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# Metapopulation and metacommunity processes, dispersal strategies and life-history trade-offs in epiphytes

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#### **Abstract**

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The aim of this thesis was to increase knowledge about metapopulation and metacommunity processes in patchy, dynamic landscapes, using epiphytic bryophytes as a model system. Host trees and deciduous forest stands in the coniferous landscape are patchy, temporal and undergo changes in habitat quality during succession. Epiphytes must track this dynamic habitat network for their long-term survival. Community patterns at different spatial scales were explored and linked to regional metapopulation processes and local population dynamics.

Spatial structuring in species richness both at a local and regional scale indicated stronger dispersal limitation but lower sensitivity to habitat quality in species with large asexual than in species with small sexual diaspores. In sexually dispersed species, a strong rescue effect was indicated by a bimodal frequency distribution of the species and by increasing local abundance with increasing patch connectivity. Present connectivity to other deciduous forest patches had positive effects on richness of asexually dispersed species, whereas richness of sexually dispersed species was instead related to the landscape connectivity 30 years ago. A study of local growth and reproduction suggested that this is caused by delayed sexual, but not asexual, reproduction. Habitat conditions affected the production of sporophytes, but not of asexual diaspores. No differences in either growth rates or competitive abilities among species with different dispersal and life-history strategies were found. *In vitro* experiments showed that establishment is higher from large asexual diaspores than from small sexual. Establishment of all diaspore types was limited by pH. There were indications of trade-offs between high germination and protonemal growth rates, desiccation tolerance and a rapid development of shoots from protonema.

The results indicated that the epiphyte metacommunity is structured by two main trade-offs: dispersal distance (diaspore size) versus age at first reproduction, and dispersal distance versus sensitivity to habitat quality. Trade-offs in species traits may have evolved as a consequence of conflicting selection pressures imposed by habitat turnover, connectivity and irregular water supply rather than by species interactions. Syndromes of interrelated species traits imply that fairly small changes in habitat conditions can lead to distinct changes in metacommunity diversity: the results indicate that increasing distances among patches cause most harm to asexually dispersed species, whereas cuttings of forests of high age and quality as well as increasing patch dynamics are most harmful to sexually dispersed species.

*Keywords:* asexual, biodiversity, bryophytes, dispersal limitation, establishment, evolution of reproductive traits, germination, growth, habitat fragmentation, landscape dynamics, local processes, patch-tracking, pH, reproduction, species richness, species interactions

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*Till alla som har hjälpt mig  
att bli frisk igen*



# List of Papers

This thesis is based on the following papers, which are referred to in the text by their Roman numerals.

- I Löbel, S., Snäll, T., Rydin, H. (2006a) Species richness patterns and metapopulation processes – evidence from epiphyte communities in boreo-nemoral forests. *Ecography*, 29(2):169–182
- II Löbel, S., Snäll, T., Rydin, H. (2006b) Metapopulation processes in epiphytes inferred from patterns of regional distribution and local abundance in fragmented forest landscapes. *Journal of Ecology*, 94(4): 856–868
- III Löbel, S., Snäll, T., Rydin, H. (2009) Mating system, reproduction mode and diaspore size affect metacommunity diversity. *Journal of Ecology*, 97(1): 176–185
- IV Löbel, S., Rydin, H. (in press) Dispersal and life-history strategies in epiphyte metacommunities: alternative solutions to survival in patchy, dynamic landscapes. *Oecologia*, DOI: 10.1007/s00442-009-1402-1
- V Löbel, S., Rydin, H. Bottle-necks and trade-offs in the establishment of epiphytes. *Manuscript*

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I planned all studies, conducted the field and laboratory work, analyzed the data and wrote the texts. T. Snäll and H. Rydin contributed with valuable discussions of the study concepts, data analyses, results and manuscripts.



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# Introduction

## Habitat loss and fragmentation as threats to biodiversity

Habitat loss and fragmentation are major threats to biodiversity (Heywood 1995). In present day landscapes many forest species are restricted to remnants of a formerly more or less contiguous forest cover. In Fennoscandia, modern forestry has led to a great decrease of old-growth forests and a low proportion of deciduous trees (Berg *et al.* 2002).

Host trees and deciduous forest stands in the coniferous landscape are patchy, temporal and undergo changes in habitat quality during succession. Many species must track this dynamic habitat network for their long-term survival (Snäll *et al.* 2005a). Increased dispersal distance, as imposed by landscape fragmentation, may lead to species extinctions and reduced biodiversity. Reduced habitat quality of small forest fragments due to forest edge effects may be fatal for many highly specialized species (Harrison & Bruna 1999; Moen & Jonsson 2003). Forest fires were the main disturbance regime in the natural forest landscape which stochastically varied in space and time (Niklasson & Granström 2000). Current forestry practice promotes conifers, and thus does not provide alternative means of host tree generation. Cutting rotation times are often shorter than natural forest fire rotation times, potentially causing harm to species with slow population dynamics such as many epiphytes (Snäll *et al.* 2005a, b).

## Metapopulation theory

Metapopulation theory has increased our understanding of the dynamics of species in fragmented landscapes, and has become an important tool for nature conservation. According to theory, the most critical aspects of habitat fragmentation are reduced patch sizes and increasing distances between habitat patches (Hanski & Gaggiotti 2004). Population sizes are expected to increase with the patch size which reduces the local extinction risk (Hanski 1999). In addition, with increasing patch size the ‘target area’ for dispersing diaspores increases. In temporary habitats such as trees, the patch area includes yet an additional dimension: the time, as reflected by tree diameter, under which a patch has been available for colonization (Snäll *et al.* 2003). However, empirical data suggest that reduced habitat quality of small

patches and edge effects are more important than area or distance effects *per se* (Debinsky & Holt 1999; Moen & Jonsson 2003). Further complexity is added by the fact that the time-lag between passing the extinction threshold and regional metapopulation extinction can be long, implying that effects of habitat fragmentation may first be detected after many years (Ovaskainen & Hanski 2002). Epiphytes that have inertia to stochastic local extinctions belong to this group of species (Snäll *et al.* 2005a; Ellis & Coppins 2009).

The core-satellite hypothesis (Hanski 1982) suggests that the importance of metapopulation processes can be assessed from regional frequency distributions and local abundances. The model predicts that within a region, most species are either core species, which are abundant within patches and occur in > 90% of all patches, or satellite species, which are sparse within patches and occur in < 10% of all patches. This bimodality is explained by metapopulation dynamics including a rescue effect, i.e. recurrent immigration reduces the rate of local extinction (Hanski & Gaggiotti 2004). Inferences about metapopulation processes can be further made from spatial species occupancy patterns by applying the incidence function model approach (Hanski 1994), and rescue effects may be detected by analyzing the impact of patch connectivity (*sensu* Hanski 1999) on local species abundances. Declining local abundances may be detected long before species extinctions, and thus, may serve as an early warning system.

## Metacommunity theory

The metacommunity approach extends the metapopulation concept to the community level. The most basic issue is to address what regulates coexistence of species in a system of connected habitat patches (Leibold & Miller 2004). There are four main frameworks: ‘patch dynamics’, ‘species-sorting’, ‘mass-effects’ and the ‘neutral model’ (Leibold & Miller 2004). The patch dynamics perspective highlights the importance of classical metapopulation dynamics of single species; patches are assumed to be homogeneous, but differ in the degree of connectivity. The metapopulation dynamics of single species should be reflected in aggregated species richness patterns, and increasing species number with increasing habitat patch size. The focus of the species-sorting perspective is on habitat heterogeneity among patches and niche specialization. The ‘mass-effects’ perspective addresses the effects of dispersal from high to low quality patches (source-sink dynamics). The ‘neutral’ perspective highlights the importance of stochastic metapopulation processes. Metacommunities may be ruled by several, rather than by a single theoretical framework (Ellis *et al.* 2006; Moullot 2007), and the predominating framework may be strongly related to dispersal rates and types (Van de Meuter *et al.* 2007; Vanschoenwinkel *et al.* 2007).

It is commonly assumed that long-term coexistence of species requires some trade-off among important biological traits (Chase *et al.* 2005). Metacommunity theory draws attention to traits that operate at regional scales, especially dispersal and associated life-history trade-offs (Leibold & Miller 2004). Most work has focused on competition-colonization trade-offs (e.g. Chase *et al.* 2005; Mouquet *et al.* 2005). In plants, seed number versus seed size has often been used as a surrogate for this trade-off; nonetheless the species traits that determine competitive and dispersal abilities are complex (Kneitel & Chase 2004), and very few empirical studies have adequately assessed both the colonization and competition process (Cadotte *et al.* 2006). Neutral lottery models and theories of unstable coexistence further challenge classical theories of species coexistence: colonization differences among species can theoretically be part of an equalizing trade-off where species end up having equal fitness (Chesson 2000). In addition, in communities of sessile organisms, competition is a neighbourhood phenomenon, rather than a Lotka-Volterra type of global interaction. This, together with spatial aggregation of species may reduce rates of competitive exclusion (Silvertown *et al.* 1992; Bengtsson *et al.* 1994). Possibly, many communities consist of species that interact so weakly that interactions can be largely ignored (Hanski 1999). Alternative dispersal strategies offer several trade-offs to be explored: life-history parameters do not vary independently of each other and are constrained by trade-offs with other biological parameters (Söderström & Herben 1997).

## Dynamic landscapes and system non-equilibrium

Classical biodiversity, metapopulation and community theories assume system equilibrium and static landscapes. Given that dynamic habitats and system non-equilibrium may be the rule rather than an exception (e.g. Stelter *et al.* 1997; Snäll *et al.* 2003), applications of the original theories in nature conservation can be questioned. ‘Patch-tracking’ metacommunities, characterized by a short life-time of the habitat patches in relation to the slow local population dynamics of the inhabiting species (Snäll *et al.* 2003, 2005a), may never reach the assumed colonization-extinction equilibrium. Such metacommunities may be mainly structured by dispersal patterns rather than by competition-colonization trade-offs (cf. Zartman & Shaw 2006).

Species inhabiting dynamic landscapes have to cope with an ever-changing number, quality and spatial arrangement of habitat patches over time (Johst *et al.* 2002). Persistence and abundance of such species are the results of a dynamic balance between habitat duration and the ability of species to disperse and colonize habitat patches. Successful dispersal involves three main processes: the production, transport and establishment of diaspores. Most studies focus on diaspore transport, and mean dispersal dis-

tance has been shown to be an important species trait for dispersal success in dynamic landscapes (Johst *et al.* 2002; Bossuyt & Honnay 2006). For wind dispersal, a negative relation between diaspore size or weight and dispersal distance has been shown (Tackenberg *et al.* 2003), but a higher establishment probability from large diaspores (Moles & Westoby 2004, 2006) may counteract the advantage of small diaspores, especially if habitat fragmentation is associated with alteration in habitat quality. However, bottle-necks during the establishment stage generally have gained very little attention in metacommunity studies, but may be a major cause for species rarity and distribution (Wiklund & Rydin 2004b).

Johst *et al.* (2002) theoretically showed that high growth rates are important for species survival, even in non-competitive metacommunities: long-range dispersal loses its advantage in dynamic landscapes if numbers of potential emigrants are low due to low local population growth rates. If habitat turnover is fast, patch longevity can be the most critical parameter for species persistence (Holyoak *et al.* 2005; Miller & Kneitel 2005; Bossuyt & Honnay 2006). In such situations, age at first reproduction and dispersal frequency, and hence mating systems and reproduction modes, may play an important role for dispersal success. Self-fertility and asexual reproduction have evolved in many sessile organisms that inhabit patchy and dynamic habitats (Longton 1994), providing means to overcome long distances between mates (Kalisz *et al.* 2004). Asexual reproduction may also be an adaptation to the dynamic nature of certain habitats as it often occurs continuously and at younger age than sexual reproduction (Pohjamo & Laaka-Lindberg 2004; Pohjamo *et al.* 2006). This aspect of asexual reproduction has rarely been considered.

## Epiphytic bryophytes as model organisms

Epiphytic bryophytes confined to deciduous trees interspersed among dominant conifers provide an excellent model system for exploring dispersal and metacommunity processes in dynamic landscapes. The dynamics of single host trees are rapid compared to the long life span of most epiphytes, and local extinctions are mainly governed by tree fall (Snäll *et al.* 2005a).

Dispersal limitation and metapopulation dynamics of epiphytes have been indicated by dispersal experiments, recorded colonizations of trees, spatial genetic structuring, and spatially aggregated species distributions (e.g. Dettki & Esseen 2003; Snäll *et al.* 2003, 2004a, b, 2005a). Metapopulation persistence may be significantly affected by the dynamics of the habitat patches (Snäll *et al.* 2005a, b). Species show high habitat specificity, and substrate quality may be particularly important during the establishment phase (Wiklund & Rydin 2004b). It has been suggested that competition among bryophytes is of minor importance for community structure and rarely leads to

species exclusion (e.g. Rydin 2009), but it has not been clarified whether epiphytes form 'interactive' metacommunities or not. Generally, most research has focused on single epiphyte metapopulations, whereas studies at the community level are rare.

Epiphytic bryophytes have evolved different mating systems, and their dispersal units, which are either produced sexually or asexually, differ widely in size. Bryophyte dispersal strategies are viewed as alternative solutions to the problem of survival in dynamic and patchy landscapes with long-lived dioecious species inhabiting stable habitats, marked by low reproductive effort, viewed as the most primitive strategy (Longton 1994). From that starting point, two principal evolutionary trends are suggested: monoecism and the production of asexual diaspores, which is much more common among dioecious than monoecious species (During 2007). Most asexual diaspores are distinctly larger than sexual spores, with shorter dispersal distances but higher establishment rates (Kimmerer 1994; Laaka-Lindberg *et al.* 2003, 2006). Studies have indicated lower energetic costs, less sensitivity to habitat conditions and reproduction at a younger age of asexual compared to sexual reproduction (e.g. Pohjamo *et al.* 2006). During (1979, 1992) proposed a classification of bryophyte life-history strategies based on trade-offs between gametophyte longevity and reproductive effort, and between spore size and spore number.

A diaspore encounters several bottle-necks before a new gametophyte is established. Diaspores may be dispersed across environments that differ much from the typical shady and humid source habitat of the old-growth forest, and desiccation tolerance determines diaspore viability when a suitable patch is reached (Proctor *et al.* 2007). Bark is prone to desiccation, and wet periods offer brief windows of opportunity for establishment. Survival until favourable germination conditions occur thus may be crucial. Germination may depend on habitat conditions, especially bark pH (Wiklund & Rydin 2004b), and diaspore types may differ in their habitat requirements for germination. Protonemal tissues are more sensitive to drought than both the diaspores and the gametophyte (Proctor *et al.* 2007). Hence, protonemal growth rates and the time it takes for the first shoots to develop may be central for the establishment success. Establishment from asexual diaspores may be less sensitive to habitat conditions and faster than from spores if establishment occurs directly, rather than via protonema production.

## Aims of this thesis

The general aim of this thesis was to increase ecological knowledge about metapopulation and metacommunity processes in patchy, dynamic landscapes, using epiphytic bryophytes as a model system. Community patterns at different spatial scales were explored and linked to regional dispersal and

metapopulation processes, and to local population dynamics (growth, species interactions, reproduction and establishment) of epiphytes with contrasting reproductive and dispersal strategies. The hypothesis that patch-tracking metacommunities are structured by reproductive and dispersal strategies rather than by competition-colonization trade-offs was tested. Trade-offs in dispersal and life-history strategies, as well as critical life-history traits for survival in patchy, dynamic landscapes, were identified and used to predict metacommunity responses to habitat fragmentation, alteration in habitat quality and landscape dynamics. Hypotheses about the evolution of alternative dispersal strategies in patch-tracking metacommunities were developed.

More specifically, the following questions were addressed:

- Does species richness show spatial aggregation at a local within-stand scale, and how much of the spatial aggregation can be attributed to local environmental conditions and to dispersal limitation and metapopulation dynamics? (I)
- Do regional distributions and local abundances of epiphytes show a bimodal pattern as predicted by the core-satellite hypothesis? Is it possible to assign these patterns to dispersal processes and metapopulation dynamics of single epiphyte species? (II)
- What is the relative importance of forest stand size, quality, connectivity and landscape history for species occupancy patterns and local abundances (II), and species richness patterns (III) at a regional scale?
- Do species with different mating systems, reproduction modes and diaspore sizes respond in different ways to habitat fragmentation, alteration in habitat quality and changes in landscape dynamics? Is the scale of spatial structuring related to diaspore size? (III)
- Do species with different reproduction modes and life-history strategies differ in local growth rates, sensitivity to habitat conditions, competitive ability or reproductive age and frequency? (IV)
- Which are the most critical stages in the establishment of epiphytic bryophytes with different diaspore types and sizes? How is establishment success affected by habitat conditions? (V)

# Material and methods

## Study system, species and sites

In paper I, I included all obligate ('specialists') and facultative ('generalists') epiphytic bryophytes and lichens growing on deciduous trees with a nutrient rich bark (*Acer platanoides*, *Fraxinus excelsior*, *Populus tremula*, *Prunus padus*, *Quercus robur*, *Salix caprea*, *Tilia cordata* and *Ulmus glabra*, 'host trees' henceforth). In this thesis, I focus on the bryophytes. For papers II-V, studies were restricted to obligate epiphytic bryophytes. Other tree species, namely *Picea abies*, *Pinus sylvestris*, *Betula* spp. and *Alnus glutinosa*, have a distinctly lower bark pH and none of the obligate epiphytes occur on them. In the coniferous forest landscape, host trees and host tree forest stands form distinct habitat patches for the epiphytic specialists.

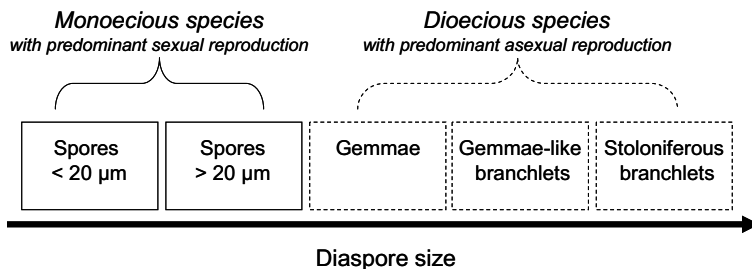


Figure 1. Epiphytic bryophyte groups differing in dispersal strategies. Grouping was done according to mating system, reproduction mode and diaspore size.

I distinguished between specialist species with predominant sexual or asexual reproduction (I, II). In paper III, I further differentiated among mating systems and diaspore sizes (Fig. 1). For paper IV, I studied growth and reproduction of 12 species (Table 1), i.e. all main obligate epiphytes occurring within the study forest. I grouped species according to their reproduction mode and life-history strategy (During 1979, 1992). Colonists reproduce by numerous light spores (< 20 μm); the reproductive effort is high and the potential life span short. Short- and long-lived shuttles reproduce by fewer, larger spores (> 20 μm). Perennial stayers reproduce only rarely by small spores; their potential life spans are several decades. For the establishment

experiments (V), I used 14 species: three mosses with small spores, three with large spores, two liverworts with large spores, three mosses with gemmae and three with gemmae-like branchlets.

Table 1. Mating system, spore size and production of asexual diaspores of the species included in the study of local population dynamics (IV) and the establishment experiments (V). Life-history strategies according to the During classification system (1979, 1992; Dierßen 2001; Hill *et al.* 2007) were listed with the exception that within the study region, *Pylaisia polyantha* and *Platygyrium repens* act as colonists, rather than as perennial stayers.

Species	Mating system	Spore size (µm)	Asexual diaspores	Life-history strategy
<b>Mosses with predominant sexual reproduction</b>				
<i>Homalia trichomanoides</i> <sup>IV, V</sup> (Hedw.) B.S.G	monoecious	14 – 16	stoloniferous branchlets	perennial stayer
<i>Isoetecium alopecuroides</i> <sup>IV, V</sup> (Dubois) Isov.	dioecious	12 – 16	none	perennial stayer
<i>Neckera pennata</i> <sup>IV, V</sup> Hedw.	monoecious	22 – 24	stoloniferous branchlets	long-lived shuttle
<i>Orthotrichum speciosum</i> <sup>IV, V</sup> Nees	monoecious	20 – 28	none	short-lived shuttle
<i>Pylaisia polyantha</i> <sup>IV, V</sup> (Hedw.) Schimp.	monoecious	13 – 16	none	colonist
<i>Ulota crispa</i> <sup>IV, V</sup> (Hedw.) Brid.	monoecious	24	none	short-lived shuttle
<b>Liverworts with predominant sexual reproduction</b>				
<i>Frullania dilatata</i> <sup>IV, V</sup> (L.) Dum.	dioecious	40 – 60	gemmae	long-lived shuttle
<i>Radula complanata</i> <sup>IV, V</sup> (L.) Dum.	monoecious	25 – 30	gemmae	long-lived shuttle
<b>Mosses with predominant asexual reproduction</b>				
<i>Anomodon longifolius</i> <sup>V</sup> (Brid.) Hartm.	dioecious	13	stoloniferous branchlets	perennial stayer
<i>Bryum flaccidum</i> <sup>IV, V</sup> Brid.	dioecious	9 – 13	gemmae	colonist
<i>Leucodon sciuroides</i> <sup>IV, V</sup> (Hedw.) Schwaegr.	dioecious	20 – 28	gemmae-like branchlets	long-lived shuttle
<i>Orthotrichum gymnostomum</i> <sup>V</sup> Brid.	dioecious	20	gemmae	long-lived shuttle
<i>Orthotrichum obtusifolium</i> <sup>V</sup> Brid.	dioecious	20	gemmae	short-lived shuttle
<i>Platygyrium repens</i> <sup>IV, V</sup> (Brid.) Schimp.	dioecious	16 – 20	gemmae-like branchlets	colonist
<i>Pseudoleskeella nervosa</i> <sup>V</sup> (Brid.) Nyh.	dioecious	16	gemmae-like branchlets	perennial stayer
<b>Liverworts with predominant asexual reproduction</b>				
<i>Metzgeria furcata</i> <sup>IV, V</sup> (L.) Dum.	dioecious	20 – 28	gemmae	long-lived shuttle



All studies were performed in the boreo-nemoral region in central Eastern Sweden. For paper I, I studied the epiphyte species richness patterns in two forest stands (Erken: 2.8 ha, Valkrör: 2.4 ha). The stands are eutrophic elm-ash forests with transition to eutrophic alder-ash forests (Diekmann 1999). The forests show traces of tree cuttings, but are not affected by recent forestry. Valkrör is a nature reserve in a late successional stage. Diaspores used in the establishment experiments (V) originated from Valkrör, Erken and two other forests. The study for paper IV was conducted at Valkrör.

The regional studies (II, III) were conducted in a landscape within the same region (Fig. 2). Today, the landscape consists of a mosaic of managed and unmanaged forests with a total of 135 forest stands harbouring the host tree species (0.01–15 ha). During the 16<sup>th</sup>–18<sup>th</sup> centuries the area was more densely inhabited, mainly by crofters. In the 19<sup>th</sup> century many fields were abandoned and developed into forests. Forestry was extensive until the 1970s. Thereafter, many old deciduous forests have been cut and replaced by forests dominated by *Picea abies* (Eriksson 1997).

## Species richness pattern at a local scale (I)

In 2003, I surveyed all epiphytic bryophytes growing on all host trees within the two study forests of Erken and Valkrör (1021 trees). Habitat conditions were recorded for each tree (diameter at breast height (DBH), bark structure, bark surface pH, light conditions, soil moisture, stem inclination). The bark surface pH was measured using a pH-electrode for surface measurements (Hamilton single pore flat). Light conditions were assessed by measuring canopy openness (%) using digital hemispherical photography. To describe host tree connectivity, maps were made of the positions of all broad-leaved deciduous trees, snags and logs within the stands.

I analyzed the species-area relationship (area = tree diameter). The effects of environmental variables on patterns of total and group specific species richness were tested by fitting generalized linear models (GLM; McCullagh & Nelder 1989). In order to test for spatial correlation among trees in total and in group specific species richness, I applied semi-variance analyses. I fitted exponential variogram models to the residuals of the GLMs as

$$\text{Semi-variance} = \tau^2 + \sigma^2 (1 - \exp^{-D_{ij}/\Phi});$$

$\tau^2$  is the nugget,  $\sigma^2$  is the sill,  $\Phi$  is the range parameter and  $D_{ij}$  is the Euclidian distance between host trees.  $\tau^2$  is the short range variance;  $\sigma^2$  is the difference between  $\tau^2$  and the overall variance in the study area.  $\Phi$  determines the scale of spatial aggregation. The variogram models inform us first, about how much of the variation in species richness is explained by spatial aggregation, and second, about the scale of spatial aggregation.

## Community pattern at a regional scale (II, III)

All host tree forest stands within the study landscape were visited, positioned by GPS (Global Positioning System) and mapped in a GIS (Geographic Information System, Fig. 2). Isolated groups of host trees were considered as separate stands if they were separated by at least 25 m of wetland or other forest types. The state of the historical landscape was recorded from infra-red aerial photographs from 1977. On these photos, it is difficult to separate most host trees from other deciduous trees, but it is possible to distinguish *F. excelsior*. I therefore used the past spatial distribution of *F. excelsior* to indicate patches suitable in 1977 for the studied epiphytes (Fig. 2).

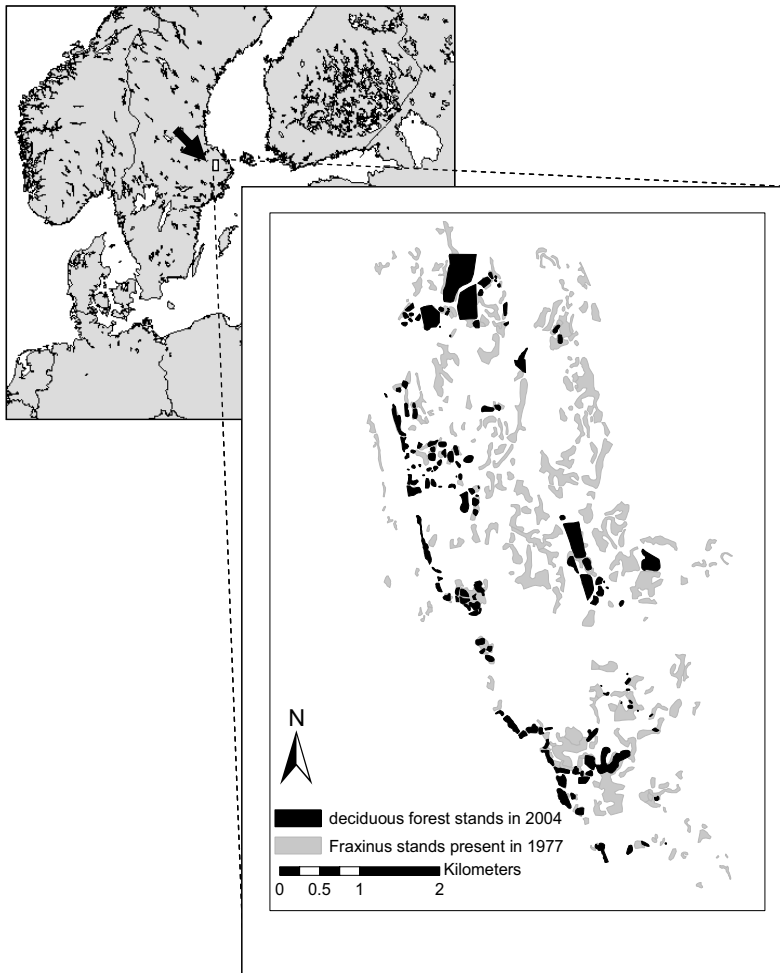


Figure 2. The study landscape of paper II and III with the surveyed host tree forest stands and *Fraxinus excelsior* stands in 1977, and its location in Eastern Sweden.

In each forest stand, all host trees  $\geq 15$  cm DBH were counted, and the tree species was noted. All obligate epiphytic bryophytes were recorded. In stands with  $\leq 100$  host trees, I measured the DBH and noted species presence/absence for each tree, in stands with  $> 100$  trees I did the same for every 5<sup>th</sup> tree, and in stands with  $> 1000$  trees I did it for every 10<sup>th</sup> tree. The number of occupied host trees by a species was extrapolated to the whole stand. I estimated the soil moisture, the cover of boulders, and the total basal area of trees per ha.

The ‘regional frequency’ of a species was defined as the number of forest stand patches occupied by the species. The ‘regional frequency distribution’ described the distribution of regional frequencies among species. The ‘absolute local abundance’ was the number of occupied host trees in a local forest stand; it scales the rate of diaspore output (emigration) from a stand. The ‘relative local abundance’ was the proportion of occupied trees in a stand. It is determined by immigration from surrounding stands and by colonization-extinction dynamics among trees within stands.

I investigated the species-area relationship, and the relationship between regional frequency and local species abundance. I used Tokeshi’s (1992) test for bimodality to determine whether species frequency distributions were significantly unimodal or bimodal. To test whether these patterns can be assigned to dispersal and metapopulation processes of single species, I tested the effects of forest patch area, host tree number, maximum tree diameter, patch quality, forest edge, forest patch area and *F. excelsior* density in 1977, as well as of present and historic connectivity on species occupancies and species relative local abundances. Connectivity was defined as

$$S_i = \sum_{j \neq i} p_j \exp(-\alpha (\ln(d_{ij}))^2) Q_j^\gamma;$$

the indices  $i$  and  $j$  refer to the focal and surrounding stands, respectively. The effect of the surrounding stand was quantified by the log-normal function of the distance  $d_{ij}$  (m) between the centroids of the stands  $i$  and  $j$ . For the present connectivity variable,  $p_j = 1$  if the species occurred in the surrounding stand  $j$ , and  $p_j = 0$  if it did not occur;  $Q_j$  was the absolute local species abundance in stand  $j$ . In case of the historic connectivity variable,  $Q_j$  denoted the area in 1977 of the surrounding stand  $j$ , and  $p_j$  was set to one. The parameter  $\alpha$  controls the rate of decay,  $\gamma$  is a scaling parameter. The larger the  $\alpha$ -parameter in the connectivity variable, the smaller is the scale at which species show spatial aggregation (Hanski 1999).

In the same way, I tested whether epiphyte species with different mating systems, reproduction modes and diaspore sizes respond in different ways to habitat fragmentation, alteration in habitat quality and landscape dynamics. In this case, I used species richness of the different epiphyte groups (Fig. 1) as response variable, and in the present connectivity variable,  $Q_j$  was the species richness of the surrounding forest patch  $j$ , and  $p_j$  was set to one.

## Growth, reproduction and species interactions (IV)

Colony growth and reproduction in 12 obligate epiphytes were studied during September 2004 and September 2005. About 40 colonies of each species were marked and their peripheries drawn on transparent plastic sheets. I noted the number of sporophytes as well as the presence of asexual diaspores. Colony drawings were digitized using a scanner. Colony area was calculated by counting pixels inside the perimeter (using *Image*, Karlsson 2007). For each colony, I recorded tree species, height above ground, DBH, bark surface pH, depth of bark crevices, stem inclination, light conditions and soil moisture. To analyze the effects of species interactions, I noted the cover of epiphytes (%) in deciles within 2 cm periphery of each colony.

Relative growth rate was calculated for each colony as

$$RGR = (\ln A_t - \ln A_0) / \Delta t;$$

$A_0$  is the initial colony area,  $A_t$  is the colony area at time  $t$ , and  $\Delta t = 1$  year.

I grouped species according to their reproduction mode (sexual, asexual) and life-history strategy. Species of the same group were analyzed together using linear or generalized linear mixed effect models. I tested a) whether species groups differed in *RGR*, b) the effects of environmental variables and cover of adjacent epiphytes on *RGR* of the different species groups, c) whether the presence of sporophytes or asexual diaspores affected *RGR*, d) whether there was a threshold-size in colony area for the onset of sexual and asexual reproduction, and e) whether sexual and asexual reproduction was affected by environmental variables and cover of other epiphytes. To predict when different species start to reproduce, I fitted GLM with the presence of sporophytes or asexual diaspores in either 2004 or 2005 as the response variable and the logarithm of colony area as predictor variable.

## Establishment experiments (V)

Germination, protonemal growth and establishment from bryophyte diaspores are difficult to study in the field as diaspores are virtually impossible to detect on natural substrates. I therefore used *in vitro* cultivation experiments to test establishment in 14 epiphytic bryophytes.

I used a full-sterilized nutrient solution; pH was adjusted to pH 4, 5, 6, 7, 8. Spore germination experiments were performed in liquid, for cultivations of gemmae, gemmae-like branchlets and gametophyte fragments the nutrient solution was solidified with 1.5% agar. The experiments consisted of four to six replicates per species and treatment. Experiments were carried out in a growth chamber with light/dark periods of 14/10 hours at 15/7.5 °C.

The proportion of germinated spores and gemmae was assessed after 0, 2, 3, 5, 7, 9, 12, 15, 20, 25, 30 days. In germinated spores the number of devel-

oped cells in the protonema was counted, in germinated gemmae the protonema size was measured. The length of the gemmae-like branchlets was measured on day 0, 9 and 20 and the production of protonema and rhizoids was noted. To study and compare establishment from different spore types and gemmae in the longer term, I followed germination, protonemal growth and transition from protonema to gametophytes of spores and gemmae at pH 6 during 90 days. Survival of different diaspore types under dry conditions was tested by putting spores, gemmae and gemmae-like branchlets to dry filter paper kept in open Petri dishes. After 0, 12, 30 and 50 days, samples of diaspores were taken from the filter paper and their germination ability was tested. To test establishment ability from gametophyte fragments at pH 4 and pH 6, I cut off the tips of 160 gametophytes of each species. The length and weight of the fragments was measured at the start of the experiment, and after 30 days. The development of rhizoids and protonema was noted.

Cumulative germination curves of spores and gemmae were modelled for each replicate using the positive Gompertz growth model

$$\omega = \alpha \exp(-\beta e^{-kt});$$

$\omega$  is the cumulative germination at time  $t$ ,  $t$  is the number of days from the start of cultivation,  $\alpha$  is the final cumulative germination, and  $\beta$  and  $k$  describe the shape of the function. The parameters  $\alpha$ ,  $\beta$  and  $k$  were estimated by non-linear regression.  $\beta$  and  $k$  were used to calculate the time to germination of 2% of the diaspores ( $t_2$ , 'onset of germination'). For gemmae-like branchlets, I used the highest recorded proportion of germinated branchlets as a substitute for  $\alpha$ .

For spores, protonemal growth rates were determined as an average for each replicate from the number of cells in the 10% fraction of spores with the fastest germination rate as suggested by Wiklund & Rydin (2004b). It was calculated as

$$\text{Growth rate (cells day}^{-1}\text{)} = (\text{no of cells at } t_2 - \text{no of cells at } t_1) / (t_2 - t_1);$$

$t_1$  was the first day when at least 10% of the spores had germinated, and  $t_2$  was the first day when the growth rate started to slow down (day 12 to 20 in different experiments). Hence, I used the period of initial linear growth. Initial growth rates of protonema from gemmae (mm day<sup>-1</sup>) were calculated in the same way, but from the length of the protonema. Initial growth rates of gemmae-like branchlets were calculated for each replicate from the length of the branchlets at the start of the experiment and after 20 days.

Species with similar diaspore types and sizes were analyzed jointly using linear or generalized linear mixed-effect models. Effects of pH on  $\alpha$ ,  $t_2$  and protonema or branchlet growth rates of the different diaspore types were tested. I analyzed whether the protonema size of different spore types and gemmae differed after 30 days of cultivation, and when the first gametophytic shoots were developed.

# Results and discussion

## Habitat patch quality

### Local scale (I)

At the local patch scale (host tree patches within forests), local environmental habitat conditions were important for epiphyte species richness. This is in line with earlier studies: different authors reported strong effects of environmental habitat factors on single epiphyte species occurrences (e.g. Heegaard & Hangelbroek 1999; Heegaard 2000; Snäll *et al.* 2003) and epiphyte metapopulation dynamics (Snäll *et al.* 2005a).

Habitat specialist richness was mainly explained by host tree species, bark pH and DBH, whereas the host tree species did not affect generalist species richness. The data indicated a higher host tree specificity of sexually than asexually dispersed species. Positive effects of light on species richness of asexually dispersed species further suggested lower sensitivity to high-light conditions and drought of asexually compared to sexually dispersed species.

Many epiphytes show a preference to a certain host tree species (Barkman 1958), which is mainly explained by differences in bark chemistry. In this study, the bark pH was important and explained variation in species richness beyond the type of host tree. This indicates that the bark pH varies considerably among trees of the same species.

### Regional scale (II, III)

Higher sensitivity to habitat conditions of sexually than asexually dispersed epiphytes were also observed at the regional scale (deciduous forest stands within the coniferous forest landscape): the density of *Acer platanoides* (implying host trees with a high bark pH) and of the total basal area of trees (implying humid, shady conditions) affected species richness of sexually, but not of asexually reproducing epiphytes (III). Environmental habitat conditions also explained a considerable part of occurrence probabilities and relative local abundances of many sexually dispersed species, but were relatively unimportant for most asexually dispersed species (II). Forest edge had negative effects on the relative local abundance of several species (II). Several studies have provided evidence that changes in patch quality related to patch size and edge effects have important impacts on local processes in fragmented landscapes (e.g. Harrison & Bruna 1999; Moen & Jonsson 2003).

My study confirmed this; it further indicated that sexually dispersed species are more sensitive to alteration in habitat quality at forest edges than asexually dispersed ones.

#### Growth and reproduction (IV)

It has been shown that local environmental conditions determine epiphyte growth and performance (Heegaard 2000). My results confirmed this (IV): bark pH was the most important predictor of *RGR* for both sexually and asexually reproducing species. Contrary to my expectation, there were no indications that growth of sexually reproducing species was particularly sensitive to habitat conditions. Effects of habitat conditions on species richness, occupancy and local abundance in sexual species (II, III) are more likely to be caused by the fact that, as in other systems (Pohjama *et al.* 2006), sexual reproduction in bryophytes depends on habitat conditions, whereas asexual reproduction does not: bark pH affected the presence of sporophytes, but not the presence of gemmae or gemmae-like branchlets.

#### Establishment (V)

Bottle-necks during the establishment stage are considered as a major cause for species rarity and distribution (Wiklund & Rydin 2004b). My establishment experiments did only partly confirm this. Germination and protonemal growth of all diaspore types was strongly affected by pH, but there were no indications for broader pH niches in large asexual diaspores than in small sexual ones. Low and high pH reduced the proportion of diaspores that finally germinated ( $\alpha$ ) for most diaspore types (Fig. 3a). Low and high pH also increased the time until the onset of germination ( $t_2$ ) for all types of spores (Fig. 3b). Protonemal growth of small and large moss spores increased with increasing pH, whereas protonemal growth of gemmae and growth of gemmae-like branchlets showed a unimodal response to pH.

High moisture can facilitate spore germination at suboptimal pH (Wiklund & Rydin 2004b), and it is possible that germination of asexual diaspores is less sensitive to pH than spore germination under water stress. However, as far as diaspore establishment goes via the protonemal stage there is no reason to suspect this: desiccation tolerance of gemmae did not differ significantly from large spores (see below), and pH response curves indicated a higher sensitivity to low and high pH of protonemal growth for gemmae than for spores. Thus, restricted establishment possibly is not the only cause of niche differentiation (Grubb 1977) and species rarity (Cleavitt 2001, 2002); habitat limitations during other life-stages, especially reproduction, may be equally important.

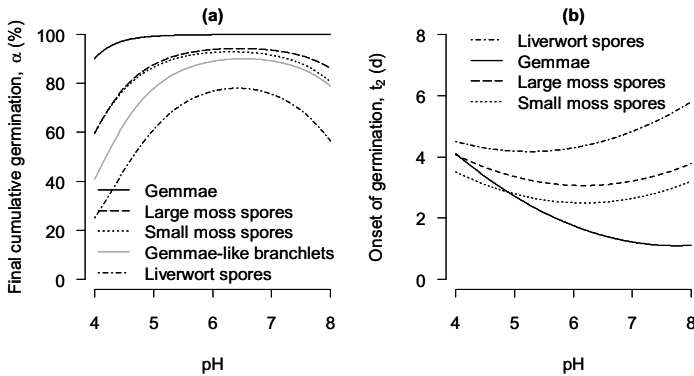


Figure 3. Effects of pH on diaspore germination (V). (a) Final cumulative germination  $\alpha$  (%) of different diaspore types. (b) Number of days until the onset of germination ( $t_2$ ) of gemmae and different spore types.

## Habitat patch size (I-III)

Host tree diameter explained only 3% of the variation in epiphyte specialist species richness among trees (I). Many studies reported a positive effect of tree diameter on the occurrence of individual epiphyte species (e.g. Uliczka & Angelstam 1999; Snäll *et al.* 2003). This has been explained by the increasing time (age), as reflected by tree diameter, under which a patch has been available for colonization (Snäll *et al.* 2003); stochastic local population extinctions from standing trees possibly are rare in the epiphyte system (Snäll *et al.* 2005a). However, there are also records of species which were not, or even negatively, affected by DBH (Hazell *et al.* 1998). Tree age and size are not independent of habitat quality (McGee & Kimmerer 2002) and for the epiphyte community, consisting of species differing in habitat requirements, the lack of a simple relationship between tree size and species number is not surprising.

Failure to observe empirical support for the predictions from island biogeography and metapopulation theory has been often assigned to the fact that the equilibrium criterion was not fulfilled (Gilbert 1980). However, at a regional scale, I observed a strong species-area effect: the number of host trees of a forest stand, which determine the within-stand metapopulation carrying capacity (Hanski & Ovaskainen 2000), explained 57% of the variation in specialist species richness among forest stands (II). It significantly enhanced species richness of both asexually and sexually dispersed specialists (III), and the occurrence probabilities of most single epiphyte species (II). The lower explanatory power of forest stand area compared to host tree number supported metapopulation dynamics as likely explanation for the observed species-area relationship. The observed  $z$ -value (0.23) lied within the range of  $z$ -values reported by many studies (0.2-0.3, see Gilbert 1980), and did not



differ significantly from the theoretical value of 0.263 under equilibrium conditions (MacArthur & Wilson 1967) for this system which is most likely not in equilibrium.

Tree falls can be the main cause of epiphyte extinction from individual trees (Snäll *et al.* 2005a), and they may even cause species extinction at the stand level. Generally, we expect lower epiphyte extinction probabilities from well connected forest stands with high local abundances and from large stands with a high number of suitable host trees and thus a large local metapopulation size (Ovaskainen & Hanski 2004). Dispersal within forest stands, establishment of new host trees and recurrent colonization of trees from surrounding stands may promote metapopulation persistence in the stand over quite long time periods (Snäll *et al.* 2005a). However, as deciduous trees are replaced by conifers during succession, the long-term metapopulation persistence over large spatial scales depends on the establishment of new deciduous stands (Snäll *et al.* 2005a, b).

## Spatial structure and dispersal

### Local scale (I)

Spatial structuring in species richness both at a local (I) and a regional (III) scale indicated stronger dispersal limitation of asexually than sexually dispersed epiphytes.

At the local scale (I), the residuals of the GLM with environmental variables as predictors showed significant spatial aggregation for all tested species groups (Fig. 4). The scale of spatial aggregation lied between 13.5 m and 36 m, corresponding well to scales at which most diaspores have been found to be deposited (e.g. Söderström & Jonsson 1989; Kimmerer 1991). For sexually dispersed specialists and for generalists, the variation in species richness explained by the spatial model was lower than the summed variation explained by environmental variables. In contrast, for asexually dispersed species, the spatial component together with the site variable superseded the effects of the local environment, indicating that strong dispersal limitation is the most important factor for species richness of this group.

Spatial aggregation of habitat generalists suggested that dispersal limitation at small spatial scales is a common phenomenon even in facultative epiphytes. The positive impact of the cover of the ground layer on generalist species richness further indicated that mass effects (Shmida & Wilson 1985), or in metapopulation terminology, source-sink dynamics (Pulliam 1988), enhance species richness: many generalists occur sporadically with a few individuals on the tree trunk, but are more abundant in the ground vegetation. Species richness of generalists thus may be mainly regulated by external factors rather than by characteristics of the host tree.

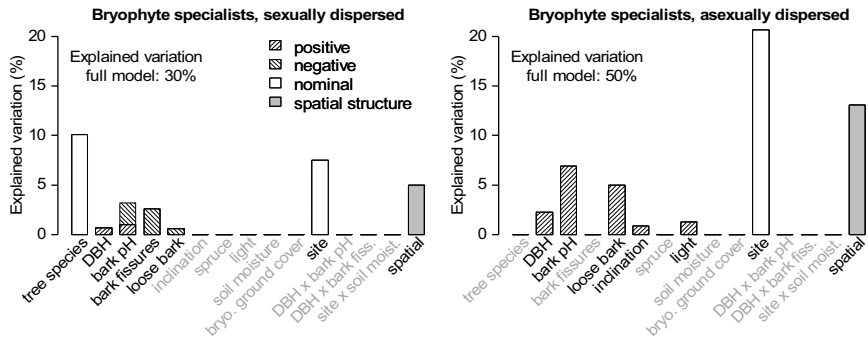


Figure 4. Factors influencing species richness of epiphytic specialists with opposing dispersal strategies (asexual vs. sexual dispersal): variation explained by environmental variables, estimated by generalized linear models, and by spatial aggregation, estimated by variogram models (I).

## Regional scale (II, III)

In the regional study, the scale of spatial aggregation in species richness was smaller in asexually than in sexually dispersed epiphytes (III). It generally increased with decreasing diaspore size. The high  $\alpha$ -parameters in the connectivity variables suggested dispersal distances of less than 100 m for large asexual diaspores. This is supported by dispersal experiments (Dettki & Esseen 2003), by a study of spatial genetic structuring (Snäll *et al.* 2004a), and by recorded colonizations of trees (Snäll *et al.* 2005a). Most asexually dispersed species were regionally rare (II), and spatial species occupancy pattern similarly indicated that this is caused by dispersal limitation.

Either present or historic stand connectivity significantly affected the relative local abundance in eight out of ten sexually dispersed species, but only in five of ten asexually dispersed species. In many asexual species dispersal among forest stands is possibly too low to enhance local population sizes. This was supported by the significantly unimodal frequency distribution of the species (II, Fig. 5). In contrast, for sexually dispersed species a strong rescue effect was indicated by a significantly bimodal frequency distribution. A weaker rescue effect in fragmented landscapes may increase species extinction risks from forest stands (Zartmann 2003).

In general, mechanisms underlying frequency distributions are poorly understood, and difficult to separate from each other (e.g. Gaston *et al.* 1998; Holt *et al.* 2002; McGeoch & Gaston 2002). Especially, the metapopulation dynamics explanation has gained very little empirical evidence (Gaston *et al.* 1998). My study (II) possibly provided the first example for a plant species assemblage in which these patterns indeed most probably were caused by metapopulation processes: metapopulation dynamics of epiphytic bryophytes were not only suggested by my analysis of species occupancy and local abundance patterns, but also by a long-term study of the colonization-

extinction dynamics in the epiphytic moss *Neckera pennata* (Snäll *et al.* 2005a). Furthermore, the niche breath hypothesis (Brown 1984) is very unlikely to explain species frequency distributions in the epiphyte community: habitat quality explained less variation in species occupancy patterns of asexually than sexually dispersed epiphytes, suggesting a lower degree of habitat specialization of the first. This was supported by the study of local growth and reproduction (IV) and the establishment experiments (V).

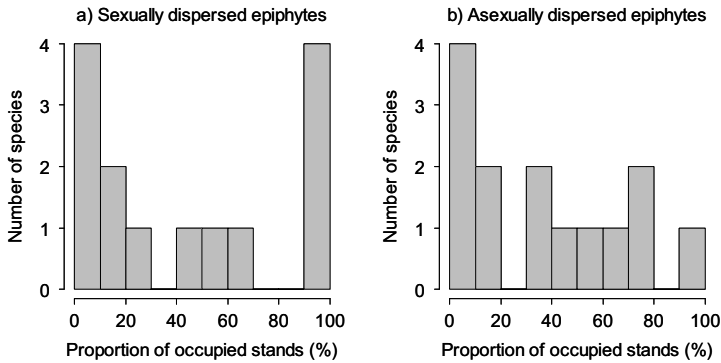


Figure 5. Regional frequency distribution of (a) sexually dispersed epiphyte specialists, and (b) asexually dispersed epiphyte specialists (II).

Variables related to the historical landscape and stand age, e.g. the maximum tree diameter, were particularly important in explaining the occupancy and abundance of rare species (II). Colonizations of the stands by these species possibly occurred long ago, and their local abundance has earlier been boosted by immigration; dispersal sources for driving these two processes were forest stands that were nearby in the past. Dispersal events in these species seem to be rare today, and regional extinctions are likely when the few occupied old trees fall.

## Landscape dynamics and species reproduction (II-IV)

Present connectivity significantly enhanced species richness of asexually reproducing epiphytes, whereas that of sexually reproducing epiphytes was affected by the historic connectivity only (III). Delayed sexual, but not asexual, reproduction most likely is the reason for this (IV): There was a threshold in colony size, and thereby age, before a species started to reproduce sexually, whereas there was no such threshold for asexual reproduction. Similar patterns have been observed within species (e.g. Pohjamo & Laaka-Lindberg 2004). In the long-term the disadvantages of short-range dispersal of asexually reproducing species may be compensated by frequent dispersal events.

Among species reproducing sexually, colony size at first reproduction increased from colonists, to short- and long-lived shuttles to perennial stayers (IV). There was a clear link between the colony size at first sexual reproduction and the observed impact of the historical landscape structure on regional species occupancy and local abundance patterns (II). The size of the colonies of the long-lived shuttle species *N. pennata* starting to reproduce for the first time was within the same range (13 – 60 cm<sup>2</sup>) as observed in an earlier study (12 – 79 cm<sup>2</sup>), corresponding to an age of 19 – 29 years (Wiklund & Rydin 2004a). Perennial stayers did not produce any sporophytes and the few fertile colonies found on host trees within the region were very large and grew on very large, i.e. old, trees. This suggests that their colonies are even older when reaching sexual maturity.

Forest stands constitute dynamic patches at the landscape level, and within these, single trees also constitute dynamic patches (Snäll *et al.* 2005a). The time scale at which new habitat occurs and habitat is lost must match the time scale at which species with different reproductive strategies are able to reproduce and disperse.

## Dispersal strategies and life-history trade-offs

### Dispersal ability versus reproductive age and frequency (I-IV)

Stronger dispersal limitation (I, II, III), but younger reproductive age (IV) of asexually compared to sexually reproducing species indicated a trade-off between dispersal distance and age at first reproduction. This may explain the parallel evolution of these alternative dispersal strategies in epiphytes. Species with asexual reproduction may perceive a given landscape to be less dynamic than species with sexual reproduction. Patch dynamics may thus be an important force in the evolution of asexual reproduction among species in transient habitats, or habitats characterized by disturbances (Rasheed 2004).

### Reproduction versus local growth and competitive ability (IV)

I observed a negative effect of the presence of sporophytes on *RGR* in sexually reproducing species. In contrast, the presence of gemmae or gemmae-like branchlets did not affect *RGR* of asexually reproducing species. Hence, there seems to be a trade-off between colony growth and sexual, but not asexual, reproduction. This in line with studies indicating a cost of sexual reproduction in mosses (Ehrlén *et al.* 2000; Bisang & Ehrlén 2002; Rydgren & Økland 2002). However, there were no indications of generally lower growth rates for sexually reproducing species compared with asexually, or that species with frequent sexual reproduction should have low growth rates: contrary to my hypothesis, colonists actually had a higher *RGR* (0.40) than

shuttles (0.23) and perennial stayers (0.31). It is most likely their short life span that prevents colonists from covering larger areas on trees. Rather than a simple trade-off between growth and reproduction, selection for high growth rates in epiphytes may occur via two different paths: in colonists it decreases the time to reach reproductive size, whereas in perennial stayers the main effect is to lower the local extinction risk. High growth rates are important for local population persistence: my data indicated that small colonies run a higher extinction risk from parts of the stem of single host trees, caused by small-scale bark-loosening, than large colonies.

My study further suggested that colony growth of epiphytes is affected by interactions with other epiphytes, especially pleurocarpous mosses, but there were no indications for differences in competitive abilities among species groups. Interaction effects were rather weak and did not support a competition-colonization trade-off: the growth of colonists was not affected by neighbouring epiphytes, and the growth of shuttle species was not more affected than that of perennial stayers. In fact, the effects of neighbours were mostly positive. In bryophytes, contact with neighbours can provide protection and a humid, shady microclimate (Mulder *et al.* 2001; Rixen & Mulder 2005; Rydin 2009). Hence, it is unlikely that competition is an important force for driving epiphyte metacommunity dynamics.

## Dispersal ability versus establishment ability (V)

The establishment experiments (V) confirmed the hypothesis of higher establishment rates from large asexual diaspores than from small sexual ones (Kimmerer 1994; Laaka-Lindberg *et al.* 2003, 2006; Pohjamo *et al.* 2006), suggesting a trade-off between dispersal distance and establishment ability. Across all stages of the establishment process, gemmae performed best: they showed the highest final cumulative germination of almost 100% and the fastest germination rate at pH > 4 (Fig. 3). Survival under dry storage (Fig. 6a) and protonemal growth were rather high, and transition times from the protonemal to gametophytic stage relatively short. Species with gemmae also had the highest fragment growth rate, possibly as the presence of protonemal gemmae on the leaf surface facilitates fragment establishment. This further enhances the advantages of asexually reproducing species in local dispersal.

Performance of gemmae-like branchlets was intermediate, but they do not have to pass through the critical protonemal stage. Hence, in nature, establishment rates from branchlets may be higher than from spores or gemmae. The same may be true for gametophyte fragments: Mishler & Newton (1988) showed that *Tortula* spp. fragments produced new shoots more quickly than spores, even though spores germinated at a higher rate.

## Trade-offs in the establishment (V)

Whereas trade-offs between dispersal distance and establishment rate may be important for the evolution of asexual dispersal in epiphytes, the evolution of spore size seems to be more complex and shaped by trade-offs becoming important during establishment. Early onset of germination, final cumulative germination and initial protonemal growth rate were linked characters, but there were indications for trade-offs between these characters, desiccation tolerance and a rapid development of shoots from protonema (Figs 3, 6).

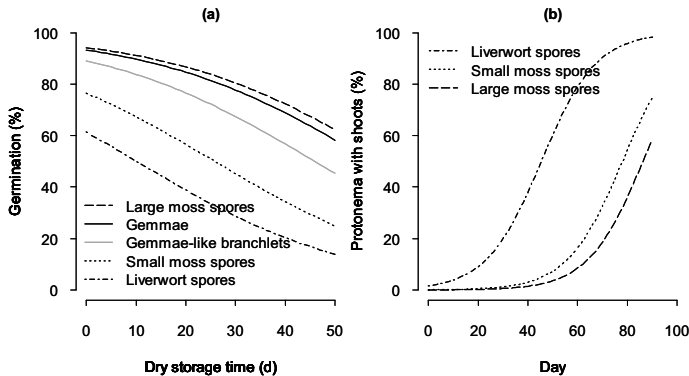


Figure 6. (a) Germination (%) of different diaspore types after dry storage. (b) Cumulative production of shoots (%) over time of protonema from spores (V).

The main advantage of large moss spores was their high desiccation tolerance: even after 50 days of dry storage models still predicted 62% germination probability. Higher establishment rates of large than small seeded vascular plants are generally assumed (Moles & Westoby 2004, 2006). In contrast, large moss spores did not show higher germination probabilities, and protonemal growth rates were much smaller than those of small moss spores. This may indicate costs of desiccation tolerance due to high nutrient requirements for the germ tube to brake the thick spore wall. Similarly, Sundberg & Rydin (2002) observed that large *Sphagnum* spores germinated more slowly than small ones.

The advantages of small moss spores were their high germination and initial protonemal growth rates, suggesting high competitive abilities during the protonemal stage. Hence, using spore number versus size as an indication for a competition-colonization trade-off, as suggested for seeds of vascular plants (e.g. Ozinga *et al.* 2004), can be misleading for epiphytes.

The main advantage of the large liverwort spores was the rapid transition from protonema to shoots. Liverworts should thus be very effective in using brief windows of wet conditions, a strategy, however, that is risky given the short survival time under dry conditions. The transition between protonema and gametophyte has been rarely considered. In line with Metha (1988) and

Sundberg & Rydin (2002), my study showed that even under optimal conditions, this takes from two weeks up to more than two months.

Desiccation tolerance and a rapid transition from protonema to shoots both seem to be powerful strategies to deal with drought of the epiphyte habitat: young twigs often are inhabited by open communities with leafy liverworts and small acrocarpous mosses with large spores. The lower tree trunk may be completely swathed in a carpet of desiccation-sensitive, pleurocarpous mosses with small spores (Bates 2009). In the competitive, but humid, environment of the tree base, a high initial protonemal growth rate may be more important than desiccation tolerance.

## Evolution of dispersal strategies in patch-tracking metacommunities

Host trees and deciduous forest stands in the coniferous landscape are patchy, temporal and undergo changes in habitat quality during succession. Bark is prone to desiccation and the epiphyte habitat is characterized by drought and irregular water supply. The conceptual model in Figure 7 suggests how epiphyte dispersal and life-history strategies have evolved in response to these habitat constraints.

Asexual reproduction is regarded as an adaptation to the temporality of patches and the spatio-temporal variation in habitat quality and water supply. First, it allows for early reproduction, second, production of asexual diaspores is rather insensitive to habitat quality, and third, establishment from large, asexual diaspores is higher than from spores, and less sensitive to irregular water supply: gemmae-like branchlets do not have to pass through the critical protonemal stage during which the bryophyte is most vulnerable to drought, and gemmae are very desiccation tolerant during and after dispersal. However, asexual diaspores are larger and fewer and have distinctly shorter dispersal distances than spores. This indicates two main trade-offs: dispersal distance versus early and frequent reproduction, and dispersal distance versus sensitivity to habitat quality and irregular water supply. The evolution of large spore sizes similarly seems to be an adaptation to irregular water supply: the largest liverwort spores showed a rapid transition from protonema to shoots, reducing the length of the sensitive protonemal stage. Large moss spores are insensitive to desiccation under and after dispersal. Large spores, however, do not only have shorter dispersal distances, but also lower germination and protonemal growth rates than small spores, and also the adult plants showed lower colony growth rates.

Rather than a simple trade-off between growth and reproduction, selection for high growth rates decreases the time to reach reproductive size (colonists) and the local population extinction risk (perennial stayers).

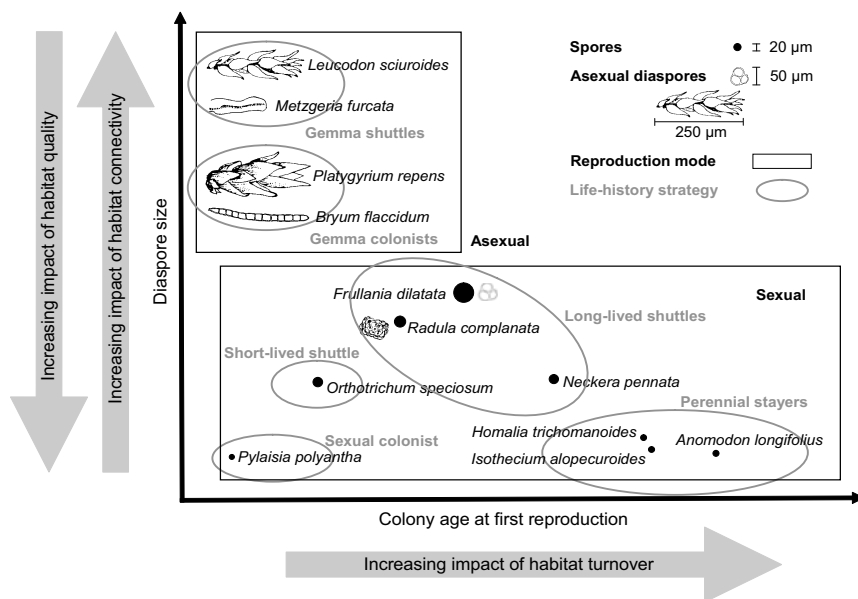


Figure 7. Conceptual model illustrating possible relationships between dispersal strategies (sexual via spores, asexual via gemmae or gemmae-like branchlets), life-history strategies based on During (1979, 1992) and Siebel & During (2006) and species responses to habitat turnover, connectivity and quality and drought (IV).

I encourage the complementation of the classical bryophyte life-history strategies by taking asexual reproduction into account (Siebel & During 2006). Arranging all main study species in the habitat template (Fig. 7), sexual colonists are least vulnerable to both habitat patchiness and dynamics, but their habitat sensitivity can prevent reproduction or establishment: in central Europe, sporophytes in *P. polyantha* have become very rare, possibly due to high air pollution (Frahm & Frey 2004). Critical species are long-lived shuttles, such as *N. pennata*, with both large spores and late onset of sexual reproduction. It is interesting to note that sexual shuttle species have developed adaptations to drought, possibly on costs of dispersal and competitive abilities. Perennial stayers with small spores are insensitive to habitat connectivity, but sensitive to drought, and their delayed reproduction is problematic if habitat turnover is fast. Gemma shuttles are a group with strong dispersal limitation, whereas gemma colonists have a better potential to colonize distant habitat – in the rare cases of sexual reproduction they have rather small spores.



## Conclusions and implications

In which ways do these findings contribute to our understanding of meta-communities characterized by fast habitat dynamics? First, this thesis confirms the hypothesis that dispersal processes are important in determining regional metacommunity diversity. Second, it shows that local population processes potentially have strong impact on metacommunity processes at larger spatial scales. A full understanding of patch-tracking metacommunity systems thus requires considering population and metapopulation dynamics as well as the dynamic nature of the patches across all spatial scales. Third, dispersal success of community members is influenced by both species traits and habitat characteristics. Metacommunities are not governed by a single process, but by a combination of factors described in the four theoretical frameworks (Ellis *et al.* 2006; Mouillot 2007); the predominating processes are strongly related to dispersal rates and types (Van de Meuter *et al.* 2007). Epiphyte metacommunity dynamics may be described by a combination of the patch dynamics (asexually dispersed species) as well as species sorting and mass effects perspectives (sexually dispersed species), but the current metacommunity frameworks lack attention to habitat dynamics and spatio-temporal niche relations among species caused by different reproductive pattern. Fourth, population processes take place on several spatio-temporal scales (Mouillot 2007; Virtanen & Oksanen 2007), and species persistence may be attained by different combinations of within patch and between patch population dynamics (Holt *et al.* 2005). Diaspore size possibly evolves as part of a spectrum of life-history traits and is not simply the result of a trade-off between producing few large diaspores with high establishment probabilities each, and many small diaspores, with lower establishment probability (Moles & Westoby 2004, 2006). Fifth, the results suggest that habitat patchiness and landscape dynamics are important forces in the evolution of species traits in patch-tracking metacommunities; constraints imposed by habitat conditions, especially drought and irregular water supply, are another major factor. Interspecific trade-offs may evolve as a consequence of conflicting selection pressures imposed by the habitat; species interactions must not necessarily be the driving force. Sixth, syndromes of interrelated species traits imply that fairly small changes in habitat conditions can lead to distinct changes in metacommunity structure and diversity. Modern forestry has led to a reduction of the overall amount of deciduous trees in the landscape, which may cause most harm to asexually dispersed species, whereas cuttings of old-growth forests of high age and quality, as well as the suppression of development of new large, deciduous stands of high quality, may be most harmful to sexually dispersed species. Sexually dispersed species are further threatened by changes in landscape dynamics, especially faster cutting or fire rotation times. In rapidly changing landscapes, we need not only be interested in how far, but also in how fast species disperse (Matlack 2005).

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# References

- Barkman, J.J. (1958) *Phytosociology and ecology of cryptogamic epiphytes*. Van Gorcum, Assen.
- Bates, J.W. (2009) Mineral nutrition and substratum ecology. *Bryophyte Biology* (eds B. Goffinet, A.J. Shaw, 2nd ed.), pp. 300–356. Cambridge University Press, Cambridge.
- Bengtsson, J., Fagerström, T. & Rydin, H. (1994) Competition and coexistence in plant communities. *Trends in Ecology and Evolution*, **9**, 246–250.
- Berg, Å., Gärdenfors, U., Hallingbäck, T. & Norén, M. (2002) Habitat preference of red-listed fungi and bryophytes in woodland key habitats in southern Sweden – analyses from a national survey. *Biodiversity and Conservation*, **11**, 1479–1503.
- Bisang, I. & Ehrlén, J. (2002) Reproductive effort and cost of sexual reproduction in female *Dicranum polysetum*. *Bryologist*, **105**, 384–397.
- Bossuyt, B. & Honnay, O. (2006) Interactions between plant life span, seed dispersal capacity and fecundity determine metapopulation viability in a dynamic landscape. *Landscape Ecology*, **21**, 1195–1205.
- Brown, J.H. (1984) On the relationship between abundance and distribution of species. *American Naturalist*, **124**, 255–279.
- Cadotte, M.W., Mai, D.V., Jantz, S., Collins, M.D., Keele, M. & Drake, J.A. (2006) On testing the competition-colonization trade-off in a multispecies assemblage. *American Naturalist*, **168**, 704–709.
- Chase, J.M., Amarasekare, P., Cottenie, K., Gonzales, A., Holt, R.D., Holyoak, M., Hoopes, M.F., Leibold, M.A., Loreau, M., Mouquet, N., Shurin, J.B. & Tilman, D. (2005) Competing theories for competitive metacommunities. *Metacommunities* (eds M. Holyoak, M.A. Leibold & R.D. Holt), pp. 335–354. The University of Chicago press, Chicago and London.
- Chesson, P. (2000) Mechanisms of maintenance of species diversity. *Annual Review of Ecology, Evolution, and Systematics*, **31**, 343–366.
- Cleavitt, N. (2001) Disentangling moss species limitations: The role of physiologically based substrate specificity for six species occurring on substrates with varying pH and percent organic matter. *Bryologist*, **101**, 59–68.
- Cleavitt, N. (2002) Stress tolerance of rare and common moss species in relation to their occupied environments and asexual dispersal potential. *Journal of Ecology*, **90**, 785–795.
- Debinsky, D.M. & Holt, R.D. (1999) A survey and overview of habitat fragmentation experiments. *Conservation Biology*, **14**, 342–355.
- Dettki, H. & Esseen, P.-A. (2003) Modelling long-term effects of forest management on epiphytic lichens in northern Sweden. *Forest Ecology and Management*, **175**, 223–238.
- Diekmann, M. (1999) Southern deciduous forests. *Acta Phytogeographica Suecica*, **84**, 33–53.
- Dierßen, K. (2001) *Distribution, ecological amplitude and phytosociological characterization of European bryophytes*. Cramer, Berlin and Stuttgart.

- During, H.J. (1979) Life strategies of bryophytes: a preliminary review. *Lindbergia*, **5**, 2–18.
- During, H.J. (1992) Ecological classification of bryophytes and lichens. *Bryophytes and lichens in a changing environment* (eds J.W. Bates & A.M. Farmer), pp. 1–31. Clarendon Press, Oxford.
- During, H.J. (2007) Relations between clonal growth, reproduction and breeding system in the bryophytes of Belgium and The Netherlands. *Nova Hedwigia, Beiheft*, **131**, 133–145.
- Ellis, C.J. & Coppins, B.J. (2009) Quantifying the role of multiple landscape-scale drivers controlling epiphyte composition and richness in a conservation priority habitat (juniper scrub). *Biological Conservation*, **142**, 1291–1301.
- Ellis, A.M., Lounibos, L.P. & Holyoak, M. (2006) Evaluating the long-term meta-community dynamics of tree hole mosquitoes. *Ecology*, **87**, 2582–2590.
- Eriksson, P. (1997) *Ekologisk landskapsplanering i Vällensområdet*. Rapport 5, Upplandsstiftelsen, Uppsala (in Swedish).
- Ehrlén, J., Bisang, I. & Hedenäs, L. (2000) Costs of sporophyte production in the moss, *Dicranum polysetum*. *Plant Ecology*, **149**, 207–217.
- Frahm, J.-P., Frey, W. (2004) *Moosflora*, 2nd ed., Ulmer, Stuttgart.
- Gaston, K.J., Blackburn, T.M. & Lawton, J.H. (1998) Aggregation and interspecific abundance-occupancy relationships. *Journal of Ecology*, **67**, 995–999.
- Gilbert, F.S. (1980) The equilibrium theory of island biogeography: fact or fiction. *Journal of Biogeography*, **7**, 209–236.
- Grubb, P.J. (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biological Review of the Cambridge Philosophical Society*, **52**, 107–145.
- Hanski, I. (1982) Dynamics of regional distributions: the core and satellite species hypothesis. *Oikos*, **38**, 210–221.
- Hanski, I. (1994) A practical model of metapopulation dynamics. *Journal of Animal Ecology*, **63**, 151–162.
- Hanski, I. (1999) *Metapopulation ecology*. Oxford University Press, Oxford.
- Hanski, I. & Ovaskainen, O. (2000) The metapopulation capacity of a fragmented landscape. *Nature*, **404**, 755–758.
- Hanski, I. & Gaggiotti, O.E. (eds, 2004) *Ecology, genetics, and evolution of metapopulations*. Elsevier, San Diego.
- Harrison, B. & Bruna, E. (1999) Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography*, **22**, 225–232.
- Hazell, P., Kellner, O., Rydin, H. & Gustafsson, L. (1998) Presence and abundance of four epiphytic bryophytes in relation to density of aspen (*Populus tremula*) and other stand characteristics. *Forest Ecology and Management*, **107**, 147–158.
- Heegaard, E. (2000) Patch dynamics and/or the species-environmental relationship in conservation bryology. *Lindbergia*, **25**, 85–88.
- Heegaard, E. & Hangelbroek, H.H. (1999) The distribution of *Ulota crispa* at a local scale in relation to both dispersal- and habitat-related factors. *Lindbergia*, **24**, 65–74.
- Heywood, V.H. (1995) *Global biodiversity assessment*. Cambridge University Press, Cambridge.
- Hill, M.O., Preston, C.D., Bosanquet, S.D.S., Roy, D.B. (2007) *Bryoatt – Attributes of British and Irish mosses, liverworts and hornworts*. CEH, NERC, Norwich.
- Holt, A.R., Gaston, K.J. & He, F. (2002) Occupancy-abundance relationships and spatial distribution: A review. *Basic and Applied Ecology*, **3**, 3–13.

- Holt, R.D., Holyoak, M. & Leibold, M.A. (2005) Future directions in metacommunity ecology. *Metacommunities* (eds M. Holyoak, M.A. Leibold & R.D. Holt), pp. 465–489. The University of Chicago press, Chicago and London.
- Holyoak, M., Leibold, M.A., Mouquet, N.M., Holt, R.D. & Hoopes, M.F. (2005) Metacommunities: A framework for large-scale community ecology. *Metacommunities* (eds M. Holyoak, M.A. Leibold & R.D. Holt), pp. 1–31. The University of Chicago press, Chicago and London.
- Johst, K., Brandl, R. & Eber, S. (2002) Metapopulation persistence in dynamic landscapes: the role of dispersal distance. *Oikos*, **98**, 263–270.
- Kalisz, S., Vogler, D.W. & Hanley, K.M. (2004) Context-dependent autonomous self-fertilization yields reproductive assurance and mixed mating. *Nature*, **430**, 884–887.
- Karlsson, S. (2007) *Image*. <http://www.sk-biometri.se>
- Kimmerer, R.W. (1991) Reproductive ecology of *Tetraphis pellucida* II. Differential fitness of sexual and asexual propagules. *Bryologist*, **94**, 284–288.
- Kimmerer, R.W. (1994) Ecological consequences of sexual versus asexual reproduction in *Dicranum flagellare* and *Tetraphis pellucida*. *Bryologist*, **97**, 20–25.
- Kneitel, J.M. & Chase, J.M. (2004) Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters*, **7**, 69–80.
- Laaka-Lindberg, S., Korpelainen, H. & Pohjama, M. (2003) Dispersal of asexual propagules in bryophytes. *Journal of the Hattori Botanical Laboratory*, **93**, 319–330.
- Laaka-Lindberg, S., Korpelainen, H. & Pohjama, M. (2006) Spatial distribution of epixylic hepatics in relation to substrate in a boreal old-growth forest. *Journal of the Hattori Botanical Laboratory*, **100**, 311–323.
- Leibold, M.A. & Miller, T.E. 2004. From metapopulations to metacommunities. *Ecology, Genetics, and Evolution of Metapopulations* (eds I. Hanski & O.E. Gaggiotti), pp. 133–150. Elsevier, Burlington, San Diego and London.
- Longton, R.E. (1994) Reproductive biology in bryophytes. The challenge and the opportunities. *Journal of the Hattori Botanical Laboratory*, **76**, 159–172.
- MacArthur, R.H. & Wilson, E.O (1967) *The theory of island biogeography*. Princeton University Press, Princeton.
- Matlack, G.R. (2005) Slow plants in a fast forest: local dispersal as a predictor of species frequencies in a dynamic landscape. *Journal of Ecology*, **93**, 50–59.
- McCullagh, P. & Nelder, J.A. (1989) *Generalised linear models*. Chapman and Hall/CRC, New York.
- McGee, G.G. & Kimmerer, R.W. (2002) Forest age and management effects on epiphytic bryophyte communities in Adirondack northern hardwood forests, New York, USA. *Canadian Journal of Forest Research*, **32**, 1562–1576.
- McGeoch, M.A. & Gaston, K.J. (2002) Occupancy frequency distribution: patterns, artefacts and mechanisms. *Biological Reviews*, **77**, 311–331.
- Metha, P. (1988) In-vitro studies on spore germination, protonemal differentiation and bud formation in three mosses grown in vitro. *Journal of the Hattori Botanical Laboratory*, **64**, 401–410.
- Miller, T.E. & Kneitel, J.M. (2005) Inquiline communities in pitcher plants as a prototypical metacommunity. *Metacommunities* (eds M. Holyoak, M.A. Leibold & R.D. Holt), pp. 122–145. University of Chicago Press, Chicago and London.
- Mishler, B.D. & Newton, A.E. (1988) Influences of mature plants and desiccation on germination of spores and gametophytic fragments of *Tortula*. *Journal of Bryology*, **15**, 327–342.

- Moen, J. & Jonsson, B.G. (2003) Edge effects on liverworts and lichens in forest patches in a mosaic of boreal forest and wetland. *Conservation Biology*, **17**, 380–388.
- Moles, A.T. & Westoby, M. (2004) Seedling survival and seed size: a synthesis of the literature. *Journal of Ecology*, **92**, 372–383.
- Moles, A.T. & Westoby, M. (2006) Seed size and plant strategy across the whole life cycle. *Oikos*, **113**, 91–105.
- Mouillot, D. (2007) Niche-assembly vs. dispersal-assembly rules in coastal fish metacommunities: implications for management of biodiversity in brackish lagoons. *Journal of Applied Ecology*, **44**, 760–767.
- Mouquet, N., Hoopes, M.F. & Amarasekare, P. (2005) The world is patchy and heterogeneous! Trade-offs and source-sink dynamics in competitive metacommunities. *Metacommunities* (eds M. Holyoak, M.A. Leibold & R.D. Holt), pp. 335–354. The University of Chicago press, Chicago and London.
- Mulder, C.P.H., Uliassi, D.D. & Doak, D.F. (2001) Physical stress and diversity-productivity relationships: The role of positive interactions. *Proceedings of the National Academy of Sciences*, **98**, 6704–6708.
- Niklasson, M. & Granström, A. (2000) Numbers and sizes of fires: long-term spatially explicit fire history in a Swedish boreal landscape. *Ecology*, **81**, 1484–1499.
- Ovaskainen, O. & Hanski, I. (2002) Transient dynamics in metapopulation response to perturbation. *Theoretical Population Biology*, **61**, 285–295.
- Ovaskainen, O. & Hanski, I. (2004) Metapopulation dynamics in highly fragmented landscapes. *Ecology, Genetics, and Evolution of Metapopulations* (eds I. Hanski & O.E. Gaggiotti), pp. 275–303. Elsevier, San Diego.
- Ozinga, W.A., Bekker, R.M., Schaminée, J.H.J. & van Groenendael, J.M. (2004) Dispersal potential in plant communities depends on environmental conditions. *Journal of Ecology*, **92**, 767–777.
- Pohjamo, M. & Laaka-Lindberg, S. (2004) Demographic structure of a leafy epixylic hepatic *Anastrophyllum hellerianum* (Nees ex Lindenb.) R.M. Schust. *Plant Ecology*, **173**, 73–81.
- Pohjamo, M., Laaka-Lindberg, S., Ovaskainen, O. & Korpelainen, H. (2006). Dispersal potential of spores and asexual diaspores in the epixylic hepatic *Anastrophyllum hellerianum*. *Evolutionary Ecology*, **20**, 415–430.
- Proctor, M.C.F., Oliver, M.J., Wood, A.J., Alpert, P., Stark, L.R., Cleavitt, N.L. & Mishler, B.D. (2007) Desiccation-tolerance in bryophytes: a review. *Bryologist*, **110**, 595–621.
- Pulliam, H.R. (1988) Sources, sinks, and population regulation. *American Naturalist*, **132**, 652–661.
- Rasheed, M.A. (2004) Recovery and succession in a multi-species tropical seagrass meadow following experimental disturbance: the role of sexual and asexual reproduction. *Journal of Experimental Marine Biology and Ecology*, **310**, 13–45.
- Rixen, C. & Mulder, C.P.H. (2005) Improved water retention links high species richness with increased productivity in arctic tundra moss communities. *Oecologia*, **146**, 287–299.
- Rydgren, K. & Økland, R.H. (2002) Ultimate costs of sporophyte production in the clonal moss *Hylocomium splendens*. *Ecology*, **83**, 1573–1579.
- Rydin, H. (2009) Population and community ecology of bryophytes. *Bryophyte Biology* (eds B. Goffinet, A.J. Shaw, 2<sup>nd</sup> ed.), pp. 393–444. Cambridge University Press, Cambridge.
- Shmida, A. & Wilson, M.V. (1985) Biological determinants of species diversity. *Journal of Biogeography*, **12**, 1–20.

- Siebel, H.N. & During, H.J. (2006) *Beknopte mosflora van Nederland en België*. K.N.N.V., Utrecht.
- Silvertown, J., Holtier, S., Johnson, J. & Dale, P. (1992) Cellular automaton models of interspecific competition for space – the effect of pattern on process. *Journal of Ecology*, **80**, 527–534.
- Snäll, T., Ribeiro Jr., P.J. & Rydin, H. (2003) Spatial occurrence and colonizations in patch-tracking metapopulations: local conditions versus dispersal. *Oikos*, **103**, 566–578.
- Snäll, T., Fogelqvist, J., Ribeiro Jr., P.J. & Lascoux, M. (2004a) Spatial genetic structure in two congeneric epiphytes with different dispersal strategies analysed by three different methods. *Molecular Ecology*, **13**, 2109–2119.
- Snäll, T., Hagström, A., Rudolphi, J. & Rydin, H. (2004b) Distribution pattern of the epiphyte *Neckera pennata* on three spatial scales – importance of past landscape structure, connectivity, and local conditions. *Ecography*, **27**, 757–766.
- Snäll, T., Ehrlén, J. & Rydin, H. (2005a) Colonization-extinction dynamics of an epiphyte metapopulation in a dynamic landscape. *Ecology*, **86**, 106–115.
- Snäll, T., Pennanen, J., Kivistö, L. & Hanski, I. (2005b) Modelling epiphyte dynamics in a dynamic forest landscape. *Oikos*, **109**, 209–222.
- Söderström, L. & Jonsson, B.G. (1989) Spatial pattern and dispersal in the leafy hepatic *Ptilidium pulcherrimum*. *Journal of Bryology*, **15**, 793–802.
- Söderström, L. & Herben, T. (1997) Dynamics in bryophyte metapopulations. *Advances in Bryology*, **6**, 205–240.
- Stelter, C., Reich, M., Grimm, V. & Wissel, C. (1997) Modelling persistence in dynamic landscapes: Lessons from a metapopulation of the grasshopper *Bryodema tuberculata*. *Journal of Animal Ecology*, **66**, 508–518.
- Sundberg, S. & Rydin, H. (2002) Habitat requirements for establishment of *Sphagnum* from spores. *Journal of Ecology*, **90**, 268–278.
- Tackenberg, O., Poschod, P., & Bonn, S. (2003) Assessment of wind dispersal potential in plant species. *Ecological Monographs*, **73**, 191–205.
- Tokeshi, M. (1992) Dynamics of distribution in animal communities: theory and analysis. *Researches on Population Ecology*, **34**, 249–273.
- Uliczka, H. & Angelstam, P. (1999) Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. *Ecography*, **22**, 396–405.
- Van de Meuter, F., De Meester, L. & Stoks, R. (2007) Metacommunity structure of pond macroinvertebrates: effects of dispersal mode and generation time. *Ecology*, **88**, 1687–1695.
- Vanschoenwinkel, B., de Vries, C., Seaman, M. & Brendonck, L. (2007) The role of metacommunity processes in shaping invertebrate rock pool communities along a dispersal gradient. *Oikos*, **116**, 1255–1266.
- Virtanen, R. & Oksanen, J. (2007) The effects of habitat connectivity on cryptogam richness in boulder metacommunity. *Biological Conservation*, **135**, 415–422.
- Wiklund, K. & Rydin, H. (2004a) Colony expansion of *Neckera pennata*: Modelled growth rate and effect of microhabitat, competition, and precipitation. *Bryologist*, **107**, 293–301.
- Wiklund, K. & Rydin, H. (2004b) Ecophysiological constraints on spore establishment in bryophytes. *Functional Ecology*, **18**, 907–913.
- Zartman, C.E. (2003) Habitat fragmentation impacts on epiphyllous bryophyte communities in Central Amazonia. *Ecology*, **84**, 948–954.
- Zartman, C.E. & Shaw, A.J. (2006) Metapopulation extinction thresholds in rain forest remnants. *American Naturalist*, **167**, 177–189.



# Biologisk mångfald av trädlevande mossor

Mossor står för en väsentlig del den av biologiska mångfalden i svenska skogar. Det intensiva skogsbruket har lett till mindre andel gamla skogar och färre lövträd. De flesta trädlevande mossor (så kallade epifyter) växer bara på träd som uppfyller speciella krav på barkens kemiska sammansättning. De viktigaste trädslagen är ask, alm, lönn och asp. Längre norrut är aspen det enda gynnsamma trädslaget. Bland epifyterna finns flera arter som är hotade, och förekomst av många sällsynta eller mindre allmänna mossarter tyder på miljöer med höga naturvärden. För att bevara den biologiska mångfalden är kunskaper om skogsekosystemet och arternas populationsbiologi viktiga.

- Vad påverkar mossornas mångfald i det svenska skogslandskapet? Hur kan vi bibehålla deras mångfald?
- Vilken roll spelar miljöfaktorer som ljus, fuktighet, barkstruktur och näring i barken å ena sidan, och landskapstrukturen å andra sidan?
- Påverkas arter med olika spridnings- och livsstrategier på olika sätt?
- Behöver vi några få naturreservat med hög miljö kvalitet eller är det bättre att satsa på att knyta ihop de isolerade bestånden med värdträd i landskapet?

Jag forskade kring dessa frågor i Upplands skogar, som är bland de rikaste i Sverige. Jag undersökte vilka trädlevande mossor det finns på samtliga ädel-lövträd och asp i två skogsbestånd (1200 värdträd). Jag mätte olika miljöfaktorer och gjorde kartor av var träden står. Kartorna användes för att undersöka isoleringsgraden hos ett träd och dess betydelse för artikedomen.

För att undersöka arternas utbrednings- och artrikedomsmonster på större skala inventerade jag alla trädlevande mossor i 135 bestånd (0,01–15 ha) med ädellöv, asp och sälg i ett landskap vid sjön Vällen i östra Uppland. Kartor och flygfotografier visade isoleringsgraden hos skogsbestånden. Eftersom många mossor växer ganska långsamt är det viktigt att också undersöka hur landskapet såg ut för 20 till 100 år sedan. Jag använde infraröda flygfotografier från 1977 till det.

Trädstammar är substrat med begränsad livslängd: Träd etablerar sig, växer och faller. För epifyter är därför reproduktion, spridning till nya värdträd, och en framgångsrik etablering på dessa, nyckelprocesser för arternas överlevnad i ett landskap. Jag studerade tillväxt och reproduktion i kolonier av 12 olika trädlevande mossor i fält under ett år. Via tillväxtmodeller skattade jag vid vilken kolonistorlek – och därmed ålder – mossor med olika

förökningsformer börjar reproducera sig. Jag undersökte också hur tillväxt och reproduktion påverkas av miljöfaktorer. I flera odlingsexperiment på laboratorium testade jag betydelsen av pH för groningen och etablering av 14 mossor med olika typ av diasporer (spridningsorgan). Jag undersökte också om olika diasportyper skiljer sig i etableringsförmåga och hur känsliga de är för uttorkning.

#### *Hur förökar och sprider sig mossor?*

Mossor förökar sig på många olika sätt. Mossor sprider sig med mycket små sexuella spridningsorgan som kallas sporer eller med speciella vegetativa spridningsorgan som ofta är betydligt större, till exempel flercelliga groddkroppar eller groddgrenar som bildas i bladaxlarna av moderplantan. Den enklaste typen av vegetativ förökning är att en ny mossa etablerar sig direkt från blad- eller bålbitar. Mina resultat visade att arter med vegetativa spridningsorgan har svårt att sprida sig över långa avstånd, men samtidigt är chansen relativt stor att en ny mossaindivid etableras. Arter med vegetativa spridningsorgan reproducerade sig också oftare och tidigare än mossor som förökar sig sexuellt. Det tog lång tid innan mossorna började reproducera sig sexuellt; för vissa arter tar det troligen mer än 20–30 år tills de första sporkapslarna produceras. Min forskning visade att beroende på förökningsform påverkas arterna olika starkt av beståndets miljö kvalitet, isolering och historia.

#### *Hur påverkas mossorna av miljön?*

Mossor påverkas av miljön på flera olika sätt. Som alla gröna växter behöver de ljus för att växa, men nackdelen med en solig växtplats är ofta den låga luftfuktigheten. Min forskning visade att många mossor föredrar fuktiga och skuggiga miljöer. Det förklarar den negativa effekt av skogskanter jag hittade för flera arter. Hög markfuktighet hade också en positiv effekt på tillväxten hos de flesta mossorna. Barken på olika trädslag skiljer sig i sin struktur, och små, unga träd har vanligtvis en slätare bark än äldre, grova träd. Mina studier visade att artrikedomen av mossor ökar med trädens ålder. De flesta trädlevande mossor är knutna till näringsrik bark med högt pH. Min forskning visade att antalet mossarter ökar med barkens pH, och att effekten är större för arter som sprider sig sexuellt än för arter som sprider sig vegetativt. Det kan förklaras med att den sexuella, men inte den vegetativa, förökningen påverkades tydligt av barkens pH. Tillväxten hos de flesta mossor ökade med barkens pH, men vid  $\text{pH} > 7$  sjönk den igen. Odlingsexperimenten visade att groningen och etableringen av alla mossdiasporer påverkas mycket av pH, och båda är högst vid  $\text{pH} 6 - 7$ . Hur lång tid det tar innan diasporer börjar gro, och hur lång tid det tar tills de första skotten utvecklas från protonema kan ha stor betydelse i naturen eftersom diasporer bara kan gro och växa när substraten är fuktiga. Etableringsförsöken visade också att stora mossporer och vegetativa groddkorn är mindre känsliga mot uttorkning

än små mossporer och levermossporer. Uttorkningståligheten kan ha stor betydelse för etableringschansen eftersom det kan ta lång tid innan gynnsamma förhållanden för groningen uppstår.

#### *Hur påverkas mossor av landskapsstrukturen och historien?*

Idag ligger många skogar med värdräd som små habitatöar i ett landskap där jord- och skogsbruk är dominerande. Innan en art kan etablera sig på en av habitatöarna måste den ha tagit sig dit. Sannolikheten att en art etablerar sig på en liten, isolerad habitatö är mycket lägre än för en större habitatö med många andra habitatöar som grannar. För att kunna förklara artrikedomen räcker det därför inte att betrakta just den speciella miljön i ett skogsbestånd eller på ett träd. Vi måste också undersöka hur landskapet ser ut runt omkring. Mina forskningsresultat visade att både landskapsstrukturen idag, och för 30 år sedan, har stor betydelse för dagens artrikedomen och arternas utbredning. Mossor som sprider sig via stora vegetativa diasporer har svårare att klara av stora spridningsavstånd än mossor som sprider sig med sexuella sporer. Det normala spridningsavståndet för stora vegetativa spridningsorgan är troligen betydligt mindre än 100 m, medan små sporer kan klara av distanser av 500 m eller mer. För mossarter som sprider sig med sporer var landskapsstrukturen för 30 år sedan betydligt viktigare än dagens landskap.

#### *Olika arter har olika behov – hur kan vi då bevara den biologiska mångfalden?*

Min forskning har visat att det är många faktorer som påverkar den biologiska mångfalden av trädlevande mossor. Behoven hos arter med olika spridningsstrategier varierar mycket, och det krävs en kombination av olika naturvårdsåtgärder för att kunna bevara hela artrikedomen.

För arter med sexuell spridning är det viktigast att bevara stora, gamla bestånd med ädellöv, asp och sälg av hög kvalitet, t.ex. i form av naturreservat. Dessa kan fungera som spridningskällor för kolonisationen av nya områden. Eftersom lövträd blir utkonkurrerade av gran under successionen, så krävs det dock på lång sikt att nya, stora bestånd med värdräd får utvecklas fritt. För arter som sprider sig vegetativt är det viktigt att satsa på att knyta ihop isolerade lövskogar och öka antalet värdräd i landskapet. Även små bestånd med lägre kvalitet kan troligen bli koloniserade av dessa arter och kan då fungera som broar för spridningen mellan naturreservaten.

# Folgen der Flächenreduktion und Verinselung natürlicher Wälder für die Artenvielfalt epiphytischer Moose

Die Landnutzung Skandinaviens ist heute durch intensive Forstwirtschaft geprägt. Die drastische Flächenreduktion natürlicher Wälder und die Verinselung der verbliebenen Lebensräume während der letzten Jahrzehnte werden als eine der Hauptursachen für den Rückgang vieler Pflanzen- und Tierarten angesehen. Die starke Abnahme der Anzahl von Laubbäumen insgesamt, und insbesondere von alten Laubbäumen, ist eines der zentralen Probleme des schwedischen Naturschutzes. In der natürlichen Waldlandschaft konnten sich Laubbäume auf offenen Freiflächen nach Waldbränden und starken Stürmen ansiedeln. Da aber in Skandinavien die Rotfichte konkurrenzkräftiger ist und Laubbäume langfristig ersetzt, erfordert der Erhalt von Laubbäumen in der Nadelwaldlandschaft die regelmäßige Schaffung von Freiflächen. Heute werden natürliche Waldbrände jedoch weitgehend unterdrückt; die Waldrodung ersetzt solche natürlichen Störungen nicht, da Kahlschläge in der Regel nicht ihrer natürlichen Entwicklung überlassen, sondern erneut mit Nadelbäumen bepflanzt werden.

Laubbäume mit nährstoffreicher Borke (Ahorn, Esche, Ulme, Pappel, Linde und Eiche) bieten Lebensraum für viele hoch spezialisierte Arten, darunter epiphytische („auf Bäumen lebende“) Moose. Sie stehen für einen bedeutenden Teil der Artenvielfalt schwedischer Wälder; ein Teil von ihnen ist heute gefährdet und viele werden als Indikatoren für Wälder von für den Naturschutz hoher Wertigkeit genutzt. Bäume haben nur eine begrenzte Lebensdauer, und der Erhalt solcher Arten in der Landschaft erfordert, dass ständig neuer Lebensraum entsteht, der besiedelt werden kann. Der Abstand zwischen Bäumen und Baumbeständen muss zudem für seine Bewohner überwindbar sein. Viele Moosarten wachsen nur sehr langsam, und es kann Jahrzehnte dauern, bis eine Fortpflanzung erfolgt. Sowohl Wachstum, Fortpflanzung als auch Keimung hängen von den jeweiligen Umweltgegebenheiten ab und können in kleinen, vereinzelter Baumbeständen, die u.a. oft eine geringere Luftfeuchte aufweisen, gehemmt sein.

Meine Forschung hat gezeigt, dass sowohl die zunehmenden Abstände zwischen Laubbäumen und Laubbaumbeständen als auch die Veränderungen der Umweltbedingungen in kleinen, isolierten Beständen die Artenvielfalt

der Baumbewohner gefährden. In welcher Form einzelne Arten von diesen Faktoren beeinträchtigt werden, hängt jedoch stark von deren Fortpflanzungs- und Ausbreitungsstrategien ab. Moose pflanzen sich sowohl sexuell mit Hilfe von Sporen, als auch mit Hilfe von vegetativ gebildeten Ausbreitungsorganen, z. B. Brutkörpern und Brutästen, fort. Sporen sind in der Regel deutlich kleiner als vegetative Ausbreitungsorgane. Meine Untersuchungen haben gezeigt, dass Arten, die sich sexuell vermehren, weitere Ausbreitungsdistanzen haben als Arten mit vegetativer Vermehrung. Kleine Moossporen können vermutlich über Entfernungen von mehr als 500 m transportiert werden, wohingegen für große Brutkörper und –äste bereits Entfernungen von weniger als 100 m unüberwindbar sein können. Gleichzeitig sind Arten mit vegetativer Vermehrung wesentlich unempfindlicher gegenüber Umweltverhältnissen als Arten mit sexueller Vermehrung. Insbesondere bei niedrigen pH-Werten der Borke – wie sie oft bei Laubbäumen in dichten Nadelbaumbeständen oder an Waldrändern auftritt – ist die sexuelle Fortpflanzung stark gehemmt, die vegetative Fortpflanzung hingegen nicht beeinträchtigt. Keimungs- und Etablierungsexperimente haben außerdem gezeigt, dass Brutkörper und Brutäste höhere Etablierungschancen besitzen als Sporen, u. a. weil diese während der Etablierungsphase weniger empfindlich gegenüber Austrocknung sind. Ein weiterer bedeutender Nachteil der sexuellen Vermehrung ist, dass viele Arten vermutlich erst nach mehr als 20 bis 30 Jahren sexuelle Reife erlangen, wohingegen eine vegetative Vermehrung bereits frühzeitig möglich ist. Für Arten, die sich sexuell ausbreiten, ist daher die Landschaftsstruktur vor 30 Jahren wesentlich bedeutsamer als die heutige. In jungen Baumbeständen ist keine sexuelle Fortpflanzung möglich, und zunehmend kürzere Rodungsintervalle stellen eine besondere Gefahr für diese Arten dar.

Verschiedene Moosarten haben unterschiedliche Ansprüche; dies erfordert kombinierte Naturschutzstrategien. Der Erhalt von großen Laubbaumbeständen hohen Alters und hoher Qualität, z.B. in Form von Naturschutzgebieten, ist zentral für den Erhalt der Vielfalt von Arten mit sexueller Vermehrung. Da jedoch im Zuge der natürlichen Entwicklung Laubbäume durch Fichten ersetzt werden, ist es langfristig auch notwendig, dass große Flächen geschaffen werden, die sich frei zu neuen Laubwäldern hoher Qualität entwickeln können. Der Schutz von Arten mit vegetativer Ausbreitung erfordert demgegenüber eine Erhöhung der Laubbaumdichte in der Landschaft insgesamt und das Einrichten von Korridoren, die die einzelnen Laubbaumbestände verknüpfen. Selbst kleine Bestände geringen Alters und Qualität können vermutlich von diesen Arten besiedelt werden.

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