



A functional relationship between species richness of spiders and lichens in spruce

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Abstract. Modern forestry has created stands with even age distribution of trees and fragmentation of the habitat. In boreal forests, the effects on biodiversity within many taxa need to be examined. We tested the hypothesis that species richness of foliose and fruticose lichens and spiders is positively related in the lower canopy of spruce (*Picea abies*) in forests with, or without, management in central Sweden. High species richness of lichens may increase the structural complexity of the microhabitat on spruce branches, and bring a higher species richness also in the spider community. In six areas, spruce branches were sampled in old-growth and managed boreal forest stands, respectively. Forest management did not affect the species richness of spiders or lichens, but an effect due to sampling area was found in the latter taxon. There was a significant covariation between species richness of lichens and spiders, and the hypothesised positive correlation was confirmed by separate analyses for each area and combining the probabilities. Moreover, regression analysis on mean values from each site revealed a positive relationship. We conclude that species richness of lichens and spiders covary on spruce branches for functional reasons, i.e. more lichen species promotes a more diverse spider community by increasing the structural heterogeneity. Our results might provide a 'shortcut' for assessing biodiversity in boreal forests.

Introduction

There is an increasing interest among conservation biologists to find covariation between species richness of different taxa. Such relationships may be used as 'shortcuts' for assessments of biodiversity (Kareiva 1993). The search for surrogate taxa has been intensive. For instance, Reid (1998) reviewed many correlative patterns of species richness between certain taxa at a coarse-grained scale from various regions. In contrast, Prendergast et al. (1993) found little covariation between 'diversity hotspots' at the scale of 50 × 50 km in Britain. These results suggest that patterns of covariation are inconclusive.

Another important aspect is the scale-dependency of covariation. Studies at finer scales may reveal other patterns than at coarser scales. In Switzerland, recent studies at a local scale showed a positive relationship between the overall total number of species and species richness of different taxa (mainly arthropods) (Duelli and Obrist 1998). However, in 31 Swedish seminatural grasslands, correlations between species richness of six taxa were few and inconsistent in direction (Vessby et al.

2002). Taken together, these studies suggest that there are no consistent patterns of covariation. The conclusion holds both at coarse-grained and finer scales.

Here we suggest that functional relationships between taxa should be examined in connection with studies on species richness. Such an approach has been used in other cases. For instance, insect communities associated with different tree species have been shown to be a function of tree abundance in recent geological history (e.g. Southwood 1961; Southwood et al. 1982). We put forward another functional hypothesis, namely, the occurrence of high species richness in one taxon creates opportunities for high diversity in another taxon, resulting in a positive covariation. In our study system, there are several lines of evidence for functional relationships affecting covariation of species richness between taxa.

In boreal forests of Scandinavia, a neglected species-rich habitat being part of the vast taiga (Hanski and Hammond 1995), spiders and epiphytic lichens are common taxa which contribute significantly to the biodiversity in canopies of Norwegian spruce *Picea abies* (Norberg 1978; Gunnarsson 1988, 1995, 1996; Pettersson et al. 1995; Pettersson 1996; Esseen et al. 1996). Earlier studies in this habitat have shown that the spider community is influenced by vegetation structure on spruce branches. Mean size and density of spiders increase with a more complex vegetation structure on the branches. Variations in the needle density (Gunnarsson 1988, 1990, 1996) and the occurrence and amount of macroscopic fruticose and foliose lichens (Pettersson et al. 1995; Pettersson 1996) cause this. Moreover, there is strong bird predation pressure on spiders in the system, and earlier experiments revealed interactions between vegetation structure and bird predation (Gunnarsson 1996).

Modern forestry has created stands of even age distribution of trees, low amounts of dead wood and spatial fragmentation. These habitat changes may affect forest arthropods (Heliövaara and Väisänen 1984) as well as epiphytic lichens (Stevenson 1990). Studies in northern Scandinavia have shown that the biomass of lichens on spruce branches can be six times higher in old-growth stands than in managed ones (Esseen et al. 1996). In addition, spider abundance and number of species per branch were higher in lichen-rich, natural spruce forests than in managed forests of northern Sweden (Pettersson 1996).

Here we focus on a previously untested hypothesis for the system described above; is there a positive relationship between species richness of lichens and spiders? High species richness of macroscopic lichens might create a more complex microhabitat due to a higher variability of different growth forms. A high structural complexity may harbour more spider species, since more refuges should be available, which means that coexistence between spiders can be facilitated. If this were true, we would expect a positive covariation between species richness of lichens and spiders for functional reasons. We also examine the effects of forestry on our study system by comparing the relationship between epiphytic lichens and spiders in old-growth and managed forests.

Methods

Six sampling areas were selected in the Svealand region (central Sweden), i.e. the

southern part of the boreal forests in Scandinavia. The old-growth sites were nature reserves: Nybrännberget (NY) in Dalarna County, Fäntjärnsskogen (FÄ) and Höljberget (HÖ) in Värmland County, Fermansbo (FB) in Västmanland County, and Börningsberget (BB) and Digerberget (DB) in Gävleborg County. In addition, each area contained a matching managed forest. Each forest was at least ca. 20 ha. In all forests, the predominant ground vegetation was *Vaccinium myrtillus* and different mosses. The forests were closed or sometimes half-open, with spruce as the dominant tree. Occasionally, single trees of birch (*Betula* spp.) and pine (*Pinus sylvestris*) were present. The old-growth forests (ca. 150–200 year) had large amounts of dead wood, they were more or less multi-layered and there were no signs of logging, i.e. there had been no recent (>150 year) activities connected to forestry. Near (<10 km) the old-growth forest, we selected a mature, managed forest with even age distribution of trees (ca. 70–90 year). The ground conditions, canopy closure and tree size were similar to those of the old-growth forests. The mean size of trees (assessed by dbh) was 330 mm (SD = 99, $n = 30$) in old-growth forests and 301 mm (SD = 68, $n = 30$) in managed forests (t -test, $t = 1.341$, $P = 0.19$).

In each forest, five spruce trees were randomly selected, giving 10 trees per area. One branch per tree was sampled. Starting at an arbitrary point inside each forest, a random direction and distance (up to 50 m) was followed to the sampling spot, where the closest spruce tree (\geq dbh 200 mm) was selected. Starting from the same point, this procedure was repeated for all trees included in the sample. At each tree, a new random direction was taken, and the branch pointing out from the trunk in best agreement with this direction (up to ca. 2.5 m above the ground) was carefully cut down into a plastic sack, which was sealed and taken to the laboratory (see Gunnarsson 1983). The branches were ca. 1.0–1.5 m long and the mean dry weight was 0.534 kg (SD = 0.183, $n = 60$). Sampling was performed in June and September 1997 and 1998.

In the laboratory the branches were cut into small pieces, and each piece was shaken and carefully examined over a white bowl. Spiders were collected and stored in 70% ethanol. Foliose and fruticose lichens were carefully removed from each branch. The branches were then left in open sacks at room temperature. After several months, the dry weight of each branch was recorded. Spiders and lichens were identified at species level by B.G. and S.H., respectively (the species composition will be reported elsewhere).

The mean number of spiders per branch did not differ between old-growth and managed forests (t -test, $t = 1.48$, $n_{\text{old growth}} = n_{\text{managed}} = 30$, $P = 0.14$). We used the size (dry mass) of branches to correct for unequal sample size. This was done because species numbers of both lichens ($R = 0.369$, $n = 60$, $P = 0.004$; test on log-transformed data) and spiders ($R = 0.295$, $n = 60$, $P = 0.029$) were positively correlated with branch size (dry weight in kg). For each branch, we therefore adjusted the species number of lichens and spiders according to branch size (number of species per kg dry branch-mass).

Data on species number of spiders and lichens, and dry mass of branches, were tested for significant departures from the normal distribution by the Kolmogorov–Smirnov goodness-of-fit test (Sokal and Rohlf 1981). When appropriate, data were log-transformed to produce non-significant deviations from the normal distribution.

Table 1. ANCOVA of spider species richness [(log) species number per kg dry branch-mass] in relation to spruce forest type (old-growth or managed) and lichen species richness [covariate; (log) species number per kg dry branch-mass] on spruce branches in six areas in middle Sweden ($n = 60$ branches).

Factor	df	F-value	P
Forest type	1	0.403	0.528
Lichen species richness	1	9.828	0.003
Interaction: forest type \times lichen species richness	1	0.541	0.465
Residual	56		

Our hypothesis regarding a relationship between species richness of lichens and spiders, and the influence of forest management on spiders was analysed by ANCOVA. The effect of forest management on the species richness of lichens was examined by a split-plot ANOVA. In our original hypothesis, we assumed that sampling area did not affect the ecological mechanisms behind the possible relationship. However, sampling time differed between the areas (June and September during 2 years) and there were obvious differences in spider species composition (B. Gunnarsson et al., unpublished data). Therefore, correlation analyses between species richness of lichens and spiders were performed separately for each of the six areas to examine the direction of possible correlations. To test our hypothesis, we then combined these independent tests according to the Fisher method (Sokal and Rohlf 1981). Moreover, in an overall test of the relationship between lichens and spiders we used mean values from each site as independent data points. Parametric analyses were performed using the SuperANOVA (Abacus Concepts 1989) and StatView 5.0 (SAS 1998) software packages.

Results

There was no indication of any effect of forest management on species richness of spiders (Table 1, $P = 0.53$, class variable 'Forest type', i.e. 'old-growth' and 'managed forest'). However, species richness of lichens (covariate in the analysis) covaried significantly ($P = 0.003$) with species richness of spiders.

We examined the effect of forest type on log species number of lichens per kg branch mass in a split-plot ANOVA, where 'Forest type' ('old-growth', 'managed forest') was used as main plots and 'Area' (NY, FÄ, HÖ, FB, BB, DB) was split plots with branch (i.e. tree) as replication. The analysis showed that 'Forest type' did not affect species richness of lichens ($P = 0.14$), but 'Area' clearly did ($P = 0.038$).

Separate analyses for each area revealed a positive relationship between log species richness of lichens and spiders in all areas, and the correlation coefficients ranged between 0.005 and 0.727 (Table 2). The probability (P) for each correlation to be different from zero was transformed to $\ln P$, and the six probabilities were combined according to Fisher's method (Sokal and Rohlf 1981), i.e. $-2 \sum \ln P = 24.420$, which is greater than $\chi^2_{0.02[12]} = 24.05$, and consequently $P < 0.02$.

Overall, there was a positive relationship between mean species richness of

Table 2. Tests of the hypothesis of a positive relationship between lichen species richness [(log) species number per kg dry branch-mass] and spider species richness [(log) species number per kg dry branch-mass] on spruce branches in six areas in middle Sweden. Probabilities were combined according to Sokal and Rohlf (1981) ($n = 10$ branches in each area).

Area	Regression coefficient	Correlation coefficient (R)	P	$\ln P$
NY	0.325	0.397	0.257	-1.361
FÄ	0.341	0.413	0.235	-1.446
HÖ	0.302	0.444	0.198	-1.617
FB	0.426	0.727	0.017	-4.057
BB	1.146	0.700	0.024	-3.717
DB	0.017	0.005	0.988	-0.012
			Total	-12.210

lichens and spiders in each site, combining old-growth and managed forests (Figure 1). Data were combined because the separate regressions were similar (old-growth, $Y = 0.941X + 0.793$, $R = 0.548$; managed, $Y = 0.984X - 0.566$, $R = 0.551$).

Discussion

The results of the present study suggest a functional, positive relationship between species richness of macrolichens and spiders in boreal forests of central Sweden. An increase in species richness of fruticose and foliose lichens probably creates a more complex microhabitat, which allows more spider species to occur on spruce branches. Structural complexity of lichen shape is known to influence the size

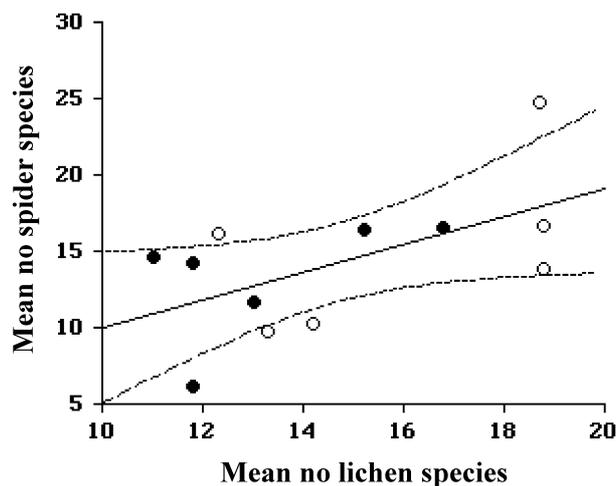


Figure 1. Relationship between mean species richness (number of species per kg dry branch-mass) of lichens and spiders on spruce branches in 12 forests in central Sweden. Filled circles are old-growth sites and open circles are managed sites. The regression line [mean spiders = $0.905 \times$ mean lichens + 0.997, $R = 0.574$, $P = 0.051$ (slope)] is shown with 95% confidence limits.

distribution of arthropods associated with macroscopic lichens (Shorrocks et al. 1991). Lichens are probably important to many arthropod taxa because they provide resources such as food, shelter, oviposition sites, etc. Earlier studies have shown that the abundance of potential prey of spiders (e.g. mites, springtails, psocids) was positively correlated with lichen biomass (Stubbs 1989; Pettersson et al. 1995). It is also known that spider communities are strongly affected by vegetation structure in general (e.g. Hatley and McMahon 1980; Greenstone 1984; Gunnarsson 1992), and in the present system on spruce branches (Gunnarsson 1988, 1990, 1995, 1996). Experimental manipulation of needle density on branches, both in the field and in the laboratory, revealed changes in spider abundance and size distribution (Gunnarsson 1990, 1996). These studies were performed in managed forests in southwestern Sweden, where epiphytic lichens are quite rare on branches, and there was no test of the hypothesis of covariation between species richness of lichens and spiders.

In a study on old deciduous forests in southern Sweden, Nilsson et al. (1995) used tree-dependent lichens and beetles as biodiversity indicators. They found that species richness of Red-listed lichens and Red-listed wood beetles living in hollow trees was strongly correlated. There was also a weaker positive relationship between all species of Red-listed lichens and wood beetles. These relationships were probably not functional, but caused by a common habitat demand, i.e. old deciduous trees. There are, however, several other studies supporting our results. In similar systems in North America, Halaj et al. (1998, 2000) investigated arboreal arthropod assemblages in e.g. noble fir (*Abies procera*) and Douglas fir (*Pseudotsuga menziesii*) canopies. They concluded that species richness of spiders was higher in structurally complex microhabitats. Another experimental study showed that growth forms of lichen thalli affected numbers of Collembola, Psocoptera and Acarina, all potential prey of spiders, positively on tree trunks (Prinzing and Wirtz 1997). Moreover, Clausen (1984, 1986) found a negative correlation between air pollution (measured as SO₂ concentrations) and number of spider species on trees. He attributed this relationship to the variation in the abundance of epiphytic lichens.

We found no effect of forest type (old-growth vs. managed) on spider species richness. Studies in northern Sweden have shown differences in spider abundance and diversity between old-growth and managed forests (Pettersson 1996). However, these quantitative differences were probably due to higher biomass of the branches and higher lichen abundance in old-growth stands (Pettersson et al. 1995; Esseen et al. 1996). No analyses of possible covariation between species richness were made in these studies. In the present study, there was no difference in lichen species richness in old-growth and managed forests. In northern Sweden, Esseen et al. (1996) found that species number of lichens was similar in old-growth and managed forest stands. The biomass of lichens was, however, much higher in old-growth stands, as it was strongly related to branch size and age.

In a recent study of biodiversity in Swedish spruce forests, Jonsson and Jonsell (1999) investigated covariation between many taxa (vascular plants, bryophytes, epiphytic lichens, wood-inhabiting fungi, and beetles). They concluded that correlations between species richness among organisms were few and scale dependent. The investigation by Jonsson and Jonsell (1999) showed that it is unlikely that a few taxa could be used as biodiversity indicators in boreal forests.

Our results suggest that by choosing functionally connected organisms, relationships between species richness of different taxa could be found. These data are probably scale dependent and need to be tested at coarser scales. Development of predictive models, incorporating the scaling aspect, would be useful for applications in conservation biology. However, there are difficulties with predictive models even if some scale dependency is included, as illustrated by a study on species presence of different taxa in fragments of ancient woodland in Britain (Bailey et al. 2002). It seemed that variables used in the models worked well for certain taxa (e.g. birds), but not for others (e.g. butterflies and plants). In the present study, a general relationship emerged from means of the different sites, but R^2 was only 0.33, leaving most of the variation unexplained. Still, there may be reasons to explore the relation between epiphytic lichens and arthropods. Many insect taxa are known to respond to structural complexity by means of their species diversity (e.g. Southwood et al. 1979; Morris 1991; Tschardtke and Greiler 1995). We therefore suggest that high species richness of epiphytic macrolichens indicates high species richness of arthropods in general. This hypothesis warrants studies in many different habitats with macrolichen communities.

Finally, we suggest more effort to be put into studies of biodiversity in systems with well-known species interactions. This includes both intra- and inter-trophic interactions. If knowledge about the major ecological processes that affect local species richness is combined with sensible habitat-specific management, then the loss of biodiversity can probably be stopped.

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References

- Abacus Concepts 1989. SuperANOVA. Abacus Concepts, Berkely, California.
- Bailey S.-A., Haines-Young R.H. and Watkins C. 2002. Species presence in fragmented landscapes: modelling of species requirements at the national level. *Biological Conservation* 108: 307–316.
- Clausen I.H.S. 1984. Notes on the impact of air pollution (SO₂ & Pb) on spider (Araneae) populations in North Zealand, Denmark. *Entomologiske Meddelelser* 52: 33–39.
- Clausen I.H.S. 1986. The use of spiders (Araneae) as ecological indicators. *Bulletin of the British Arachnological Society* 7: 83–86.
- Duelli P. and Obrist M.K. 1998. In search of the best correlates for local organismal biodiversity in cultivated areas. *Biodiversity and Conservation* 7: 297–309.
- Esseen P.-A., Renhorn K.-E. and Pettersson R.B. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: effect of branch quality. *Ecological Applications* 6: 228–238.

- Greenstone M.H. 1984. Determinants of web spider species diversity: vegetation structural diversity vs. prey availability. *Oecologia* 62: 299–304.
- Gunnarsson B. 1983. Winter mortality of spruce-living spiders: effect of spider interactions and bird predation. *Oikos* 40: 226–233.
- Gunnarsson B. 1988. Spruce-living spiders and forest decline: the importance of needle-loss. *Biological Conservation* 43: 309–319.
- Gunnarsson B. 1990. Vegetation structure and the abundance and size distribution of spruce-living spiders. *Journal of Animal Ecology* 59: 743–752.
- Gunnarsson B. 1992. Fractal dimension of plants and body size distribution in spiders. *Functional Ecology* 6: 636–641.
- Gunnarsson B. 1995. Arthropods and passerine birds in coniferous forest: the impact of acidification and needle-loss. *Ecological Bulletins* 44: 248–258.
- Gunnarsson B. 1996. Bird predation and vegetation structure affecting spruce-living arthropods in a temperate forest. *Journal of Animal Ecology* 65: 389–397.
- Halaj J., Ross D.W. and Moldenke A.R. 1998. Habitat structure and prey availability as predictors of the abundance and community organization of spiders in western Oregon forest canopies. *Journal of Arachnology* 26: 203–220.
- Halaj J., Ross D.W. and Moldenke A.R. 2000. Importance of habitat structure to the arthropod food-web in Douglas-fir canopies. *Oikos* 90: 139–152.
- Hanski I. and Hammond P. 1995. Biodiversity in boreal forests. *Trends in Ecology and Evolution* 10: 5–6.
- Hatley C.L. and McMahon J.A. 1980. Spider community organization: seasonal variation and the role of vegetation architecture. *Environmental Entomology* 9: 632–639.
- Heliövaara K. and Väisänen R. 1984. Effects of modern forestry on northwestern European forest invertebrates: a synthesis. *Acta Forestalia Fennica* 189: 5–29.
- Jonsson B.G. and Jonsell M. 1999. Exploring potential biodiversity indicators in boreal forests. *Biodiversity and Conservation* 8: 1417–1433.
- Kareiva P. 1993. No shortcuts in new maps. *Nature* 365: 292–293.
- Morris M.G. 1991. The management of reserves and protected areas. In: Spellerberg I.F., Goldsmith F.B. and Morris M.G. (eds), *The Scientific Management of Temperate Communities for Conservation*. Blackwell, Oxford, UK, pp. 323–347.
- Nilsson S.G., Arup U., Baranowski R. and Ekman S. 1995. Tree-dependent lichens and beetles as indicators in conservation forests. *Conservation Biology* 9: 1208–1215.
- Norberg R.Å. 1978. Energy content of some spiders and insects on branches of spruce (*Picea abies*) in winter; prey of certain passerine birds. *Oikos* 31: 222–229.
- Pettersson R.B. 1996. Effect of forestry on the abundance and diversity of arboreal spiders in the boreal forest. *Ecography* 19: 221–228.
- Pettersson R.B., Ball J.P., Renhorn K.-E., Esseen P.-A. and Sjöberg K. 1995. Invertebrate communities in boreal forest canopies as influenced by forestry and lichens with implications for passerine birds. *Biological Conservation* 74: 57–63.
- Prendergast J.R., Quinn R.M., Lawton J.H., Eversham B.C. and Gibbons D.W. 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365: 335–337.
- Prinzling A. and Wirtz H.-P. 1997. The epiphytic lichen, *Evernia prunastri* L., as a habitat for arthropods: shelter from desiccation, food-limitation and indirect mutualism. In: Stork N.E., Adis J. and Didham R.K. (eds), *Canopy Arthropods*. Chapman & Hall, London, pp. 477–494.
- Reid W.V. 1998. Biodiversity hotspots. *Trends in Ecology and Evolution* 13: 275–280.
- SAS 1998. *StatView Reference*. 2nd edn. SAS Institute Inc., Cary, North Carolina.
- Shorrocks B., Marsters J., Ward I. and Evennett P.J. 1991. The fractal dimension of lichens and the distribution of arthropod body lengths. *Functional Ecology* 5: 457–460.
- Sokal R.R. and Rohlf F.J. 1981. *Biometry*. 2nd edn. Freeman, New York.
- Southwood T.R.E. 1961. The number of species of insect associated with various trees. *Journal of Animal Ecology* 30: 1–8.
- Southwood T.R.E., Brown V.K. and Reader P.M. 1979. The relationships of plant and insect diversities in succession. *Biological Journal of the Linnean Society* 12: 327–348.

- Southwood T.R.E., Moran V.C. and Kennedy C.E.J. 1982. The richness, abundance and biomass of the arthropod communities on trees. *Journal of Animal Ecology* 51: 635–649.
- Stevenson S.K. 1990. Managing second-growth forests as caribou habitat. *Rangifer* 3: 139–144.
- Stubbs C.S. 1989. Patterns of distribution and abundance of corticolous lichens and their invertebrate associates on *Quercus rubra* in Maine. *Bryologist* 92: 453–460.
- Tscharntke T. and Greiler H.-J. 1995. Insect communities, grasses, and grasslands. *Annual Review of Entomology* 40: 535–558.
- Vessby K., Söderström B., Glimskär A. and Svensson B. 2002. Species-richness correlations of six different taxa in Swedish seminatural grasslands. *Conservation Biology* 16: 430–439.