

Vascular plants as a surrogate species group in complementary site selection for bryophytes, macrolichens, spiders, carabids, staphylinids, snails, and wood living polypore fungi in a northern forest

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Abstract

Vascular plants were investigated as a potential surrogate group in complementary small scale site selection, such as woodland key habitats in Scandinavia. We compared the response of vascular plants to environmental gradients to that of seven other plant, fungal and animal groups within a forest reserve in western Norway using data from 59 plots of 0.25 ha. We also examined whether the spatial changes in species (beta-2 index) of vascular plants matched that of the other groups. All seven groups responded to the same gradients in nutrient richness and humidity as the vascular plants. Furthermore, changes in species composition of vascular plants were reflected in comparable degrees of change among the “target” groups. The lower the degree of change in species composition between plots in the “target” groups relative to that of vascular plants, the higher the percentage “target” species encompassed in a complementary selection of sites based on vascular plants. We conclude that in practical site selection of small scale sites of conservation value, such as woodland key habitats, vascular plants may be used in combination with an inventory of important habitats for rare and/or redlisted forest species, such as dead wood, old trees, deciduous trees, and cliffs.

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1. Introduction

In recent years small scale site selection, as a part of a management strategy, has been applied in Fennoscandian forests. Woodland key habitats (sensu Gustafsson, 2002) are being mapped and subject to public and private protection programs in Sweden (National Board of Forestry, 1998; Gustafsson, 2002), Finland (Tenhola and Yrjönen, 2000), and Norway (Levende Skog, 1998). Woodland key habitats are small forest stands or habitat patches that can be expected to host red-listed species, excluding species with strong landscape scale

requirements for survival (Hansson, 2001). In Sweden, the number of forest patches mapped and identified as woodland key habitats is ca. 40 000, and the median area of these forest patches is 1.4 ha (Johansson and Gustafsson, 2001; Gustafsson, 2002). However, the expected number of woodland key habitats to be selected in Sweden is ca. 70 000 (National Board of Forestry, 1998). As stated by Gustafsson (2002) the methodology for selection of woodland key habitats seems to be biased toward sites with red-listed plants (vascular plants and cryptogams). If important sites for species groups other than plants (e.g. invertebrates) are primarily found in other places than plants the present methodology of site selection will clearly miss important sites for these groups. For example, whereas most red-listed bryophytes

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prefer shady or moist sites, most (59%) red-listed saproxylic invertebrates in Sweden are found to prefer sun-exposed sites (Jonsell et al., 1998). Recently, it has been argued that the best strategy to maintain overall species richness when selecting woodland key habitats is to select sets of forest patches based on the concept of complementarity (e.g. Similä et al., 2002). Such a selection will ensure that the full variation in species composition along important environmental gradients is included in the set of sites. The present study aims at investigating the use of vascular plants as a surrogate species group in complementary site selection at a small scale for this purpose.

How to select surrogate taxonomic groups in site selection is not straightforward (Margules and Pressey, 2000; Cabeza and Moilanen, 2001). Obviously, vascular plants cannot adequately represent diversity for large mobile animals but they are potentially a well suited surrogate taxon for groups such as invertebrates, fungi, lichens and bryophytes. They have, in fact, been widely used for this purpose because they are taxonomically well described, they are easily identified in the field, and many biologists know them. However, two basic requirements are of vital importance for any surrogate group. First, it should respond to the same underlying main gradient as the species groups it is supposed to indicate. Secondly, the assemblage of species should be at least as sensitive to conditions as the groups it is supposed to represent (Oliver et al., 1998; Pharo et al., 1999; Williams et al., 2000). If the surrogate group consists of species with wide ecological amplitude, it may not adequately reflect changes in the non target groups. These two criteria are investigated in this study of vascular plants as a surrogate species group for a broad range of organisms within a mixed forest in western Norway.

Using a dataset from 59 plots (0.25 ha each) within a nature forest reserve in western Norway the aim of this study is to answer the following questions:

1. Do vascular plants respond to the same underlying main ecological gradient as spiders, carabids, staphylinids, snails, wood living polypore fungi and epiphytic, epixylic and epilithic bryophytes and macrolichens?
2. Is species richness (alpha-diversity) in vascular plants correlated with species richness in the other seven species groups?
3. Are complementary sets of sites based on vascular plants able to capture species diversity of the other seven species groups?
4. Does spatial turnover of species composition (beta-diversity) in vascular plants adequately reflect changes in species composition in these seven taxa in complementary site selection?

2. Methods

2.1. Study area

The study area is situated within Geitaknottane Nature Reserve, which is located in Hordaland county, western Norway (Ihlen et al., 2001). The study area covers a forested area of ca. 140 ha. and the altitude ranges from 100 to 300 m.a.s.l. The area is heterogeneous, containing primarily Scots pine (*Pinus sylvestris*) forest, but broad-leaved deciduous forest is found on southeast-facing slopes. The area belongs to the borenemoral region. The climate is oceanic, with a mean annual precipitation of ca. 2600 mm (Førland, 1993), and a mean annual temperature of 7.2 °C (Aune, 1993).

2.2. Species surveys

All field work was carried out in 1997 and 1998. The study area was divided into 1-ha grid cells superimposed on the area, and a 50×50 m (0.25 ha) sample plot was located in the southeastern corner of each 1 ha plot. Fifty-nine plots were selected to cover the major variation within the area. Hence a stratified representative sampling was performed, reflecting the distribution of the major forest types within the area. Care was taken to include plots representing different topography within each forest type. Thus, nine plots were classified as thermophilous deciduous woodland, three plots as low herb woodland, 21 plots as bilberry (*Vaccinium myrtillus*)—woodland, and 26 plots as heather (*Calluna vulgaris*)—bog bilberry (*Vaccinium uliginosum*)—Scots pine woodland. All species of vascular plants were recorded within the 59 plots by thorough field identification. Bryophytes and macrolichens (Krog et al., 1994) were recorded on dead wood (snags and logs), rocks, bare soil, trees, and rock walls <2 m above the ground. All fruit bodies of wood living polypore fungi were recorded on trees and dead wood (snags and logs). Ground-living beetles (Carabidae and Staphylinidae) and spiders were recorded using pitfall traps. Eight pitfall traps were situated in each sample plot of 0.25 ha. The trapping period was from end of April to end of November. The traps were emptied four times during the trapping period, and the individuals sampled in the eight traps were pooled and treated as one sample. Snails were recorded by sifting of ground litter (Waldén, 1962). Six ground litter samples were collected within each sample plot, and care was taken to sample all types of possible snail habitat.

Total field inventory varied between 1 and 10 h for each of the sample plots, depending on taxonomic group and species richness.

2.3. Environmental variables

In order to relate the major gradients in species composition to potentially important environmental variables

the following environmental variables were recorded within each sample plot:

1. Potential productivity: the value “H40 index”, indicating the height of 40-year old trees (Tveite and Braastad, 1981).
2. Vegetation index: ranking of vegetation types, reflecting the richness of the vegetation (Fremstad 1997). Heather-bog bilberry–Scots pine forest (1), bilberry forest (2), low-herb forest (3), and deciduous woodlands (4).
3. Topographic position: 1 = flat, 2 = upper part of a south-facing slope, 3 = lower part of a south-facing slope, 4 = upper part of a north-facing slope, 5 = lower part of a north-facing slope, 6 = bottom of valley or gorge.
4. Aspect: dominating aspect of the plot. Measured as deviation from SW.
5. Inclination: measured as the difference (metres) between the highest and lowest point of the plot.
6. Soil depth: subjective estimate of the dominating soil depth within the plot, ranging from 1 to 4. 1 = <25 cm, 2 = 26–50 cm, 3 = 50–100 cm, 4 = >100 cm.
7. Deciduous tree index: the sum of rank values of the deciduous trees within the plot, according to the likely richness of the epiphytic flora of each tree species. 1 = *Betula*, 2 = *Populus*, 3 = *Alnus*, *Prunus*, *Quercus*, *Sorbus*, *Salix*, and *Tilia*, 4 = *Corylus*, *Fraxinus*, and *Ulmus*.

2.4. Numerical analyses

To investigate the major gradients in the species data for the various species groups involved detrended correspondence analysis (DCA) was performed for each group (Hill and Gauch, 1980). Rare species were down-weighted. Other options followed the default settings for DCA in CANOCO 4 (terBraak and Smilauer, 1998).

Possible covariation between the main gradients for the various species groups was tested by Kendall rank correlation. To test for possible covariation between species richness for the various groups Pearson product–moment correlation was applied to the data. Only *P*-values <0.01 were considered statistically significant.

A heuristic procedure (Sætersdal et al., 1993) was used to select the complementary set needed to include all vascular plant species. The algorithm is set to select new samples by the greatest number of new species in each sample. The selection continues until all species are selected.

The beta-2 measure of turnover was used to quantify spatial changes of species composition (Wilson and Shmida, 1984; Harrison et al., 1992). Beta-2 determines the relationship between the number of species in the

most species-rich plot and the total number of species in the dataset: $(S/(\alpha_{\max} - 1))/(N - 1) \times 100$, where *S* is the total number of species in the dataset, α_{\max} is the number of species in the most species rich plot, and *N* is the total number of plots.

3. Results

Altogether a total of 1083 species were found in the eight species groups studied. The most species-rich group was bryophytes with 347 species. The least species-rich group was snails with a total of only 30 species (Table 1). As a first step, detrended correspondence analysis was used in order to detect the major gradients in vascular plant species composition of the 59 plots within the study area (Fig. 1). The first axis (eigenvalue=0.31, Table 2) is interpreted as representing the gradient from plots in broad-leaved deciduous forest to plots situated in nutrient-poor pine forest (heather-bog bilberry–Scots pine forest). Axis 2 (eigenvalue=0.07, Table 2) is less clear, but seems to be related to the topographic position of the plots.

As can be seen from Table 3, the interpretations are generally supported when the sample scores from the DCA are correlated with measured environmental variables using Kendall rank correlation. Axis 1 is highly correlated to aspects of soil nutrient richness, such as stand productivity and vegetation index. Axis 2 is significantly correlated to topographic position and soil depth.

To investigate to what extent the other seven species groups respond to the same underlying gradient as the vascular plants (our first question) a Kendall rank correlation was performed on the sample scores from the DCA axis 1 for the various groups. Table 4 shows that the correlations between the sample scores of axis 1 for the different species groups are statistically significant for most comparisons. However, generally, the weakest correlations are found between the polypores and the other groups (Table 4). In Fig. 2 the sample

Table 1
Mean number of species per plot (S.D.) and total number of species found in all 59 plots for each species group

Species group	Mean no. of species (S.D.)	Total no. of species
Vascular plants	68 (22.0)	236
Bryophytes	89 (30.2)	347
Lichens	15 (7.1)	77
Spiders	32 (8.6)	150
Carabids	9 (3.5)	31
Staphylinids	26 (11.9)	174
Snails	9 (5.2)	30
Polypore fungi	3 (2.2)	38
Total		1083

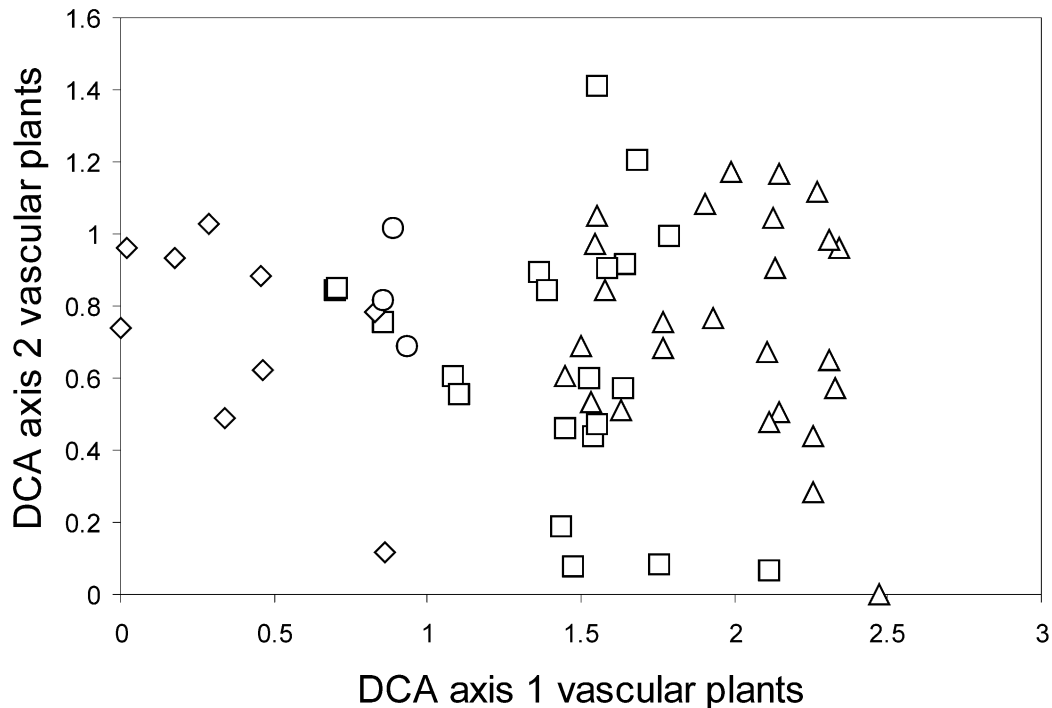


Fig. 1. Detrended correspondence analysis diagram of the 59 plots based on the vascular plant data. The dominating vegetation types of the plots are indicated: \triangle = heather-bog-Scots pine forest, \square = bilberry forest, \circ = low herb forest, \diamond = deciduous forest.

Table 2
Detrended correspondence analysis results for the vascular plant data from the 59 sample plots

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalue	0.31	0.07	0.04	0.04
Lengths of gradient	2.47	1.41	1.11	1.19
Cumulative% variance explained	21	26	29	31

Table 3
Kendall rank correlation coefficients (Kendall tau) between sample plot positions relative to DCA axes 1 and 2, based on the vascular plant species data set, and measured environmental variables

Environmental variable	DCA axis 1	DCA axis 2
Potential productivity	-0.74***	-0.04
Vegetation index	-0.69***	-0.02
Topographic position	-0.27*	-0.22*
Aspect	-0.16	0.18
Inclination	-0.52***	0.10
Soil depth	-0.49***	-0.30**
Deciduous tree index	-0.64***	0.18

* $P < 0.05$.

** $P < 0.01$.

*** $P < 0.001$.

scores of axis 1 for vascular plants are plotted against the sample scores of axis 1 for the other groups in order to give a visual impression of the relationships. The covariations seem to be least pronounced within the

nutrient-poor pine forest. For example, staphylinids and carabids show large variation in sample scores within this type of pine forest, whereas the variation in sample scores of vascular plant species is low.

In order to answer our second question about possible correlations between species richness (alpha-diversity) for the different groups of organisms in the 59 plots, Pearson product-moment correlation was performed (Table 5). As can be seen from Table 5, species richness in vascular plants is significantly correlated with species richness of all the other seven species groups. However, the species richness of spiders is negatively correlated with that of all other species groups including vascular plants: spiders were most speciose in nutrient-poor pine forest whereas the species richness of the other seven species groups is highest in deciduous forest.

Our third question was on the extent to which a complementary selection based on vascular plants encompasses the total species richness of the other groups of organisms. Twenty out of the 59 plots (34% of area) were needed to include all vascular plant species (Fig. 3). These 20 plots encompassed 94% of the lichen species, 93% of the snails, 89% of the bryophytes, 77% of the staphylinids, 76% of the spiders, 74% of the carabids and 68% of the polypore fungi species. Of the 1083 species in all eight groups, the 20 plots needed to include all vascular plant species encompassed 942 species overall (87%). In comparison, a random selection

Table 4

Kendall rank correlations (Kendall tau) between sample plot positions relative to DCA axis 1 (59 plots) for the various species groups

	Vascular plants	Bryophytes	Lichens	Spiders	Carabids	Staphylinids	Snails	Polypore fungi
Vasc. Plants	–	0.69***	0.67***	0.66***	0.59***	0.58***	0.55***	0.24**
Bryophytes		–	0.65***	0.53***	0.49***	0.45***	0.59***	0.23
Lichens			–	0.59***	0.40***	0.46***	0.46***	0.18
Spiders				–	0.56***	0.57***	0.39***	0.21
Carabids					–	0.59***	0.36***	0.31
Staphylinids						–	0.47***	0.31***
Snails							–	0.24
Polypore fungi								–

** $P < 0.01$.*** $P < 0.001$.

of 20 plots encompassed on average (50 random selections) 862 species overall (80%). Further analysis revealed that the first six plots (10% area) selected in the complementary analysis encompassed on average 65% of the total species richness in the other groups, and the first three plots (5% area) encompassed 52% of the total species richness of the other groups.

The degree of species change between samples (beta-2 index) was lowest in snails and highest in polypore fungi (Table 6). Vascular plants had a relatively low spatial species turnover compared with the other groups. Generally, the turnover rates of the various species groups were low.

To test whether the spatial turnover in species composition of vascular plants adequately reflected changes in the other seven groups, we plotted relative differences in beta-2 index (for each of the other seven groups minus vascular plants) against % species richness of each of the other groups included in the complementary selection (Fig. 4). The null hypothesis of no relationship was rejected (Kendall tau = -0.714 , $P < 0.05$). Indeed, the % species richness included of a given group was negatively related to the spatial turnover in species composition relative to vascular plants. Thus we conclude that polypores, the species group with highest species change between samples relative to vascular plants, were least well represented (ca. 40%) by vascular plants, while snails with the lowest change in species composition were much better represented ($> 80\%$). It can be seen from Fig. 4 that the lower the degree of change in species composition between plots in the “target” groups relative to that of vascular plants, the higher the percentage “target” species encompassed in a complementary selection of sites based on vascular plants. Unfortunately, vascular plants seem to have a rather low species turnover compared to polypores, spiders and staphylinids. Hence, the percentages species included in the complementary selection are low in these three groups in comparison with those of the other species groups.

4. Discussion

4.1. Methodological aspects

The number of scientist-hours required for an “all-taxa biological inventory” for a “representative hectare” of forest is in the order of 10–20% of the global workforce of systematists (Lawton et al., 1998). Practical conservation is therefore forced to use some surrogate information to decide on conservation priorities (e.g. Faith and Norris, 1989; McKenzie et al., 1989; Pressey and Nicholls, 1989; Margules et al., 1994; Gaston, 1996; Wessels et al., 1999). Generally, there are two types of biodiversity surrogates. First, surrogates, or indicators, of species richness can be habitat and substratum variables (e.g. Ferris and Humphrey, 1999; Jonsson and Jonsell, 1999). Second, surrogates can be species, or species groups (so-called surrogate taxonomic groups) (e.g. Prendergast et al., 1993; Williams et al., 1996; Flather et al., 1997; Howard et al., 1998; van Jaarsveld et al., 1998; Reyers et al., 2000).

Howard et al. (1998) found that different species groups showed similar patterns of biogeography in Uganda, and therefore that complementary sets of one species group represented other species groups well. Other studies have found less encouraging results (e.g. Sætersdal et al., 1993; van Jaarsveld et al., 1998). However, as stated by Pimm and Lawton (1998) it is possible that, in regions with a strong and persistent gradient, complementarity across different species groups may represent a route to efficient reserve selection. In this study the eight species groups studied were all found to respond to the same underlying gradient in productivity and humidity among the sample plots (Table 4 and Fig. 2). Hence, an important requirement for a successful use of a surrogate species group in complementary selection is fulfilled.

Our results resemble those of Virolainen et al. (2000) who found that, for small patches within old-growth forests in Finland and Sweden, most complementary

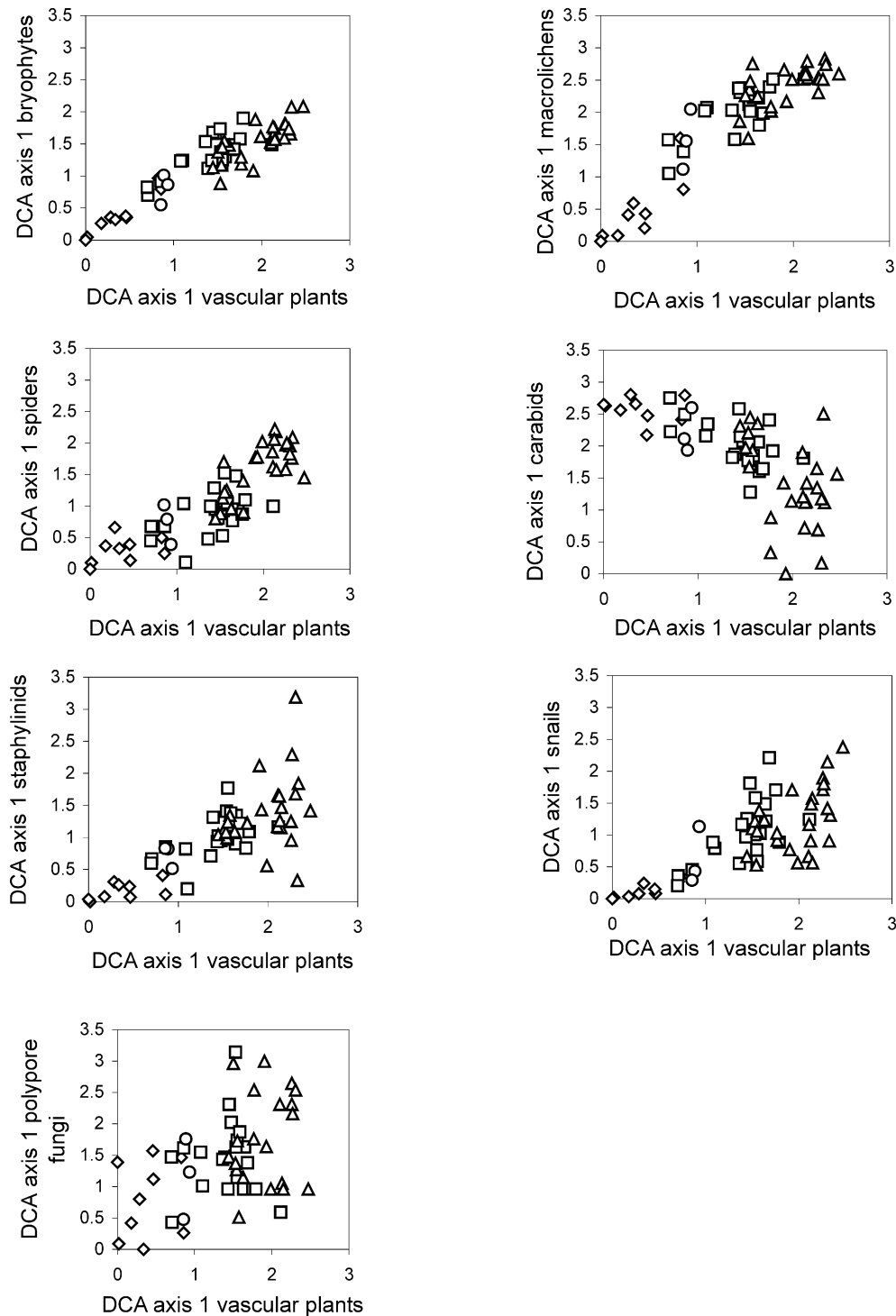


Fig. 2. Plots of the covariation between sample scores DCA axis 1 based on vascular plants and sample scores DCA axis 1 based on the other 7 groups of organisms of the 59 plots. The dominating vegetation types of the plots are indicated: \triangle = heather-bog-Scots pine forest, \square = bilberry forest, \circ = low herb forest, \diamond = deciduous forest.

networks based on one taxonomic group captured species richness of all groups with a high efficiency. As suggested by Pimm and Lawton (1998) and Margules and Pressey (2000) the potential success of the use of surrogate species groups in complementary reserve selection will presumably depend on the environmental heterogeneity of

the area. It is a well documented pattern that the major gradients in species composition of field layer vascular plants, bryophytes and lichens are related to soil nutrient richness and humidity (e.g. Tonteri et al., 1990; Økland, 1996; Grime et al., 1997). Although soil nutrient richness and humidity in principle are independent, they often are

Table 5

Pearson product moment correlation coefficients between number of species (species richness) in each plot (59 plots) for the eight species groups

	Vascular plants	Bryophytes	Lichens	Spiders	Carabids	Staphylinids	Snails	Polypore fungi
Vasc. plants	–	0.80***	0.58***	–0.44***	0.32**	0.40***	0.67***	0.65***
Bryophytes		–	0.56***	–0.54***	0.37***	0.46***	0.55***	0.64***
Lichens			–	–0.33**	0.52***	0.65***	0.66***	0.47***
Spiders				–	–0.20	–0.32	–0.30	–0.42***
Carabids					–	0.51***	0.34***	0.22
Staphylinids						–	0.57***	0.41***
Snails							–	0.48***
Polypore fungi								–

** $P < 0.01$.

*** $P < 0.001$.

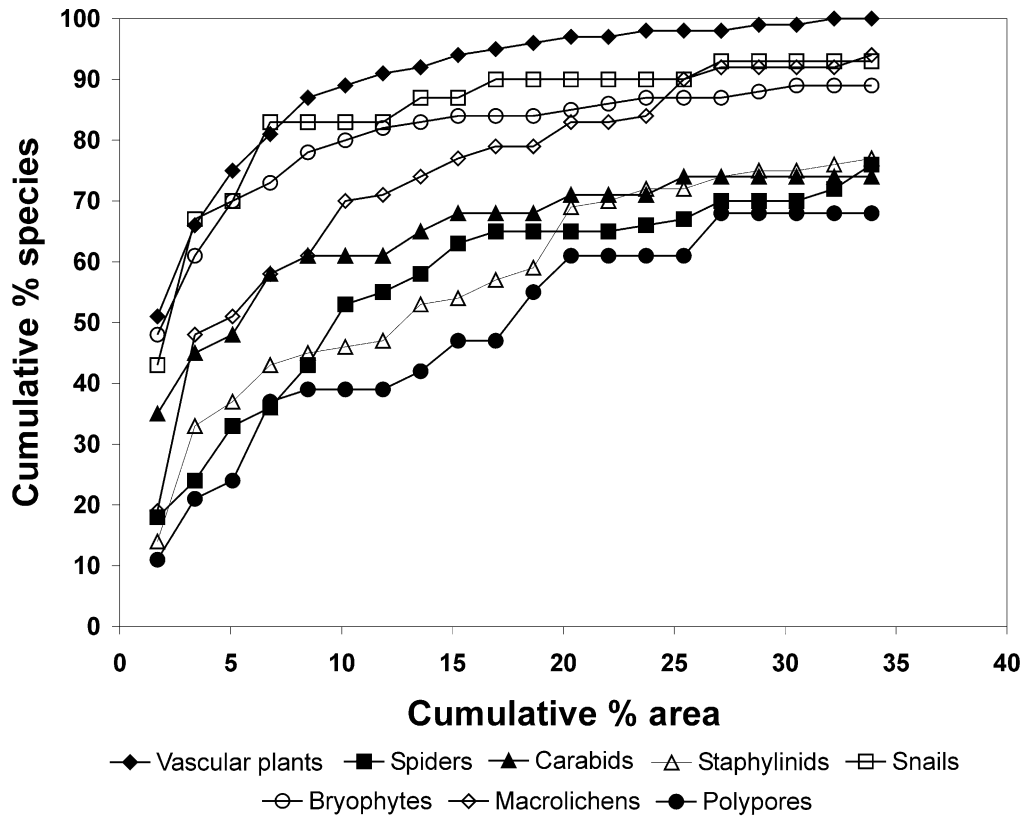


Fig. 3. Cumulative percentage of species of the different species groups captured as a function of cumulative percentage area from a complementary selection of sites based on vascular plant species.

Table 6

Measures of species turnover for the eight species groups. Beta-2 index and length of compositional DCA axis 1 gradient

	Vascular plants	Bryophytes	Lichens	Spiders	Carabids	Staphylinids	Snails	Polypore fungi
Beta-2	1.6	1.9	1.9	3.6	1.6	3.6	0.6	6.3
DCA-SD	2.47	2.08	2.83	2.22	2.80	3.19	2.38	5.75

$$\text{Beta-2} = (S/\alpha_{\max} - 1)/(N - 1) \times 100.$$

correlated (Økland, 1996), as in this study. The factors contributing to the gradient in nutrient conditions are, among others, soil pH, content of soil nitrogen, and the concentration of exchangeable Ca and Mg. These parameters make up a so-called complex gradient in nutrient

richness (Whittaker, 1956; Økland, 1990). The classification of Norwegian forest vegetation types is primarily based on the gradients in soil nutrient richness and humidity (Fremstad, 1997). This study is the first to demonstrate that the same underlying gradients also

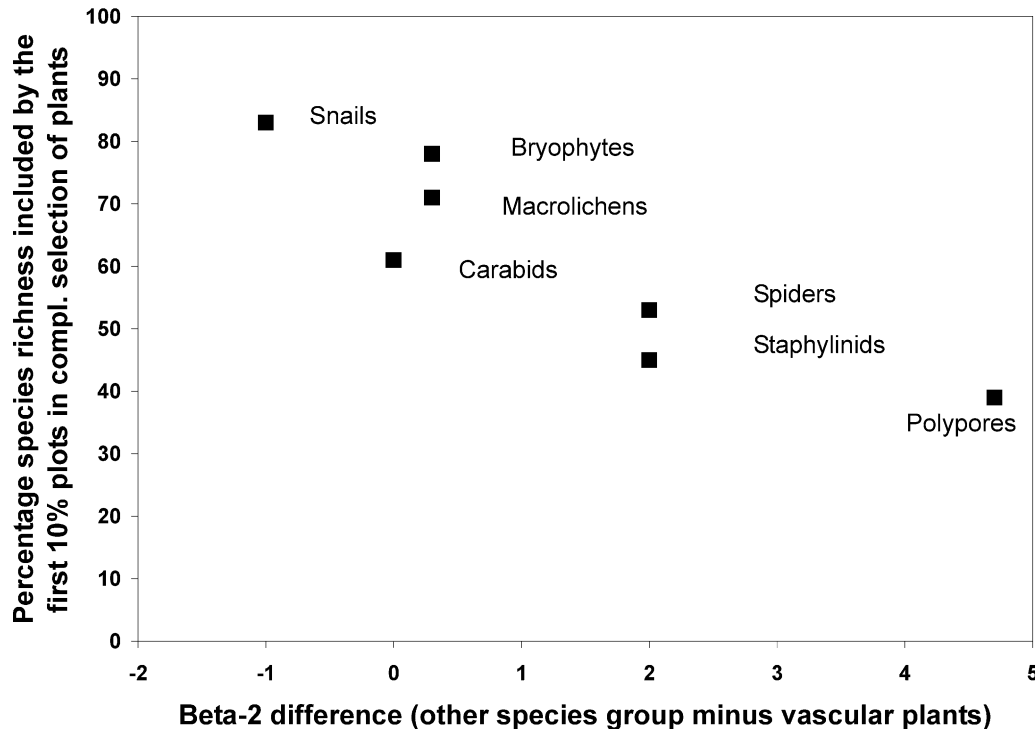


Fig. 4. Percentage of species for the various species groups included in a set of sites selected (after 10% area is included) from a complementary selection of sites based on vascular plants (see Fig. 3) plotted against the difference in beta-2 index between the other species groups and vascular plants (beta-2 index of the other species groups minus beta-2 index vascular plants).

determine the species composition of epiphytic, epixylic, and epilithic bryophytes and macrolichens as well as wood-living polypore fungi and several groups of ground-living invertebrates at the scale of forest stands. Hence, it can be argued that the various vegetation types will generally indicate complementary species assemblages in all the groups of organisms included in this study. In a study from USA, Hughes et al. (2000) found that dipteran and hymenopteran communities were differentiated by dominant vegetation at the scale of hundreds of metres. Recently, MacNally et al. (2002) investigated the use of vegetation types (in 1 ha plots in Australia) as surrogates for patterns of species richness in tree species, birds, mammals, reptiles, terrestrial invertebrates, and nocturnal flying insects using generalised Mantel tests. They conclude that the use of vegetation units as surrogates for species composition in other groups may be justified for birds, mammals, and trees, but not for reptiles and invertebrates.

The lowest correlation in this study was found between DCA axis 1 for vascular plants and DCA axis 1 for wood-living polypore fungi (Table 4 and Fig. 2). This is reflected by the relatively low success of the complementary set based on vascular plants to capture species richness of wood-living polypore fungi (Fig. 3). A similar result was found by Virolainen et al. (2000). It is possible that the scattered distribution of dead wood (lack of dead wood habitat within several plots) within the study area is partly responsible for this result. We

therefore hypothesise that a stronger covariation between gradients in vascular plants and wood-living polypore fungi would be observed in forests with dead wood habitat present in all samples.

Because of the negative correlation between species richness of spiders and vascular plants, a hot-spot for one would not be a hot-spot for the other. However, as spiders are found to respond to the same underlying gradient in soil nutrient richness and humidity, a complementary selection based on plants will include sites along the whole gradient and should therefore also sample spiders adequately (Fig. 3). This is an important observation because covarying patterns of species richness may not be particularly important in complementary site selection. Instead, covarying gradient patterns may be more important (Kremen et al., 1993; Howard et al., 1998) as they will ensure that a complementary selection based on one species group will also represent the variation in species composition in other species groups.

Williams et al. (2000) investigated how well the use of selected flagship species indicated important areas for other species in complementary site selection. They concluded that, in order to represent overall diversity of species, the selected flagship species had to show little spatial overlap (i.e. a high degree of turnover in species composition) in their distribution. In the present study, species turnover of vascular plants turned out to be among the lowest of the investigated species groups.

This implies that a single vascular plant species assemblage, at a certain scale, may be associated with several species assemblages in the other species groups. It seems therefore that vascular plants, as a group, fail to fulfil the last requirement of a good surrogate species group in that it does not fully represent the spatial turnover in species composition in the other species groups. Possible explanations for variations in species composition turnover between the species groups are poorly understood. However, we suggest that differences in niche breadths and the spatial structure of important habitats may possibly offer an explanation in this study (Harrison et al., 1992).

Earlier studies have demonstrated differences in spatial species turnover in species composition between different groups of organisms (e.g. Sætersdal and Birks, 1993; Rey Benayas, 1995; Oliver et al., 1998; Pharo et al., 1999). However, to the best of our knowledge this study is the first to demonstrate the effects of relative species spatial turnover in a surrogate species group compared to the species groups it is supposed to indicate, for the ability to capture species richness of these species groups during complementary selection.

An important question is whether the major results from this study would change if the extent of study was increased. One possible effect would be that other environmental variables (e.g. factors related to climate) would become predominantly responsible for the main gradient in species composition (Willis and Whittaker, 2002). However, it is unclear to what extent the relative differences in turnover between the species groups would be altered. Nevertheless, the important point is that differences in spatial species composition turnover between surrogate species groups and the other species groups do affect the success of a complementary site selection (irrespective of scale).

4.2. Conservation aspects

In the more or less continuous forest landscape of the northern forests red-listed species are not confined to well-defined small patches. Gustafsson (2002) found red-listed species (vascular plants, bryophytes, and lichens) in 86% of 2 ha plots within the production forest. Gjerde et al. (in preparation) found that 18% of 0.25 ha plots within mature production forest in Norway contained red-listed species (bryophytes, macrolichens, and polypore fungi). As large parts of the northern forests contain red-listed forest species a selection of sites is clearly needed. As is shown in this study a complementary selection based on vascular plants seems to adequately represent the variation in species composition within several groups of organisms including selected groups of cryptogams and invertebrates.

Our study was done within an area of only ca. 200 ha. In practical forest management, complementary selection

should be done at a larger scale for two reasons. First, planning areas in Scandinavia are typically at a scale of 10⁵ ha. Second, a complementary selection at too small a scale can lead to a “Noah’s Ark” effect: all species are captured in a combination of sites, but the populations are all too small to persist (Pimm and Lawton, 1998).

Some of the results of this study (e.g. % species within the various species groups included in the complementary selection) should not, as a matter of course, be extrapolated to larger scales, such as the selection of nature reserves. However, the major conclusions of this study concerning common compositional gradients are relevant at a larger scale of study (Berg et al., 2002), as is the effect of relative differences in spatial species turnover between species groups in complementary site selection.

The main conservation targets of the Fennoscandian woodland key habitats are the rare and/or threatened (red-listed) forest species. Many of these species are confined to habitats such as dead wood, old trees, deciduous trees, and cliffs (e.g. Berg et al., 1994; Jonsell et al., 1998; Thor and Arvidsson, 1999; Berg et al., 2002). As the results from this study show that species associated with these habitats respond to the same gradients as vascular plants, plant lists or vegetation types may be used as indicators of habitats with different species compositions in complementary selection. These habitats are primarily found more or less patchily distributed, therefore the selection of sites can not be based on vascular plants or vegetation types alone, but in a combination with an inventory of these habitats. Different sites may have a similar vascular plant flora but differ greatly in presence of species associated with, for instance, dead wood or old trees, due to a lack of these habitats in some of the sites. In practical site selection of small scale sites of conservation value, such as woodland key habitats, the use of vascular plants, or vegetation types, will be to ensure that the total variation in habitat conditions for the rare and/or red-listed species associated with dead wood, old trees, deciduous trees and cliffs are represented in the set of selected sites. Hence, vascular plants may be used to classify the ground moisture and nutrient conditions of sites with similar important habitats for red-listed forest species. It is necessary to include the full spectrum of habitat conditions related to soil moisture and humidity in order to include complementary sets of species associated with the same type of habitats in the woodland key habitat selection.

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