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# At which spatial and temporal scales does landscape context affect local density of Red Data Book and Indicator species?

*Heidi Paltto*[a,*], *Björn Nordén*[a], *Frank Götmark*[b], *Niklas Franc*[b]

[a]*Department of Plant and Environmental Sciences, Göteborg University, Box 461, 405 30 Göteborg, Sweden*
[b]*Department of Animal Ecology, Göteborg University, Box 463, 405 30 Göteborg, Sweden*

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ABSTRACT

The landscape context is crucial for forest conservation in regions where the natural forest is fragmented. The focus of practical conservation is currently shifting from local stands to a landscape perspective, but few studies have tested the relative effect of different spatial and temporal scales for occurrence and persistence of species of conservation concern. We studied Red Data Book and Indicator species (the latter proposed to indicate presence of Red Data Book species) of vascular plants, lichens, bryophytes and wood-inhabiting fungi in 22 old temperate broadleaved forests in southern Sweden. We analysed at which scales these species respond to habitat proportion in surrounding landscape. The proportion of suitable habitat was measured at two temporal scales (present-day and historic) and at two spatial scales (about 0–1 km and 1–5 km of study sites). Local density of Red Data Book species increased with increasing proportion of suitable habitat in the current landscape (within 1–5 km of study sites) while Indicator species were unaffected. The response to landscape differed between organism groups. Vascular plants (near significantly) and wood-inhabiting fungi showed a time delay of 120 years in their response, indicating a possible regional extinction debt. An appropriate minimum landscape scale for conservation of Red Data Book species in temperate broadleaved forests in Sweden seems to be about 5 km (radius), but smaller landscapes may be important for vascular plants and wood-inhabiting fungi of conservation concern. In addition, restoration is urgent to counteract the effect of time delays in species responses to recent habitat loss.



## 1. Introduction

The landscape perspective is crucial for forest conservation in regions where the forest is fragmented (Lindenmayer and Franklin, 2002). The field of landscape ecology and other fields addressing temporal and spatial scales have progressed rapidly (Caldow and Racey, 2000; Nobis and Wohlgemuth, 2004), and the focus of conservation is currently shifting from local stands as main units of conservation to a broader landscape perspective (Groom et al., 1995; Swedish EPA and NBF, 2005). Multiscaled biodiversity planning, matrix management (Lindenmayer and Franklin, 2002; Lindenmayer et al., 2006) and conservation priority of landscapes with dense occurrence of natural habitats (Andersson, 2002; and Swedish EPA and NBF, 2005) are recommended in forest conservation

* *Corresponding author:* Tel.: +46 31 773 48 04 (Institute); +46 500 49 13 13 (Home); +46 733 79 80 10 (Mobile).
E-mail addresses: heidi.paltto@botany.gu.se (H. Paltto), bjorn.norden@botany.gu.se (B. Nordén), frank.gotmark@zool.gu.se (F. Götmark), niklas.franc@zool.gu.se (N. Franc).
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planning, but in most cases the recommendations about minimum landscape size are vague or lacking. The reason for this may be a lack of studies testing the relative effect of different spatial and temporal scales for occurrence and persistence of species of conservation concern, especially for vascular plants and cryptogams despite common use of these groups in conservation planning (NBF, 1999; Andersson et al., 2003). Red Data Book species are usually rare and therefore difficult to study, yet important in conservation research.

Processes that operate at broader spatial scales likely influence the occurrence and persistence of organisms at local scales (With, 2004; Hanski, 2005). According to metapopulation and landscape ecological theory, habitat loss and fragmentation should reduce species density of habitat specialists due to (1) an area-related decrease in population sizes and (2) decreased colonization rates after isolation of remaining habitats (Saunders et al., 1991; Eriksson and Ehrlén, 2001; Hanski and Gaggiotti, 2004; With, 2004; Hanski, 2005; Vellend et al., 2006). Long-lived species, however, with low colonization and extinction rates may show considerable time delay in their response to changing configuration of the landscape (Debinski and Holt, 2000; Lindborg and Eriksson, 2004; Helm et al., 2006; but see also Hanski and Ovaskainen, 2002; With, 2004). The time delay is called extinction debt when habitat conditions for survival are no longer met, but the species is still present (Tilman et al., 1994; Hanski and Ovaskainen, 2002). The theories are largely based on models and many empirical studies report effects of habitat loss and fragmentation (e.g., Ferraz et al., 2003; Helm et al., 2006; Vellend et al., 2006). However, few of the empirical studies analyzed the relative effect of different temporal and spatial scales for local species densities, especially for vascular plants (but see Lindborg and Eriksson, 2004) and cryptogams.

Lists of Indicator species are often used to locate 'hotspots' of forest biodiversity (Lindenmayer et al., 2000). Woodland Key Habitat (WKH) inventories in several countries in northern Europe (NBF, 1999; Andersson et al., 2003) aim at identifying forest stands of high conservation value. By definition, a WKH is a forest where Red Data Book species occur or probably occur (Nitare and Norén, 1992). Since Red Data Book species are rare and difficult to find, a list of Indicator species was established by the Swedish National Board of Forest (Norén et al., 1995) to be used together with aspects of forest structure as Indicators of valuable forests. The Indicator species concept is widely used in national WKH inventories, but few studies have thoroughly evaluated the Indicator species ability to predict local density of Red Data Book species (but see Gustafsson et al., 2004) or their dependence of the surrounding landscape.

We studied habitat specialists of Red Data Book and Indicator species among vascular plants, lichens, bryophytes and wood-inhabiting fungi in 22 semi-natural broadleaved forests (WKHs) in southern Sweden. We analysed at which scales these species respond to habitat proportion in the surrounding landscape. The proportion of suitable habitat in the surrounding landscape was measured at two temporal scales (120 years BP, and current landscape) and two spatial scales (within radii of about 1 km and 5 km from the study plots).

## 2. Materials and methods

### 2.1. Study area

Southern Sweden (Fig. 1) is located in the boreonemoral zone; a transition zone between the boreal forest in northern Europe and the temperate (nemoral) forest in the central parts of Europe (Ahti et al., 1968; Esseen et al., 1997). Temperate broadleaved forest predominated in southern Sweden 9000–1000 years ago (Gustafsson and Ahlén, 1996; Lindbladh et al., 2000), but only 6% of the current forests consist of temperate broadleaved trees (Ekberg, 2003). These trees are defined in Sweden as 'noble' broadleaved trees and the forest type is called 'noble broadleaved forest' to exclude broadleaved trees that also occur in the boreal zone ('trivial' broadleaved forest). In Swedish legislation, 13 broadleaved trees are defined as 'noble' ('ädellöv' in Swedish). The seven most common in decreasing abundance are pedunculate oak *Quercus robur* L., sessile oak *Quercus petraea* (Matt.) Liebl., beech *Fagus sylvatica* L., common ash *Fraxinus excelsior* L., wych elm *Ulmus*

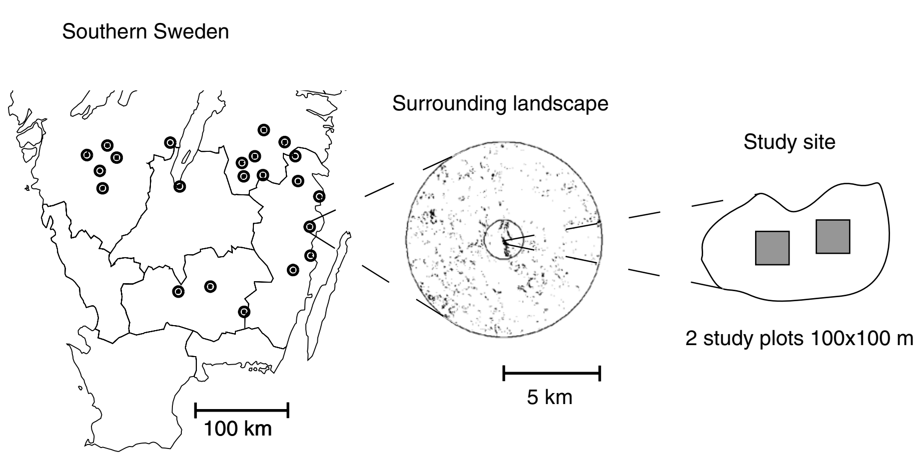


**Fig. 1 – Study design: map of the study area, study sites (*n* = 22) and the surrounding landscape with broadleaved forest patches marked in black.**

*glabra* Huds., small-leaved lime *Tilia cordata* Mill. and Norway maple *Acer platanoides* L.

The 22 study sites are former oak wood pastures or meadows abandoned about 25–75 years ago, characterized by remnant large oaks and other broadleaved/coniferous trees of smaller dimensions, due to secondary succession. The proportion of pedunculate/sessile oak was 50% (range 13–86%) of the basal area at breast height. Corresponding figures for other noble broadleaved trees was 16% (0–62%), coniferous trees 12% (0–48%) and trivial broadleaved trees and shrubs 23% (4–56%). The forest communities were oligotrophic oak forests or mesotrophic mixed broadleaved forests (Diekmann, 1994).

The study sites (Fig. 1) lie 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 study sites are nature reserves ($n = 5$) or woodland key habitats (WKHs, $n = 17$), called WKHs below for simplicity as the habitat structure and conservation quality of both study site types in our study were equally high. Information about sites was obtained through conservation authorities and forest owners. The study sites are situated mainly on mesic moraine soils, on rather level surfaces, with almost closed canopies. In each stand, we delimited two plots (each 1 ha), usually $100 \times 100$ m or $83 \times 120$ m. The mean distance between the plots at a site was 50 m (range 10–250 m).

### 2.2. *Species measures*

Six surveys were conducted at the 22 study sites: (1) epiphytic Red Data Book and Indicator species (bryophytes and lichens), (2) ground-living bryophytes and lichens; (3) epixylic bryophytes and lichens and (4) epiphytic bryophytes and lichens on the largest oak trees; (5) wood-inhabiting fungi and (6) ground-living herbaceous vascular plants. The first inventory included only Red Data Book species (nationally listed according to criteria developed by the World Conservation Union, IUCN; Gärdenfors, 2000) and Indicator species (Swedish WKH Inventory lists; Norén et al., 2002), and data on such species was also used from the other five inventories. Species listed as both Indicator and Red Data Book species were only included as Red Data Book species.

To focus on species characteristic of noble broadleaved forests and their dependence on deciduous forests in the surrounding landscape, we omitted 19 species associated with coniferous substrates, species associated with both coniferous and deciduous substrates and ground-living species that are as common in coniferous forests as in deciduous forests. We calculated the species number per study site for each species group. 'Red Data Book species' and 'Indicator species' include species from all four organism groups. Organism group data (vascular plants, lichens, bryophytes, wood-inhabiting fungi) include both Red Data Book and Indicator species. The area sampled differs among organism groups within sites, but since surveys at sites were standardized to a certain area or a certain number of substrates, the sites are comparable with respect to species diversity of a particular organism group. We refer to the species number as species density and the unit is "minimum number of species per 2 ha".

To analyze habitats for the species groups, we used the substratum (ground, stone, living and/or dead trees), as reported by Hallingbäck (1995, 1996) and Hallingbäck and Aronsson (1998). The total number of each substratum type was summed for each tested species group (Red Data Book, Indicator and the four organism groups) and the proportion of each substratum type of the sum was calculated.

We surveyed Indicator and Red Data Book species of epiphytic lichens and bryophytes on tree trunks up to 1.7 m in height along 10 m wide transects covering about 64% of the plot area (10 m along plot border excluded). All Red Data Book species and a selection of Indicator species were recorded: the bryophytes *Anomodon* spp., *Antitrichia curtipendula* (Hedw.) Brid., *Frullania tamarisci* (L.) Dum., *Neckera* spp., *Porella* spp., and the lichens *Collema* spp., *Lobaria* spp., *Nephroma* spp., *Peltigera* spp. and *Sphaerophorus globosus* (Huds.) Vain.

Vascular plants were surveyed along transects with a total length of 400 m per study site (8 transect sections of 25 m each in the plots of size $100 \times 100$ m; 10 transect sections of 20 m each in the plots of size $83 \times 120$ m; transects placed about 20 m apart). We recorded all species within one meter from a measuring tape, on one side (summer flora) or two sides (spring flora). We walked slowly along each transect, recording all encountered species in sections of 20–25 m.

Wood-living fungi were surveyed along transects with a total length of 600 m per study site; the transects partially overlapped with the vascular plant transects. We recorded all species within two sides from a measuring tape walking slowly along each transect, recording all encountered species.

Bryophytes and fruticose lichens living on ground and stone (but not on dead wood and living trees) were recorded in 16 subplots per study site. One subplot ($1 \times 5$ m) was randomly placed in each 20–25 m transect section. We selected a new plot if it had $\geqslant 25\%$ stones. Species on $\geqslant 2$ cm deep soil, soft dead wood (class 5; Renwall, 1995) or on at least two litter components (fallen bark, twigs etc) were defined as ground-living.

Epixylic lichens and bryophytes were recorded on 10 logs and 6 stumps at each study site. Species on remaining bark on logs/stumps were included. The diameter of logs was 10–90 cm and of stumps 10–110 cm.

Epiphytic lichens were investigated on 10 oaks per study site, randomly selected among the 20% largest oaks in each plot. We inventoried one $40 \times 40$ cm$^2$ on the south facing and one on the north facing side of each oak stem, at a height of about 1.5 m.

Indicator/Red Data Book species were surveyed in March–June 2002. Vascular plants were surveyed 14 May-4 June (spring flora) and 16 July–4 August (summer flora), either 2001 (8 sites) or 2002 (17 sites). Wood-inhabiting fungi were inventoried twice in September–November 2000 and September–October 2001, ground-living bryophytes and lichens in March–September 2002, epixyles in September–November 2000 and epiphytes in February–June 2001.

### 2.3. Environmental measures

Current forest data at a landscape level was obtained from a project at the Swedish University of Agricultural Sciences in Umeå working with mapping and estimating of different forest variables in Sweden with a method termed "kNN" (Reese et al., 2003). The kNN-data are based on satellite maps from 1999 calibrated against field data from the National Forest Inventory 1990–1999 (Fridman, 2000). The pixel resolution is 25 m × 25 m. We calculated the proportional area of forest (of total circle area) within circles of different radii around the study sites (0–0.5 km, 0.5–1 km, 1–5 km and 1–8 km). This study design refers to a 'focal patch landscape study' design according to Brennan et al. (2002). Four classes of broadleaved trees are used in kNN: Oaks, beech, birches and other broadleaved trees. All four classes were used to estimate the area of "all broadleaved forest" and three of the four classes (birch excluded) to estimate the area of "noble broadleaved forest". We excluded forest <30 years old to avoid young successional forests on felled conifer forests (aspen and birch the most common species). Forest pixels with ⩾30%-volume of broadleaved and ⩾30% noble broadleaved trees, respectively, were included in the calculations. The area of "mature noble broadleaved forests of at least WKH-quality" (called WKHs below) was obtained from the Regional Forestry Boards (WKHs) and County Administration Boards (nature reserves). We excluded mature trivial broadleaved and conifer forests from the WKH/nature reserve-data, but also mixed broadleaved-conifer forests were excluded as we could not easily separate stands with noble broadleaved trees from those without such trees. To classify WKHs and reserves similarly, descriptions and maps of the reserves were evaluated. We calculated the proportional area of WKHs within circles of radii 0–1 km, 1–5 km and 1–10 km. We used the GIS-program ArcView 3.2 and Spatial Analyst 2.0a to calculate areas.

The proportion of historic broadleaved forest was estimated from the cadastral map "Generalstabskartan" (Ottoson and Sandberg, 2001), which covers Sweden at a scale of 1:100 000. The maps used were from 1863 to 1894 (average 1877). Since "Generalstabskartan" was produced earlier than this period for four study sites, we used "Häradskartan" (scale 1:20,000 or 1:50,000) for these calculations.

We measured forest stand area for each site using infrared aerial photographs (scale 1:30,000) from 1982 to 1997 and a stereoscope. Continuous forest (including parkland, woodland and gardens) with ⩾30% noble broadleaved trees was included. We defined "continuous" as all forest patches less than 90 m apart.

The mean monthly precipitation (July) was obtained from Raab and Vedin (1995). Soil-pH ($H_20$) was based on eight pooled samples of topsoil (0–5 cm depth, litter removed, each sample 150 $cm^3$), taken in April 2002 in each plot. A mean value was calculated for the two plots per site. We measured light conditions (canopy closure) from 16 photographs taken in July–August 2001 with a digital camera (28 mm) from ground level towards the sky, and calculated mean proportion of sky visible for each site. The colour pixels were converted to binary black-and-white pixels, and the white pixels were counted with the program NIH Image 1.62 (National Institute of Health, USA).

We calculated the proportion of noble broadleaved trees (of total tree basal area) based on a tree inventory (April–September 2001 and 2002) in about half of the plot area, for all trees ⩾5 cm in diameter at breast height. The density of large noble broadleaved trees with a diameter ⩾50 cm was calculated (trees/ha). Coarse dead wood (logs, snags, stumps ⩾10 cm in diameter) was surveyed along four 100 × 10-m transects (4000 $m^2$) and fine dead wood (1–10 cm in diameter) in 32 2 m × 2.5 $m^2$ (160 $m^2$) per study site, see Nordén et al. (2004) for details. The total volume ($m^3$) of dead wood per hectare was estimated for each study site.

### 2.4. Data analyses

We used Spearman's rank correlation to explore relationships between species density of the four organism groups (tests pairwise), and between environmental variables to be selected for the multiple regression analyses. We chose the biologically most relevant explanatory variable within pairs of strongly correlated variables ($R^2 > 0.50$, which corresponds to Spearman $r_s > 0.707$). A total of 13 out of 21 potential variables remained for further analyses.

Landscape and local variables were related to the six measures of species density using multiple log linear regression models (Genmod; SAS 8.02, SAS Institute, 1999–2001). The local variables were included to contrast and control for variation caused by abiotic and biotic local factors; an approach that is rare but powerful in landscape analyses of species strongly dependent on local factors. The explanatory variables were divided into four groups to facilitate interpretation of results: current landscape (5 variables), historic landscape (2 variables), stand-associated abiotic factors (3 variables) and stand-associated biotic factors (3 variables). The variable "dead wood" was omitted from the analyses of vascular plants. Due to the fact that the response variables were species counts, we used logarithmic link function and Poisson distribution of errors (McCullagh and Nelder, 1989). We interpreted a species group as sensitive to habitat loss in the landscape if the association between species density and any landscape measure was positive. If a species group showed a positive association with historic but not current landscape data, we concluded that its response to habitat change is delayed.

The model residuals were tested for autocorrelation by calculating Moran's I and correlograms for 9 equidistant distance classes among the pairs of study sites. We used the program AUTOCOR in R package version 4.0d9 (Casgrain and Legendre, 2001). The correlograms did not show any spatial pattern (see Legendre and Legendre, 1998) and only two out of 54 $p$-values (6 models × 9 distance classes) were below 0.05 (in distance classes 7 and 8), which is less than expected by chance. Since no autocorrelation was found in the residuals, we did not include the spatial covariance structure in our models (see Diniz-Filho et al., 2003). Residuals were plotted from predicted values of response variable to evaluate the regression fit. Estimate values (regression coefficients) were back-transformed from the original model: $E_t = \text{Exp}(E_m)$, where $E_t$ is the back-transformed estimate value and $E_m$ is the original model estimate value. The back-transformed value expresses the proportional change of species density per unit change in a predictor variable.

## 3. Results

### 3.1. Species

Indicator species were found at all study sites while Red Data Book species were found at 18 of 22 sites (82%; Table 1). We found in total 18 Red Data Book and 53 Indicator species (10 species belong to both categories) characteristic for noble broadleaved forest: 17 vascular plants, 20 lichens, 12 bryophytes and 12 wood-inhabiting fungi (Appendix). The most common species in the study were the epiphytic lichen *Arthonia vinosa*, the vascular plant *Anemone hepatica*, the wood-living fungi *Skeletocutis nivea* and *Plicatura crispa* and the bryophytes *Antitrichia curtipendula* and *Herzogiella seligeri* (Appendix). The Red Data Book species consisted of one vascular plant (6% of all vascular plants in this study), eight lichens (38% of the lichens), one bryophyte (9% of the bryophytes) and eight wood-inhabiting fungi (67% of the fungi); 17 species were from the Red Data Book category near threatened and one endangered (Gärdenfors, 2000). Species densities of the organism groups were not significantly correlated to each other (bryophytes-lichens $r_s = 0.41$; $n = 22$; $p = 0.060$; vascular plants-wood-inhabiting fungi $r_s = 0.37$; $n = 22$; $p = 0.094$, other correlations $p > 0.200$). Neither the density of Red Data Book species was correlated with the density of Indicator species ($r_s = 0.197$; $n = 22$; $p = 0.380$).

The Red Data Book species found in our study mainly occur on temporary substrates such as living and dead trees, while the Indicator species live on all types of both temporary and stable substrates (Fig. 2a). Vascular plants of conservation concern live on ground, bryophytes mainly on living trees and stone, lichens mainly on living trees and wood-inhabiting fungi mainly on dead wood (Fig. 2b).

### 3.2. Environmental variables

The proportions of broadleaved forest, noble broadleaved forest and noble broadleaved WKHs of the total area were higher in the inner circles near the study sites in comparison with the outer circles (Table 2). The proportion of noble broadleaved forest of total broadleaved forest decreased from 80% (0–0.5 km from study sites) to 56% (1–8 km) and the noble broadleaved WKHs of total noble broadleaved forest decreased from 28% (0–1 km) to 7% (1–8 km), indicating that the aggregations of broadleaved forests close to study sites are of higher conservation quality than the surrounding forests of this type.

At a scale of 0–5 km, the average cover of historic broadleaved forest (criteria ⩾30% broadleaved trees) was 15.2%; the corresponding current cover was 11.2%, indicating an average decrease by 26% of the broadleaved forest in 120 years (the historic data with criteria ⩾30% were not included in Table 2 and analyses, since data could not be obtained for different radii). The proportion of broadleaved forest decreased at 16 sites and increased at 6 sites during the 120 year period.

### 3.3. Impact of landscape and local factors on Red Data Book and Indicator species

Local Red Data Book species density was best explained by a current landscape measure: the proportion of noble broadleaved forest within 1–5 km from the study sites (multiple loglinear regression model, Table 3). In contrast, Indicator species density was not positively related to any landscape measure. Both Red Data Book and Indicator species were affected by abiotic factors. The Indicator species increased with increasing precipitation (and near significantly with increasing soil-pH), and Red Data Book species increased with increasing soil-pH.

### 3.4. Impact of landscape and local factors on different organism groups of conservation concern

Current landscape measures were important predictors of lichens and bryophytes of conservation concern, while the density of vascular plants (nearly significantly; $p = 0.054$) and wood-inhabiting fungi were predicted by historic landscape measures (multiple loglinear regression model, Table 3). The most important spatial scale was 0–1 km for wood-inhabiting fungi and vascular plants and 1–5 or 1–10 km for bryophytes and lichens. The proportion of WKH forests in the surrounding landscape was more important for lichens (see estimate-values in Table 3) than the proportion of total broadleaved forest for any other organism groups. Contrary to expectation, the species density of lichens was negatively affected by stand area and historic landscape.

Abiotic stand-level factors were important for all four groups of organisms. The species density of wood-inhabiting

**Table 1 – Red Data Book and Indicator species: density (minimum species number per 2 ha) in noble broadleaved forest ($n = 22$)**

| | Red Data Book species | | Indicator species[a] | | Sum | |
|---|---|---|---|---|---|---|
| | Mean ± STD | Range (min–max) | Mean ± STD | Range (min–max) | Mean ± STD | Range (min–max) |
| Vascular plants | 0.0 ± 0.2 | 0–1 | 2.9 ± 2.0 | 0–7 | 2.9 ± 2.1 | 0–8 |
| Lichens | 0.8 ± 0.9 | 0–3 | 2.5 ± 1.6 | 0–6 | 3.3 ± 2.2 | 0–8 |
| Bryophytes | 0.0 ± 0.2 | 0–1 | 2.2 ± 1.5 | 0–6 | 2.3 ± 1.5 | 0–6 |
| Wood-inhabiting fungi | 0.9 ± 1.1 | 0–4 | 1.4 ± 1.2 | 0–4 | 2.3 ± 1.5 | 0–5 |
| Sum | 1.7 ± 1.6 | 0–6 | 9.0 ± 3.5 | 3–15 | 11.9 ± 5.3 | 4–26 |

a Species on both Red Data Book and Indicator species lists were excluded.

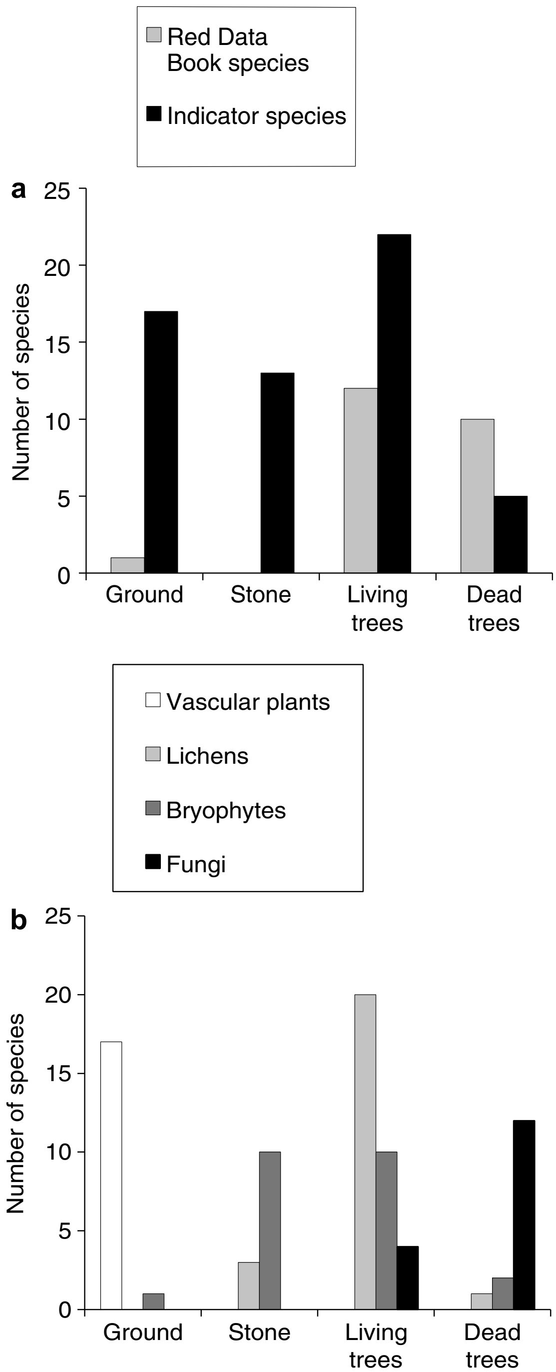


**Fig. 2 – Substratum for the studied species: proportion of all substratum preferences within each group of (a) Red Data Book and Indicator species and (b) organism groups. Sixty-one species were registered 80 times (single species can live on several substratum types). Data on ecological preferences compiled from Hallingbäck (1995, 1996) and Hallingbäck and Aronsson (1998).**

fungi and vascular plants increased with increasing soil-pH, and the species density of lichens and bryophytes increased with increasing precipitation.

## 4. Discussion

### 4.1. *Impact of landscape context on Red Data Book versus Indicator species*

The diversity of Red Data Book species was positively related to the proportion of suitable habitat in the surrounding landscape at the large scale (1–5 km of study sites), while no such relationship was observed for Indicator species. This indicates that Red Data Book species mostly do not survive in, or cannot colonize, small and/or isolated noble broadleaved forests. As the area of broadleaved forest around our study sites has decreased (by 20–30% during the past 120 years), our results suggest that the local occurrences of Red Data Book species suffer from habitat loss in the surrounding landscape. The studied species are generally not well studied and the red-listing is mainly based on qualified guesses about their geographical ranges and ecology in combination with knowledge/guesses about the status of their habitat rather than measurements of their dependence of habitat in the landscape.

Two possible explanations for the different responses for Red Data Book and Indicator species are that Red Data Book species have (1) a narrower habitat preference and therefore more uniform response and/or (2) inferior dispersal capacity compared to Indicator species. The species in both groups are specialists of noble broadleaved forests, but the studied Red Data Book species seem to have narrower habitat ranges: they have a higher proportion of lichens and wood-inhabiting fungi, which more often occur on temporary substrates (living and dead trees). The Indicator species use both temporary (trees) and permanent substrates (ground, stone) and if the permanent substrates are available to some extent outside the broadleaved forests, the Indicator species' response to broadleaved forest in the landscape could be weaker. The strong association of lichens to high quality forests (WKHs) indicates narrower habitat preference than in the other organism groups that showed weak associations to the proportion of total broadleaved forest. The exclusion of mixed forest WKHs from the figures of 'proportion noble broadleaved WKHs in the landscape' may have contributed to the different effects of landscape for the Indicator and Red Data Book species, if Indicator species are to higher extent generalists compared to the Red Data Book species.

Our results may not support the second explanation – inferior dispersal capacity for Red Data Book species – since the Red Data Book species found in our study consisted mainly of lichens and wood-inhabiting fungi (89%) with several species probably less limited by dispersal than many ancient forest vascular plants (Nordén and Appelqvist, 2001). This may be because the group of Indicator species is more heterogeneous than Red Data Book species with respect to dispersal capacity; all four organism groups are represented, especially ancient forest vascular plants that are considered to be slow dispersers (Hermy et al., 1999; Kolb and Diekmann, 2005). This heterogeneity may be a reason for the lack of clear association between Indicator species density and habitat proportion in the landscape. This is also supported by the analyses of different organism

**Table 2 – Environmental variables: potentially important environmental variables to explain density of Red Data Book/Indicator species in noble broadleaved forests (n = 22)**

| Environmental variable | Mean | SD | Min | Max |
|---|---|---|---|---|
| *Current landscape (1999)* | | | | |
| Broadleaved forest[a] 0–0.5 km (% of total area)[b] | 30.4 | 12.3 | 10.7 | 54.9 |
| Broadleaved forest[a] 0.5–1 km (% of total area)[b] | 15.6 | 5.6 | 4.4 | 26.5 |
| Broadleaved forest[a] 1–5 km (% of total area)[b] | 10.9 | 3.9 | 5.1 | 20.7 |
| Broadleaved forest[a] 1–8 km (% of total area)[b] | 10.3 | 3.4 | 3.8 | 18.2 |
| Noble broadl. Forest[c] 0–0.5 km (% of total area) | 24.3 | 11.1 | 7.2 | 52.5 |
| Noble broadl. Forest[c] 0.5–1 km (% of total area)[b] | 10.1 | 5.3 | 2.1 | 22.3 |
| Noble broadl. Forest[c] 1–5 km (% of total area) | 6.3 | 3.2 | 2.5 | 15.1 |
| Noble broadl. Forest[c] 1–8 km (% of total area)[b] | 5.8 | 2.8 | 1.7 | 12.9 |
| Noble broadleaved WKHs 0–1 km (% of total area) | 3.66 | 5.68 | 0.00 | 26.0 |
| Noble broadleaved WKHs 1–5 km (% of total area)[b] | 0.46 | 0.48 | 0.02 | 1.59 |
| Noble broadleaved WKHs 1–10 km (% of total area) | 0.40 | 0.35 | 0.06 | 1.61 |
| Stand area (ha) | 29.4 | 30.5 | 6.2 | 130 |
| *Historic landscape (1863–1894)* | | | | |
| Hist. broadleaved forest[d] 0–1 km (% of total area) | 20.6 | 11.0 | 3.2 | 50.3 |
| Hist. broadleaved forest[d] 1–5 km (% of total area) | 11.5 | 6.0 | 3.0 | 23.9 |
| Hist. broadleaved forest[d]1–8 km (% of total area)[b] | 11.0 | 5.4 | 1.5 | 25.4 |
| *Stand-associated abiotic factors* | | | | |
| Soil-pH | 5.4 | 0.4 | 4.4 | 6.1 |
| Light (% visible sky from ground level) | 14.5 | 3.4 | 8.8 | 22.9 |
| Precipitation (mm/July, mean 1961–1990) | 64.5 | 8.0 | 50 | 90 |
| *Stand-associated biotic factors* | | | | |
| Noble broadleaved tree proportion (% of basal area) | 64 | 17 | 27 | 93 |
| Large noble broadleaved trees ⩾50 cm breast height (no./ha) | 23.8 | 9.0 | 9.1 | 43.3 |
| Dead wood ($m^3$/ha)[e] | 25.8 | 9.0 | 13.2 | 46.7 |

a ⩾30%-Volume of broadleaved trees.
b Excluded from regression analyses due to strong correlation to at least one other variable.
c ⩾30%-Volume of noble broadleaved trees.
d ⩾70% Cover of broadleaved forest.
e Excluded from models with vascular plants.

groups (see next chapter) that obviously differ in their spatiotemporal response to landscape factors.

The relationship between Red Data Book species and amount of suitable habitat in the landscape may also be reinforced by a positive relationship between habitat amount and its average quality within each measured habitat type. A general problem in studies of local versus landscape factors is that the latter are difficult to measure in detail, due to large area. This study included, however, two quality classes of forests (all noble broadleaved forests and noble broadleaved WKHs) in the analyses, to cover some of the variation in habitat quality.

### 4.2. *Impact of landscape context on different organism groups of conservation concern*

The adjustment of species distributions to changing landscapes includes dispersal to new patches and extinction from old (often isolated) patches. A specialist species with slow dispersal and delayed local extinction should show a delayed response to changed habitat configuration. Shortly after habitat loss, delayed local extinctions should result in over-saturation of the species and after an increase of habitat in landscape, slow dispersal should result in under-saturation until a new equilibrium is reached (but this increase requires that the species still are extant in nearby landscapes). Contrasting results for different organism groups may reflect differences in adjustment rate of their distributions. Bryophytes and lichens of conservation concern (significant effect of current landscape, 1–5 and 1–10 km) seem to have faster adjustment rates than forest vascular plants (nearly significant effect of historic landscape 120 years BP, 0–1 km). The results are reasonable since most cryptogams are considered to be more easily dispersed than the ancient forest vascular plants (Nordén and Appelqvist, 2001). Many ancient forest vascular plants are long-lived but inferior at dispersal (Kolb and Diekmann, 2005) and can survive for long periods as remnant populations (Eriksson, 1996), while bryophytes and lichens living on temporary substrates regularly go extinct when trees die or logs decay. Few empirical studies have explored the effect of landscape on vascular plants, lichens and bryophytes of conservation concern in forest habitats. The occurrence of an epiphytic Red Data Book moss *Neckera pennata* was dependent on habitat connectivity in a fragmented forest landscape (Snäll et al., 2004), and its response was stronger to the old than the current landscape (the old landscape data were about 20 years older than the current data). Similarly, the epiphytic Red Data Book lichen *Lobaria pulmonaria* was more abundant in landscapes with high habitat connectivity (Snäll et al.,

**Table 3 – The predictive ability of environmental variables to explain species density: Results from multiple log linear regression models**

| Species group<br>Environmental variable | Env. variable category | Estimate[a] | Lower conf. limit[a] | Upper conf. limit[a] | $\chi^2$ | $p$[b] |
|---|---|---|---|---|---|---|
| *Red Data Book species* | $R^2 = 0.70$ | | | | | |
| Noble broadleaved 1–5 km (%) | Current landsc. | 1.42 | 1.08 | 1.87 | 6.40 | 0.011 |
| Soil-pH | Stand – abiotic | 6.45 | 1.48 | 28.1 | 6.16 | 0.013 |
| Noble broadl. WKHs 0–1 km (%) | Current landsc. | 1.10 | 1.00 | 1.22 | 3.60 | 0.058 |
| Hist broadleaved 1–5 km (%) | Hist. landsc. | 0.89 | 0.78 | 1.01 | 3.26 | 0.071 |
| Noble broadleaved 0–0.5 km (%) | Current landsc. | 0.89 | 0.78 | 1.02 | 2.86 | 0.091 |
| *Indicator species* | $R^2 = 0.88$ | | | | | |
| Precipitation (mm/July) | Stand – abiotic | 1.05 | 1.02 | 1.09 | 8.88 | 0.003 |
| Stand area (ha) | Current landsc. | 0.98 | 0.97 | 1.00 | 5.92 | 0.015 |
| Soil-pH | Stand – abiotic | 1.71 | 0.98 | 2.96 | 3.59 | 0.058 |
| *Vascular plants*[c] | $R^2 = 0.40$ | | | | | |
| Soil-pH | Stand – abiotic | 3.85 | 1.38 | 10.7 | 6.62 | 0.010 |
| Hist broadleaved 0–1 km (%) | Hist. landsc. | 1.03 | 1.00 | 1.07 | 3.71 | 0.054 |
| Noble broadl. WKHs 0–1 km (%) | Current landsc. | 1.06 | 0.99 | 1.13 | 2.38 | 0.123 |
| *Lichens*[c] | $R^2 = 0.75$ | | | | | |
| Precipitation | Stand – abiotic | 1.10 | 1.03 | 1.17 | 8.79 | 0.003 |
| Stand area (ha) | Current landsc. | 0.97 | 0.94 | 0.99 | 8.75 | 0.003 |
| Noble broadl. WKHs 1–10 km (%) | Current landsc. | 7.20 | 1.47 | 35.2 | 5.95 | 0.015 |
| Hist broadleaved 0–1 km (%) | Hist. landsc. | 0.96 | 0.92 | 0.99 | 4.97 | 0.026 |
| Hist broadleaved 1–5 km (%) | Hist. landsc. | 0.94 | 0.87 | 1.01 | 2.88 | 0.090 |
| *Bryophytes*[c] | $R^2 = 0.65$ | | | | | |
| Noble broadleaved 1–5 km (%) | Current landsc. | 1.31 | 1.02 | 1.69 | 4.58 | 0.032 |
| Precipitation | Stand – abiotic | 1.07 | 1.01 | 1.14 | 4.57 | 0.033 |
| Large noble trees (no./ha) | Stand – biotic | 0.93 | 0.87 | 1.00 | 3.81 | 0.051 |
| Noble trees (% of basal area) | Stand – biotic | 1.03 | 0.99 | 1.08 | 2.83 | 0.093 |
| Stand area (ha) | Current landsc. | 0.96 | 0.91 | 1.01 | 2.25 | 0.134 |
| *Wood-inhabiting fungi*[c] | $R^2 = 0.78$ | | | | | |
| Hist broadleaved 0–1 km (%) | Hist. landsc. | 1.06 | 1.01 | 1.11 | 5.52 | 0.019 |
| Soil-pH | Stand – abiotic | 4.38 | 1.24 | 15.5 | 5.23 | 0.022 |
| Light | Stand – abiotic | 0.83 | 0.68 | 1.02 | 3.20 | 0.074 |
| Large noble trees (no./ha) | Stand – biotic | 0.94 | 0.88 | 1.01 | 2.47 | 0.116 |
| Noble broadl. WKHs 0–1 km (%) | Current landsc. | 1.10 | 0.97 | 1.24 | 2.19 | 0.139 |
| Noble broadl. WKHs 1–10 km (%) | Current landsc. | 0.21 | 0.02 | 1.78 | 2.06 | 0.152 |

a Back-transformed from model values. The back-transformed value gives a measure of proportional change per unit in the environmental variable, i.e., estimate 2.0 means a predicted doubling of species density per unit increase in the environmental variable. Estimate values below 1.0 predict a decrease in species density with an increase in the environmental variable.
b Variables with $p$-values above 0.200 not shown.
c Includes both Indicator and Red Data Book species.

2005). The lichens and bryophytes in the present study might show short time delays (about 20 years) in response to habitat change as was found for *Neckera pennata* (Snäll et al., 2004). Since the habitat proportion in the studied landscapes has decreased during the last 120 years, the current species density of vascular plants of conservation concern may be higher than can be maintained in the long term, and future species losses may be expected at a regional level even if the present landscape configuration is maintained, i.e., there may be a regional extinction debt.

The local density of wood-inhabiting fungi was explained by the historic (120 BP) but not current amount of suitable forest in the landscape, and this effect was even stronger than for vascular plants (Table 3). Similar results were obtained for single Red Data Book species of wood-inhabiting fungi in boreal forests in Norway (Sverdrup-Thygeson and Lindenmayer, 2003; one species tested) and Finland (Gu et al., 2002; three out of four species). Due to the fact that wood-inhabiting fungi are probably more easily dispersed than lichens and bryophytes (Nordén and Appelqvist, 2001), the time-delay in response to habitat change may seem contradictory. We suggest that the response to historic landscape depends on a delay in dead wood production compared to changes in the amount of forest at a landscape level. When broadleaved forest stands are invaded by shade-tolerant Norway spruce *Picea abies* (L.) H. Karst., the stands are no longer defined as broadleaved, but there are still large amounts of dead wood of broadleaved trees until the dead wood is completely decayed. There may also be a temporary peak in dead wood production due to death of light-demanding broadleaved trees (such as oak) following shading. Alternatively, there may be a lack of dead wood in newly established broadleaved forests. The first possibility seems more important since the average proportion of broadleaved forest in the landscape decreased during the last 120 years. Due to the fact that the production of living trees precedes the production of dead wood in forest successions, it is more likely that wood-inhabiting fungi show a longer time delay to the change of proportion habitat in landscape (as measured here: deciduous forest calculated from maps) than do epiphytic lichens and bryophytes. If the suggestion of prolonged production of dead wood in stands overgrowing to coniferous stands is true, local extinctions should be likely to occur in the future (when this dead wood is completely decayed). In addition, this phenomenon may also be linked to a possible extinction debt for wood-inhabiting fungi at a regional level.

In our analyses a species groups' response to historic landscape (120 years BP) was linked to the response at a small scale (0–1 km), while the response to current landscape was linked to the large scale (1–5 or 1–10 km). This pattern may be related to dispersal, since dispersal capacity depends on time.

The *negative* effect of stand area on two species groups ("Indicator species" and "lichens of conservation concern") was contrary to expectation. Stand area was delineated from infra-red photographs to get comparable measures for all the study sites. These measures are, however, correlated to the stand area as measured in the WKH inventory and the areas from nature reserve descriptions. The negative impact of stand area may be a consequence of the selection criteria of WKHs and nature reserves in southern Sweden: Small patches may be considered valuable only if these are of very high conservation value, while large areas are recognized at least partly because they are large. Subsequently, the average conservation value per unit area should be higher in small WKHs/reserves (Götmark and Thorell, 2003). However, in the present study two of three local biotic qualities (proportion of noble broadleaved trees and density of large noble broadleaved trees) are positively, but weakly, correlated to stand area and the third (dead wood volume) is unaffected. Even if it seems that WKHs/nature reserves of different sizes in our study do not show bias in their forest structure, there may be a systematic (but probably small) error in the WKH/nature reserve-data used in the landscape measures (small forests with high quality forest structure but few indicator species underrepresented). This may have weakened an eventual relationship between the local species densities and the proportion of WKHs in the landscape.

### 4.3. *Impact of stand-associated abiotic and biotic factors*

Abiotic factors were important to explain the local densities of all tested species groups. The results indicate that Red Data Book species are favoured by high soil-pH and Indicator species by high precipitation. Among the four organism groups, bryophytes and lichens are favoured by high precipitation and vascular plants and wood-inhabiting fungi by high soil-pH. Wood-inhabiting fungi were more strongly affected by soil-pH than vascular plants. Other studies have shown a dependence on pH for vascular plants (Gustafsson, 1994; Pärtel et al., 2004) and for macrofungi sensu lato (Rydin et al., 1997) but not specifically for wood-inhabiting fungi. Red Data Book species were more strongly affected by soil-pH than both vascular plants and wood-inhabiting fungi. Areas with high soil-pH are scarce and unevenly distributed in southern Sweden. The vegetation differs considerably from the surrounding more acid soils and many of the Red Data Book and Indicator species are characteristic of these vegetation types (Rydin et al., 1999). Similarly, sub-oceanic climate with high precipitation is confined to south-western Sweden (Degelius, 1935; Ahti et al., 1968), and many rare sub-oceanic species are found in the Red Data Book and on the Indicator species list.

Stand-level biotic factors such as tree size and dead wood are probably important for many Indicator and Red Data Book species (Berg et al., 2002; Gustafsson, 2002). The lack of impact of these factors may reflect our focus on forests of relatively high conservation value, with many large trees and dead trees. There was, however, also considerable variation in these variables among our sites, indicating that landscape and abiotic factors may be more important than biotic factors when explaining density of species of conservation concern in these forests.

## 5. Implications for nature conservation

The local density of Red Data Book species seems to be better predicted by the proportion of suitable habitat in the landscape than by local density of Indicator species or local biotic factors. Therefore, we suggest that conservation planning should be carried out at the landscape rather than local level. Local data are important but should be used in a landscape context. Data from Woodland Key Habitat inventories (or other equivalent inventories) and nature reserves databases could be used together with other forest data to search for priority landscapes with (1) high proportion of noble broadleaved WKHs and/or (2) high proportion of total noble broadleaved forests. For northern Europe higher priority should be given to landscapes with high precipitation and forests on base-rich soils. Potential priority landscapes for Red Data Book species should include both core areas and the surrounding landscape of about 5 km radius, but considerably smaller landscapes (1 km) may be important for vascular plants and wood-inhabiting fungi of conservation concern. In addition, there is a need for habitat restoration, since the responses of wood-inhabiting fungi and vascular plants to habitat loss were delayed, indicating a current extinction debt. Restoration and increased biodiversity consideration in forestry is probably most effective if carried out within such suggested priority landscapes.

The density of Indicator species was not related to the density of Red Data Book species, and they were not explained by the landscape factors. Different organism groups seem to respond to the landscape at different spatio-temporal scales and therefore no general pattern appears when the Indicator species from several organism groups are pooled. The Indicator species belonging to different organism groups probably indicate different things. Nordén, Paltto, Götmark and Wallin (manuscript in review: Species indicators of biodiversity, what do they indicate? – Lessons for conservation of cryptogams in oak-rich forest) found that the indicator species group of lichens indicated Red Data Book species of lichens. Additional studies in such relationships are needed.

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## Appendix. Red Data Book and Indicator species included in the study of 22 noble broadleaved forests in southern Sweden

| Species[a] | Indicator species | Red Data Book category[b] | Frequency (number of sites) |
|---|---|---|---|
| Vascular plants | | | |
| *Actaea spicata* L. | X | | 5 |
| *Anemone hepatica* L. | X | | 17 |
| *Bromopsis benekenii* (Lange) Holub | X | NT | 1 |
| *Cardamine bulbifera* (L.) Crantz | X | | 7 |
| *Crepis paludosa* (L.) Moench | X | | 3 |
| *Elymus caninus* (L.) L. | X | | 1 |
| *Gagea spathacea* (Hayne) Salisb. | X | | 1 |
| *Galium odoratum* (L.) Scop. | X | | 2 |
| *Hedera helix* L. | X | | 1 |
| *Lathraea squamaria* L. | X | | 6 |
| *Lathyrus niger* (L.) Bernh. | X | | 3 |
| *Lathyrus vernus* (L.) Bernh. | X | | 6 |
| *Listera ovata* (L.) R. Br. | X | | 2 |
| *Polygonatum multiflorum* (L.) All. | X | | 3 |
| *Polygonatum verticillatum* (L.) All. | X | | 1 |
| *Sanicula europaea* L. | X | | 1 |
| *Viola mirabilis* L. | X | | 4 |
| Lichens | | | |
| *Acrocordia gemmata* (Ach.) A. Massal. | X | | 2 |
| *Arthonia spadicea* Leight. | X | | 2 |
| *Arthonia vinosa* Leight. | X | | 20 |
| *Bacidia biatorina* (Körb.) Vain. | | NT | 4 |
| *Bacidia rubella* (Hoffm.) A. Massal. | X | | 5 |
| *Buellia violaceofusca* G. Thor & Muhr | | NT | 2 |
| *Calicium adspersum* Pers. | X | | 3 |
| *Cliostomum corrugatum* (Ach.: Fr.) Fr. | X | NT | 2 |
| *Gyalecta ulmi* (Sw.) Zahlbr. | X | NT | 1 |
| *Lobaria pulmonaria* (L.) Hoffm. | X | | 3 |
| *Lopadium disciforme* (Flot.) Kullh.(1870) | X | | 6 |
| *Micarea adnata* Coppins | | EN | 2 |
| *Nephroma parile* (Ach.) Ach. | X | | 2 |
| *Nephroma sp.* | X | | 1 |
| *Normandina pulchella* (Borrer) Byl. | X | NT | 1 |
| *Peltigera collina* (Ach.) Schrad. | X | | 2 |
| *Schismatomma decolorans* (Turner & Borrer ex Sm.) Clauzade and Vĕzda in Vĕzda | X | NT | 1 |
| *Schismatomma pericleum (Ach.)* Branth & Rostr. | X | NT | 4 |

(*continued on next page*)

## Appendix – *continued*

| Species[a] | Indicator species | Red Data Book category[b] | Frequency (number of sites) |
|---|---|---|---|
| *Sclerophora pallida* (Pers.) Y.J. Jao & Spooner | X | | 2 |
| *Sphaerophorus globosus* (Huds.) Vain | X | | 3 |
| *Thelotrema lepadinum* (Ach.) Ach. | X | | 1 |
| Bryophytes | | | |
| *Anomodon longifolius* (Brid.) Hartm. | X | | 1 |
| *Antitrichia curtipendula* (Hedw.) Brid. | X | | 14 |
| *Frullania tamarisci* (L.) Dum. | X | | 4 |
| *Herzogiella seligeri* (Brid.) Iwats | X | | 10 |
| *Homalia trichomanoides* (Hedw.) Schimp. | X | | 3 |
| *Homalothecium sericeum* (Hedw.) Schimp. | X | | 4 |
| *Lejeunea cavifolia* (Ehrh.) Lindb. | X | | 4 |
| *Neckera sp.* | X | | 1 |
| *Plagiothecium latebricola* Schimp. | | NT | 1 |
| *Porella cordaeana* (Hüb.) Moore | X | | 2 |
| *Porella platyphylla* (L.) Pfeiff. | X | | 1 |
| *Porella sp.* | X | | 1 |
| *Ulota crispa* (Hedw.) Brid. | X | | 4 |
| Wood-inhabiting fungi | | | |
| *Antrodia pulvinascens* (Pilát) Niemelä | X | NT | 3 |
| *Ceriporia purpurea* (Fr.) Donk | | NT | 6 |
| *Clavicorona pyxidata* (Pers.: Fr.) Doty | X | NT | 2 |
| *Dichomitus campestris* (Quél.) Domański & Orlicz | X | | 6 |
| *Fistulina hepatica* (Schaeff.: Fr.) Fr. | X | NT | 1 |
| *Lentinellus vulpinus* (Sowerby) Kühner & Maire | | NT | 2 |
| *Oxyporus corticola* (Fr.) Ryvarden | X | | 1 |
| *Perenniporia medulla-panis* (Jacq.: Fr.) Donk | | NT | 2 |
| *Plicatura crispa* (Pers.: Fr.) Rea | X | | 10 |
| *Pluteus umbrosus* (Pers.: Fr.) Kumm | | NT | 1 |
| *Skeletocutis nivea* (Jungh.) Keller | X | | 14 |
| *Xylobolus frustulatus* (Pers.: Fr.) Boidin | X | NT | 2 |

a The vascular plant *Paris quadrifolia* was omitted because of its low indicator value in south Sweden.
b EN, endangered; NT, near threatened.

## REFERENCES


Ahti, T., Hämet-Ahti, L., Jalas, J., 1968. Vegetation zones and their sections in northwestern Europe. Annales Botanici Fennici 5, 169–211.

Andersson, L., 2002. Mapping nature protection values – a habitat-wise presentation of regional variation in rare and vulnerable species richness. Svensk Botanisk Tidskrift 96, 313–322 (in Swedish; English summary).

Andersson, L., Martverk, R., Külvik, M., Palo, A., Varblane, A., 2003. Woodland key habitat inventory in Estonia 1999–2002. Regio Publishing, Tartu, Estonia.

Berg, Å., Gärdenfors, U., Hallingbäck, T., Norén, M., 2002. Habitat preferences of red-listed fungi and bryophytes in woodland key habitats in southern Sweden – analyses of data from a national survey. Biodiversity and Conservation 11, 1479–1503.

Brennan, J.M., Bender, D.J., Contreras, T.A., Fahrig, L., 2002. Focal patch landscape studies for wildlife management: optimizing sampling effort across scales. In: Jianguo, L. (Ed.), Integrating Landscape Ecology into Natural Resource Management. Cambridge University Press, Port Chester, NY, USA, pp. 68–91.

Caldow, R.W.G., Racey, P.A., 2000. Large-scale processes in ecology and hydrology. Journal of Applied Ecology 37, 6–12.

Casgrain, P., Legendre, P., 2001. The R Package for Multivariate and Spatial Analysis, version 4.0 d9 – User's Manual. Département de sciences biologiques, Université de Montréal. Available from: <http://www.fast.umontreal.ca/BIOL/legendre/>.

Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. Conservation Biology 14, 342–355.

Degelius, G., 1935. Das ozeanische element de strauch- und laubflechtenflora von Skandinavien. Acta Phytogeographica Suecica. Svenska växtgeografiska sällskapet, Uppsala, Sweden.

Diekmann, M., 1994. Deciduous Forest Vegetation in Boreo-nemoral Scandinavia. Opulus press, Uppsala, Sweden.

Diniz-Filho, J.A.F., Bini, L.M., Hawkins, B.A., 2003. Spatial autocorrelation and red herrings in geographical ecology. Global Ecology and Biogeography 12, 53–64.

Ekberg, K. (Ed.), 2003. Statistical Yearbook of Forestry 2003. National Board of Forestry. Jonkoping, Sweden.

Eriksson, O., 1996. Regional dynamics of plants: a review of evidence for remnant, source-sink and metapopulations. Oikos 77, 248–258.

Eriksson, O., Ehrlén, J., 2001. Landscape fragmentation and the viability of plant populations. In: Silvertown, J., Antonovics, J.

(Eds.), Integrating Ecology and Evolution in a Spatial Context. Blackwell Science, Oxford, UK, pp. 157–175.
Esseen, P.-A., Ehnström, B., Ericson, L., Sjöberg, K., 1997. Boreal forests. Ecological Bulletins 46, 16–47.
Ferraz, G., Russell, G.J., Stouffer, P.C., Bierregaard, R.O.J., Pimm, S.L., Lovejoy, T.E., 2003. Rates of species loss from Amazonian forest fragments. Proceedings of the National Academy of Sciences USA 100, 14069–14073.
Fridman, J., 2000. Conservation of forest in Sweden: a strategic ecological analysis. Biological Conservation 96, 95–103.
Gärdenfors, U. (Ed.), 2000. The Red List of Swedish Species. ArtDatabanken, SLU, Uppsala, Sweden.
Götmark, F., Thorell, M., 2003. Size of nature reserves: densities of large trees and dead wood indicate high value of small conservation forests in Southern Sweden. Biodiversity and Conservation 12, 1271–1285.
Groom, M.J., Meffe, G.K., Carroll, C.R. (Eds.), 1995. Principles of Conservation Biology, third ed. Sinauer Associates, Sunderland, Massachusetts, USA.
Gu, W., Heikkilä, R., Hanski, I., 2002. Estimating the consequencess of habitat fragmentation on extinction risk in dynamic landscapes. Landscape Ecology 17, 699–710.
Gustafsson, L., 1994. A comparison of biological characteristics and distribution between Swedish threatened and non-threatened forest vascular plants. Ecography 17, 39–49.
Gustafsson, L., 2002. Presence and abundance of red-listed plant species in Swedish forests. Conservation Biology 16, 377–388.
Gustafsson, L., Ahlén, I. (Eds.), 1996. Geography of Plants and Animals. National atlas of Sweden. Almqvist and Wiksell International, Stockholm, Sweden.
Gustafsson, L., Hylander, K., Jacobson, C., 2004. Uncommon bryophytes in Swedish forests – key habitats and production forests compared. Forest Ecology and Management 194, 11–22.
Hallingbäck, T., 1995. The Lichens of Sweden and Their Ecology. ArtDatabanken, SLU, Uppsala, Sweden (in Swedish; English summary).
Hallingbäck, T., 1996. The Bryophytes of Sweden and Their Ecology. ArtDatabanken, SLU, Uppsala, Sweden (in Swedish; English summary).
Hallingbäck, T., Aronsson, G. (Eds.), 1998. Macrofungi and Myxomycetes of Sweden and Their Ecology. ArtDatabanken, SLU, Uppsala, Sweden (in Swedish; English summary).
Hanski, I., 2005. The Shrinking World: Ecological Consequences of Habitat Loss. International Ecology Institute, Oldendorf/Luhe, Germany.
Hanski, I., Gaggiotti, O.E., 2004. Metapopulation biology: past, present, and future. In: Hanski, I., Gaggiotti, O.E. (Eds.), Ecology Genetics and Evolution of Metapopulations. Elsevier Academic Press, London, UK, pp. 3–22.
Hanski, I., Ovaskainen, O., 2002. Extinction debt at extinction threshold. Conservation Biology 16, 666–673.
Helm, A., Hanski, I., Pärtel, M., 2006. Slow response of plant species richness to habitat loss and fragmentation. Ecology Letters 9, 72–77.
Hermy, M., Honnay, O., Firbank, L., Grashof-Bokdam, C., Lawesson, J.E., 1999. An ecological comparison between ancient and other forest plant species of Europe, and implications for forest conservation. Biological Conservation 91, 9–22.
Kolb, A., Diekmann, M., 2005. Effects of life-history traits on responses of plant species to forest fragmentation. Conservation Biology 19, 929–938.
Legendre, P., Legendre, L., 1998. Numerical Ecology, second ed. Elsevier Amsterdam, Netherlands.
Lindborg, R., Eriksson, O., 2004. Historical landscape connectivity affects present plant species diversity. Ecology 85, 1840–1845.
Lindbladh, M., Bradshaw, R., Holmqvist, B.H., 2000. Pattern and process in south Swedish forests during the last 3000 years, sensed at stand and regional scales. Journal of Ecology 88, 113–128.
Lindenmayer, D., Franklin, J.F., 2002. Conserving Forest Biodiversity – A Comprehensive Multiscaled Approach. Island press, Washington, DC, USA.
Lindenmayer, D.B., Margules, Chris, R., Botkin, D.B., 2000. Indicators of biodiversity for ecologically sustainable forest management. Conservation Biology 14, 941–950.
Lindenmayer, D.B., Franklin, J.F., Fischer, J., 2006. General management principles and a checklist of strategies to guide forest biodiversity conservation. Biological Conservation 131, 433–445.
McCullagh, P., Nelder, J.A., 1989. Generalized Linear Models. University Press, Cambridge, UK.
NBF, 1999. Nyckelbiotopsinventeringen 1993–1998. Slutrapport (The Woodland Key Habitat Inventory 1993–1998, Final Report). Meddelande 1 – 1999. National Board of Forestry, Jönköping, Sweden.
Nitare, J., Norén, M., 1992. Woodland key-habitats of rare and endangered species will be mapped in a new project of the Swedish National Board of Forestry. Svensk Botanisk Tidskrift 86, 219–226 (in Swedish; English summary).
Nobis, M., Wohlgemuth, T., 2004. Trend words in ecological core journals over the last 25 years (1978–2002). Oikos 106, 411–421.
Nordén, B., Appelqvist, T., 2001. Conceptual problems of ecological continuity and its bioindicators. Biodiversity and Conservation 10, 779–791.
Nordén, B., Götmark, F., Tönnberg, M., Ryberg, M., 2004. Dead wood in semi-natural temperate broadleaved woodland: Contribution of coarse and fine dead wood, attached dead wood and stumps. Forest Ecology and Management 194, 235–248.
Norén, M., Hultgren, B., Nitare, J., Bergengren, I., 1995. Instruktion för Datainsamling vid Inventering av Nyckelbiotoper (Directions for data collection in Key Habitat Inventories). National Board of Forestry, Jonkoping, Sweden.
Norén, M., Nitare, J., Larsson, A., Hultgren, B., Bergengren, I., 2002. Handbok för inventering av nyckelbiotoper (Directions for Key Habitat Inventories). Skogsstyrelsen, Jonkoping, Sweden.
Ottoson, L., Sandberg, A., 2001. Generalstabskartan 1805–1979. Kartografiska Sällskapet, Stockholm, Sweden.
Pärtel, M., Helm, A., Ingerpuu, N., Reier, Ü., Tuvi, E.-L., 2004. Conservation of Northern European plant diversity: the correspondence with soil pH. Biological Conservation 120, 525–531.
Raab, B., Vedin, H. (Eds.), 1995. Climate, Lakes and Rivers. National Atlas of Sweden. Almqvist and Wiksell International, Stockholm, Sweden.
Reese, H., Nilsson, M., Granqvist-Pahlén, T., 2003. Countrywide estimates of forest variables using satellite data and field data from the National Forest Inventory. Ambio 32, 542–548.
Renwall, P., 1995. Community structure and dynamics of wood-rotting basidiomycetes on decomposing conifer trunks in Northern Finland. Karstenia 35, 1–51.
Rydin, H., Diekmann, M., Hallingbäck, T., 1997. Biological characteristics, habitat associations, and distribution of macrofungi in Sweden. Conservation Biology 11, 628–640.
Rydin, H., Snoeijs, P., Diekmann, M. (Eds.), 1999. Swedish Plant Geography, vol. 84. Svenska Växtgeografiska Sällskapet, Uppsala, Sweden.
Saunders, D.A., Hobbs, R.J., Margules, C.R., 1991. Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5, 18–32.
Snäll, T., Hagström, A., Rudolphi, J., Rydin, H., 2004. Distribution pattern of the epiphyte *Neckera pennata* on three spatial scales - importance of past landscape structure, connectivity and local conditions. Ecography 27, 757–766.

Snäll, T., Pennanen, J., Kivistö, L., Hanski, I., 2005. Modelling epiphyte metapopulation dynamics in a dynamic forest landscape. Oikos 109, 209–222.

Sverdrup-Thygeson, A., Lindenmayer, D.B., 2003. Ecological continuity and assumed indicator fungi in boreal forest: The importance of the landscape matrix. Forest Ecology and Management 174, 353–363.

Swedish EPA, NBF, 2005. National Strategy for the Formal Protection of Forest. Swedish Environmental Protection Agency, Stockholm, and National Board of Forestry, Jönköping, Sweden (in Swedish; English summary).

Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. Nature 371, 65–66.

Vellend, M., Verheyen, K., Jacquemyn, H., Kolb, A., van Calster, H., Peterken, G., Hermy, M., 2006. Extinction debt of forest plants persists for more than a century following habitat fragmentation. Ecology 87, 542–548.

With, K.A., 2004. Metapopulation dynamics: perspectives from landscape ecology. In: Hanski, I., Gaggiotti, O.E. (Eds.), Ecology, Genetics and Evolution of Metapopulations. Elsevier Academic Press, London, UK, pp. 23–44.