountered in landscapes with a high amount of suitable habitat, surveys may be concentrated there, possibly increasing the efficiency of conservation work.

5. Conclusions and implications

For cryptogams, Signal species as evaluated here did not unequivocally predict richness of Red List species among oak-rich forest stands. Therefore, if all WKHs cannot be protected in the future, separate inventories of Red List species or other better evaluation tools should probably be considered to prioritize forests among WKHs for the aim of protection of these more or less threatened species.

The Signal species approach may also be useful for other purposes. By redefining Signal species as indicating ‘environments with high natural values’, as did Nitare (2000, p. 8), or as habitat specialists indicating rare forest types, they could complement the more rare Red List species.

Red List species are a minor component of the fauna and flora (e.g. 6% of all Swedish species). Our results suggest that Signal species of lichens and especially wood-living fungi are useful indicators of species richness within these groups. Moreover, wood-living fungi seem to indicate cryptogam hotspots well in oak-rich and mixed forests; to some extent, lichens and bryophytes also may be useful in this respect, but more studies are needed. One problem that needs to be addressed is the paucity of mycologists and identification guides for wood-living fungi. Additional studies similar to ours and of subsets of cryptogam species as indicators (in different forest types) would be valuable.

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