# Effects of Habitat Conditions and Disturbance on Lichen Diversity

## Studies on Lichen Communities in Nemoral, Boreal and Grassland Ecosystems

Per Johansson
*Faculty of Natural Resources and Agricultural Sciences*
*Department of Conservation Biology*
*Uppsala*

**Doctoral thesis**
**Swedish University of Agricultural Sciences**
**Uppsala 2006**

**Acta Universitatis Agriculturae Sueciae**
2006: 6

ISSN 1652-6880
ISBN 91-576-7055-2

Tryck: SLU Service/Repro, Uppsala 2006

# Abstract

Johansson, P. 2006. *Effects of habitat conditions and disturbance on lichen diversity: studies on lichen communities in nemoral, boreal and grassland ecosystems*. Doctor's dissertation.
ISSN 1652-6880, ISBN 91-576-7055-2

This thesis includes five papers from four studies on lichen diversity in its broad sense. The overall objectives were to examine species richness, composition, distribution, and abundance of lichens at tree and stand-level, after forest fire, and after prescribed burning. Based on these studies I develop two themes in the thesis: 1) The epiphytic lichen metacommunity – how tree-level lichen diversity depends on local and regional processes, whose importance may vary over time. 2) How disturbance induced habitat loss and mortality may affect lichen diversity and the extinction risk of rare species. Nemoral, epiphytic lichen communities were examined in Uppland, Sweden. Species distribution, richness, and composition were related to factors at both tree and stand-level, e.g. tree age, stand size (number of trees), surrounding landscape, and isolation. Species abundance was mainly related to tree size and stand size (number of trees). For *Pleurosticta acetabulum* the results indicated an effect of connectivity on stand-level abundance, i.e. a 'mass-effect'. For species richness, the relationship with tree age was asymptotic and levelled off at ca. 65 years of age. Boreal, epiphytic lichen communities were examined eight years after a forest fire in Minnesota, USA. Lichen abundance was proportionally lower than species richness at burned sites compared with unburned sites. Post-fire colonization was related to species post-fire abundance, and was higher for common species and dead wood preferring species. Crustose, shade preferring, and rare lichens seemed especially vulnerable to the fire. Grassland lichens were surveyed before and after prescribed burning of two old, abandoned fields in central Minnesota. After a low intensity fire, cover of *Cladonia* spp. was still relatively high and positively related to pre-fire cover. After a high intensity fire no such relationship was seen, and all lichens had experienced high mortality rates. The studies demonstrate that lichen community structure depends on a multitude of local and regional factors, whose importance may vary between diversity measures. They also demonstrate that lichen community response to disturbance depends on disturbance intensity and may vary between diversity measures. Post-disturbance colonization rates are higher for species with high post-disturbance population size, which in turn, may be a function of pre-disturbance population size. However, if disturbance intensity exceeds critical thresholds for species mortality, population size does not matter – all individuals are killed.

*Keywords*: biodiversity, community assembly, connectivity, disturbance, epiphytic lichens, extinction risk, forest fire, life-history traits, *Parmelina tiliacea*, *Pleurosticta acetabulum*

*Author's address*: Per Johansson, Department of Conservation Biology, Swedish University of Agricultural Sciences, SE-750 07 Uppsala, Sweden.
E-mail: per.johansson@nvb.slu.se

# Contents

# Appendix

## Papers I-V

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

I. Johansson, P., Rydin, H. & Thor, G. Tree age and epiphytic lichen diversity – community composition and life-history traits. *Submitted manuscript*.

II. Johansson, P. & Ehrlén, J. 2003. Influence of habitat quantity, quality and isolation on the distribution and abundance of two epiphytic lichens. *Journal of Ecology 91*, 213-221.

III. Johansson, P., Reich, P.B., Carlson, D., Wetmore, C.M. & Thor, G. The legacy of wildfire for lichens in the boreal forest. *Manuscript*.

IV. Johansson, P., Wetmore, C.M., Carlson, D., Reich, P.B. & Thor, G. Habitat preference, growth form and population size of lichens along a wildfire severity gradient*. Submitted manuscript*.

V. Johansson, P. & Reich, P.B. 2005. Population size and fire intensity determine post-fire abundance in grassland lichens. *Applied Vegetation Science 8*, 193-198.

Paper II is reproduced with permission from Blackwell Publishing; Paper V is reproduced with permission from Opulus Press.

As first author, for each paper I contributed with major parts of study set up, field work, lab work, data analysis, and preparing the papers.

# Introduction

Biodiversity is a highly variable phenomenon that continuously keeps intriguing ecologists and ecological research. To quote Hansson (2003): "The very obstacle for understanding and predicting ecological relationships locally is actually the high level of 'biodiversity'." Disturbance, succession, heterogeneity in resources and physical factors, and interactions between trophic levels and along resource gradients, are some factors that generate this large variability in species composition at temporal as well as at spatial scales (Huston, 1994; Hansson, 2003). This variability cannot easily be examined, but can be approached by tactical case studies, that may permit at least some preliminary synthesis, and predictive and testable hypotheses. This is the approach that I have chosen for my thesis work on lichen diversity, here defined in a broad sense including community composition, species richness, and species abundance (cf. Hooper *et al.*, 2005).

The thesis includes five papers from four studies in three ecosystems on two continents; the nemoral forest in Sweden (paper I and II), the boreal forest in North America (III and IV), and the North American prairie (V). The studies from Sweden focus on habitat prerequisites for epiphytic lichen communities, e.g. the effects of tree age, number of trees available for colonization, and habitat isolation. The North American studies, on the other hand, centre on the destruction of lichen communities, i.e. the legacy of fire.

## Objectives of thesis work

The overall objective in paper I and II was to examine tree and stand-level effects on lichen diversity, including species richness, composition, and species abundance. Although tree and stand-level effects separately have been the subject in numerous prior studies, there are relatively few which include combined effects of such factors when examining lichen diversity.

The overall objective in paper III, IV, and V was to examine the effects of fire on lichen diversity. Considering the extensive interest in the effects of forestry on lichen diversity in boreal forests there are surprisingly few studies on the consequences of natural disturbance, such as fire, in these ecosystems. During my two years spent in Minnesota, USA, I could use sample-plots established after a wildfire in pristine, boreal forest to examine lichen diversity and colonization along a fire severity gradient. The work further led me to recognize the role of heterogeneity within disturbances, which was the incentive to set up the study on grassland lichens before and after prescribed burning at Cedar Creek, USA (paper V). The main objective of this study was to examine the nature and consequences of heterogeneity within grassland fires for post-fire lichen abundance.

## Thesis aims

Rather than summarizing the results from the studies included in this thesis I attempt to develop some general hypotheses on two main themes based on results from these studies. Doing this I acknowledge they are case studies of limited extent in space and time. For reference, I provide extended summaries of paper I-V last in the thesis.

The first theme has its starting point in the relationship between tree age and lichen species richness (paper I, Figure 8). It is my notion that the basic assumptions on this topic are rarely developed or explicitly stated. Therefore, I will attempt to outline some general assumptions and predictions of tree-level lichen diversity, put in a metacommunity context.

A metacommunity is broadly defined as a set of local communities that exchange colonists of multiple species (Leibold *et al.*, 2004). Emphasis on regional influence on local community dynamics is not new (e.g. MacArthur & Wilson, 1967), and the extensive field of metapopulation ecology has dissected local and dispersal processes for single species dynamics. The metacommunity concept emphasizes linkages between spatial scales for whole communities, and is rapidly gaining foothold in contemporary community ecology (Leibold & Miller, 2004; Figure 1). Epiphytes, such as tree-living lichens, form very dynamic 'patch-tracking' communities (cf. Snäll *et al.*, 2003). Habitat patches, trees, continuously appear and disappear. The local communities, delimited at tree-level, are strongly affected by local (tree-level) processes, e.g. tree growth. Dispersal is presumably very important, since all species continuously have to 'track' new habitat patches. Therefore, I believe it is an appealing approach to study epiphytic lichens within a metacommunity context, which would contribute to the growing field of metacommunity ecology.

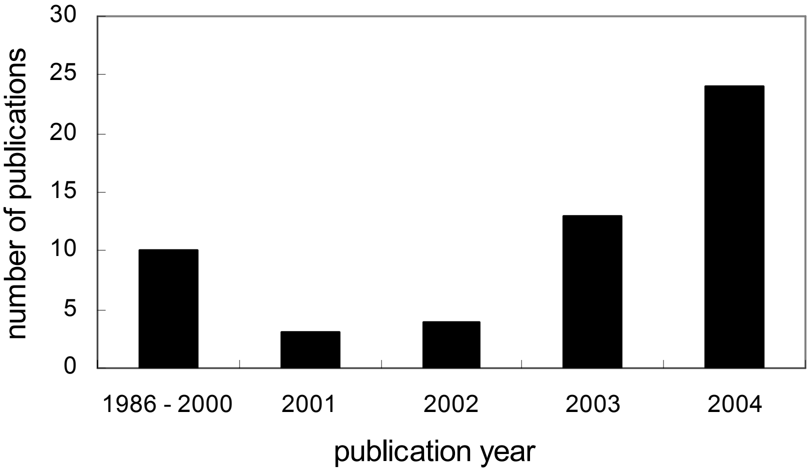

*Fig. 1.* The number of published papers between 1986-2004, including "metacommunity" somewhere in title, abstract or key-words (Web of Science, on the 1st of December 2005).

The second theme is based on papers III to V and deals with disturbance. From these studies I infer a general scenario for the immediate community response to disturbance as an effect of disturbance induced habitat loss and direct mortality. I also provide a short overview of disturbances in lichen communities.

# The epiphytic lichen metacommunity

Basically any community is determined by factors and processes operating at multiple spatial and temporal scales (Ricklefs, 1987; Levin, 1992; Loreau, 2000; Srivastava, 2005). For example, the equation, $D\gamma = D\alpha + D\beta$, describing how landscape diversity ($D\gamma$) is the sum of local diversity ($D\alpha$) and 'environmental heterogeneity' ($D\beta$), illustrate that various scales interact through 'bottom-up and top-down' effects (Loreau, 2000).

It may be intuitive that species occurrence and community structure depend on processes at multiple scales. But although large-scale processes have been emphasized in evolutionary, taxonomic, and biogeographic contexts, it is not until the last 20 years that community ecology has shifted its focus from local, to both local and regional processes (Loreau, 2000; Ricklefs, 2004). In contemporary ecology, this insight has resulted in an increasing number of studies that evaluate the effects of both local and regional factors on local community structure (Cottenie & De Meester, 2004; He *et al.*, 2005; Srivastava, 2005).

Local scales have often been defined as the spatial extent of community interactions, where factors such as competition, predation, mutualism, niche differentiation, disturbance, and resource availability govern the membership and abundance of species in the local community (Mouquet *et al.*, 2003; Cottenie & De Meester, 2004; Foster & Dickson, 2004; Ricklefs, 2004; He *et al.*, 2005). Regional scales are often defined by the geographical distributions of species that potentially can colonize the local community (Ricklefs, 1987; Dupré, 2000; Foster & Dickson, 2004; Srivastava, 2005). Species distributions are determined by factors such as history, dispersal and abiotic factors.

Defining the scales where decisive processes occur is, however, not easy (Bellehumeur & Legendre, 1998; Huston, 1999; Holland *et al.*, 2004). For example, Loreau (2000) has remarked, referring to Whittaker's α, β, and γ-scales, that "it has proved extremely difficult to identify these scales in operational terms" and that "there is essentially no prescription in ecology on how to define the spatial scale of a local community". Ricklefs (2004) even advocate that "ecologists should abandon circumscribed concepts of local communities". He suggests that they should be thought of as point estimates of overlapping regional species distributions, except in cases of highly discrete resources or sharp ecological boundaries. However, describing ecological phenomena in nested spatial scales may help to understand how communities are structured (cf. Bellehumeur & Legendre, 1998).

For epiphytic lichens, two such nested spatial scales are the tree and the stand-level (Figure 2). The scale-dependence is manifested by the fact that the host trees for these lichens often occur in stands that are themselves more or less well-defined patches at the landscape-level. Especially the tree is a highly discrete resource. The stand is a somewhat arbitrary delineation for the surrounding landscape where regional processes operate, but is often encompassed by similar abiotic conditions and land-use history. These scales, the tree and stand-level, are often referred to in management contexts; forests are managed at stand-level, where retention of old trees is becoming a common management practice (Fries *et al.*, 1997; Niemelä, 1999). Therefore, the tree and the stand scale should be highly operational and relevant in a conservation biology context, and conceptually useful for a local-regional perspective on epiphytic lichens.

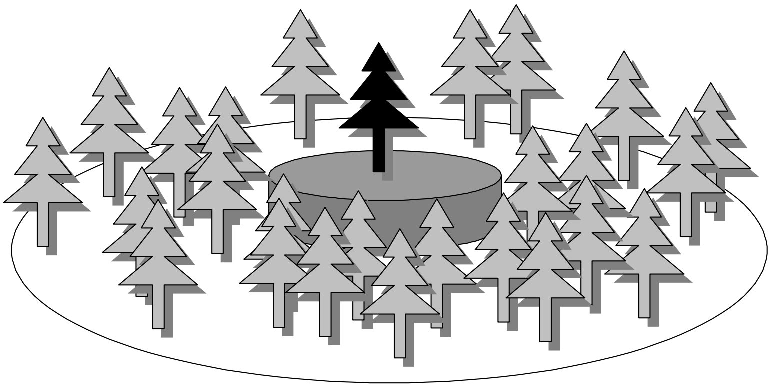

*Fig. 2*. The tree and the stand-level may provide two operational and conceptually useful spatial scales that help to understand how scale-dependent factors and processes structure epiphytic lichen metacommunities.

## Brief review of tree and stand-level influence on lichen diversity

Any inherent properties of the tree, such as its identity and age, are potential ‘bottom effects’ that set the prerequisites for the lichen community. Relationships between epiphytic lichens and tree properties have accordingly been emphasized for more than a century (see Almborn, 1948, and earlier references therein).

Thorough, quantitative analyses of lichen communities with regard to tree species and other tree properties were presented fifty years ago by Culberson (1955) and Hale (1955), and a few years later, Barkman (1958) published an extensive account on the topic. Associations between tree species and lichen community characteristics have since then repeatedly been reported, from tropical, temperate, and boreal forest ecosystems (Jesberger & Sheard, 1973; Degelius, 1978; Halonen *et al.*, 1991; Arup *et al.*, 1997; Wolseley & Aguirre-Hudson, 1997;

Uliczka & Angelstam, 1999; Eversman *et al.*, 2002; Sillett & Antoine, 2004; Mistry & Berardi, 2005; paper II).

As well as there are differences among tree species, the lichen community can vary among and within trees of the same species as a function of variation in light, humidity, and temperature (Hale, 1952; Edwards *et al.*, 1960; Yarranton, 1972; Øvstedal, 1980; McCune, 1993; McCune *et al.*, 1997; McCune *et al.*, 2000; Campbell & Coxson, 2001; Sillett & Antoine, 2004). Varying soil conditions can also provide an explanation for lichen community variability among conspecific trees. There are still few studies on this topic but those studies indicate that bark chemistry can be a function of soil conditions that translate into the tree and the lichen community (Gauslaa, 1985; Bates, 1992; Gustafsson & Eriksson, 1995; Gauslaa *et al.*, 1998).

Tree age, or tree size, is another important factor for lichen diversity (Almborn, 1948; Yarranton, 1972; Jesberger & Sheard, 1973; Pedersen, 1980; Uliczka & Angelstam, 1999; Boudreault *et al.*, 2000; Kantvilas & Jarman, 2004, paper I & II, Figure 8, 9 & 10). In conservation contexts, the importance of old trees for rare and red-listed species is often emphasized, with important consequences for management and conservation practices because it calls for old-tree retention and recruitment (e.g. Thor, 1998).

It may be difficult, however, to separate the effect of tree age from that of tree size, since age and size correlate. While physical and chemical bark conditions can be functions of both age and size, there are other factors that specifically relate to either age or size. Increasing tree size simply implies an area effect and should be positively correlated with the number of species for that reason, while high age also means a longer time for colonization (Rolstad & Rolstad, 1999; Snäll *et al.*, 2003; Kantvilas & Jarman, 2004). Besides the area effect, large trees may also display larger gradients in environmental factors among the different parts of the tree, which should allow a broader range of species (see above). Thus, the tree size effect on species richness should increase with the sampled proportion of a tree. Most studies, however, for practical reasons include only the basal part of tree trunks, especially when sampling the complete lichen community. This scale, and even smaller, are, however, relevant scales to study the local lichen community development over time, i.e. succession. However, few studies of tree-trunk lichen communities have tried to separate the effects of age and size, which I attempted to do in paper I (Figure 8).

Stand-level conditions that affect the tree-level lichen community can include macroclimate, topography, landscape configuration, and productivity gradients (e.g. Almborn, 1948; Hale, 1955; Adams & Risser, 1971; Jesberger & Sheard, 1973; Halonen *et al.*, 1991; Peterson & McCune, 2001; Jovan & McCune, 2004; Werth, 2005, paper II). That such effects can override local effects was shown, for example by Oksanen (1988), who analysed data collected by Koskinen in the 1940s. He found that site conditions (forest type) were more important for lichen species composition than the host tree species identity.

In the 1970s, Rose (1976) published his classical account of how lichen diversity in English woodlands depends on ecological continuity. This work generated many subsequent studies on the importance of stand history. It is within this context that studies on local and regional influence on lichen diversity, defined either at tree versus stand-level or at stand versus landscape-level, have seen most development over the last two decades. For example, Peck & McCune (1997), Peterson & McCune (2001), and Hedenås & Ericson (2004) have showed how stand-level species composition depends on both stand history and macroclimate or surrounding landscape. Dettki & Esseen (1998) found effects of landscape history on stand-level lichen abundance, while Esseen *et al.* (1996) found effects of stand history on tree-level lichen abundance.

## Local and regional processes that structure the epiphytic lichen metacommunity

It should be evident that both tree and stand-level factors are important to explain lichen diversity patterns. But how do such factors, as reviewed above, apply to a local-regional perspective on the development (assembly) of local (tree-level) lichen communities? To understand how epiphytic metacommunities are structured it is, for example, essential to ask: When do local or regional processes dominate in local community assembly (Figure 3), and do local processes propagate within the metacommunity? To answer such questions it is necessary to define the local and regional processes that operate at the local and regional scales, respectively.

Local processes could be defined as processes that are expressed in the performance of species within the local community, i.e. establishment, growth, reproduction, and mortality. For epiphytic lichens such factors and processes are related to tree properties, species interactions, small-scale disturbance, productivity, and climate. Climate can refer to the microclimate of the immediate surroundings, but also to macroclimate, which may be viewed as a spatially autocorrelated local factor (J. Ehrlén, pers. comm.). This view may be applied to all environmental variability at larger scales than the tree-level, which show some form of spatial autocorrelation, and have potential effects on the local lichen community, e.g. topography and productivity.

Regional processes are those that are expressed in species dispersal into the local communities, and the assembly of species in the regional species pool. Dispersal is a prerequisite for species colonization of local communities, but can also maintain species local population size through ‘mass effects’ (Leibold & Miller, 2004). The assembly of the regional species pool will be affected by factors such as land-use history, large-scale disturbance regimes, macroclimate, and at longer time-scales, also by evolutionary processes.

Another important feature of the regional species pool is species niche differentiations and life-history trade-offs. If the species exhibit differentiation in resource use, or life-history strategies, this can lead to species sorting along environmental gradients, and contribute to explain the metacommunity structure (Leibold *et al.*, 2004; Leibold & Miller, 2004).

Considering how the studies reviewed in the earlier section apply to this local and regional perspective they mainly deal with the influence of tree properties and climate on local lichen performance, and with regional factors that affect the assembly of the regional species pool. The consequences of species interactions, small and large-scale disturbance, niche differentiation and life-history trade-offs are generally poorly understood. In the subsequent section I will therefore attempt to outline some assumptions on these factors, and use these for predictions of the development of local (tree-level) lichen diversity.

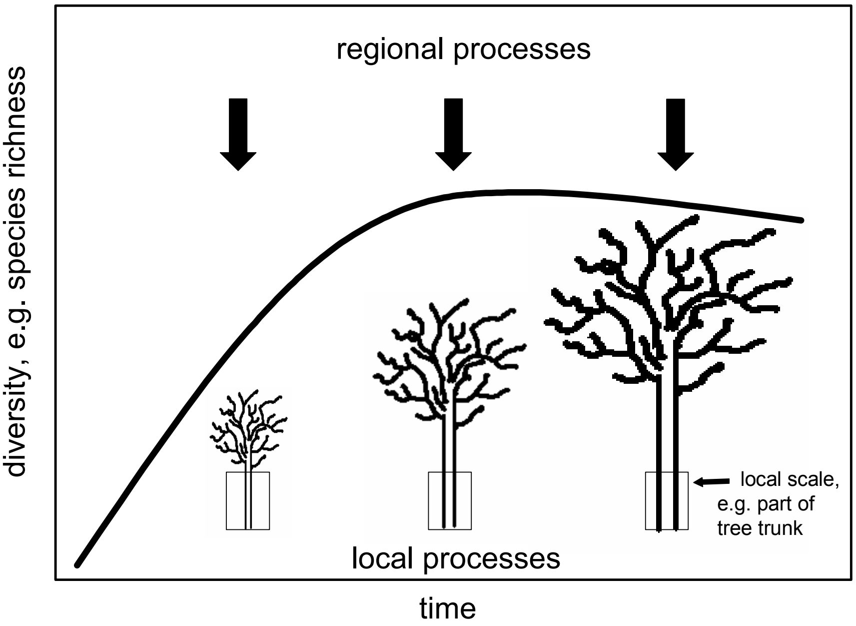

*Fig. 3*. The development (assembly) of the local lichen community on tree trunks is ultimately set by the lifespan of the tree. Local processes are expressed in species establishment, growth, reproduction, and mortality, and may include competition, climate, tree growth, and disturbance. Colonization of the tree-level community results from regional processes, expressed in dispersal. The relationship between tree age and lichen diversity (here as asymptotic, cf. Figure 8) will depend on the relative influence of local and regional processes, and on the level of species niche differentiation and life-history trade-offs in the regional species pool. The relative influence from local and regional processes may also vary over time.

## *Local processes: tree properties, climate, interactions, and disturbance*

From prior studies on epiphytic lichens it is clear that establishment and growth depend on tree properties and the local climate. For example, for tree species with qualities that favour a wide range of the regional species pool, the establishment rates will likely be higher than for ‘low quality’ tree species. Further, as a tree grows, at least some of its properties will change, e.g. the bark ruptures and the tree crown enlarges. In this way tree growth may affect lichen reproduction and mortality, e.g. caused by bark rupture or bark scaling. While bark rupture is a continuous process, bark scaling is best viewed as a disturbance. Herbivory by snails and moth larvae, as well as infestation by parasitic fungi may also act as disturbances to the local community (see *Disturbance in lichen communities*). Senecense is, however, not considered to be an important factor of mortality since all lichens are assumed to have continuous growth of new tissue.

Species interactions, e.g. competition, is sometimes seen as unimportant within lichen communities. For example, Lawrey (1991) discussed the possibility that competition may not occur due to the slow development rates of lichens, and the fact that large proportions of unoccupied habitat are often observed in 'equlibrium' lichen communities, e.g. on old trees. Unfortunately there are only few studies on species interactions among epiphytic lichens. These and other studies on presumed successional gradients, do, however, suggest that both competition and facilitation occur (Rogers, 1988; Stone, 1989; Hilmo, 1994; Ruchty *et al.*, 2001). Further, at humid sites epiphytic bryophytes can become abundant, and they may have strong competitive effects on the lichen community (cf. Ruchty *et al.*, 2001; Wiklund & Rydin, 2004). Thus, interactions can likely be important within local lichen communities, and even more within epiphytic communities including both lichens and bryophytes.

### *Regional processes: dispersal*

From the basic nature of the epiphytic lichen community and its habitat follows that dispersal is a crucial process. The lichen populations continuously have to track new habitat patches (trees) for their long-term persistence in the regional pool (cf. Snäll *et al.* 2003, 2005). Dispersal in terms of the number of species that potentially can colonize the local communities (i.e. the regional species pool) will depend on factors such as land-use history, macroclimate, and large-scale disturbance. Dispersal among local communities may then vary due to varying distances among habitat patches (trees), mass effects, and differentiation in dispersal related life-history traits (see below). Dispersal can also be assumed to link processes in the local communities (growth, reproduction) within the metacommunity. This is supported by studies of both epiphytic lichens and bryophytes that have demonstrated distance-dependent colonization and that species are spatially aggregated at tree and landscape-levels (Tapper, 1976; Dettki *et al.* 2000; Gu *et al.*, 2001; Hedenås *et al.*, 2003; Snäll *et al.*, 2003, 2004, 2005; Öckinger *et al.*, 2005; paper II).

The role of dispersal for tree-level diversity will vary depending on the mortality rates. With high mortality rates, dispersal can maintain tree-level diversity, but mortality processes will ultimately limit diversity. On the other hand, with low mortality rates dispersal will limit diversity. Vandvik & Goldberg (2004) argued that dispersal also limit local diversity in circumstances when increased dispersal will lead to higher diversity. This would be the case when the propagules of all species do not reach all habitat patches, and when species experiencing enhanced dispersal actually may establish once dispersed to a new patch. Dispersal limited diversity should likely be common in epiphytic lichen communities since there are often large patches of seemingly unoccupied habitat open for colonization (see above). As referred to above, there is also evidence for spatial variation in propagule loads.

### *Niche differentiation and life-history trade-offs*

Numerous accounts of lichen species lists show that certain species are often confined to young or old tree bark (cf. Figure 9). The occurrence of early and late successional species indicates species niche differentiation. In this context, I use niche differentiation in the meaning that there are inherent differences among the species that are manifested in terms of their occurrence along tree age related resource gradients. These differences can result from adaptations driven both by the environment and competition. Whether any particular local epiphytic community then is assembled on the basis of similar phenotypic traits or competition (see Cavender-Bares *et al.*, 2004) is, however, beyond the scope of this thesis.

A consequence of niche differentiation is that species likely exhibit different life-history traits. The classic trade-off between colonization and competitive ability infer that early successional species have high fecundity and dispersal ability, while late species are good competitors (Huston, 1994). Pioneer lichens have consequently been characterized by reduced thalli, low ability to compete, abundant spore production, and short time to reproduction (Topham, 1977; Hilmo, 1994; Richardson, 2002; paper I). Although these trade-offs are generally accepted there seems to be little support so far that they are important for species coexistence in metacommunities (Leibold & Miller, 2004). However, they should have potential consequences for species colonization and mortality rates.

## Predictions of tree-level lichen diversity

For the ash trees that were examined in paper I, the relationship between tree age and species richness was asymptotic or even slightly hump-shaped (Figure 8). Other studies have reported on both linear positive and asymptotic or humped lichen diversity-tree age/tree size relationships (Adams & Risser, 1971; Pedersen, 1980; Uliczka & Angelstam, 1999; Kantvilas & Jarman, 2004). The contrasting results provoke questions on when and why we should expect linear, asymptotic, or other kinds of relationships between lichen diversity and tree age. It is likely that both local and regional processes can affect both the shape and magnitude of these relationships. It is also likely that the relative importance of these processes vary over time (cf. Mouquet *et al.*, 2003; Figure 3). In this section I attempt to formulate some general predictions of the development of local (tree-level) lichen diversity, within a local-regional perspective.

A positive relationship between tree age and lichen diversity should occur with low levels of niche differentiation, and with low mortality rates (Figure 4a). For any lichen species, the probability of successful colonization should increase over time. Together, these assumptions result in an increasing number of species with increasing tree age (Figure 4a). This scenario implies that regional processes, enhancing dispersal and subsequent colonization of the local community, will be more important than local processes. The influence of dispersal may, however, be affected by tree species quality as substrate for the species in the regional pool. Dispersal should be more important for diversity on tree species that potentially can host a large proportion of the regional species pool.

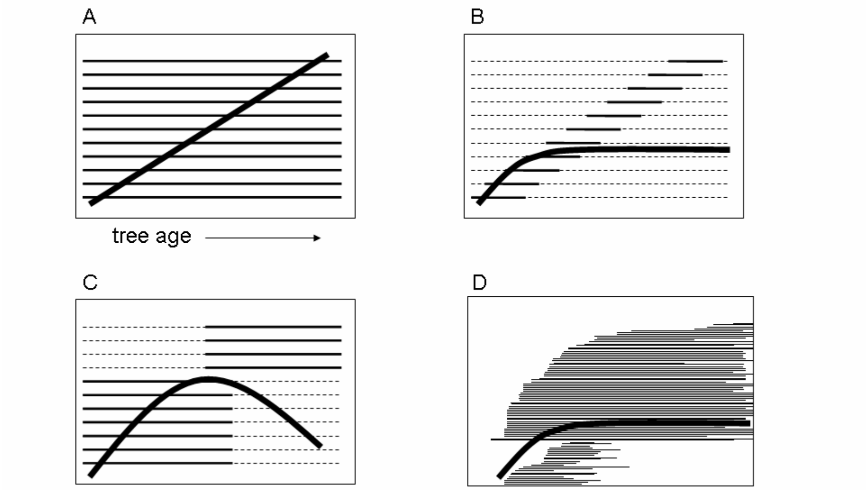

*Fig. 4*. Predictions of lichen diversity (species richness) - tree age relationships, irrespective of tree size effects. The bold horizontal lines indicate hypothetical species niches along tree age related resource gradients. A) A positive relationship should occur with low levels of niche differentiation among species, and with low mortality rates. For any lichen species, the probability of colonization should increase over time. B) An asymptotic relationship should occur when colonizations are balanced by species extinctions, after an initial phase with high colonization rates and low mortality rates. This should occur with high levels of niche differentiation, or with moderate to high mortality rates caused by tree growth or disturbance. High mortality rates, however, will have to be balanced by high colonization rates in order to maintain high diversity. C) A hump-shaped relationship should occur with skewed species niche differentiation, where only few species in the regional species pool can occur on old trees, or with high mortality rates on old trees. D) Simplified illustration of species niche differentiation along the tree age gradient (0-140 years) for 86 lichen taxa found on ash trees in Uppland (paper I). Niche width is described as the interval between the youngest and oldest tree with occurrence of each species. The curve shows the approximate relationship between tree age and species richness that was found for 143 ash trees (Figure 8).

An asymptotic relationship should occur when colonizations are balanced by species extinctions, after an initial phase with high colonization rates and low mortality rates (Figure 4b). This should occur with high levels of niche differentiation (Figure 4b), or with moderate to high mortality rates. Such mortality could result from species interactions, bark rupture, herbivory, and disturbance. High mortality rates, however, will have to be balanced by high colonization rates in order to maintain high diversity, which seems unlikely considering the relatively slow growth rates of lichens. Asymptotic relationships should thus result from both local and regional processes that affect the mortality rates and colonization rates (dispersal), respectively.

A hump-shaped relationship should occur with skewed species niche differentiation, where few species occur on old trees (Figure 4c), or with high mortality rates on old trees. High mortality rates could result from increased rupture of the tree bark, unfavourable bark environment, and disturbance from e.g. bark scaling. As for the asymptotic relationship, both local and regional processes are involved.

Negative or irregular relationships should basically not exist, because of the time lag for any species to colonize a growing tree. For example, the youngest tree included in paper I was 11 years, and hosted only two species, compared with an overall mean number of 17 lichen species per tree. Irregular relationships between age and lichen diversity could possibly occur if both colonization and mortality rates are high, e.g. for tree species with very scaly bark, readily colonized by pioneer species.

### *The Fraxinus example*

For the lichens found on at least three ash trees (paper I), I used the age interval between the youngest and the oldest tree for each species occurrence as a crude estimate of species niche differentation (Figure 4d). Acknowledging this as a very crude measure, it suggests that there is some niche differentiation among these species. About 25% only occurred on trees younger than ca. 75 years (cf. Figure 9), and only a few lichens were confined to the oldest trees (Figure 4d). The majority of species seem to be able to use a wide range of the tree age gradient. Their occurrence may be determined by stochastic colonization and mortality events, but the sequential appearance of species with increasing tree age may also suggest differentiation among these species caused by life-history traits related to colonization ability. Examination of selected life-history traits indicated for example that spore size increased for species that occurred most frequently on old trees.

The figure (Figure 4d) also suggests that something happens on the trees at 60-70 years of age, since that is when one-fourth of the species disappear. There are at least two possible explanations. One is competitive exclusion, which is somewhat supported by the fact that for species within Arthoniales and Ramalinaceae, species with immersed or thin crustose thalli, which may suggest inferior competitive ability, occurred most often on young trees (paper I). The second explanation is that this is the point in time when the ash trees change from having a fairly smooth bark, to rupture and get the more rough bark of older trees. This process could lead to mortality among early species, while late species may be favored by this new microenvironment.

### *Do the regional influence vary over time?*

Recently, Mouquet *et al.* (2003) suggested that local-regional diversity relationships depend on assembly time. Based on modelling experiments they found that in early assembly stages species richness saturate because only a subset of the species pool can colonize the local community – and they do. At intermediate assembly stages, local communities are unsaturated due to extended periods of competitive exclusion which results in non-equilibrium conditions. At later stages they found saturation as a result of resource competition.

Epiphytic communities provide a very suitable system to test the hypothesis by Mouquet *et al.* (2003) because local community age (assembly time) is easy to determine; it is related to tree age. Further, it is reasonable to assume that a subset of species in regional lichen species pools are fast colonizers, and that non-equilibrium conditions can occur on old trees (see above).

Using the data from paper I, as a preliminary examination, seems to support the hypothesis of Mouquet *et al.* (2003). There is no difference in species richness among stands when comparing young ash trees, while there are such differences for older trees (Figure 5). These results may indicate that there is a subset of lichens that readily colonize young trees irrespective of regional diversity, while diversity of old trees potentially is limited by dispersal. The data does not, however, allow further dissecting of such patterns.

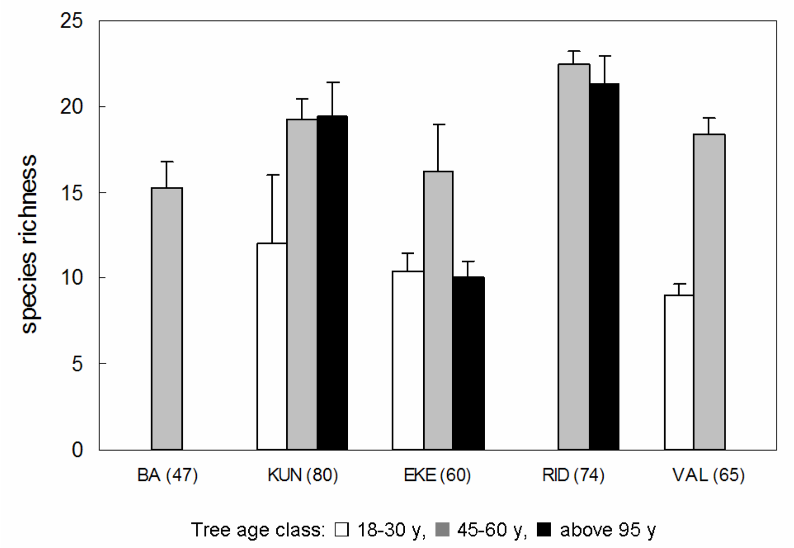

*Fig. 5*. Mean lichen species richness (and standard error) on ash trees grouped in tree age classes from young trees to old trees. The letter code under each bar denotes the stand name (see Figure 9), and the figure in brackets is the total number of lichens that were recorded in each stand, respectively. Data from paper I.

# Disturbance

Disturbance is a potentially important influence on the processes that structure lichen metacommunities and has briefly been touched upon in previous sections. In this and subsequent sections I will therefore provide an overview of disturbance in lichen communities. I will then, based on paper III-V, infer a general scenario for the immediate response to disturbance in species richness and abundance.

Disturbance is generally considered to be the amount of mortality and damage to individuals, that reduce biomass, and that directly or indirectly create possibilities for new individuals to establish (Sousa, 1984; Huston, 1994). The amount of mortality is referred to as disturbance severity, while disturbance intensity is the amount of energy released by the physical process of disturbance (Frelich, 2002).

However, it is not easy and unambiguous to define disturbance (cf. Pickett & White, 1985). What initially can act as disturbance to a community and its individuals may over time constitute the normal conditions, and lead to adaptations and stabilization to these new conditions. Sousa (1984) described disturbance as an event that “lies near one extreme of the continuum of natural perturbations that affect organisms” and that it is “a discrete, punctuated killing, displacement, or damaging of one or more individuals […].” Huston (1994) defined disturbance as “any process or condition external to the natural physiology of living organisms that results in the sudden mortality of biomass in a community on a time scale significantly shorter (e.g. several orders of magnitude faster) than that of the accumulation of the biomass.” Pickett *et al.* (1989) further aimed at specifying disturbance as an external process to the scale or level of interest causing change in its minimal structure. However, since the effects of disturbance at any given level likely can propagate to all components of the metacommunity (cf. Rykiel, 1985 in Pickett *et al.*, 1989), disturbance may ultimately have to be defined within the metacommunity concept.

## Disturbance in lichen communities

Compared with other organisms, such as vascular plants, lichens have slow growth rates. Therefore, disturbance, such as fire, should have long-lasting effects on the lichen community, which is also often the case (Bliss & Wien, 1972; Schulten, 1985; Wolseley & Aguirre-Hudson, 1997; Mistry, 1998; Johansen, 2001). Long-lasting effects of disturbance also seem to agree with the often-observed high abundance and diversity of lichens in old-growth forest, in contrast to younger forest stages (Lesica *et al.*, 1991; McCune, 1993; Dettki & Esseen, 1998; Haeussler *et al.*, 2002). The slow growth rates further imply that disturbance in lichen communities can include events extended in time. Reviewing and understanding the role of disturbance in lichen communities, however, suffers from a general lack of published studies on this topic.

Searching 24 major journals* in ecology and related subjects, using Web of Science on the 26th of November 2005 (back to 1986), resulted in 39 records for the combination of disturbance and lichens, of which 25 referred to soil living (terricolous) lichens, 10 to epiphytic lichens, and four to lichens on rocks. This can be compared with 4235 records for disturbance alone, 1311 records for disturbance and diversity, and 812 records for disturbance and plants. Extending the search on disturbance and lichens to include two of the major journals for lichenology; The Bryologist and Lichenologist, added another 11 records regarding lichens. Thus, only 50 papers including lichens and disturbance have been published in 26 major journals in ecology/plant biology in the last 20 years.

However, even if not explicitly stated, as evident from the search statistics above, there are studies on external perturbations on lichens and lichen communities that can qualify as disturbance. According to the synthesis of earlier definitions, I have here tried to identify these as: any event, resulting in extreme perturbations in relation to the natural range of variation, that results in discrete, punctuated killing or damaging of individuals, that is external to the level of interest or natural physiology of the lichens, repeated on time scales shorter than the accumulation of lichen biomass or development of the lichen community. By this definition I consider processes such as such tree bark scaling, tree fall, logging, and fire as potential disturbances in lichen communities.

Direct and indirect effects of predation (grazing, trampling by large herbivores) may in most ecosystems best be described as continuous processes. However, grazing and trampling may also occur stochastically due to predator behaviour, and then qualify as true disturbances. In this account of disturbance effects I will include rather than exclude predation, while I do not include effects of tree growth, climate change, or air pollution. Severe weather episodes clearly qualify as disturbance to lichen communities, and should be related to the extensive research on lichen physiological response to climate variables. However, that is beyond the scope of this thesis, and here I only recognize the importance of extreme weather episodes on growth, reproduction, and survival of lichens.

*American Naturalist, Applied Vegetation Science, Basic and Applied Ecology, Biodiversity and Conservation, Biological Conservation, Canadian Journal of Botany, Canadian Journal of Forest Research, Conservation Biology, Ecography, Ecological Applications, Ecological Monographs, Ecology, Ecology Letters, Écoscience, Journal of Applied Ecology, Journal of Biogeography, Journal of Ecology, Journal of Vegetation Science, Landscape Ecology, Oecologia, Oikos, Plant Ecology, Restoration Ecology

### *Disturbance in terricolous lichen communities*

For terricolous lichens there are far more explicit studies on disturbance than for epiphytes (see below). The impact of fire, grazing, and animal trampling on lichens in grasslands and on biological soil crusts have been studied by e.g. Antos *et al.* (1983), Schulten (1985), Shay *et al.* (2001), Scutari *et al.* (2004), and Holt & Severns (2005). In boreal forests, the effects of reindeer grazing receive a lot of attention (den Herder *et al.*, 2003; Boudreau & Payette, 2004). From boreal forests there are also studies on successional patterns following fire (Maikawa & Kershaw, 1976; Brulisauer *et al.*, 1996; Uotila & Kouki, 2005), and studies comparing the effects of logging and fire (Nguyen-Xuan *et al.*, 2000; Coxson & Marsh, 2001; Rees & Juday, 2002; Uotila & Kouki, 2005). The reason terricolous lichens are studied more often than epiphytes is that fire and grazing have important and obvious consequences in these systems. Another reason, however, is probably that epiphytic communities are more difficult to study in this respect.

### *Small-scale disturbance from herbivores and fungal parasites*

The consequences of small-scale herbivory by invertebrates and infestation by fungal parasites for lichen communities are poorly understood and seemingly often viewed as unimportant. One reason for this may be that damage from invertebrate herbivory is rarely observed in nature, and that lichens have ‘lichen compounds’, which are assumed to act as herbivore defence (see Gauslaa, 2005). Recent experiments have confirmed that these compounds do reduce herbivory from snails (Gauslaa, 2005) and moth larvae (Pöykkö *et al.*, 2005). However, Fröberg *et al.* (1993) have demonstrated effects of grazing on calcicolous lichen communities, and similar effects could be expected on tree trunks. This topic is, however, to my knowledge so far only touched upon as scattered observations (Hazell & Gustafsson, 1999; Gauslaa, 2005). Infestation by the parasitic fungus *Athelia arachnoidea* is another potential disturbance effect on tree-level lichen communities (Thor & Kannesten, 1989; Bates *et al.*, 2001; Gauslaa, 2002). This fungus seems to be favored by mild winters, when it probably can attack, and effectively kill selected epiphytic lichens (Gauslaa, 2002; G. Thor, pers. comm.).

### *Disturbance in forest ecosystems and the gap of knowledge*

A fairly extensive line of research on disturbance effects on lichens is concerned with the consequences of land-use, mainly forestry, on epiphytic lichens in boreal or other conifer forests. These studies include, for example, comparisons of lichen diversity between old growth and secondary forest (Lesica *et al.*, 1991; Dettki & Esseen, 1998; Kuusinen & Siitonen, 1998), and of lichen response to forest edges (Renhorn *et al.*, 1997; Rheault *et al.*, 2003).

In contrast to the numerous studies on the impact of forestry and forest age on epiphytic lichens, there are, however, surprisingly few studies on epiphytic lichens and natural disturbance, such as wildfire. Longan *et al.* (1999) remarked that "literature about the impact of fire on the diversity of epiphytic lichens is scarce". Most work seems to originate from temperate to tropical areas, while few studies are from boreal forest ecosystems. Longan *et al.* (1999), studied post-fire colonization in Spain, and Romagni & Gries (2000) have studied post-fire lichen recovery in southwestern USA. In Minnesota, Wetmore (1983) studied lichens on oak trees in oak savannas experiencing different fire regimes, and in the cerrado region of Brazil, Mistry (1998), and Mistry & Berardi (2005) have studied the lichen flora in relation to fire frequency. In Thailand, Wolseley & Aguirre-Hudson (1997) described how lichen composition can be used to assess forest fire regime.

Thus, it is evident that there is a gap regarding our understanding of the role of natural disturbances for epiphytic lichens in forest ecosystems. Filling this gap is especially urgent in a conservation biology context, where the importance of old-growth forest is often stressed and used as reference when evaluating biodiversity in managed landscapes. Fire is a major natural disturbance in many forest ecosystems that can retain these forests in a ‘primary state’ while simultaneously eliminating old-growth. Therefore, as formulated by Nordén & Appelqvist (2001), the "use of ecological continuity may lead to underestimation of the importance of forest dynamics and dispersal, and to overestimation of the importance of local land use history."

## Lichen community response to forest fire: a general description of community response to disturbance?

Forest fire consumes and kills both trees and their lichens. The community response to any disturbance that reduces the resources (habitat) shared by a species guild can be assumed to be a function of this habitat loss, as well as of direct mortality. Further, it may be assumed that habitat loss is proportional to disturbance intensity, and that population size is proportional to habitat availability (cf. Fahrig, 1997). These assumptions will result in a negative linear relationship between disturbance intensity and species population size/abundance (Figure 6a). If the disturbance in itself kills individuals at a higher rate than habitat is reduced, the negative response will be even stronger (Figure 6a). For species richness on the other hand, response to habitat loss could be expected to follow a species-area function (Brooks *et al.*, 1997; Thomas *et al.*, 2004):

$$\%\text{species lost} = 1 - (\text{HA post-disturbance}/\text{HA pre-disturbance})^z$$

HA is habitat area, and z will depend on the spatial scale and arrangement of the habitat (Brooks *et al.*, 1997; Ulrich & Buszko, 2004). Simplified assumptions on random distribution and nested habitat loss, using a value of $z = 0.25$, will predict low declines in species richness at low to moderate levels of disturbance intensity (habitat loss), and a strong decline first when a high proportion of habitat is lost (Figure 6b). If the disturbance in itself causes species extinction at a higher rate than habitat is reduced, the negative response will be even stronger (Figure 6b).

The results from paper III may lend some support to these predictions in that the abundance of the common lichens *Evernia mesomorpha* and *Usnea* spp. was proportionally lower than species richness at burned sites than at unburned sites (Figure 11 & 12). The actual relationship between habitat availability and disturbance intensity, however, is not described by the fire severity gradient used in paper III.

The response to disturbance intensity in terms of habitat loss or species mortality may not, however, be linear. On the contrary it is likely that there will be threshold levels where the response to disturbance intensity changes dramatically (Romme *et al.*, 1998; Spiller *et al.*, 1998; Frelich, 2002; Figure 6c). In paper V this was demonstrated for the response to prescribed fire for grassland lichens. During a low intensity fire, many lichens survived and post-fire abundance was a function of pre-fire population size. In contrast, after a fire of higher intensity, basically all lichens were killed and there was low lichen cover everywhere, irrespective of pre-fire population size (Figure 15).

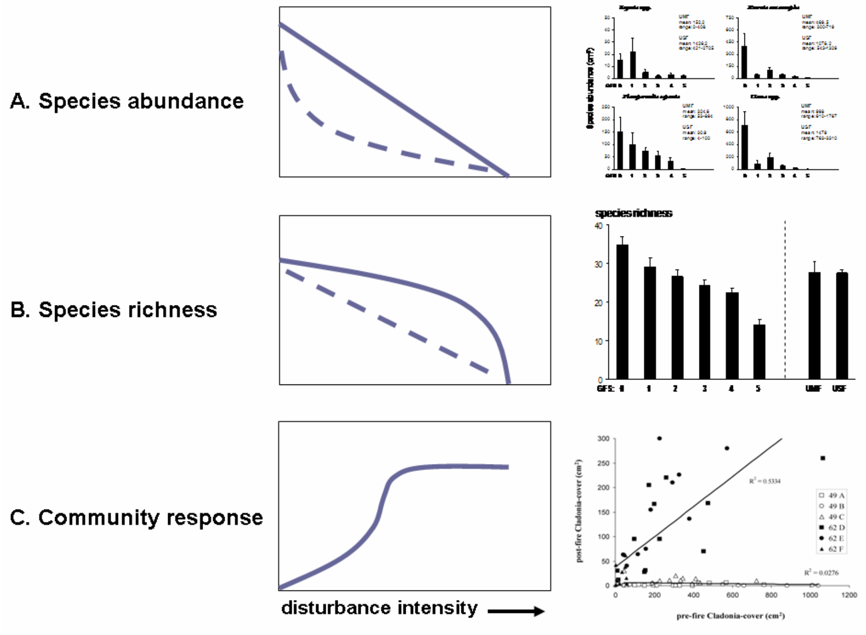

*Fig. 6*. General predictions of the immediate community response to disturbance intensity, illustrated with figures from paper III and V (Fig. 11, 12, 15). In A and B, disturbance intensity is assumed to be proportionally related to habitat loss. A) Species abundance is reduced proportionally to disturbance intensity, or at higher rates if disturbance cause mortality at higher rates than habitat loss (dashed line). Figure from paper III show drastically reduced abundance in burned vs. unburned plots for two abundant, fruticose lichens, and a more gradual decline for a foliose species. B) Species richness is reduced at high rates first at high disturbance intensity, as predicted from a species-area power function, or at higher rates if disturbance cause higher species extinction rates than habitat loss alone (dashed line). Figure from paper III show a gradual decline with increasing increments in fire severity, but a low number of species in the most severely burned plots. C) In reality there will often be threshold levels, where community response (in e.g. species abundance and richness) to disturbance intensity changes dramatically. Above a certain intensity level all individuals are killed. Figure from paper V show how lichen abundance is still high and proportional to pre-fire abundance after a low intensity fire, but very low, irrespective of pre-fire abundance, after a high intensity fire.

### *Which species go extinct from disturbance?*

During a disturbance it is likely that species will differ in terms of their vulnerability to go extinct. In general, rare species face higher risk of extinction than common species (Pimm *et al.*, 1988; O'Grady *et al.*, 2004). However, rarity can refer to either low abundance, or small distribution range, or both (Gaston, 1994). Reynolds (2003) recently argued that it is important to separate the form of vulnerability species exhibit, low abundance or small range size, from the factor that causes vulnerability to extinction: mortality or habitat loss. He suggested that for species with small range sizes, habitat loss may be more critical than mortality. For species with low abundance, on the other hand, mortality may be the most important factor causing extinction (Reynolds, 2003).

Considering disturbance intensity thresholds it is likely that the effects of disturbance induced habitat loss versus mortality on species extinction risk change along the intensity gradient. When disturbance intensity is below a critical threshold for species mortality, reduction in species abundance (extinction risk) should be proportional to disturbance intensity or habitat loss (Figure 6c & 7). In that case, species with small distribution range should be most vulnerable to extinction (Figure 7). The extinction risk for these species will then increase proportionally with increasing disturbance intensity, assuming random distribution of species and disturbance effects (Figure 7). Species with low abundance but fairly wide distributions will however most likely survive (Figure 7). Above the critical intensity threshold for extensive mortality, however, the effect of mortality will override the effect of habitat loss, and low abundant species will also experience severe extinctions (Figure 7).

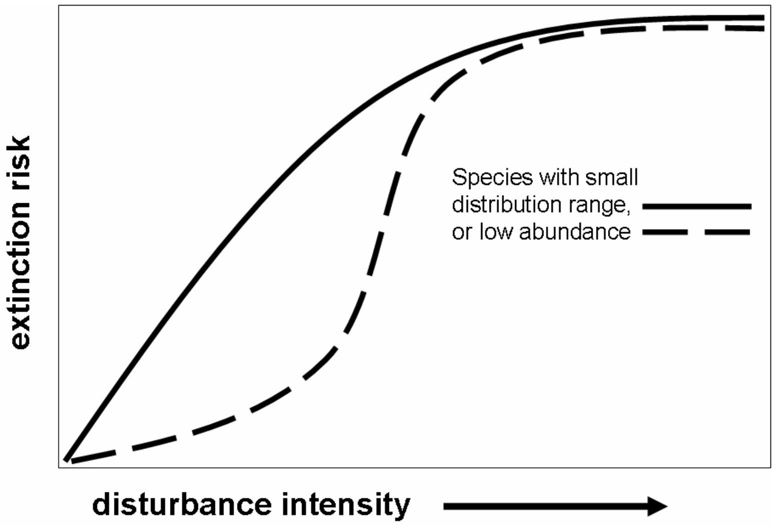

*Fig. 7*. Predicted extinction risk/species loss as a function of disturbance intensity for rare species with either small distribution range or low abundance. Below critical intensity thresholds for extensive mortality, the extinction risk of species with low range size is proportional to disturbance intensity, while species with low abundance have low extinction risk. Low abundant species face high extinction risk first when disturbance intensity exceeds the threshold.

When examining various species groups, both low abundance and small range size are repeatedly found to be correlated with species extinction risk (Pimm *et al.*, 1988; Manne & Pimm, 2001; Duncan & Young, 2000; Reynolds, 2003; O'Grady *et al.*, 2004). The results in paper IV and V also suggest that rare species were more prone to extinction during the fire. Examining the lichen species along the fire severity gradient in paper IV, indirectly suggests that rare species have been locally extinct at intermediate to severely burned sites (Figure 14). In this case, I cannot tell whether these species were mainly of low abundance or limited distribution range. At Cedar Creek, the results demonstrated a linear relationship between pre and post-fire abundance below a critical fire intensity threshold (Figure 15). Further, the overall low-abundant *Diploschistes muscorum* was extinct from all sample-plots but one, burned by low fire intensity (V).

Besides distribution range and population size, there are of course other explanations and potential predictors of disturbance induced extinctions. For example, spatial aggregation of populations and disturbance effects will affect species extinction risk (Kallimanis *et al.*, 2005). Species distribution and abundance are further often manifestations of species-specific life-history traits. Such traits may be the ultimate explanations of species vulnerability to disturbance. Reynolds (2003) suggested that life-history traits associated with species extinction risk may be late age at maturity and habitat specialization.

Extinction risk may also depend on the ecosystem characteristics and type of disturbance. In paper IV, the results suggest that shade preferring, crustose lichens were over-represented among species in unburned plots, suggesting that these species in particular were vulnerable to the fire. These species often occurred on balsam fir, a flammable tree species that is often eliminated by fire (Frelich & Reich, 1995). In the fire that burned the study area in Boundary Waters, a high proportion of the black spruce-balsam fir forest suffered high crown fire damage (Carlson, 2001). This reduced the occurrence of balsam firs and other shaded habitats. Thus, it is very likely that the lichens that prefer shaded balsam fir trunks had wider distribution in the study area before the fire. In that case their absence from burned sites really depends on their habitat preference, which in turn should be a function of their life-history traits. This point to the vulnerability of this habitat in this particular forest system, when subjected to fire, but also that habitat specialists are more vulnerable to local extinction than habitat generalists. High extinction risk for habitat specialists seems to be a general phenomenon (Reynolds, 2003).

# Summary of papers

## I. Tree age and epiphytic lichen diversity – community composition and life-history traits

In this study, I examined the effects of tree age, tree size, crown and understory vegetation cover, and stand location on tree-level lichen diversity. I sampled the basal tree trunks, up to 130 cm, of 143 ash trees, *Fraxinus excelsior*, in five deciduous stands in Uppland, Sweden. In total, 113 lichen species were recorded on these trees, from 2 to 30 species per tree. Some red-listed and other rare species were encountered, including *Agonima allobata* (NT), *Bacidia polychroa* (VU), *Bacidina caligans* (DD), *Biatora sphaeroidiza*, *Biatoridium monasteriense* (NT), *Eopyrenula leucoplaca* (NT), *Lecanora impudens* (VU), *Opegrapha ochrocheila* (NT), *Schismatomma pericleum* (NT), and *Thelenella pertusariella* (Red List categories according to Gärdenfors, 2005). Five of these species were found at Riddersholm, where the oldest tree was 140+ years, four at Vällen (63 y), four at Kungsträdgården on Biskops Arnö (140+ y), one at Ekebyholm (122 y), and none at the second Biskops Arnö site (50 y).

Tree age and tree size were strongly related to tree-level species richness, which increased with trunk diameter over all trees (Figure 8). Species richness increased only up to c. 65 y of age. Above that age, the number of species levelled off or even decreased (Figure 8). Species composition also shifted with tree age, which presumably reflects a successional gradient driven both by tree growth and species interactions (Figure 9). The age gradient mainly coincided with axis two in the ordination, and the older trees all appeared in the lower part of the ordination diagram (Figure 9). The ordination was based on only presence or absence of the species. Thus, it illustrates that trees above c. 75 years of age hosted several different lichen species than younger trees (Figure 9).

Internal site conditions, included as stand identity, influenced both species richness and composition. For example, two-thirds of all species were over-represented in a particular stand. With only five stands no firm conclusions can be drawn of which stand conditions that were most influential on the results. In this case, however, stand age and macroclimate are candidates. Stand age, if estimated as the oldest tree, varied from 50 to 140+ years, and the stands were located at both inland and coastal sites.

Tree-level light conditions, estimated by crown and understory cover, also showed significant relationships with both lichen cover and species richness. These relationships likely also explain the positive correlation between lichen cover and species richness. A model with lichen cover and trunk diameter alone, explained one third of the variation in tree-level species richness. The cover-richness relationship suggests a random placement of species, and that there are no dominant competitors in this system. However, understanding the nature of this relationship needs further research, preferably also at various spatial scales.

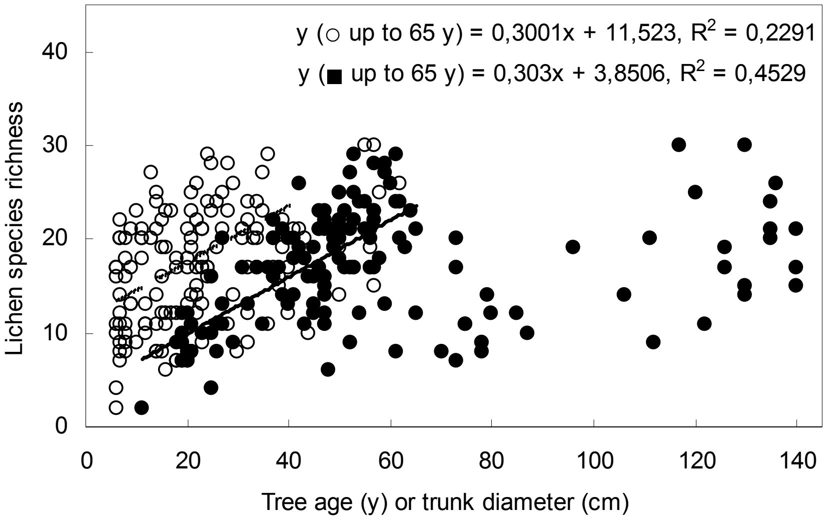

*Fig. 8*. Tree-level lichen species richness versus tree age (●) and trunk diameter, dbh (○), for all ash trees *Fraxinus excelsior* at the five study sites (143 trees). Linear equations include trees up to 65 y. age. Adopted from paper I.

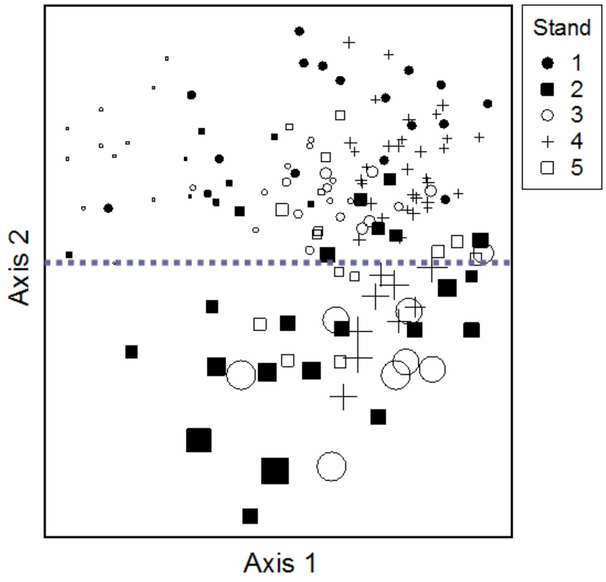

*Fig. 9*. NMS ordination graph of 142 ash trees in species space (the youngest tree with only two species present, was excluded from this analysis). (●=1.Biskops Arnö, ■=2.Ekeby, ○=3.Kungsträdgården, + = 4.Riddersholm, □=5.Vällen). Size of symbols represents tree age (from 18 to 140). The dashed line separates trees below and above 75 years; all trees below the line were older than 75 years of age. Adapted from paper I.

I also aimed at evaluating whether there were associations between some life-history traits of the lichen species encountered in this study, and their preference for young or old trees. Examining spore length, spore size, thallus height, growth form, dispersal mode, photobiont, pH preference, and Swedish distribution range, I found indications that spore size was associated with species preference for tree age; species most often found on old trees had longer and larger spores. For species within Arthoniales and Ramalinaceae, the results also suggested that species with immersed or thin crustose thalli occurred on younger trees than species with thick, crustose thalli. These results seem to agree with general theory and empirical data on dispersal traits and competitive ability as important traits that generally shift in species assemblages during succession.

## II. Influence of habitat quantity, quality and isolation on the distribution and abundance of two epiphytic lichens

In this study, I assessed the relative importance of tree- and stand-level effects on tree and stand-level occupancy and abundance of two foliose lichens, *Parmelina tiliacea* and *Pleurosticta acetabulum*, in a 9 $km^2$ landscape SW of Uppsala. These species were assumed to be similar in terms of habitat ecology, but represent one rare, mainly vegetatively dispersed species, and one common, sexually dispersed species, respectively. I also compared the predictive effect of three measures of isolation on species stand-level occurrence. In total, I surveyed 3237 trees in 94 stands, ranging from 1 to 198 surveyed trees per stand. *P. tiliacea* occurred on 563 of these trees and *P. acetabulum* on 692 trees.

At tree-level, for both species, occupancy was most related to tree size and stand identity, while abundance was most of all an effect of tree size (Figure 10). However, ca 80% of the variation in species abundance at tree-level remained unexplained. There was also an effect of tree species; *Parmelina tiliacea* seemed to prefer *Ulmus glabra* before *Acer platanoides*, *Fraxinus excelsior*, *Quercus robur*, and *Tilia cordata*. *P. acetabulum* seemed to prefer *Acer platanoides* and *Fraxinus excelsior*, before *Quercus robur*, *Tilia cordata*, and *Ulmus glabra*.

At stand-level, species presence was explained by the number of large trees (as an estimate of habitat availability), the amount of adjacent conifer forest (a negative effect), and proximity to conspecific lichen populations. In addition, *P. tiliacea* occurred more often in stands with a high proportion of edge to interior, which likely reflects its preference for exposed trees close to farmland. For both species, stand-level abundance was most of all explained by the number of large deciduous trees (patch size). For *P. acetabulum* abundance, there was also an effect of proximity to other stands and conspecific populations, indicating an effect of dispersal also for its local population size – a 'mass effect'..

Both species were similar in their response to isolation. However, the results indicated a stronger effect of isolation, and a stronger level of spatial aggregation for *P. tiliacea*. Together with the positive effect of 'connectivity' on stand-level abundance for *P. acetabulum*, this might suggest a stronger dispersal constraint on landscape-level distribution for *P. tiliacea*.

In conclusion this study suggests that species presence (colonization) is affected by factors at multiple spatial scales, e.g. tree and stand-level. Species abundance, on the other hand, was mainly related to habitat availability, in terms of tree size and tree number. However, only one-fifth of the variation in tree-level abundance could be explained in this study. Other factors and processes that can affect lichen species local abundance (net growth on individual trees) are species interactions, herbivory, substrate productivity, and disturbance. The significance of these factors in lichen communities is, however, poorly understood and needs further research.

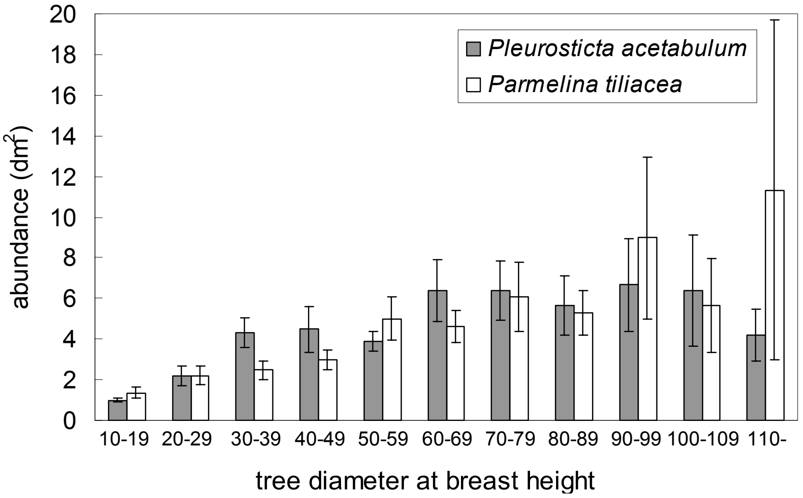

*Fig. 10*. Mean abundance in tree size classes according to diameter in breast height, of *Parmelina tiliacea* (515 trees) and *Pleurosticta acetabulum* (623 trees). Adapted from Paper II.

## III. The legacy of wildfire for lichens in the boreal forest

In 1995, a wildfire burned 1200 ha in the pristine, southern boreal forest of Boundary Waters Canoe Area Wilderness (BWCAW), in northern Minnesota. Two months after the fire, Daren Carlson, Lee Frelich and Peter Reich established sample-plots within the fire perimeter. The plots were located 35 m apart in squared grids, at three sites. Fire severity was estimated in the sample-plots by duff, litter, and canopy foliage consumption, in six classes, from unburned to severely burned sites. In this study I used a subset of these plots (84) to examine lichen species richness, composition, abundance, and colonization, along the fire severity gradient eight years post-fire.

In total, I found 135 lichen species (120 in the sample-plots) of which several are rarely or never recorded before in central or eastern North America, e.g. *Cheiromycina flabelliformis*, *Lecidea betulicola*, *Rinodina degeliana*, and *Ropalospora viridis*. For one species, *Biatora ocelliformis*, there were no earlier confirmed records from North America (Printzen & Otte, 2005).

As expected, fire severity was an important factor explaining lichen diversity eight year post-fire. Lichen abundance and species richness declined with increasing fire severity (Figure 11 & 12). Species accumulation over plots grouped by fire severity classes further indicated that the 'landscape'-level species richness was reduced with increasing fire severity, from low to intermediate to high (figure 6c).

Comparing richness and abundance along the fire severity gradient revealed somewhat different patterns between these measures, especially when comparing with the most common focal lichens, *Evernia mesomorpha* and *Usnea* spp. Their abundances were proportionally lower than species richness at burned sites than at unburned sites (Figure 11 & 12). Species richness declined with every incremental increase in fire severity, most of all at the most severely burned plots.

Also species composition was different among the fire severity classes (figure 6a). Of all 120 species that were found, 79 occurred in the unburned plots (7 plots) compared with a total of 67 species in all of the GFS 4-5 plots together (33 plots). Among species only found in unburned plots were *Cheiromycina flabelliformis*, *Lepraria lobificans*, and *Mycoblastus fucatus*. Species found in unburned or lightly burned plots were e.g. *Bacidia laurocerasi*, *Heterodermia speciosa*, and *Phlyctis argena*. At severely burned sites, common species were *Cladonia botrytes*, *Micarea misella*, and *Placynthiella dasea*.

Lichen colonization was measured as abundance of *Evernia mesomorpha* and *Usnea* spp. on birch and pin cherry saplings. The saplings were ca eight years old, i.e. of post-fire origin. The abundance of *E. mesomorpha* and *Usnea* spp. on the saplings correlated with fire severity and the overall plot abundance of these species, respectively (which was a separate measure).

In conclusion this study suggests the following scenario for the lichen community following a forest fire: The fire drastically reduces lichen abundance, but most species may persist unless fire intensity is both high and spatially uniform. Increased mortality with increased fire intensity, and overall slow recovery rates lead to reduced beta-diversity across the fire gradient, which could be hypothesized as a general pattern for organisms with high disturbance induced mortality rates and low recovery rates. After the fire, the colonization rates are highest close to propagule sources, i.e. at sites where lichens escaped the fire, which also suggests that rare species will colonize at lower rates than common species. The time lag for recovery to pre-fire lichen diversity and abundance will depend on forest characteristics. In north-eastern North America, studies indicate that the epiphytic lichen community in boreal forest can recover within 100 years which is about the natural fire interval in the BWCAW.

Finally, small- and large-scale heterogeneity within wildfire events needs to be acknowledged in the application of natural disturbance as a template for forestry practices as well as in conservation biology. Applying such templates should, however, be done with an overly cautious approach because any disturbance in the often fragmented boreal forest landscape, where populations are already reduced, may increase species extinction rates.

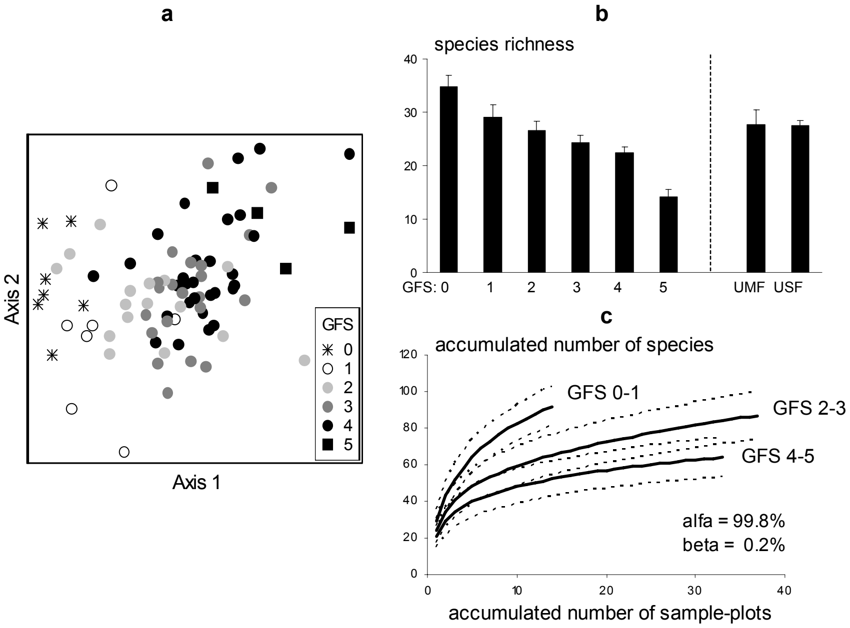

*Fig. 11*. Species composition (a), species richness (b), and species accumulation curves (c) for the GFS classes 0-5. In the two-dimensional NMS ordination the accumulated r-square between original space and distances (a) was 0.83 (0.60 for axis 1, and 0.23 for axis 2), indicating a good representation of the underlying structure in the species composition matrix. For species richness (b), bars show average species number with standard error for plots grouped by GFS class. For comparison the reference plots in unburned mixed forest (UMF) and swamp forest (USF) are shown in the two rightmost bars. Randomized species accumulation curves, with 95% confidence intervals (dashed lines), are shown for lumped GFS classes 0-1, 2-3 and 4-5. The alfa-diversity component is calculated from the weighted average of Hurlbert´s probability of interspecific encounter (the average curve) for these three classes, which expressed a high similarity to the overall species accumulation curve (the gamma-diversity). Adopted from paper III.

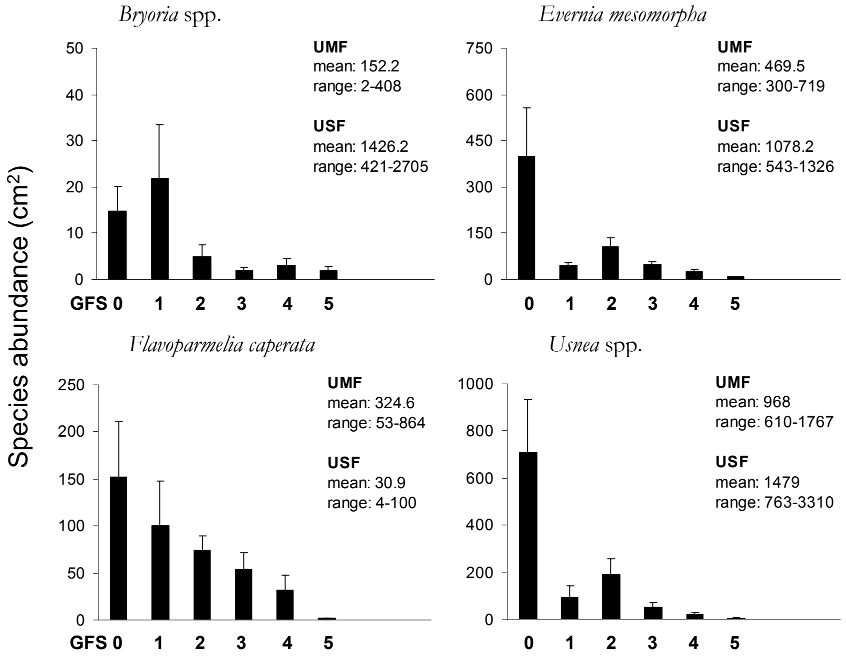

*Fig. 12*. Mean species abundance and standard error for the focal lichen species along the ground fire severity gradient (GFS). Mean abundance and range are shown for the unburned mixed forest (UMF) reference plots, and the unburned swamp forest (USF) reference plots. Adopted from paper III.

## IV. Habitat preference, growth form and population size of lichens along a wildfire severity gradient

This paper is based on the same study as paper III, and provides a closer examination of the species that were recorded along the fire severity gradient. Species response to disturbance such as fire may depend on species life-history traits. Therefore, the aim of this paper was to examine possible associations between the lichen species occurrence at burned versus unburned or lightly burned sites, and life-history related features of these lichens; habitat preference, growth form, dispersal mode, and overall population size.

I included all species recorded in at least three sample-plots, in total 79 taxa. Growth form was described as one of the major growth form types in lichens; crustose, foliose, or fruticose. *Cladonia* spp. were separated from other fruticose species due to their distinct morphology and common habitat use, i.e. soil, horizontal dead wood, and tree bases. Dispersal mode was described as vegetative or sexual, based on the presence of soralia (character for vegetative dispersal). Species habitat preference was described as shade preferring, aspen preferring, dead wood preferring, or as generalist. The rationale for using these habitat categories is that they represent important lichen habitat in boreal forest, and are assumed to reflect species life-history traits that otherwise can be difficult to measure. They also represent a habitat generalist – specialist comparison. The relative population size in the Boundary Waters region was estimated using the number of collections in the Minnesota lichen herbarium from the counties covering BWCAW. As for habitat preference, population size is not a true life-history trait, rather a consequence of such traits. Population size is, however, often used to predict species extinction risk, and may reflect response of traits that are otherwise difficult to evaluate.

The results showed that species that were over-represented in unburned to lightly burned plots were associated with shade-preference and crustose growth form (Figure 13). Examples of such species were *Arthonia radiata*, *A. didyma*, *Biatora laurocerasi*, *B. ocelliformis*, *B. pycnidiata*, *Lecanora impudens*, *L. thysanophora*, *Lecidea betulicola*, *Ochrolechia arborea*, *Pertusaria ophthalmiza*, *Phlyctis argena*, *Rinodina efflorescens*, and *Ropalospora viridis*. Foliose and fruticose species that were over-represented in these plots were e.g. *Heterodermia speciosa*, *Punctelia perreticulata*, *Ramalina dilacerata*, and *Usnea cavernosa*. Few species were over-represented in burned plots; *Cladonia botrytes*, *C. gracilis*, *Micarea misella*, *Placynthiella dasea*, and *Trapeliopsis granulosa*. These were associated with preference for dead wood. Rare species (species recorded in only 1-2 sample-plots) were over-represented in unburned plots (Figure 14).

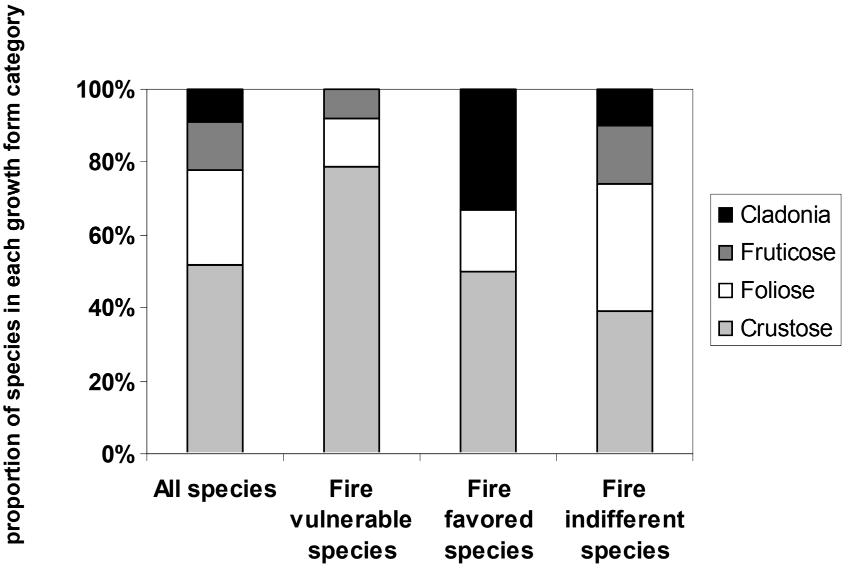

*Fig. 13.* Proportion crustose, foliose, fruticose, and *Cladonia*-species among the fire vulnerable, fire favored, and fire indifferent species, compared with the growth form distribution among all species/taxa ≥3 records (79). Adopted from paper IV.

In total, 32 species were found on charcoal, presumably indicating post-fire colonizations. These species were most of all characterized by being frequent and preferring dead wood. Two rare species were recorded on charcoal; *Cladonia parasitica* (2 records) and *Hypocenomyce friesii* (1).

In conclusion, this study suggests that habitat associations and population size are presumably important for species response to disturbance, through habitat susceptibility to fire, habitat availability and the mere likelihood of getting extinct. For example, balsam fir is an important tree for lichen diversity in the southern boreal forests of North America. Balsam fir hosts many of the shade preferring, crustose lichens found in this study. Balsam fir is sensitive to fire, and often eliminated by forest fires. Thus, the lichens on these trees are particularly vulnerable to fire, while habitat generalists and dead wood preferring species may survive depending on population size. Post-fire colonization rates will be highest for common species and dead wood preferring lichens.

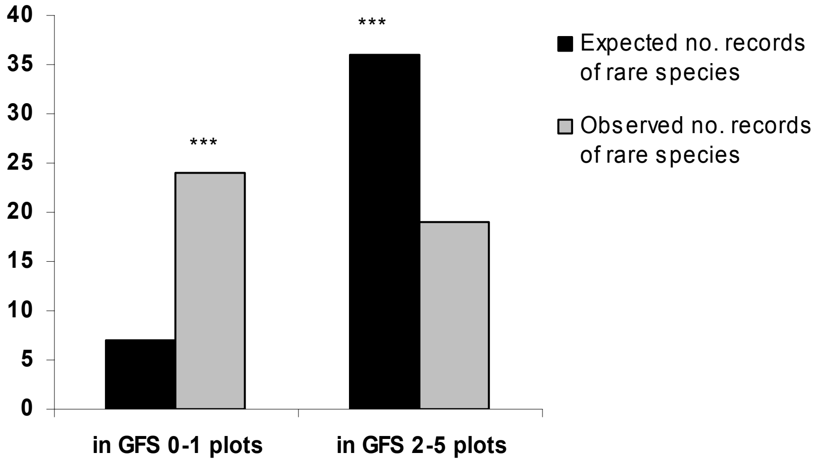

*Fig. 14.* The expected versus the observed number of rare species records (= species found in 1-2 sample-plots) in unburned (0-1) and burned (2-5) grid-plots within the Gabbro fire perimeter. The expected number was calculated as total number of rare species records (43) × the proportion of sample-plots in each GFS category (0-1: 14/84 and 2-5: 70/84, respectively). The likelihood of getting the observed number was calculated as a probability function of the Binomial distribution (*** = p<0.001). Adopted from paper IV.

## V. Population size and fire intensity determine post-fire abundance in grassland lichens

This study was set up on short notice before prescribed burning of two old, abandoned fields at Cedar Creek Natural History Area in east-central Minnesota. The fields had been abandoned since the 1950s, and had not been burned before. The soils in the area are sandy and poor in nitrogen. Therefore these fields are still open and dominated by grasses and forbs, and have a fairly extensive cover of terricolous lichens, mainly *Cladonia* spp. The objective of the study was to examine variability, in terms of lichen mortality, within and between grassland fires.

In each of the two fields, I established 12 sample-plots (0.5 × 0.5 m) at three sites. At each site, the sample-plots were arranged in a squared grid, 1 m apart. The rationale for this design was to examine small and large-scale variability within the fires. Before the burning I surveyed lichen cover, as well as litter, plant, bare soil, and moss cover in the plots. I expected that especially litter cover, providing fuel, could increase fire intensity, while cover of bare soil and moss potentially could decrease fire intensity at the plot-level. Before the burning I identified nine species of *Cladonia* in the sample-plots. The most common species were *C. cariosa*, *C. cervicornis*, and *C. rei*. Additional species were *Diploschistes muscorum* and *Peltigera didactyla*. Both were relatively rare and found in 16 and 18 sample-plots, respectively. The sample-plots were surveyed again almost exactly one year post-fire. I then estimated only the cover of living lichens, and did not identify *Cladonia* spp. to species-level. One year post-fire most *Cladonia* species occurred only as vegetative 'phyllocladia' and could not be identified. Therefore, when analysing pre and post-fire lichen cover, *Cladonia* spp. were treated together.

It turned out that the fires burned with different intensities, most likely due to different weather conditions. The first burn was on a fairly warm and dry day and the fire burned most of the litter layer on that field. The fire intensity was estimated as similar or slightly above a mean savanna fire at Cedar Creek. The second fire, on the other hand, was of low fire intensity and burned only about one-third of the litter layer. The weather was colder and wetter than during the first fire, and this fire was estimated to be of lower fire intensity than a mean savanna fire at CCNHA.

The post-fire survey clearly mirrored the differences between the fires. In field 62 (the low intensity fire), post-fire cover of *Cladonia* spp. was still relatively high and showed a strong positive relationship with pre-fire cover (Figure 15). In field 49 (the high intensity fire) no such relationship was seen. *Cladonia* spp. had experienced high mortality rates, irrespective of pre-fire cover (Figure 15). No other variables than pre-fire cover explained post-fire cover of *Cladonia* spp., i.e. there were no effects of litter, moss or bare soil cover.

In conclusion, this study provides an example of a non-linear relationship between pre and post-disturbance population size as a function of disturbance intensity. There are few explicit examples of this in the literature and to my knowledge none for lichens.

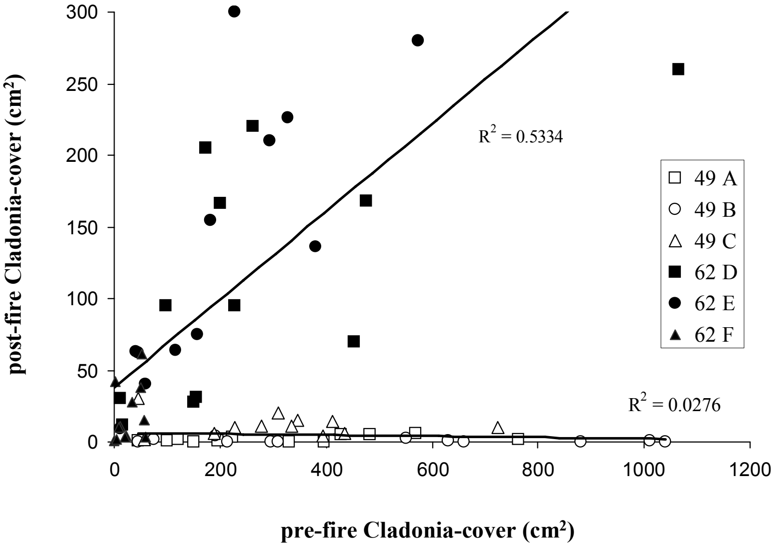

*Fig 15.* Relationships between pre- and one year post-fire cover of Cladonia spp. in 0.5 × 0.5 m sample plots grouped by site (A-F), in two fields (49 and 62) subjected to prescribed fire. Field 49 experienced high fire intensity, while field 62 experienced low fire intensity. The linear relationships for the observed pre-and post-fire *Cladonia* cover and their $r^2$-values are shown for the sites grouped by field. Adopted from paper V.

# Conclusions

Lichen community structure depends on a multitude of local and regional factors, whose importance may vary over time and between diversity measures. For example, explanations of species distributions in fragmented landscapes must include spatial configuration of species habitat, which also may affect species abundance through 'mass effects'.

Lichen community response to disturbance depends on disturbance intensity and may vary between diversity measures. Post-disturbance colonization rates are higher for species with high post-disturbance population size, which in turn, may be a function of pre-disturbance population size. However, if disturbance intensity exceeds critical thresholds for species mortality, population size does not matter – all individuals are killed.

To some extent, species occurrence, both for epiphytic lichens on deciduous trees and for lichens along the fire severity gradient in boreal forest, could be understood from their life-history traits. For lichens, the role life-history traits in community assembly is, however, still poorly understood.

# References

Adams, D.B. & Risser, P.G. 1971. Some factors influencing the frequency of bark lichens in North central Oklahoma. *American Journal of Botany 58*, 752-757.

Almborn, O. 1948. Distribution and ecology of some South Scandinavian lichens. *Botaniska Notiser 1(2)*, Lund, Sweden.

Antos, J.A., McCune, B. & Bara, C. 1983. The effect of fire on an ungrazed western Montana grassland. *American Midland Naturalist 110*, 354-364.

Arup, U., Ekman, S., Kärnefelt, I. & Mattsson, J.-E. (eds.) 1997. *Red-listed lichens and changes in the lichen flora of southwestern Sweden*. SBF-förlaget, Lund, Sweden.

Barkman, J.J. 1958. *Phytosociology and ecology of cryptogamic epiphytes*. Van Gorcum, Assen, The Netherlands.

Bates, J.W. 1992. Influence of chemical and physical factors on *Quercus* and *Fraxinus* epiphytes at Loch Sunart, western Scotland: a multivariate analysis. *Journal of Ecology 80*, 163-179.

Bates, J.W., Bell, J.N.B. & Massara, A.C. 2001. Loss of *Lecanora conizaeoides* and other fluctuations of epiphytes on oak in SE England over 21 years with declining $SO_2$ concentrations. *Atmospheric Environment 35*, 2557-2568.

Bellehumeur, C. & Legendre, P. 1998. Multiscale sources of variation in ecological variables: modeling spatial dispersion, elaborating sampling designs. *Landscape Ecology 13*, 15-25.

Bliss, L.C. & Wien, R.W. 1972. Plant community response to disturbances in the western Canadian Arctic. *Canadian Journal of Botany 50*, 1097-1109.

Boudreau, S. & Payette, S. 2004. Growth performance of *Cladina stellaris* following caribou disturbance in subarctic Quebec. *Écoscience 11*, 347-355.

Boudreault, C., Gauthier, S. & Bergeron, Y. 2000. Epiphytic lichens and bryophytes on *Populus tremuloides* along a chronosequence in the southwestern boreal forest of Québec, Canada. *The Bryologist 103*, 725-738.

Brooks, T.M., Pimm, S.L. & Collar, N.J. 1997. Deforestation predicts the number of threatened birds in insular Southeast Asia. *Conservation Biology 11*, 382-394.

Brulisauer, A.R., Bradfield, G.E. & Maze, J. 1996. Quantifying organisational change after fire in lodgepole pine forest understorey. *Canadian Journal of Botany 74*, 1773-1782.

Campbell, J. & Coxson, D.S. 2001. Canopy microclimate and arboreal lichen loading in subalpine spruce-fir forest. *Canadian Journal of Botany 79*, 537-555.

Carlson, D.J. 2001. *Causes and consequences of the heterogeneity of wildfire in the southern boreal forest of Minnesota, USA*. Master thesis, University of Minnesota, U.S.A.

Cavender-Bares, J., Ackerly, D.D., Baum, D.A. & Bazzaz, F.A. 2004. Phylogenetic overdispersion in floridan oak communities. *The American Naturalist 163*, 823-843.

Cottenie, K. & De Meester, L. 2004. Metacommunity structure: synergy of biotic interactions as selective agents and dispersal as fuel. *Ecology 85*, 114-119.

Coxson, D.S. & Marsh, J. 2001. Lichen chronosequences (postfire and postharvest) in lodgepole pine (*Pinus contorta*) forests of northern interior British Columbia. *Canadian Journal of Botany 79*, 1449-1464.

Culberson, W.L. 1955. The corticolous communities of lichens and bryophytes in the upland forests of northern Wisconsin. *Ecological Monographs 25*, 215-231.

Degelius, G. 1978. Further studies on the epiphytic vegetation on twigs. *Botanica Gothoburgensia 7*, 1-58.

den Herder, M., Kytöviita, M.M. & Niemelä, P. 2003. Growth of reindeer lichens and effects of reindeer grazing on ground cover vegetation in a Scots pine forest and a subarctic heathland in Finnish Lapland. *Ecography 26*, 3-12.

Dettki, H. & Esseen, P.-A. 1998. Epiphytic macrolichens in managed and natural forest landscapes: a comparison at two spatial scales. *Ecography 21*, 613-624.

Dettki, H., Klintberg, P. & Esseen, P.-A. 2000. Are epiphytic lichens in young forests limited by dispersal? *Écoscience 7*, 317-325.

Duncan, R.P. & Young, J.R. 2000. Determinants of plant extinction and rarity 145 years after European settlement of Auckland, New Zealand. *Ecology 81*, 3048-3061.

Dupré, C. 2000. How to determine a regional species pool: a study in two Swedish regions. *Oikos 89*, 128-136.

Edwards, R.Y., Soos, J. & Ritcey, R.W. 1960. Quantitative observations on epidendric lichens used as food by caribou. *Ecology 41*, 425-431.

Esseen, P.-A., Renhorn, K.-E. & Petersson, R.B. 1996. Epiphytic lichen biomass in managed and old-growth boreal forests: Effect of branch quality. *Ecological Applications 6*, 228-238.

Eversman, S., Wetmore, C.M., Glew, K. & Bennett, J.P. 2002. Patterns of lichen diversity in Yellowstone National Park. *The Bryologist 105*, 27-42.

Fahrig, L. Relative effects of habitat loss and fragmentation on population extinction. *Journal of Wildlife Management 61*, 603-610.

Foster, B.L. & Dickson, T.L. 2004. Grassland diversity and productivity: the interplay of resource availability and propagule pools. *Ecology 85*, 1541-1547.

Frelich, L.E. 2002. *Forest dynamics and disturbance regimes: studies from temperate evergreen-deciduous forests*. Cambridge studies in ecology, Cambridge University Press, Cambridge, Great Britain.

Frelich, L.E. & Reich, P.B. 1995. Spatial patterns and succession in a Minnesota southern-boreal forest. *Ecological Monographs 65*, 325-346.

Fries, C., Johansson, O., Pettersson, B. & Simonsson, P. 1997. Silvicultural models to maintain and restore natural stand structures in Swedish boreal forests. *Forest Ecology and Management 94*, 89-103.

Fröberg, L., Baur, A. & Baur, B. 1993. Differential herbivore damage to calcicolous lichens by snails. *Lichenologist 25*, 83-95.

Gaston, K.J. 1994. *Rarity*. Population and community biology series 13, Chapman & Hall, London, United Kingdom.

Gauslaa, Y. 1985. The ecology of *Lobarion pulmonariae* and *Parmelion caperatae* in *Quercus* dominated forests in South-west Norway. *Lichenologist 17*, 117-140.

Gauslaa, Y. 2002. Die back of epiphytic lichens in SE Norway – can it be caused by high rainfall in late autumn? *Graphis Scripta 13*, 33-35.

Gauslaa, Y. 2005. Lichen palatability depends on investment in herbivore defence. *Oecologia 143*, 94-105.

Gauslaa, Y., Ohlson, M. & Rolstad, J. 1998. Fine-scale distribution of the epiphytic lichen *Usnea longissima* on two even-aged neighbouring *Picea abies* trees. *Journal of Vegetation Science 9*, 95-102.

Gu, W.D., Kuusinen, M., Konttinen, T. & Hanski, I. 2001. Spatial pattern in the occurrence of the lichen *Lobaria pulmonaria* in managed and virgin boreal forest. *Ecography 24*, 139-150.

Gustafsson, L. & Eriksson, I. 1995. Factors of importance for the epiphytic vegetation of aspen *Populus tremula* with special emphasis on bark chemistry and soil chemistry. *Journal of Applied Ecology 32*, 412-424.

Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y. & Kranabetter, J.M. 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. *Silva Fennica 36*, 307-327.

Hale, M.E. 1952. Vertical distribution of cryptogams in a virgin forest in Wisconsin. *Ecology 33*, 398-406.

Hale, M.E. 1955. Phytosociology of corticolous cryptogams in the upland forests of southern Wisconsin. *Ecology 36*, 45-63.

Halonen, P., Hyvärinen, M. & Kauppi, M. 1991. The epiphytic lichen flora on conifers in relation to climate in the finnish middle boreal subzone. *Lichenologist 23*, 61-72.

Hansson, L. 2003. Why ecology fails at application: should we consider variability more than regularity? *Oikos 100*, 624-627.

Hazell, P. & Gustafsson, L. 1999. Retention of trees at final harvest – evaluation of a conservation technique using epiphytic bryophyte and lichen transplants. *Biological Conservation 90*, 133-142.

He, F., Gaston, K.J., Connor, E.F. & Srivastava, D.S. 2005. The local-regional relationship: immigration, extinction, and scale. *Ecology 86*, 360-365.

Hedenås, H., Bolyukh, V.O. & Jonsson, B.G. 2003. Spatial distribution of epiphytes on *Populus tremula* in relation to dispersal mode. *Journal of Vegetation Science 14*, 233-242.

Hedenås, H. & Ericson, L. 2004. Aspen lichens in agricultural and forest landscapes: the importance of habitat quality. *Ecography 27*, 521-531.

Hilmo, O. 1994. Distribution and succession of epiphytic lichens on *Picea abies* branches in a boreal forest, Central Norway. *Lichenologist 26*, 149-169.

Holland, J.D., Bert, D.G. & Fahrig, L. 2004. Determining the spatial scale of species' response to habitat. *BioScience 54*, 227-233.

Holt, E.A. & Severns, P.M. 2005. The effect of prescribed burning on wet prairie lichen communities. *Natural Areas Journal 25*, 130-136.

Hooper, D.U., Chapin III, F.S., Ewel, J.J., Hector, A., Inchausti, P. *et al.*, 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs 75*, 3-35.

Huston, M.A. 1994. *Biological diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge, Great Britain.

Huston, M.A. 1999. Local processes and regional patterns: appropriate scales for understanding variation in the diversity of plants and animals. *Oikos 86*, 393-401.

Jesberger, J.A. & Sheard, J.W. 1973. A quantitative study and multivariate analysis of corticolous lichen communities in the southern boreal forest of Saskatchewan. *Canadian Journal of Botany 51*, 185-201.

Johansen, J.R. 2001. Impacts of fire on biological soil crusts. In: Belnap, J. & Lange, O.L. (eds.). *Biological soil crusts: structure, function and management*. Ecological studies vol. 150, Springer Verlag, Berlin, Germany.

Jovan, S. & McCune, B. 2004. Regional variation in epiphytic macrolichen communities in northern and central California forests. *The Bryologist 107*, 328-339.

Kallimanis, A.S., Kunin, W.E., Halley, J.M. & Sgardelis, S.P. 2005. Metapopulation extinction risk under spatially autocorrelated disturbance. *Conservation Biology 19*, 534-546.

Kantvilas, G. & Jarman, S.J. 2004. Lichens and bryophytes on *Eucalyptus obliqua* in Tasmania: management implications in production forests. *Biological Conservation 117*, 359-373.

Kuusinen, M. & Siitonen, J. 1998. Epiphytic lichen diversity in old-growth and managed *Picea abies* stands in southern Finland. *Journal of Vegetation Science 9*, 283-292.

Lawrey, J.D. 1991. The species-area curve as an index of disturbance in saxicolous lichen communities. *The Bryologist 94*, 377-382.

Leibold, M.A. & Miller, T.E. 2004. From metapopulations to metacommunities. In: Hanski, I. & Gaggiotti, O.E. (eds.). *Ecology, genetics, and evolution of metapopulations*. Elsevier Academic Press, Burlington, U.S.A. pp. 133-150.

Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M. *et al.*, 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecology Letters 7*, 601-613.

Lesica, P., McCune, B., Cooper, S.V. & Hong, W.S. 1991. Differences in lichen and bryophyte communities between old-growth and managed 2nd-growth forests in the Swan valley, Montana. *Canadian Journal of Botany 69*, 1745-1755.

Levin, S.A. 1992. The problem of pattern and scale in ecology. *Ecology 73*, 1943-1967.

Longan, A., Gaya, E. & Gomez-Bolea, A. 1999. Post-fire colonization of a Meditteranean forest stand by epiphytic lichens. *Lichenologist 31*, 389-395.

Loraeu, M. 2000. Are communities saturated? On the relationship between α, β and γ diversity. *Ecology Letters 3*, 73-76.

MacArthur, R.H. & Wilson, E.O. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, U.S.A.

Maikawa, E. & Kershaw, K.A. 1976. Studies on lichen-dominated systems. XIX. The postfire recovery sequence of black spruce-lichen woodland in the Abitau Lake region, N.W.T. *Canadian Journal of Botany 54*, 2679-2687.

Manne, L.L. & Pimm, S.L. 2001. Beyond eight forms of rarity: which species are threatened and which will be next? *Animal Conservation 4*, 221-229.

McCune, B. 1993. Gradients in epiphyte biomass in three Psuedotsuga-Tsuga forests of different ages in western Oregon and Washington. *The Bryologist 96*, 405-411.

McCune, B., Amsberry, K.A., Camacho, F.J., Clery, S., Cole, C. *et al.* 1997. Vertical profile of epiphytes in a Pacific Northwest old-growth forest. *Northwest Science 71*, 145-152.

McCune, B., Rosentreter, R., Ponzetti, J.M. & Shaw, D.C. 2000. Epiphyte habitats in an old conifer forest in western Wasington, USA. *The Bryologist 103*, 417-427.

Mistry, J. 1998. Corticolous lichens as potential bioindicators of fire history: a study in the cerrado of the Distrito Federal, central Brazil. *Journal of Biogeography 25*, 409-441.

Mistry, J. & Berardi, A. 2005. Effects of phorophyte determinants on lichen abundance in the cerrado of central Brazil. *Plant Ecology 178*, 61-76.

Mouquet, N., Munguia, P., Kneitel, J.M. & Miller, T.E. 2003. Community assembly time and the relationship between local and regional species richness. *Oikos 103*, 618-626.

Nguyen-Xuan, T., Bergeron, Y., Simard, D., Fyles, J.W. & Pare, D. 2000. The importance of forest floor disturbance in the early regeneration patterns of the boreal forest of western and central Quebec: a wildfire versus logging comparison. *Canadian Journal of Forest Research 30*, 1353-1364.

Niemelä, J. 1999. Management in relation to disturbance in the boreal forest. *Forest Ecology and Management 115*, 127-134.

Nordén, B. & Appelqvist, T. 2001. Conceptual problems of ecological continuity and its bioindicators. *Biodiversity and Conservation 10*, 779-791.

Öckinger, E., Niklasson, M. & Nilsson, S.G. 2005. Is local distribution of the epiphytic lichen *Lobaria pulmonaria* limited by dispersal capacity or habitat quality? *Biodiversity and Conservation 14*, 759-773.

O'Grady, J.J., Reed, D.H., Brook, B.W. & Frankham, R. 2004. What are the best correlates of predicted species extinction risk? *Biological Conservation 118*, 513-520.

Oksanen, J. 1988. Impact of habitat, substrate and microsite classes on the epiphyte vegetation: Interpretation using exploratory and canonical correspondence analysis. *Annales Botanici Fennici 25*, 59-71.

Øvstedal, D.O. 1980. Lichen communities on *Alnus incana* in North Norway. *Lichenologist 12*, 189-197.

Peck, J.E. & McCune, B. 1997. Remnant trees and canopy lichen communities in western Oregon: A retrospective approach. *Ecological Applications 7*, 1181-1187.

Pedersen, I. 1980. Epiphytic lichen vegetation in an old oak wood, Kaas Skov. *Botanisk Tidsskrift 75*, 105-120.

Peterson, E.B. & McCune, B. 2001. Diversity and succession of epiphytic macrolichen communities in low-elevation managed conifer forests in western Oregon. *Journal of Vegetation Science 12*, 511-524.

Pickett, S.T.A. & White, P.S. 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, London, United Kingdom.

Pickett, S.T.A., Kolasa, J., Armesto, J.J. & Collins, S.L. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. *Oikos 54*, 129-136.

Pimm, S.L., Jones, H.L. & Diamond, J. 1988. On the risk of extinction. *American Naturalist 132*, 757-785.

Pöykkö, H., Hyvärinen, M. & Bačkor, M. 2005. Removal of lichen secondary metabolites affects food choice and survival of lichenivorous moth larvae. *Ecology 86*, 2623-2632.

Printzen, C. & Otte, V. 2005. *Biatora longispora*, new to Europe, and a revised key to European and Macaronesian *Biatora*-species. *Graphis Scripta 17*, 56-61.

Rees, D.C. & Juday, G.P. 2002. Plant species diversity on logged versus burned sites in central Alaska. *Forest Ecology and Management 155*, 291-302.

Renhorn, K.-E., Esseen, P.-A., Palmqvist, K. & Sundberg, B. 1997. Growth and vitality of epiphytic lichens. I. Responses to microclimate along a forest edge-interior gradient. *Oecologia 109*, 1-9.

Reynolds, J.D. 2003. Life histories and extinction risk. In: Blackburn, T.M. & Gaston, K.J. (eds.). *Macroecology: concepts and consequences*. Symposium of the British Ecological Society 43. Blackwell Publishing, Oxford, United Kingdom, pp. 195-217.

Rheault, H., Drapeau, P., Bergeron, Y. & Esseen, P.-A. 2003. Edge effects on epiphytic lichens in managed black spruce forests of eastern North America. *Canadian Journal of Forest Research 33*, 23-32.

Richardson, D.H.S. 2002. Reflections on lichenology: achievements over the last 40 years and challenges for the future. *Canadian Journal of Botany 80*, 101-113.

Ricklefs, R.E. 1987. Community diversity: relative roles of local and regional processes. *Science 235*, 167-171.

Ricklefs, R.E. 2004. A comprehensive framework for global patterns in biodiversity. *Ecology Letters 7*, 1-15.

Rogers, R.W. 1988. Succession and survival strategies in lichen populations on a palm trunk. *Journal of Ecology 76*, 759-776.

Rolstad, J. & Rolstad, E. 1999. Does tree age predict the occurrence and abundance of *Usnea longissima* in multi-aged submontane *Picea abies* stands? *Lichenologist 31*, 613-625.

Romagni J.G. & Gries, C. 2000. Post-fire recolonization of dominant epiphytic lichen species on *Quercus hypoleucoides* (Fagaceae). *American Journal of Botany 87*, 1815-1820.

Romme, W.H., Everham, E.H., Frelich, L.E., Moritz, M.A. & Sparks, R.E. 1998. Are large, infrequent disturbances qualitatively different from small, frequent disturbances? *Ecosystems 1*, 524-534.

Rose, F. 1976. Lichenological indicators of age and environmental continuity in woodlands. In: Brown, D.H., Hawksworth, D.L. & Bailey, R.H. (eds.). *Lichenology: Progress and problems*. Academic Press, London, United Kingdom, pp. 279-307.

Ruchty, A., Rosso, A.L. & McCune, B. 2001. Changes in epiphyte communities as the shrub, *Acer circinatum*, develops and ages. *The Bryologist 104*, 274-281.

Rykiel, E.J. 1985. Towards a definition of ecological disturbance. *Australian Journal of Ecology 10*, 361-365.

Schulten, J.A. 1985. The effects of burning on the soil lichen community of a sand prairie. *The Bryologist 88*, 110-114.

Scutari, N.C., Bertiller, M.B. & Carrera, A.L. 2004. Soil-associated lichens in rangelands of north-eastern Patagonia. Lichen groups and species with potential as bioindicators of grazing disturbance. *Lichenologist 36*, 405-412.

Shay, J., Kunec, D. & Dyck, B. 2001. Short-term effects of fire frequency on vegetation composition and biomass in mixed prairie in south-western Manitoba. *Plant Ecology 155*, 157-167.

Sillett, S.C. & Antoine, M.E. 2004. Lichens and bryophytes in forest canopies. In: Lowman, M.D. & Rinker, H.B. (eds.). *Forest canopies*. Elsevier Academic Press, London, United Kingdom, pp. 151-174.

Snäll, T., Ribeiro, P.J. & Rydin, H. 2003. Spatial occurrence and colonisations in patch-tracking metapopulations: local conditions versus dispersal. *Oikos 103*, 566-578.

Snäll, T., Fogelqvist, J., Ribeiro, P.J. & Lascoux, M. 2004. Spatial genetic structure in two congeneric epiphytes with different dispersal strategies analysed by three different methods. *Molecular Ecology 13*, 2109-2119.

Snäll, T., Ehrlén, J. & Rydin, H. 2005. Colonization-extinction dynamics of an epiphyte metapopulation in a dynamic landscape. *Ecology 86*, 106-115.

Sousa, P.W. 1984. The role of disturbance in natural communities. *Annual Review of Ecology and Systematics 15*, 353-391.

Spiller, D.A, Losos, J.B. & Schoener, T.W. 1998. Impact of a catastrophic hurricane on island populations. *Science 281*, 695-697.

Srivastava, D.S. 2005. Do local processes scale to global patterns? The role of drought and the species pool in determining treehole insect diversity. *Oecologia 145*, 205-215.

Stone, D.F. 1989. Epiphyte succession on *Quercus garryana* branches in the Willamette valley of western Oregon. *The Bryologist 92*, 81-94.

Tapper, R. 1976. Dispersal and changes in the local distributions of *Evernia prunastri* and *Ramalina farinacea*. *New Phytologist 77*, 725-734.

Thomas, C.D., Cameron, A., Green, R.E., Bakkenes, M., Beaumont, L.J. *et al*. 2004. Extinction risk from climate change. *Nature 427*, 145-148.

Thor, G. 1998. Red-listed lichens in Sweden: habitats, threats, protection, and indicator value in boreal coniferous forests. *Biodiversity and Conservation 7*, 59-72.

Thor, G. & Kannesten, C. 1989. *Sticta sylvatica*, ärrlav, återfunnen i Sverige. *Windahlia 18*, 31-33. [In Swedish]

Topham, P.B. 1977. Colonization, growth, succession and competition. In: Seaward, M.R.D. (ed.). *Lichen ecology*. Academic Press, London, United Kingdom, pp. 31-68.

Uliczka, H. & Angelstam, P. 1999. Occurrence of epiphytic macrolichens in relation to tree species and age in managed boreal forest. *Ecography 22*, 396-405.

Ulrich, W. & Buszko, J. 2004. Habitat reduction and patterns of species loss. *Basic and Applied Ecology 5*, 231-240.

Uotila, A. & Kouki, J. 2005. Understory vegetation in spruce-dominated forests in eastern Finland and Russian Karelia: successional patterns after anthropogenic and natural disturbances. *Forest Ecology and Management 215*, 113-137.

Vandvik, V. & Goldberg, D.E. 2005. Distinguishing the roles of dispersal in diversity maintenance and in diversity limitation. *Folia Geobotanica 40*, 45-52.

Werth, S., Tømmervik, H. & Elvebakk, A. 2005. Epiphytic macrolichen communities along regional gradients in northern Norway. *Journal of Vegetation Science 16*, 199-208.

Wetmore, C.M. 1983. Lichen survival in a burned oak savanna. *Michigan Botanist 22*, 47-52.

Wiklund, K. & Rydin, H. 2004. Colony expansion of *Neckera pennata*: Modelled growth rate and effect of microhabitat, competition and precipitation. *The Bryologist 107*, 293-301.

Wolseley, P.A. & Aguirre-Hudson, B. 1997. The ecology and distribution of lichens in tropical deciduous and evergreen forests of northern Thailand. *Journal of Biogeography 24*, 327-343.

Yarranton, G.A. 1972. Distribution and succession of epiphytic lichens on black spruce near Cochrane, Ontario. *The Bryologist 75*, 462-480.

# Acknowledgements

*Tack…*

Till er som uppmuntrade och formade mitt naturintresse. Pappa Nils, som tog med mig på otaliga utflykter till enkelbeckasinspel, avlägsna metstenar och skogsbäckar. Olof Hedlund, min mellanstadielärare, som lärde mig att föra fenologilistor. Jag minns klassresan till Öland när hela cykelkaravanen hade tvärnitat på ditt kommando, och du sade åt oss att ”Lyssna på kornknarren, det är en raritet. Det här är kanske den enda gången i ert liv ni får höra den!” Det var ett stort ögonblick i mitt tolvåriga liv!

Till lavgruppen i Lund som introducerade mig till lavarnas och lavforskarnas värld. Till Stefan Ekman, Ulf Arup och Lars Fröberg för era ändlösa och entusiastiska diskussioner om lavar. Till Louise Lindblom, Jan-Eric Mattsson, Arne Thell och Ingvar Kärnefelt. Det hade inte blivit en ”lavhandling” om det inte hade varit för er. Stenshuvud 1987 var första gången jag såg en lichenolog dra kniv, och skära loss en redig barkbit från en ask mitt i naturreservatet (Stefan). Det var då jag insåg att lavar är macho.

Till Göran Thor, som uppmuntrade mig och gav mig chansen att doktorera. Ett av mina första minnen av dig Göran, var att du undrade varför jag inte hade artbestämt *alla* Leprarior på Lunds domkyrka! Jag vet att du skulle ha gjort det. Du lämnar inte några lavar eller andra detaljer åt slumpen, och det skapar trygghet. Du har alltid utryckt stöd och uppskattning – det kan rädda dagen.

Till min handledargrupp som lotsat mig fram mellan vetenskapens grynnor och grund: Lennart Hansson, Johan Ehrlén, Håkan Rydin och Göran. Ni har givit mig en bred och trygg kompetens att luta mig mot. Ni har stark vetenskaplig integritet som ni har delat med er av. Johan, resorna till Stockholm har alltid varit värda tågbiljetterna. Håkan, tack för att du inkluderade mig bland dina (andra) mossiga doktorander. Lennart, tack för diskussionerna om ekologiska grundbegrepp. Inte minst den senaste månaden, Lennart, har du varit ett stort stöd. Tack ska ni ha för engagerad handledning under frihet och med respekt för egna initiativ!

To all great people at St Paul campus, University of Minnesota. To Peter Reich, who welcomed me to join your lab group, and shared your contagious and never ending enthusiasm for ecological research. To Clifford Wetmore, who put up full support in the lichen lab and shared your extensive knowledge in lichenology. To Lee Frelich, who shared your office with me, and learned me lots on scientific writing, disturbance ecology, the Minnesotan forests, invading earthworms, tornados, and got me to finally listen to Mahler. To Daren Carlson, who guided me into the study area in Boundary Waters. To Jeri and Shinya for your statistical knowledge. To Andy for your paper sessions at Lori´s. To the modelling folks Olivia, Barbara, Kelly, Jeanine, and Eric for the inspiring work together. To Trisha, Jamie, and Lynn for sharing the field work. To everyone else who welcomed me and helped me with small things, e.g. Jeremy, Jacek, Roy, Clarence, Jared, Steve, Janelle, Cindy. Thanks also to the Swedish America Foundation

(Sverige-Amerika Stiftelsen), to SLU, and to Anna and Gunnar Vidfelts Foundation for financial support.

Till Joachim Strengbom för tiden i Minnesota och sedan vi kom hem. Tack för mängder av vetenskaplig och annan input över oräkneliga Lattes, subs och Woks.

Till alla på hemmaplan – Naturicum. Varje gång jag går upp mot huset, mellan äppelträden, fylls jag av lugn och arbetslust. Tack alla ni som är där och bidrar till den atmosfären. Till er som har hjälpt mig att få vardagen att fungera, både här hemma och under tiden i Minnesota, särskilt till Hans Jernelid, Ulla-Bitt Petersson, Sonja Jansson, Roger Svensson och Torbjörn Persson. Till alla gamla och nya meddoktorander, för god kamp om strumpan, för hjälp med diverse småsaker, och för inspirerande diskussioner om vädret! Lite särskilt till Henrik Weibull, min käre rumskamrat under de första åren; Staffan Roos, för allt mellan himmel och jord; Åsa Berggren, som inspirerade mig att fara utomlands; Jörgen Rudolphi, för att du kom och hälsade på i Minnesota och till Sandro Caruso, för att jag kan snacka lavar med dig. Sist men inte minst till Lena Gustafsson för att du gav mig chansen att komma till Uppsala (SkogForsk), och uppmuntrande handledde mina första stapplande steg i att skriva vetenskapligt.

Till mor och far, Anne-Marie och Nils. Jag är glad och tacksam för att ni alltid självklart har stött min väg hit.

Till Maria. Det är inte bara livet jag har delat med dig den här tiden, utan också intresset för forskning och allt vad det innebär, t ex otaliga timmar med varsin laptop på en coffeeshop i Twin Cities. Romantiskt!? Du är min främsta och vassaste kritiker och pådrivare, klarsynt och logisk. Du har därmed ofta drivit det här arbetet framåt.