

# **Bryophytes on Boulders**

**Diversity, habitat preferences and conservation aspects**

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## Abstract

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The influence of different overstorey tree species on the floristic composition of bryophytes growing on boulders was studied in two deciduous forests. Covering tree species and amount of litter were the factors explaining most of the variation in bryophyte species composition. Boulders below base-rich deciduous tree species (ash, elm and maple) had a considerably different bryophyte species composition than boulders below Norway spruce, while the species composition was intermediate below oak and birch.

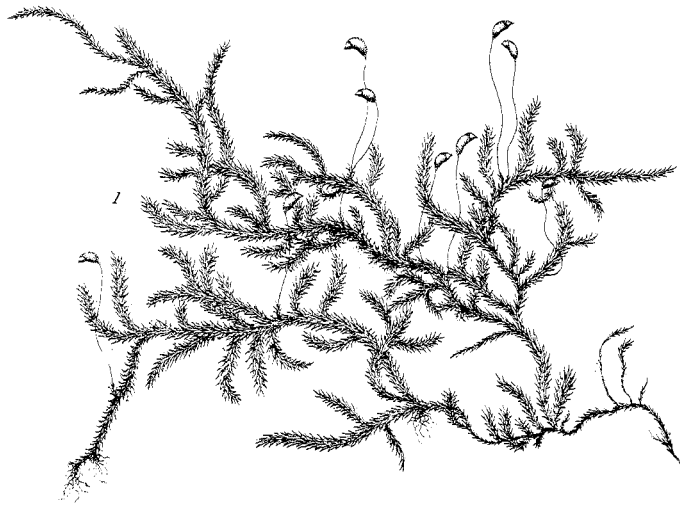
Boulders below base-rich deciduous trees had approximately twice as many species as those below Norway spruce, while boulders below oak and birch were intermediate. Individual plots (10×10 cm) were on average not more species-rich on large boulders than on small ones, even though large boulders had more species.

Transplanted patches of the moss *Tortula ruralis* were grown below the cover of five tree species. The growth was significantly lower below Norway spruce than below the deciduous tree species, which was related to lower amount of throughfall, lower pH in throughfall and lower relative light flux below Norway spruce. In laboratory experiments *Tortula ruralis* grew significantly less at pH 4.1 as compared to pH 4.5 or higher. At high RH *Antitrichia curtipendula* grew significantly more than at low RH. *Antitrichia curtipendula* grew significantly more and *T. ruralis* significantly less when watered often (every third day).

The bryophyte flora was also studied in permanent plots on boulders in a deciduous forest between 1997 and 1999, in order to study the effects of three litter treatments (deciduous, coniferous or no litter). Species richness increased in plots with deciduous litter and decreased in plots with Norway spruce litter, while it was maintained in plots without litter. There was a considerable variation between years in cover of many species, which reduced the treatment-effects.

*Key words:* disturbance, pH, hepatics, mosses, throughfall, litter, relative humidity, watering frequency, permanent plot, species richness, deciduous forest, Norway spruce, *Tortula ruralis*, *Antitrichia curtipendula*.

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# Appendix

## Papers I-IV

The present thesis is based on the following papers, which will be referred to by their Roman numerals.

- I. Weibull, H. Influence of tree species on the epilithic bryophyte flora in deciduous forests of Sweden  
*Journal of Bryology, In press*
- II. Weibull, H. & Rydin, H. Bryophyte species richness on boulders: effects of area, habitat diversity and covering tree species.  
*Manuscript*
- III. Weibull, H., Bengtsson, N. & Larsson, M. Experiments on growth of the mosses *Antitrichia curtipendula* and *Tortula ruralis*: effects of moisture and pH.  
*Manuscript*
- IV. Weibull, H. Effects of leaf litter on dynamics of epilithic bryophytes.  
*Manuscript*

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## Introduction

Vegetation patterns in boreo-nemoral forests are greatly influenced by the composition of the tree layer (Diekmann, 1994, 1999). A current topic in forest conservation biology is whether the presence of deciduous trees in an otherwise homogeneous commercial coniferous forest has a beneficial effect on ecosystem processes and biodiversity (Berg *et al.*, 1994; Bernes, 1996; Saetre, 1998). Another reason for the interest in the effects of the canopy tree species is the expansion of Norway spruce in areas of high conservation value, such as old deciduous forests, wooded pastures and other traditional cultural landscapes in southern Sweden (Berghlund *et al.*, 1996).

### Effects of canopy tree species

Tree species differ in their ability to influence the availability and chemistry of the rainwater below them. Depending on the branching pattern of the tree, the leaves and branches lead the incoming water as throughfall and stemflow (Fig. 1). Norway spruce (*Picea abies*), for example, with its strictly structured branches leads the water to the edge of the tree crown (Tamm, 1953). Most other tree species have less structured crowns, but species such as elm (*Ulmus glabra*), ash (*Fraxinus excelsior*) and especially beech (*Fagus sylvatica*) have main branches, which lead much of the water as stemflow (Wittig, 1986).

The difference between stemflow and throughfall chemistry within (Beier *et al.*, 1993) and among tree species is distinct, not only between coniferous and deciduous species, but also among different deciduous species (Nordén, 1991, 1994a; Bergkvist & Folkesson, 1995). The microclimate differs among stands of different tree species, and probably also among individual trees of different species within a stand (Barkman, 1958; Kuusipalo, 1985; Stoutjesdijk & Barkman, 1992). There are also considerable differences in the defoliation (deciduous versus evergreen trees), chemistry and decomposability of the leaves of different tree species (Sveinbjörnsson & Oechel, 1992; Nordén, 1994b).

### Why bryophytes and boulders?

Bryophyte diversity is an essential part of the overall diversity of forests. In Sweden, there are about 300 bryophyte species regularly occurring in forests (28% of all Swedish bryophytes) (Hallingbäck, 1996). This could be compared to about 300 forest vascular plant species (18%) (Ahlén *et al.*, 1996). A considerable proportion of the bryophyte species within a forest stand is found on boulders and cliffs (Berg *et al.*, 1994; Hallingbäck, 1996).

The main reasons for studying bryophytes were that they are sensitive to pH and water availability, and would probably respond to factors associated with tree species. Unlike vascular plants, bryophytes have very thin leaves and lack cuticle and stomata (Brown, 1982; Proctor, 1982). Therefore, they are sensitive to both

low and high pH (cf. Gilbert, 1968; Rao, 1982; Kellner & Weibull, 1998) and cannot control water loss during periods of drought (Meenks *et al.*, 1991; Mishler & Oliver, 1991; Giordano *et al.*, 1993). Most bryophytes do not have an efficient internal water conducting system (Meenks *et al.*, 1991; Seel *et al.*, 1992), instead they are ectohydric and primarily retain and transport water externally by capillary forces (Proctor, 1982; Giordano *et al.*, 1993). Bryophytes are therefore to a large extent dependent on free water in the environment for their growth. One feasible strategy for these species is to be desiccation tolerant, i.e. having tissues that can withstand complete desiccation without suffering injury (Tuba *et al.*, 1996). However, as bryophytes are only photosynthesising when they are hydrated, the time they spend in a hydrated state is important for their growth and is affected by the availability of water and the microclimate (Økland, 1997).

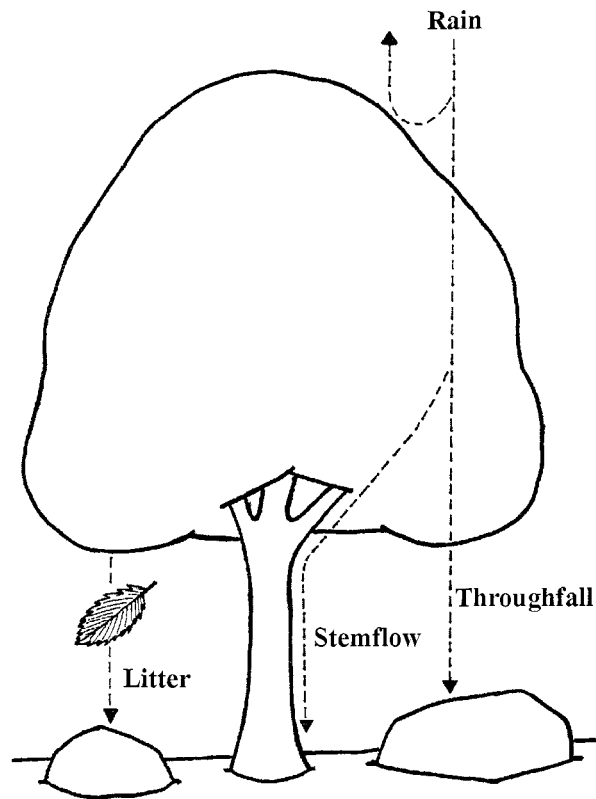


Illustration by Sofie Weibull

Figure 1. A schematic picture of how a tree affects the rain water received by boulders on the forest floor. Stemflow is the rainwater that is channelled through the canopy onto the trunk, while throughfall is water that drips from the canopy.



The studies of Du Rietz (1932) and von Krusenstjerna (1945, 1965) suggested that litter from base-rich deciduous tree species (e.g. elm and ash) increase both the availability of nutrients (e.g. nitrogen) and the pH on the substrate surface. This effect, which is similar to that of dust and bird droppings (Du Rietz, 1932), should be most obvious on siliceous substrates, e.g. granite. Granite boulders (large rocks deposited during the end of the latest glaciation) provide a chemically homogeneous substrate with low pH and low buffering capacity. Therefore, one can assume that their bryophyte flora is sensitive to the covering tree species. Sjögren (1995) found considerable changes in bryophyte species composition and a decline in species richness on boulders in Swedish deciduous forests between 1958 and 1990, presumably because of acid precipitation. However, the relation between the distribution of bryophyte species and canopy tree species is still largely unknown.

### **Species-area relations**

Boulders are patchy substrates in the forest, hosting a different set of bryophyte species than the ground. As habitat islands, their species richness is likely to depend on patch area. As an addition to the influence of tree species, as explanation for bryophyte diversity on boulders, the mechanisms behind the species-area relationship were studied.

One explanation for the ubiquitous positive species-area relationship is Williams's (1943) habitat diversity theory stating that in a larger area there will be more habitat types and thus more species present. The equilibrium theory in island biogeography (MacArthur & Wilson, 1967) states that the number of species on an island is determined by the dynamic equilibrium between immigrations and extinctions of species. A larger area will hold larger populations, and these will have lower extinction probabilities. Westman (1983) introduced an approach to separate the habitat diversity theory and the equilibrium theory for plants. Sample plots of a fixed size are placed in similar habitats, to exclude effects of habitat diversity, on islands of different size. Then, according to the equilibrium theory (MacArthur & Wilson, 1967), there will be a positive influence of island area on the number of species per sample plot. The reason is that in each plot the species have the same probability of going extinct (since this probably depends only on area in the theory). The chance of re-colonisation increases with island area, since the extinction risk on the whole island is lower on a large island and there will therefore be more species close to the plot.

A problem with the plot sampling approach is the difficulty to unambiguously define a habitat in which to place the plots. Granite boulders represent a homogeneous substrate with very little variation in nutritional value. The habitat variation that occurs on boulders is readily observable: presence of fissures, litter cover, inclination etc. In this system it is therefore feasible to test species-area relationships while controlling for habitat diversity.

## Summary

In these studies I have investigated if and how the canopy tree species influence the bryophyte flora on granite boulders. The foci have been on floristic composition, species richness, vegetative growth and bryophyte vegetation changes over time. I have combined descriptive field investigations with experimental studies both in the field and in the laboratory.

In paper **I** the aim was to study the influence of different overstorey tree species on the floristic composition of bryophytes growing on boulders. In two deciduous forests, Vårdsätra and Billingsudd in east-central Sweden, granite boulders (50-200 cm across) lying below the crown cover of elm, ash, maple (*Acer platanoides*), oak (*Quercus robur*), birch (*Betula pendula*) and Norway spruce were studied. Tree species was the factor explaining most of the variation in bryophyte species composition. Boulders below base-rich tree species (with a high bark pH: elm, ash and maple) had a similar species composition, with many bryophytes indicating high pH conditions (e.g. *Brachythecium populeum*, *Homomallium incurvatum* and *Pseudoleskeella nervosa*). On boulders below Norway spruce the species composition was very different with bryophytes indicating low pH conditions (e.g. *Ptilidium pulcherrimum*, *Dicranum montanum* and *Platygyrium repens*). Below oak and birch the species composition was intermediate between the two other groups with bryophytes indicating both high and low pH conditions (e.g. *Brachythecium reflexum* and *Hedwigia ciliata*). The amount of litter on the boulders was also an important factor explaining much of the variation. The conclusion was that throughfall chemistry and effects of leaf litter were the two most important factors explaining bryophyte species composition on boulders.

In paper **II** (together with Håkan Rydin) the aim was to study the influence of different overstorey tree species and area of the boulder on bryophyte species richness. We used data on species richness from the same boulders as in paper **I**, supplemented with data on species richness in sample plots (10×10 cm) on the boulders at Vårdsätra. Covering tree species, area of the boulder and amount of litter on the boulder were the most important variables affecting boulder species richness. Boulders below ash, elm and maple were the most species-rich, oak and birch intermediate and boulders below Norway spruce were the most species-poor. The rank order among trees was as expected from bark pH and litter decomposability in the literature. Boulders below the base-rich deciduous trees (ash, elm and maple) held approximately twice as many species as those below Norway spruce. At plot-level, intermediate levels of litter, litter seepage (i.e. the amount of litter that water is seeping through on the boulder before it reaches the plot), inclination and exposed rock promoted species richness, and also here the covering tree species had an effect. Individual plots were on average not more species-rich on large boulders than on small ones. This leads us to conclude that population extinctions on the plot-level, and re-colonisations from other parts of

the boulder, are less important for species richness than within-boulder habitat diversity. A conclusion was that Norway spruce had a negative effect on species richness in deciduous forests, and base-rich deciduous trees a positive effect.

In paper **III** (together with Niklas Bengtsson and Maria Larsson) we wanted to test experimentally if vegetative growth of the moss *Tortula ruralis* may explain the distribution of the species below different tree species, as seen in paper **I**. Intact patches of the moss were transplanted to pots and individual shoots were marked with plastic rings and the vegetative growth was measured. Vegetative growth and frequency of sporophytes in *T. ruralis* were significantly lower in pots placed below Norway spruce than in pots below the deciduous species maple, birch, oak and lime. This was related to lower amount of throughfall water, lower pH in throughfall and lower relative light flux below Norway spruce. In order to investigate the factors behind these results laboratory experiments were performed on the effects of pH, relative humidity (RH) and watering frequency on the desiccation tolerant species *T. ruralis*, and one less desiccation tolerant species, *Antitrichia curtipendula*. *Tortula ruralis* grew significantly less at pH 4.1 as compared to pH 4.5 or higher, while *A. curtipendula* showed no distinct pattern. In a factorial experiment the mosses were grown at low (40%) and at high (70%) RH, and they were watered every ninth, sixth or every third day. At high RH *A. curtipendula* grew significantly more than at low RH, while *T. ruralis* did not differ between the humidity treatments. *Antitrichia curtipendula* grew significantly more and *T. ruralis* significantly less when watered every third day. We concluded that desiccation tolerant species, such as *T. ruralis*, might not only survive desiccation, but also depend on periods of drought, whereas less desiccation tolerant species, such as *A. curtipendula*, respond positively to conditions providing longer periods of hydration. The investigated factors are probably important explanatory factors for bryophyte distribution patterns as we detected differences in vegetative growth after only a few months.

In paper **IV** I studied the bryophyte flora in permanent plots (10×10 cm) on boulders in a deciduous forest between 1997 and 1999. In order to study the effects of litter on single bryophyte species and bryophyte species richness three litter treatments were applied to totally 87 plots: no litter: all natural leaf litter removed; deciduous litter: the natural deciduous litter (consisting of leaves of ash and elm) was removed before and replaced after the inventory; and Norway spruce litter: all natural leaf litter removed and Norway spruce needles added. There was a strong effect of the litter treatment on plot species richness, which increased in plots with deciduous litter and decreased in plots with Norway spruce litter, while it was maintained in plots without litter. *Thuidium philibertii* increased in plots with deciduous litter and *Pterigynandrum filiforme* and *Orthotrichum anomalum* decreased in plots with coniferous litter, while there were minor changes in plots without litter. There was a considerable variation between years in cover of many species, which reduced the treatment-effects. The most pronounced change over the study period was a decrease in *Pseudoleskeella*

*nervosa* and an increase in *Brachythecium populeum*, which was caused by natural succession and/or weather conditions (the rainy summer of 1998). It was concluded that litter, as well as other factors affecting the fine-scale disturbance of bryophyte shoots and patches, are important for maintaining high species richness on boulders.

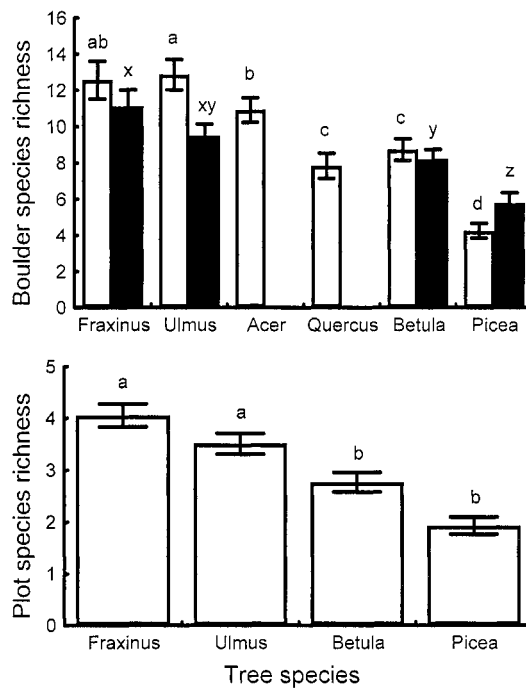


Fig. 2. Bryophyte species richness on whole boulders (upper) at both Billingsudd (open bars) and Vårdsättra (filled bars), and in plots (lower) at Vårdsättra below different tree species. Bars represent mean values and whiskers  $\pm$  one standard error, open bars represent Billingsudd and filled bars represent Vårdsättra. Different lower-case letters indicate significant differences between tree species ( $p < 0.05$ ; a, b, c and d at Billingsudd and x, y and z at Vårdsättra) (II).

## General discussion

### Influence of tree species

Boulders below the base-rich deciduous trees ash, elm and maple roughly hold twice as many species as those below Norway spruce (Fig. 2). The rank order among trees, with ash, elm and maple being richest, oak and birch intermediate

and Norway spruce poorest is precisely the one expected from bark pH (Du Rietz, 1945; Barkman, 1958; Skye, 1968) and litter decomposability (Howard & Howard, 1974; Swift *et al.*, 1979; Berg, 1986; Berg & Tamm, 1991; Nordén, 1994b; Tavakol & Proctor, 1994). This strongly supports the idea that throughfall and litter quality are the main factors regulating bryophyte species richness.

Canopy tree species was also the most important factor explaining the variation in bryophyte species composition on boulders (I). The largest differences in bryophyte species composition were between Norway spruce and deciduous trees, but there were also differences among the deciduous trees (I). Below tree species such as elm, ash and maple, bryophytes indicating base-rich substrates were abundant even on the acidic and biologically almost inert substrate granite (I).

Norway spruce had a negative influence on the vegetative growth and on the development of sporophytes in transplanted patches of *Tortula ruralis* (III). This was related to lower amount of throughfall water, lower pH in throughfall and lower relative light flux below Norway spruce (III). These results are consistent with the scarce occurrences of *T. ruralis* on boulders below Norway spruce (I).

I agree with von Krusenstjerna (1945, 1965) that litter is very important in the development of high pH levels and for the availability of nutrients on the surface of siliceous substrates in particular. But the bryophyte flora on the top of boulders, where leaf litter does not remain and therefore has no effect, also differs among tree species (Weibull, unpublished). This suggests an effect of throughfall in addition to the litter effect. Rambo & Muir (1998) also observed differences in bryophyte vegetation below coniferous and hardwood deciduous trees, presumably due to the differences in pH and the nutrients in throughfall as well as differences in light levels. Within tree species the chemistry of throughfall resembles the chemistry of litter, e.g. pH and nutrients (Nordén, 1991, 1994b).

The age of the covering tree is certainly very important to species composition and species richness on boulders. Below an old tree the species have had time to colonise and become established, but below a young tree the species composition is more complex, with bryophytes both adapted to the present tree species and to the “historical effect” of previous tree species or a gap. The changes in the chemical and physical environment can probably take at least 20-30 years to accomplish, depending on the tree type (I). For certain bryophyte species with a very low rate of colonisation the establishment can take even longer time, e.g. *Anomodon* spp., which in Sweden rarely produces sporophytes and has no specialised means of vegetative dispersal.

### **Influence of climatic factors**

In the transplant experiments *Tortula ruralis* had a higher mortality (due to fungus infections) at high RH and high watering frequency and also grew less at high watering frequency (III). This is in accordance to Dilks & Proctor (1974),



to low water pH strongly influence vegetative growth and distribution patterns of bryophytes in mixed temperate forests.

### **Influence of the substrate**

For both epilithic and epiphytic cryptogams, substrate pH is one of the most important factors explaining the species composition (Billings & Drew, 1938; Barkman, 1958; Sjögren, 1961, 1964; Bates, 1992). Species indicator values for substrate reaction (*sensu* Düll, 1991) turned out to be an important distinguishing character in the present study. As only the acidic and biologically almost inert granite boulders were included in the study, the values for substrate reaction probably reflect the influence of the covering tree species (**I**). However, the values for substrate reaction (Düll, 1991) are more complex than just measures of pH conditions. Nutrient availability certainly also plays an important role. Bryophytes growing on substrates with a low pH and slow weathering are expected to be highly dependent on both water and nutrients from the trees.

### **Influence of litter**

The effect of litter is probably one of the most important factors regulating bryophyte species composition in forests (von Krusenstjerna, 1945; Sydes & Grime, 1981; Xiong & Nilsson, 1999). Paper I confirms the results of von Krusenstjerna (1945), who suggested that the epilithic bryophyte community *Antitrichion* grows almost exclusively on substrates affected by litter from base-rich tree species (Fig. 4). Base-rich deciduous litter raises the pH on the substrate surface more than litter from gymnosperms and other trees with a low pH, e.g. *Betula* spp. (von Krusenstjerna, 1945).

The litter on a boulder in a forest mainly comes from the tree above it, but even the small and compact needles from Norway spruce are sometimes transported 10 to 20 metres. This “edge” effect of litter blowing around is probably one reason why species richness is higher at Vårdsätra than at Billingsudd (**II**). Therefore, it is concluded that the effect of a tree can be observed some distance away from the edge of the crown.

Intermediate amount of litter on the plot-level was positive for species richness, while boulder species richness was highest if the boulder was covered by a large amount of litter (Fig. 5). On the plot-level the small area (1 dm<sup>2</sup>) can be completely covered by litter. On the boulder, on the other hand, there are always more or less litter-free areas where bryophytes can grow. It is interesting to note that these results were consistent for boulders below all tree species (**II**). Even below Norway spruce the most species rich boulders were those that gathered most litter (**II**). However, these boulders have a distinctly different species composition (**I**).

In the experiment with permanent plots, deciduous litter had a positive effect on bryophyte species richness during the study period (IV). This supports the result in paper II, that plots with intermediate amounts of deciduous litter are more species rich than those without litter. As expected, there was a negative effect on species richness in the permanent plots treated with Norway spruce litter, and also on the cover of *Pterigynandrum filiforme* and *Orthotrichum anomalum* (IV). These decreases could be caused by the toxic and acidifying effect of Norway spruce litter.

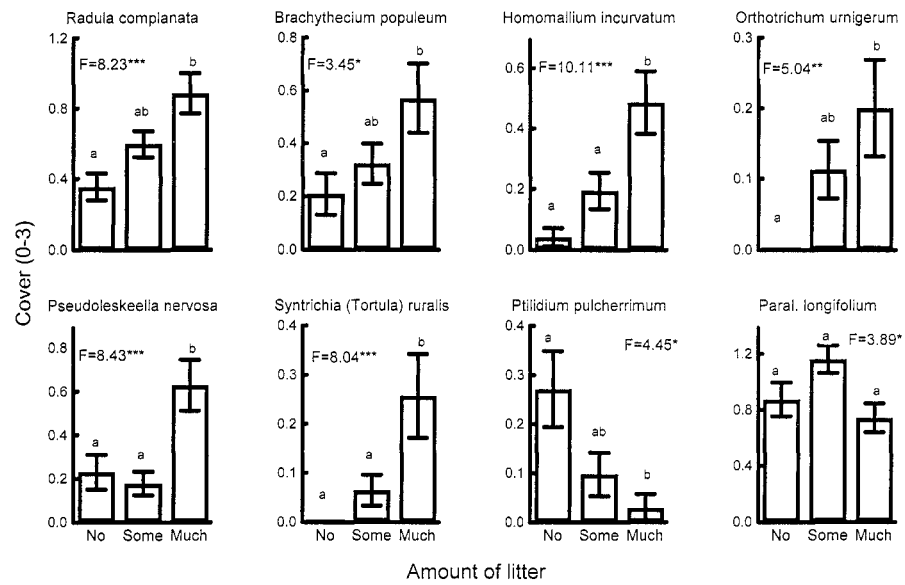


Figure 4. Mean cover (0-3) of selected bryophytes on boulders with different amounts of litter at Billingsudd. Differences among litter classes were tested with ANOVA with Tukey test for unequal sample sizes and the F-value is given in the figure with the significance of the test indicated: \*\*\*  $p < 0.001$ , \*\*  $p < 0.01$  and \*  $p < 0.05$ . Whiskers indicate  $\pm$  one standard error and lower-case letters show significant differences between litter classes ( $p < 0.05$ ) (I).

## Disturbance

The direct effects of fungi and detachment of bryophyte patches in paper IV can be viewed as disturbance: a discrete displacement, damaging or killing of one or more shoots, which directly or indirectly creates opportunities for new individuals (modified after Sousa, 1984). However, the effects of leaf litter are more indirect and act in different ways. The toxic effect of substances leaching from the litter



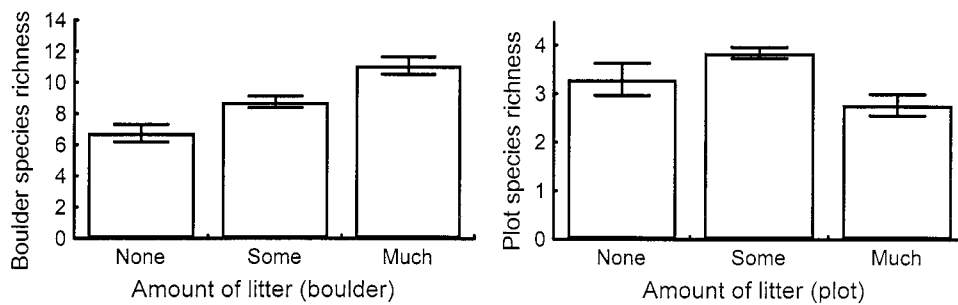


Fig. 5. Bryophyte species richness on whole boulders (left) and in plots (right) for the different classes of litter amount: none (no litter present), some (<1/4 of the boulder/plot covered) or much (>1/4 of the boulder/plot covered). Bars represent mean values and whiskers  $\pm$  one standard error (II).

(Swift *et al.*, 1979) can be viewed as a disturbance. The negative effect of litter covering the bryophytes, not allowing light to penetrate (Xiong & Nilsson, 1999) more resembles stress through asymmetric competition of light from the tree (*sensu* Grime, 1979), while the presumably positive effect of nutrients leaching from the litter can enhance growth and fitness, and thereby counteract the negative effects of litter. However, it is concluded that litter, as well as other factors affecting the fine-scale disturbance of bryophyte shoots and patches, are important for maintaining high species richness on boulders.

At plot-level the effect of litter cover is most easily explained in terms of the intermediate disturbance hypothesis (see review in Huston, 1994), with too low cover leading to competitive dominance and too high cover preventing colonisation (Fig. 6). At boulder level the positive effect of litter on species richness means that there are areas with both high and low cover of litter (II).

Plots with large area of exposed rock are probably recently disturbed and the bryophytes have been removed either because of: 1) too much litter (repeated disturbance) that results in a constant low species richness; or 2) lost bryophyte patches due to a single disturbance event. At low bryophyte cover only a few species have invaded the available substrate. At intermediate bryophyte cover most species have invaded, but there is still available bare rock. At high bryophyte cover there is little or no available bare rock and therefore the species come in such a close contact that interspecific competition and competitive exclusion can take place (Rydin, 1997). When the bryophyte cover becomes thick there is an increasing risk of patches falling off the boulder, which increases with

increasing inclination of the substrate (also shown by Hestmark, 1997). The high rate of disturbance prevents interaction between bryophyte species and therefore high species richness can be maintained.

In the study of permanent plots the detachment of bryophyte patches was quantified to 1-4%, which in most cases was caused by the detachment of an individual patch, 0.2-2 dm<sup>2</sup> in size, consisting of several species (IV). Despite the relatively large size of detached patches there were no net change of species richness (IV). Detached bryophyte patches were able to re-colonise plots with exposed rock, which shows that there can also be directly positive effects of detachment of bryophyte patches on species richness (IV). There were probably several agents behind the detachment of bryophyte patches, of which the effects of badger (*Meles meles*), birds and fungi were the most obvious.

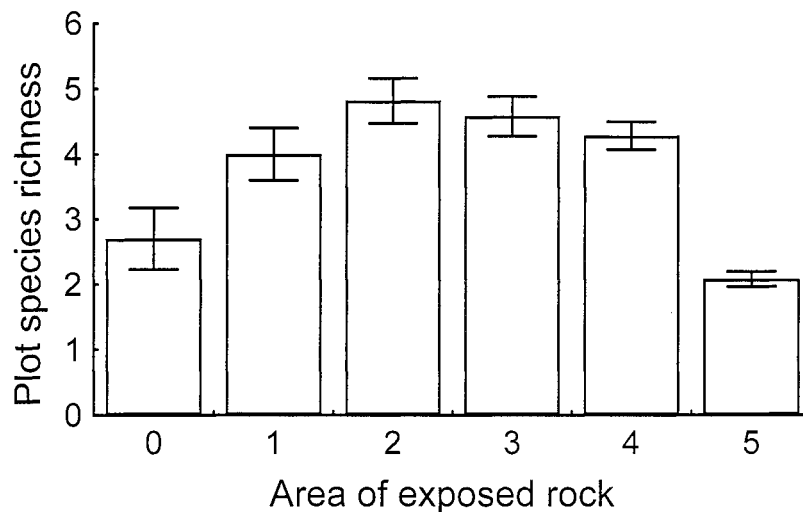


Fig. 6. Bryophyte species richness in plots for the six classes of area of exposed rock: 0 (none), 1 (<6.25%), 2 (6.25-12.5%), 3 (12.5-25%), 4 (25-50%) and 5 (50-100%). Bars represent mean values and whiskers  $\pm$  one standard error (II).

### Bryophytes and species-area relations

Individual plots were on average not more species-rich on large boulders than on small ones, even though large boulders had more species (II). Therefore, it is concluded that population extinctions on the plot-level, and re-colonisations from other parts of the boulder, are less important for species richness than within-

boulder habitat diversity. The result is consistent with the study of vascular plants on habitat islands by Köchy & Rydin (1997). However, the positive influence of area on bryophyte plot species richness, in a study by Tangney *et al.* (1990), shows that the results cannot be generalised to all types of ecosystems.

The results have implications for the long-lasting debate on the relationship between species richness and area, and the choice of model for fitting species-area curves (e.g. Rydin & Borgegård, 1988; Ekbohm & Rydin, 1990; Loehle, 1990; and review in Rosenzweig, 1997). While there are promising new ways to model the species-area relationship (He & Legendre, 1996; Leitner & Rosenzweig, 1997), the results in paper **II** suggest that it would be worthwhile to further develop general models, in which classificatory and continuous variables are explicitly used together with area to predict species richness. Despite early attempts by Buckley (1985) this field is rather poorly developed.

### **Implications for conservation**

In deciduous forest nature reserves the expansion of Norway spruce can be a threat to the bryophyte flora. In management plans for nature reserves it is often stated that the forest should be allowed to develop freely. However, such development should be monitored, and if the purpose is high diversity one should prevent the expansion of Norway spruce, and perhaps also increase the amount of base-rich deciduous trees in the forests. The higher species richness below Norway spruce at Vårdsåtra, compared to Billingsudd, was the result of an edge effect (**II**). Base-rich deciduous litter can easily reach under most Norway spruce canopies at Vårdsåtra, where ash and elm are very common (**I** and **II**). This indicates that several tree individuals are needed in the forest stand to significantly influence the species richness.

Even in areas with moderate levels of air pollution (such as southern Sweden), acid deposition has had strong impact on the bryophyte flora (Hallingbäck, 1992; Sjögren, 1995). Here it is even more important to keep or even increase the amount of base-rich deciduous trees, as their throughfall and litter to some extent can buffer the acid deposition (Stoutjesdijk & Barkman, 1992; Nordén, 1994b).

Measures that change the relative humidity in forests, e.g. clear cutting or thinning, have severe effects on the occurrence and performance of bryophytes (Hazell & Gustafsson, 1999). This is in accordance to the results in paper **III** where relative humidity and the time that the bryophyte is hydrated have effect on vegetative growth. However, the response differs between bryophyte species. Therefore, it is important to take the most sensitive species into consideration in restoration of forests with high conservation value and in commercial forestry planning.

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