

1. INTRODUCTION

Patterns and drivers of biodiversity in ecosystems have always attracted the attention of ecologists, and this field of research is today more urgent than ever. The ecosystems of the earth are today under increasing pressure from changes directly or indirectly induced by human activities (Berg et al. 2002; Heywood 2005). Changes in land use and exploitation of the natural systems supporting life interact in creating pressures on terrestrial ecosystems in the form of fragmentation and habitat loss, with negative effects on biodiversity (Fahrig 2003). Climate change is causing shifts in vegetation patterns evident e.g. in mountain regions and the Arctic (ACIA 2005), where vegetation belts and distribution of species are predicted (Spehn et al. 2010) and already documented (Pauli et al. 2007; Kullman 2010; Stöckli et al. 2011) to shift upward as the climate is getting warmer. In order to persist, plants will be dependent on their abilities to disperse and establish in suitable habitats as climate change, changes in land-use and anthropogenic disturbance will impact community structure and composition.

In this context, there is a need for increasing our understanding of how biodiversity patterns are regulated and how dispersal ability of species affects diversity and composition of plant communities. Understanding the components and patterns of biological diversity are increasingly important for the conservation and management of ecosystems. The way plants interact in space and time, how they migrate and disperse is important to the dynamics of the communities that make up the natural systems we are dependent on.

Studies of biodiversity encompass several scales, covering genetic, species and landscape levels (Heywood 2005). The total regional diversity of a landscape (γ -diversity) is made up by local (α -) diversity, as well as the difference between local communities (β -diversity). The term β -diversity was introduced by Whittaker (1960) and can be defined as “the extent of change in community composition”. It is consequently made up by the compositional difference between local assemblages in the regional species pool. The larger the difference of species composition between communities or sites, the higher is the total diversity at landscape scale (Magurran 2004). Hence it is equally important as

α -diversity in assessments of biodiversity and conservation, since species turnover influences diversity at large scales (Condit et al. 2002).

β -diversity can be measured and analyzed in several ways, which can be distinguished into three categories (Magurran 2004): i.) indices based on difference of α compared to γ for a set of compared areas or assemblages; ii.) indices of complementarity or similarity/dissimilarity focusing on differences in species composition; and iii.) indices measuring turnover in relation to species accumulation with area. There is a large number of indices, which all perform differently for different types of species assemblages (see Koleff et al. 2003 for a review).

In this thesis, differences in β -diversity have been investigated as a measure of similarity or dissimilarity. To evaluate the distinctness of the investigated communities, the Bray-Curtis and Sørensen indices have been used, which are considered as robust indices for measuring dissimilarities among communities (Faith et al. 1987; Clarke and Warwick 2001). Distance decay of similarity can be caused by environmental gradients and/or dispersal limitation which interact to explain observed patterns of community composition (Nekola and White 1999; Soininen et al 2007). Metacommunity theory provides a framework for analyzing and interpreting these patterns. A metacommunity is defined as a set of local communities, linked by dispersal of multiple potentially interacting species (Leibold et al. 2004). Metacommunity theory is based on four major paradigms, making different assumptions about e.g. similarities between patches and species composition, dispersal/interpatch movement and spatial synchrony (outlined in detail in Holyoak et al. 2005). These recently developed concepts make up a powerful approach for including spatial components into community ecology and makes it possible to investigate complex dynamic interactions between communities.

1.1 Aim of thesis

The aim of this thesis was to investigate processes shaping patterns of plant communities in cliffs and mountainous regions in terms of species distribution, composition and diversity. The investigated drivers of community structure included environmental factors, spatial factors and dispersal, disturbance from human activities and biotic interactions. It focuses on vegetation of cliffs and surrounding matrix of sub-arctic alpine tundra of northern Sweden as well as cliff vegetation in the boreo-nemoral part of south-west Sweden. In the studies performed the following questions were investigated:

1. How do the special conditions found in cliff habitats affect patterns of biodiversity and composition of cliff plant communities? (Paper I)
2. How do cliffs contribute to biodiversity on a landscape scale? (Paper I)
3. How does environmental variables and spatial configuration of cliffs in the landscape affect species distribution patterns and community composition of bryophytes in cliffs? Are cliff bryophyte communities likely to be influenced by dispersal ability? (Paper II)
4. How does recreational rock-climbing affect species richness and composition of cliff communities? (Paper III)
5. Are biotic interactions between plants likely to change over a topographic gradient in the Scandes, as reported in other alpine regions in the world? If so, how will this influence biodiversity patterns in the sub-arctic alpine tundra? (Paper IV)

1.2 Cliff ecology, diversity and species composition

1.2.1 What is a cliff?

A cliff is a tall and steep structure of rock that can be divided into some major components, each exhibiting typical features: a level or sloping plateau at the top; the cliff edge before the cliff face; a steep, near-vertical cliff face and a pediment at the base. Within the cliff environment, a number of features are frequently found, creating special kinds of microhabitats; fractures in the rock create small cracks, larger crevices, or caves; horizontal or sloping ledges offer space for soil accumulation; undercut sections of rock creates overhangs; and a talus- or scree slope may be present between the cliff face and the pediment (Larson et al. 2000). Figure 1 shows some of the cliffs surveyed in this thesis.

1.2.2 Characteristics of cliff vegetation

Cliffs differ from surrounding areas in terms of environmental conditions and the cliff face is the habitat with most clearly pronounced boundaries, differing from surrounding vegetation types, although it shares some characteristics with the cliff edge and talus in terms of environmental conditions and species composition (Bartlett et al. 1989; Larson et al. 2000). The cliff face zone constitutes unique and relatively undisturbed habitats with environmental conditions differing drastically from the rest of the landscape, creating niches for species making up a distinct vegetation, contrasting to the surrounding matrix (Bunce 1968; Pentecost 1980; Phillips 1982; Larson et al. 2000; Matthes et al. 2000).

Cliffs are landscape features found in most biomes and vegetation types that despite their life-less appearance are hosts to diverse and highly distinct plant communities, important for landscape biodiversity (Davis 1951; Bunce 1968; Jarvis 1974; Phillips 1982; Larson et al. 1989; Camp and Knight 1997; Meirelles et al. 1999; Matthes et al. 2000). They contain species that typically are poor competitors that cannot persist in the surrounding landscape (Davis 1951; Bunce 1968; Jarvis 1974). Cliff face plant communities are characterized by a dominance of lichens and epilithic bryophytes, of which many are highly specialized for this environment (Jarvis 1974; Larson et al. 1989; Meirelles et al.

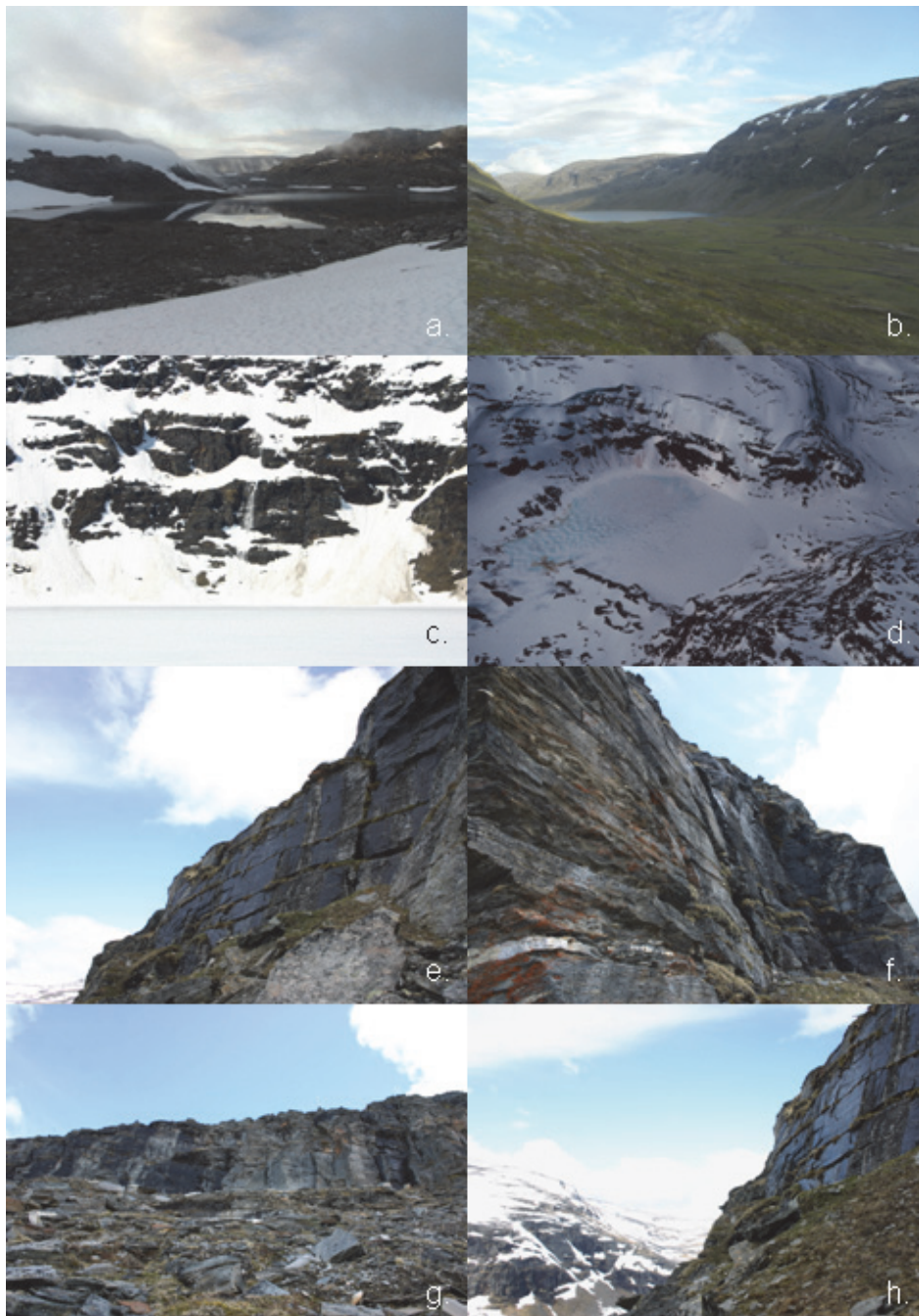




Figure 1. Some cliffs and landscapes investigated in this thesis. a-d show some examples of the dramatic landscape in the sub-arctic alpine valley Latnjavagge (Paper IV). 1c and d is taken in the beginning of June, when large parts of the valley is still covered with snow. 1e-h are examples of the investigated cliffs in Paper I. 1i-r are some of the cliffs investigated in Paper II. Photos by Henrik Antonsson except 1d by Ulf Molau.

1999; Matthes et al. 2000; Fransson 2003). Cliff ecosystems contain (1) obligate chasmophytic species that are highly specialized for cliff environments and (2) facultative chasmophytes (“rupestrals”) that can be found also in the vegetation mosaic outside cliffs. Two typical traits of obligate chasmophytes are the lack of competitive ability and low tolerance to herbivory. The cliffs therefore act as refugia for specialists, and many rare species, sometimes threatened of extinction (Davis 1951; Bunce 1968; Jarvis 1974; Larson et al. 1989; Cooper 1997; Meirelles et al. 1999; Wisser and Buxton 2009). A high proportion of the endemic species in Europe are restricted exclusively to cliffs (Ellenberg 1988). The rupestral species are also represented in the surrounding vegetation, but find more favourable conditions in the cliff environment. Both groups are species that find a refugium from conditions to which they are not adapted and benefit from the reduced levels of competition, herbivory and/or disturbance in the cliff habitat compared to the surroundings (Bunce 1968; Larson et al. 1989).

Despite being common on most continents and in most vegetation types (Larson et al. 2000), relatively little has been done to scientifically explore the role of cliffs from an ecological perspective. Most studies on cliffs are from temperate areas, while northern biomes and the Arctic are heavily underrepresented (Larson et al. 2000). Some reasons to this are their inaccessibility, low productivity and small size of typical cliff plants, which may have contributed to the moderate interest of cliffs in ecological research. However, ecological studies made on cliff communities give a picture of a landscape element that is far from dead, lifeless, or even particularly harsh for plants and animals to persist although special conditions prevail (Larson et al. 2000). Water availability can often be higher than in the surroundings, as fracturing of the rocks increase water holding capacity (Larson et al. 2000). Air humidity is high (Bunce 1968), and amplitude of temperatures is smaller compared to the surroundings.

While the composition of actual species differs, cliff vegetation is similar between geographical zones in terms of life forms and life history. Lichens dominate rock faces, also inhabited by epilithic bryophytes; vascular plants are found sparsely on ledges, cracks and crevices, where soil is accumulating. Ferns are abundant on most cliffs except sea cliffs (Larson et al. 2000). Among vascular plants, annual plants (therophytes)

are rare, and the dominant life forms are chamaephytes (Davis 1951) and hemicyptophytes (Larson et al. 1989). Knowledge about the patterns of biodiversity and processes driving these patterns is important for preserving these unique habitats in order to maintain their high biological values.

1.2.3 Environment and microclimate in cliffs

Factors driving structure and composition of cliff habitats have been investigated in a number of studies, using different methods and have reached differing, sometimes contrasting results. Except for the absence of grazing and competition (cliffs are largely inaccessible to macroherbivores and have low levels of competition due to the scattered distribution of vegetation with highly spaced individuals, see Davis 1951; Bunce 1968; Larson et al. 2000), aspect of the cliff has also been pointed out as important for structuring communities (Risbeth 1948; Ashton and Webb 1977; Fuls et al. 1992; Cooper 1997; Kuntz and Larson 2006a). Altering microclimatic conditions affect length of growing season (Larson et al. 2000). The microclimate in cliffs is correlated with the aspect of the cliff face, and compared to surrounding areas temperature is higher on south-facing cliffs and lower on north-facing (Figure 2).

Cliff habitats are characterized by large heterogeneity over small spatial scales, as cracks, fissures, pockets, ledges, corners, overhanging rock and roofs offer a mosaic of microhabitats that differ drastically over small distances. This has been recognized for different types of rock and in different geographical regions focusing on vascular plants (Davis 1951; Kuntz and Larson 2006a) and bryophytes (Fransson 2003; Weibull and Rydin 2005; Hespanhol et al. 2011). Although lichens show some correlation with differences in microtopographic structures (Pentecost 1980; Kuntz and Larson 2006a), they are more closely related to bedrock type and pH (Pentecost 1980; Larson et al. 2000). Cliffs have been observed to contain a mixture of species with contrasting ecological traits occurring together on cliffs. Alpine/arctic species have been documented to co-exist with southern plant elements on cliffs, which has been attributed to decoupling of disturbance in combination with high microsite variation (Bunce 1968; Cooper 1997).

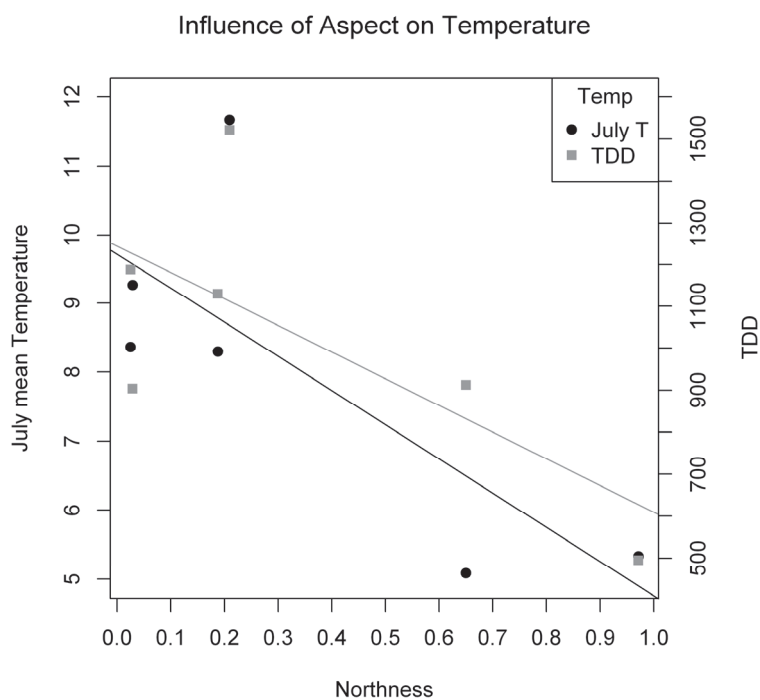


Figure 2. The influence of aspect of the investigated cliffs in Paper I on July mean temperature and Thawing Degree Days (TDD). Both variables were negatively correlated with northness ($R^2=0.58$ and 0.50 , respectively).

Bedrock type seems to have most influence on cliff lichen communities, to a moderate degree on bryophytes and less on vascular plants, for which calcicole species have been reported to exist on siliceous cliffs (Cooper 1997). Bedrock chemistry and soil pH is not always correlated since the normal processes of soil formation is absent on cliffs (Larson et al. 2000). The relationship between soil pH and vegetation is less clear for vertical cliffs compared to level ground. Soil pH has also been reported to vary drastically over small distances even on a single cliff (Hora 1947) further adding to the heterogeneity of cliff habitats.

Other factors controlling cliff vegetation is gravity, which is acting as a filter for which species included in the propagule rain that will manage to establish. Limitation of space, as well as water and nutrient availability is also important (Larson et al. 2000). Contrary to the general impression, water and nutrients are not always scarce on cliffs (Larson et al. 2000), which often have more available water than the surrounding areas. While cliff ecosystems in general are unproductive, this does not apply to all individual microsites, which may have a high nutrient availability, again adding to the mosaic nature of this habitat (Larson et al. 2000). However, the typically slow growth of plants in cliffs results in a common adaptation of cliff plants being longevity (Davis 1951). In addition to the controlling processes mentioned above, distance to the sea and elevation are also important factors for plant species composition on cliffs (Cooper 1997; Meirelles et al. 1999).

Regarding differentiation of species composition, some studies have identified typical cliff vegetation types among cliff ecosystems, correlating with differences in micro-topography and other abiotic factors (Davis 1951; Jarvis 1974; Nuzzo 1996; Fransson 2003; Kuntz and Larson 2006a; Wiser and Buxton 2009). Other studies have stated that while the occurrence of individual species may correlate with variation in abiotic factors, no distinct vegetation types exist (Bunce 1968). Some studies have shown that community composition is similar on rocks over large geographical distances (Larson et al. 1989; Haig et al. 2000; Matthes et al. 2000).

1.2.4 Diversity patterns, dispersal and connectivity

The theory of island biogeography (MacArthur and Wilson 1967) predicts that the number of species occurring on oceanic islands represents an equilibrium between immigration and extinction rates, which will vary with island area and the distance from the mainland. The mainland is assumed to be the single source from which species colonizes islands at different distance and size. This hypotheses has been tested on different kinds of terrestrial habitat islands, including cliffs (Haig et al. 2000), rocks (Armesto and Contreras 1981) and boulders (Kimmerer and Driscoll 2000; Weibull and Rydin 2005), with different results. The assumption of a single mainland source, from which species colonize habitat islands, does however rarely conform well to real landscapes. In reality, each of the islands may act as sources or sinks, depending on e.g. habitat quality and competition over resources among and within locally coexisting populations, affecting the probability for persistence or extinction. If the investigated system does not conform to a mainland-island structure, factors such as connectivity of suitable habitat patches in the landscape, as well as the permeability of the matrix of habitats surrounding the islands will affect community structure. Metacommunity theory makes more realistic assumptions for this kind of systems, and cliffs or boulder patches are likely to conform well to many of the assumptions of metacommunity theory (Virtanen and Oksanen 2007). Since metacommunity theories have been developed quite recently, it is still an urgent task to link theoretical concepts to natural systems (Holyoak and Holt 2005). Although differing in underlying assumptions, metacommunity and island biogeography theories both emphasize the importance of dispersal abilities of the species making up the communities and the connectivity of suitable patches in the landscape for predicting richness and composition of communities.

Cliffs occur as natural fragments in the landscape (Haig et al. 2000, Hunter 2003) and thus make up excellent habitats for studying how isolation and connectivity affect biodiversity and community composition (Pharo and Zartman 2007). Compared to many other habitat types, cliffs have distinct boundaries, differ drastically from surrounding vegetation, contain a high proportion of specialized species and are easy to identify.

*1.2.5 Effects of dispersal ability and connectivity on bryophyte
communities*

Bryophytes are ideal organisms for studying meta-community structures and effects of dispersal ability and connectivity on species richness and community composition, due to their substrate specificity (Virtanen and Oksanen 2007). Therefore, cliff bryophyte communities may be valuable for providing insight into the dynamics of species with narrow niches and restricted dispersal abilities.

Some studies have shown evidence that decreasing patch size, increasing fragmentation and isolation of forest stands reduce species richness of epiphytic and epiphyllous bryophytes in tropical forests (Zartman 2003; Alvarenga and Porto 2007), as well as boreal forests (Löbel and Rydin 2009). There are also examples from rocky boulder fields. Virtanen and Oksanen (2007) proved that bryophyte diversity increased with boulder size and connectivity. Weibull and Rydin (2005) concluded that species richness was positively correlated to both boulder area and within-boulder habitat diversity.

There is also evidence that spatial and environmental variables interact in structuring bryophyte communities (Snäll et al. 2003, 2004, 2005; Löbel et al. 2009). Propagule size is a crucial component in explaining biodiversity patterns for bryophytes occurring in patchy or fragmented habitats (Löbel et al. 2006a, 2006b; Gunnarsson and Söderström 2007; Hajek et al. 2011). Although many bryophytes have wide distributions, several studies have shown that their distribution may be dispersal limited on a smaller spatial scale (Snäll et al 2003; Kimmerer 2005; Pharo and Zartman 2007).

Bryophytes can disperse effectively over long distances with spores. However, species that do not regularly produce spores but reproduce asexually, by fragments or/and specialized vegetative dispersal organs, tend to be rare and have restricted distributions, which may be explained by a combination of their reproductive system and sporophyte production frequency (Longton 1992; Laaka-Lindberg et al. 2000).

1.2.6 Disturbance on cliff ecosystems from rock climbing

Cliffs receive little antropogenic disturbance, and are perhaps among the most undisturbed ecosystems on earth (Larson et al. 2000). Rock-climbing is an increasingly popular outdoor activity with increasing numbers of perpetrators (in Sweden and globally) and has been reported as an activity with negative impact on biodiversity of cliff communities. Avifaunal (Crick and Ratcliffe 1995; Brambilla et al. 2004), snail (McMillian et al. 2003; Baur et al. 2007) and plant communities (Nuzzo 1996; Camp and Knight 1998; Farris 1998; McMillian and Larson 2002; Müller et al. 2004; Rusterholz et al. 2004; Kuntz and Larson 2006b; Baur et al. 2007) have been investigated. Several studies have documented some effect on cliff habitats from rock climbing in terms of species richness, density, diversity, cover, abundance, composition, or a combination thereof (see table 1, Paper III for an overview). However, different approaches and methods have been used, and different groups of organisms sometimes show different responses.

1.3 Facilitation and nurse-plants

Facilitation has been defined as an interaction between organisms that are beneficial to at least one, and harmful to none of them (Bruno et al. 2003). This field of ecological research has received increasing amounts of attention during the last two decades, and has been shown to be important in a multitude of environments, such as for example deserts, chaparral, salt marshes and arctic and alpine tundra (see Callaway and Walker 1997 and references therein). Facilitative interactions affect individual fitness, population distributions and growth rates, species composition and diversity, across scales from individuals to landscapes.

Studies of changes in plant species interactions along environmental gradients have shown facilitation to increase with increasing stress, summarized as the Stress Gradient Hypothesis, SGH (Bertness and Callaway 1994). Although there is a large body of literature supporting the SGH, the generality of this hypothesis has been challenged and its applicability in arid and semi-arid regions questioned (Maestre 2005, 2006; Michalet 2007). In alpine and arctic environments, environmental severity often increase along elevational gradients along with worsened conditions concerning temperature, length of growing season, nutrients, exposure and substrate stability (Körner 2003). Facilitation is well doc-

umented in alpine plant communities (Callaway et al. 2002), where it may promote niche expansion into severe environments for species at their altitudinal limit (Choler et al. 2001), as well as in the form of nurse plants ameliorating conditions along gradients of increasing stress (Cavieres et al. 2002; Arroyo et al. 2003; Badano and Cavieres 2006a, b; Cavieres et al. 2006). In harsh environments this form of plant–plant interaction is of great importance for the establishment and survival of many species and for patterns of community composition and dynamics.

2. MATERIAL AND METHODS

2.1 Study sites

Paper I and IV were performed in the subarctic alpine valley Latnjavagge, making up the catchment area for Lake Latnjajaure, situated at 981 m a.s.l., 16 km west of Abisko in northern Sweden (Figure 3). The climate is typical for sub-arctic alpine regions with low mean annual temperatures and a short vegetation season (see Figure 4). The bedrock in the valley consists mainly of calcareous mica schist, forming a mosaic of rock outcrops and steep cliff faces with different aspect and inclination on the eastern and western sides of the valley (Figure 1e-h). The surrounding areas are tree-less alpine tundra and vegetation consists of a mix of alpine heaths, meadows and wetlands (Figure 1a-d).

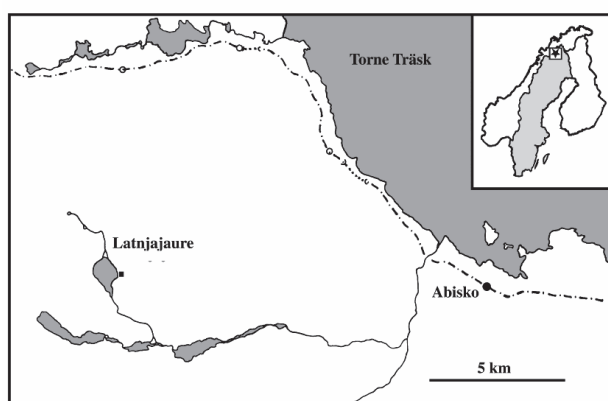


Figure 3. Location of Lake Latnjajaure in northern Sweden. Illustration by Ulf Molau.

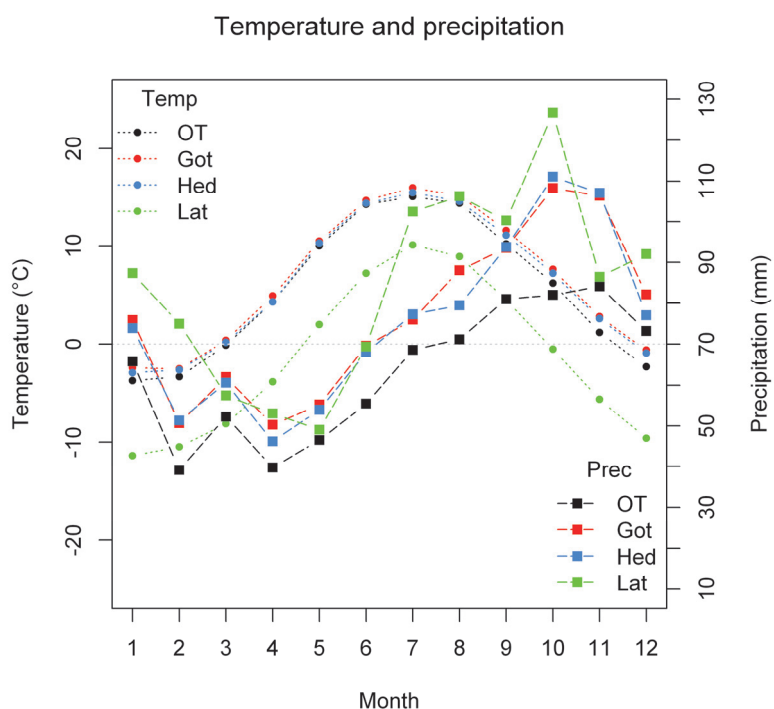


Figure 4. Illustration of differences in temperature (°C) and precipitation (mm) at the climate stations closest to the investigated areas in this thesis. The graph shows monthly means for air temperature and precipitation and is based on normal values for 1961-1990 from the Swedish Meteorological and Hydrological Institute (www.smhi.se). OT is the Orust-Tjörn area (climate data from Ljungskile), Got is the Gothenburg area (climate data from Gothenburg), Hed is the Hedekas area (climate data from Dingle) and Lat is the Latnjavagge area (climate data from Riksgränsen). The three investigated areas in Paper II had similar temperature and precipitation. The Latnjavagge sites had lower temperatures and more precipitation in autumn and winter. The x-axis represents the months of the year (1= January and 12= December). Solid dots indicate temperature and open squares indicate total monthly precipitation.

Paper II was performed on near-vertical cliff sites in the south-western part of Sweden (Figure 1i-o). Three different regions along the west coast were investigated. One region covered an area situated inland from Gothenburg, one comprised the two large coastal islands Orust and Tjörn and one was situated around Hedekas (Figure 5). The bedrock in the three areas is siliceous (granite or gneiss). Patterns in precipitation and temperature were similar between the three areas (Figure 4). Length of vegetation season is 200-210 days (normal values for 1961-1990 from the Swedish Meteorological and Hydrological Institute: www.smhi.se). The investigated cliffs were predominantly surrounded by forest, in the Hedekas area dominated by Norway Spruce (*Picea abies*), in the Gothenburg and Orust-Tjörn area mixed deciduous forest, in Orust-Tjörn with some dominance of Oak (*Quercus robur*).

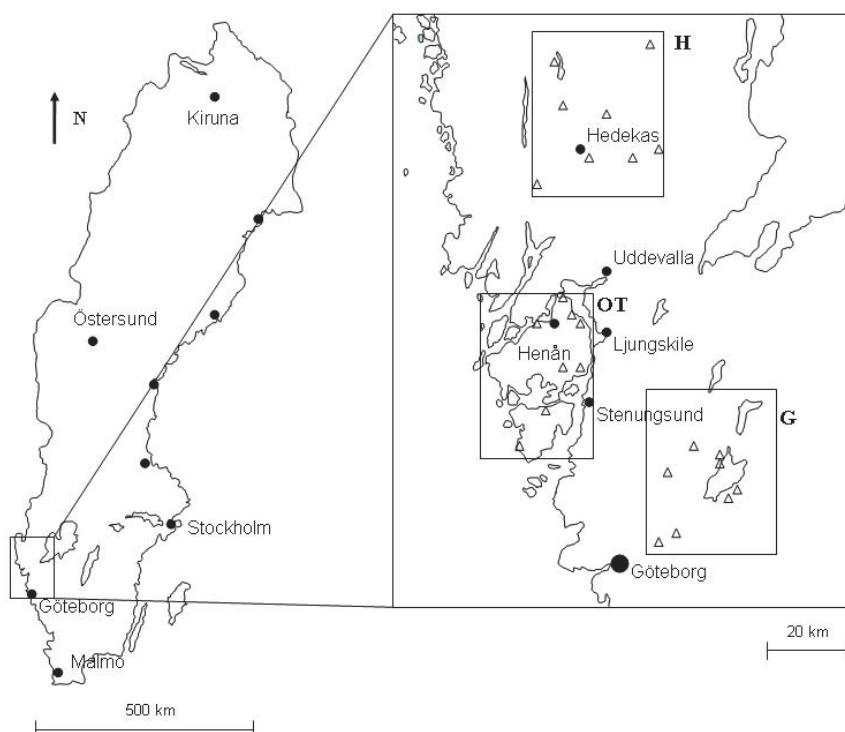


Figure 5. The investigated regions in Paper II.

Paper III was performed on cliffs around Gothenburg, used for recreational rock-climbing, and unclimbed reference cliffs. The cliffs were all of siliceous bedrock (granite or gneiss).

2.2 Field sampling

In Papers I, II and III, near-vertical cliffs were sampled. When possible, climbing equipment was used to rappel down the cliffs in focus from a belay arranged using safe belay points at the top of the cliff face (Figure 6). In the Latnjajaure catchment (Paper I), this method could not be used for many of the cliffs, due to lack of safe anchor points and/or poor quality of the rock. For these cliffs, a ladder was used instead to sample as much as possible of the cliff face.

In Paper I and III, pointframe quadrates (0.25 m^2) with 25 points were used, placed along the cliff face, to sample each site (Figure 6c). This gives an estimate of the frequencies of the species found on the cliff face.

In Paper II, the Point Centered Quarter method was used, which starts from a random point on the cliff face, from which four quadrants are assigned. In every quadrant, with the random point as the intersection, the distance to the nearest species or “feature” (see below) was measured. Density, expressed as number of bryophytes or features per square meter was calculated from Equation 1.

$$\text{Density} = 1/r^2 \quad (1)$$

where r is the average distance to the object of interest (in our case the species or feature), from the random point.

In Paper IV, four altitude transects were randomly placed along the south-west facing slope of Mt. Latnjatjårro, spaced at least 20 m apart. At every 20 meters of elevation, from the summit at 1447 m a.s.l. to 1150 m a.s.l, the nearest cushion of *S. acaulis* measuring at least 10 cm in diameter was located, and marked in order to avoid sampling it twice. The contour of each marked cushion was then taken using a soft steel wire (in a similar manner to that reported by Cavieres et al. 2002) to mark identical areas for the paired control plots.



Figure 6. Methods used for sampling steep cliffs. a.) Rapelling down the cliff to sample cliff vegetation. b.) An anchor used for fixing the rope on top of the cliff. c.) Fieldwork in these environments sometimes involves being in a painful position in a beautiful scenery.



Figure 7. A typical *Silene acaulis* cushion from Paper IV.

The number of vascular plant species within the *Silene* cushions was then noted (Figure 7). The steel wire loops marking the paired control plots were laid out in a random direction (1-360 degrees) and distance (1-10 m) from the sampled cushions.

2.3 Estimation of environmental variables

In Papers I, II and III environmental variables were estimated at the cliff sites to characterize differences between sites and relate to species richness, density and composition. The following variables were estimated in all three studies:

- i.) Inclination of the cliff face was measured using a clinometer.
- ii.) The East and North components of aspect (Eastness and Northness) were estimated using a compass (360°) at a right angle to the horizontal edge of each quadrat. The values obtained were transformed into two components, following equations 2 and 3, respectively (Roberts 1986), where x = the measured direction in radians.

$$\text{Northness} = \frac{\cos(x) + 1}{2} \quad (2)$$

$$\text{Eastness} = \frac{\cos\left(x - \left[\frac{90}{360}\right]\right) + 1}{2} \quad (3)$$

This produces a relative measure between 0 and 1 for the two components, respectively, representing the degree of north and east facing orientation of the cliffs (called Northness and Eastness).

- iii.) A feature index value was calculated to include an estimation of microtopographic heterogeneity, as recommended by Kuntz and Larson (2006a). In Papers I and III heterogeneity in terms of 'features' of the rock surface was noted at all 25 points of the quadrat. A feature was defined as the deviation (in mm) at the point from an even surface. The feature index was then obtained by dividing the sum of the size of features by the number of points. In Paper II the density and size of features was used instead, calculated using equation 1, and a minimum size of 10 mm for each feature was used.

The following variables were estimated only in Paper I:

- iv.) Soil organic matter (SOM) and soil pH were measured from soil samples, dried to constant weight at 30-35 °C and sieved through a 2-mm mesh. For pH measurements, 5 g of soil were shaken with 1M KCl (1:10), sedimented and filtered and measured with a pH meter. Soil organic matter (SOM) was determined by loss on ignition at 550 °C for 24 h after drying soil samples at 70 °C for 48 hours.
- v.) Temperature was measured using temperature sensors/loggers (TinyTags, Gemini), placed on the soil/cliff surface at one location for each site. From the hourly recordings of temperature, mean July temperature (JulyT) and Thawing Degree Days (TDD) were calculated. TDD is calculated as the cumulative integrated temperature sum above 0°C. The daily contribution to TDD is the mean over 24 h of all hourly recordings above freezing.
- vi.) Elevation of the investigated sites was recorded using a GPS.
- vii.) Habitat type (Cliff or Reference) was included as an environmental factor in the ordinations.

In Paper II and Paper III, most cliffs were surrounded by forest, and the relative canopy cover was ranked on a scale, where:

- viii.) 1 = cliff face completely open, i.e. the cliff face was above the canopy, or the distance to a closed canopy was more than 25 m; 2 = intermediate openness, with scattered trees or a closed canopy 5 – 25 m from the cliff; 3 = cliff face with a closed canopy closer than five m.

The following variables were used only in Paper II:

- ix.) Seepage was recorded as a dummy variable at each point with 1 if the spot had continuously running/seeping water and 0 if there was no continuously seeping water.
- x.) Cliff length (measured in meters at the base of the cliff) and height (average of the lengths of transect lines, in meters) was used to calculate the size of the cliff.

3. RESULTS AND DISCUSSION

3.1 Paper I

In this Paper, diversity in terms of species richness and density was investigated in six cliffs and six reference sites in the sub-arctic alpine valley Latnjavagge to quantify the contribution of the cliff habitats to the total landscape diversity. Differences between the habitat types were investigated along with an analysis of what environmental variables were important for driving differences in species density and species composition.

The results of the differences in species composition, richness and density between the cliff habitat and surrounding matrix habitat show that cliff habitats were dominated by lichens, of which very few species were shared with the matrix habitat, followed by bryophytes, occurring in lower abundance. Vascular plants were the least abundant group of species on the cliff face. The bryophyte communities on cliffs were also highly specialized for this habitat and very few species were shared between cliffs and surrounding habitats. Among the vascular plants in the cliff habitat, there were few truly chasmophytic species and a higher proportion of species were shared between the habitats (Table 1).

Table 1. Number of species and proportions (%) of the total species pool in cliff or reference sites at Latnjajaure, and number and proportion of shared species for each taxonomic group.

	Community	Vascular plants	Bryophytes	Lichens
Cliff	78 (44%)	32 (45%)	19 (32%)	27 (59%)
Reference	135 (76%)	61 (86%)	45 (75%)	29 (63%)
Shared	36 (20%)	21 (30%)	4 (7%)	10 (22%)
Total	177	71	60	46

The different organism groups (vascular plants, lichens and bryophytes) responded differently to environmental variables in terms of community structure (analyzed with Non-Metric Multidimensional Scaling). Lichens and bryophytes showed significant differences in composition between habitat types, but vascular plants did not. pH was the most important environmental variable, significant for explaining differences in composition for all groups.

Species density was significantly lower in the cliff habitat for bryophytes and vascular plants. For lichens, density did not differ significantly between cliff and reference habitats. Total species richness was lower in the cliff habitat for lichens but vascular plants and bryophytes did not differ significantly when rarified to the same number of individuals. This result differs from some previous reports on cliff vegetation in other areas, which have reported cliff communities to be more species rich than surrounding level-ground vegetation (Bunce 1968; Ward and Andersson 1988; Meirelles et al. 1999).

Feature index was significantly correlated with species density of vascular plants, but lichens and bryophytes were not, when analyzed separately. Bryophyte density was significantly higher in more north facing cliffs, where higher humidity is likely to create better growing conditions for this organism group (Hallingbäck 1996; Hespanhol et al. 2011). Lichen density was higher on east facing cliffs, which may be explained by strong westerly winds in the region creating severe conditions, unfavorable for the majority of species. Lichen density (number of species / 0.25 m²) was significantly negatively correlated with inclination of the cliff.

The results illustrate the importance of including cliff habitats when assessing landscape diversity in alpine ecosystems. Cliffs contribute to landscape diversity by high species turnover in relation to surrounding matrix habitats. Cliffs contain many species with distinct affiliation to these habitats, especially among cryptogams, which is in line with documentations by previous studies (Larson et al. 1989; Maycock and Fahselt 1992; Hallingbäck 1996; Matthes et al. 2000). The study also showed the importance of accounting for number of individuals when comparing communities with different densities (as argued by Gotelli and Colwell 2001), since the observed total richness of the two habitats

showed a different pattern than when comparisons were made on rarefied species richness. In addition, it emphasizes the importance of analyzing different species groups separately since they responded differently in terms of diversity patterns.

3.2 Paper II

In this Paper we aimed to find out the importance of spatial configuration of suitable habitats, in comparison with environmental factors, is for composition of obligate epilithic bryophyte communities on siliceous cliffs in south-western Sweden. It investigated whether the main source of beta-diversity is spatial or environmental factors and if communities are restricted by dispersal abilities of bryophytes or environmental conditions. It also sought to find out if there was a positive relationship between the size of the investigated cliffs and species richness at each site.

We found more generalist than obligate cliff bryophytes in the investigated siliceous cliffs. The generalist species occur frequently in the surrounding matrix habitats, and the spatial configuration of cliffs did not affect composition of this group of species. The composition of obligate cliff bryophytes, however, was significantly correlated with geographic distance between the cliffs sites, showing decreasing similarity with increasing distance, when partialling out the effect of environmental variables in a Partial Mantel test. This is an indication that the distribution of these species is likely to be limited by dispersal ability. This conclusion was further supported by the fact that the species scores along Axis 1 in the NMDS ordination were correlated with a ranked classification of the frequency of spore production of the species (Figure 8). This supports previous studies performed on epiphytic bryophytes showing that species rarely producing spores are dispersal limited (Löbel et al. 2006a, 2006b, 2009; Löbel and Rydin 2009). The finding is important for practical conservation work, and implies that many bryophyte species are dependent on high connectivity of suitable habitat patches for their long-term persistence.

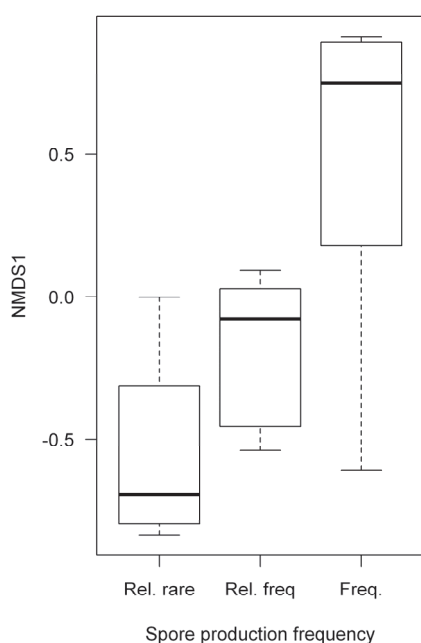


Figure 8. Frequency of spore production of the obligate bryophytes in Paper II in relation to the species scores along the first axis in the NMDS ordination. The observed pattern is an indication that dispersal ability is important for species composition of obligate bryophytes, supporting our finding in the Partial Mantel test.

Results from the tests showed that environmental variables, and not geographic distance, were the best predictors of composition of generalist bryophytes, which had a more similar community composition over large geographical distances. Of the environmental variables included in the NMDS ordination, density of the canopy of the surrounding forest was the best predictor of community composition of both generalists and obligate cliff species, most likely by increasing air humidity at the site, which favors drought-intolerant bryophytes.

There were no differences in species richness between the investigated regions. Cliff species richness was best explained by a model including northness (positively correlated), feature size and inclination (both negatively correlated). We did not find cliff size to be significant for explaining species richness, which has been reported in some previous studies of cliffs and boulders (Kubešová and Chytrý 2005; Weibull and Rydin 2005; Virtanen and Oksanen 2007)

3.3 Paper III

In this Paper we investigated the impact of rock-climbing on species richness and composition on cliffs with different popularity, receiving different number of visits from climbers. The main focus was to answer if the observed differences in species richness and composition were likely to be explained by climbing activity also when the differences in environmental conditions at the sites were taken into account.

Northness and shade from the surrounding canopy layer were good predictors of diversity on cliff site level, while the amount of microtopographic heterogeneity (feature index) was the best predictor at plot level (species density, number of species occurring in each 0.25 m² point-frame). Northness was correlated both to species richness and frequency of visits from climbers (Figure 9). However, our results show that disturbance from climbing in terms of frequency of visits was not significant when environmental variables were included in a multiple regression analysis. Northness and inclination were significant for explaining species composition, but frequency of visits from climbers was not. The results indicate that environmental variables were more important drivers of diversity patterns than the influence of climbing activity, which is in line with the conclusions by Kuntz and Larson (2006b), Nuzzo (1996) and Farris (1998).

The results emphasize the importance of including environmental variables when investigating impacts from climbing activity on cliffs, as there was a negative correlation between frequency of visits and shade from the canopy. In our study, the most reasonable explanation is that the frequently visited cliffs are the ones displaying low species richness, and that environmental processes, and not climbing activity, are controlling the observed diversity patterns in our study area (Figure 9).

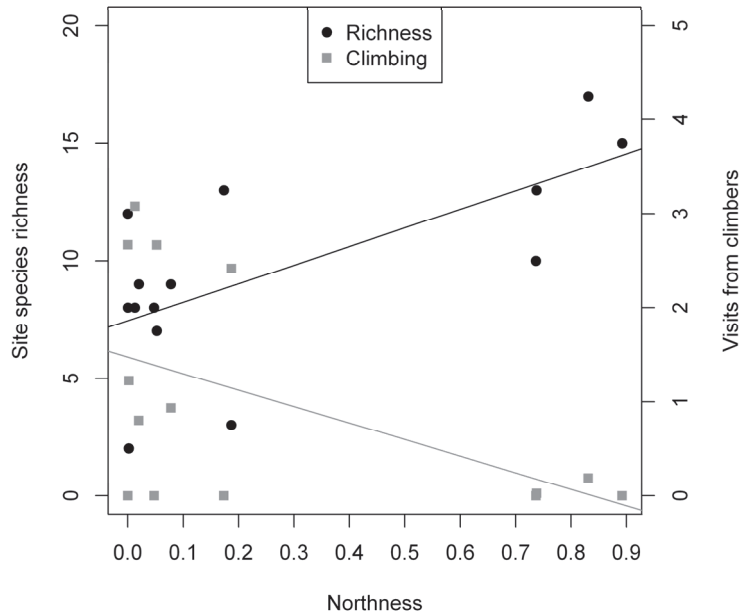


Figure 9. The plot shows relationships between northness (northern component of aspect) and species richness (black line, $R^2=0.45$) and frequency of visits from climbers (grey line, $R^2=0.27$), respectively at the cliffs investigated in Paper III. Cliffs with a northerly aspect were more species rich, but also received less visits from climbers. Climbing activity was not a significant factor explaining species richness when environmental variables (including northness) were included in a multiple regression.

There are no published reports investigating cliffs before and after climbing activity started at the cliffs. The problem of explicitly separating the causal links between human disturbance and structure of vegetation was recognized by Farris (1998), who found a significantly lower plant cover on climbed cliffs compared to pristine, but concluded that geological and environmental factors influence both human use and patterns of vegetation, which should be considered in assessments of

climbing impact on the diversity of cliffs. Nuzzo (1996) also identified a decrease in species density and cover of lichens when comparing climbed cliffs to pristine, but concluded that environmental and physical variables were the primary determinants of the cliff flora, and called for more studies to disentangle the drivers of diversity patterns. Studying climbing disturbance and changes in vegetation, Kuntz and Larson (2006b) found that when controlling for influences of microtopography, differences in vegetation could not be related to climbing disturbance, but rather that climbers select cliffs supporting less vegetation. These results, and the results of our study emphasize the importance of explicitly considering differences in environmental and microhabitat conditions between climbed and unclimbed cliffs in order to disentangle the disturbance effects of rock climbing from differences in environmental variables among the investigated sites.

3.4 Paper IV

In this Paper we focused on the nurse plant effect of the cushion forming plant *Silene acaulis* (L.) Jacq. along an altitudinal gradient in the valley Latnjavagge and explored the potential importance of cushion-forming plants for biodiversity and species distribution in alpine landscapes. Cushion plants provide favorable conditions within their closed micro-cosms, and have been shown to enhance biodiversity in other alpine sites, with different environmental conditions creating stress for plant species.

In this study we showed that there was a shift in the interaction between *Silene* cushions and the species growing inside them when conditions were shifted towards a more stressful environment along the investigated elevational gradient. Interactions shifted from competition to facilitation in the form of a nurse plant effect as temperatures became lower along the elevational gradient. We concluded that *Silene acaulis* is acting as a nurse-plant at higher elevation, increasing local biodiversity in the harsh environment of high-altitude sites (Figure 10).

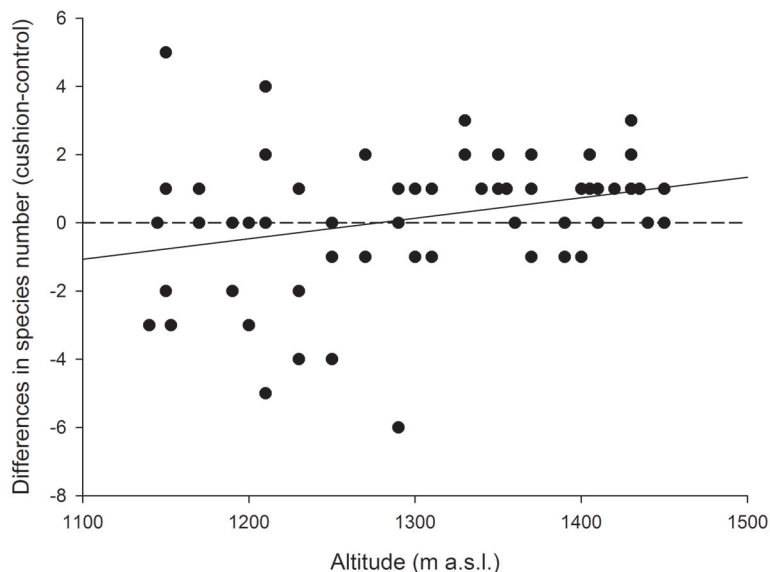


Fig. 10. Differences in species numbers between *Silene acaulis* cushions and identical-sized paired control plot as a function of altitude (Spearman correlation coefficient = 0.29, $P = 0.008$, $n = 69$), showing trend line fitted by least square regression (From Paper IV, reprinted with permission from Taylor & Francis).

The composition of species was largely similar inside and outside cushions over the whole elevational gradient, but we could observe a tendency for graminoids to be represented to a higher degree inside the *Silene* cushions. Our results support the Stress Gradient Hypothesis and previous studies from alpine regions reporting that species interactions shift from competition to facilitation as environmental severity increases (Callaway and Walker 1997; Jones et al. 1997; Choler et al. 2001; Callaway et al. 2002; Kikvidize et al. 2001, 2005). It confirms that cushion plants are acting as nurse plants in the Scandes, as observed e.g in the Andes (Nuñez et al. 1999; Cavieres et al. 2005; Cavieres et al. 2006; Badano and Cavieres 2006a, b). The positive effects from *Silene* cushions on beneficiary species is likely to be in the form accumulation of nutrients and organic soil, amelioration of disturbance, protection from herbivores, shelter from wind and protection from extreme temperatures.

3.5 Patterns of bryophyte distribution in Papers I, II and III

The investigated cliffs in Papers I, II and III contained many bryophyte species occurring in low frequencies (Figure 11). Many species were uniques, occurring just at one single site. This indicates a high species turnover between cliff sites in all three studies.

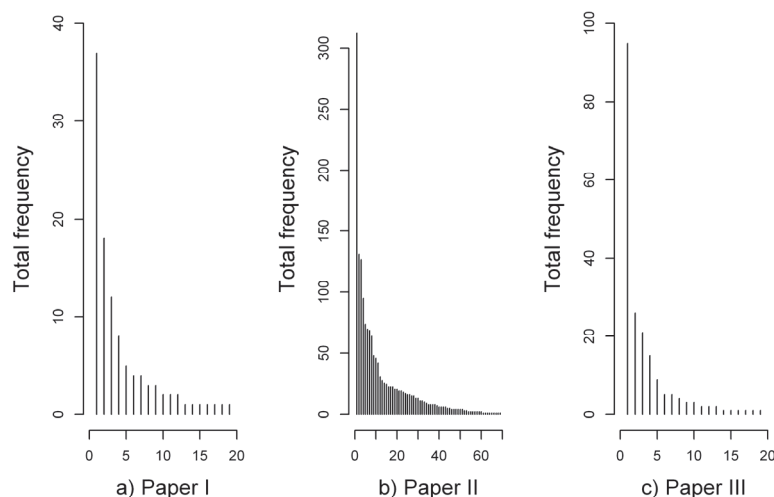


Figure 11. Frequency plots of bryophytes in Papers I, II and III, showing the total frequency of bryophytes (y-axis) for the number of species found in the survey (x-axis). The investigated cliffs contained a few very dominant species while most species occurred in low frequencies. Many bryophyte species were uniques or duplicates, occurring at one single or two sites. Note the different scales on the y axis.

The study sites were distinctly different between Paper I and Papers II and III in terms of environmental and climatic conditions (see Figure 4 and description in materials and methods), but some general patterns can be outlined (see Table 1 for an overview of the Papers in this thesis). Northness was the most important factor driving differences in species composition and promoting higher species richness of bryophytes.

Comparing the results of Paper I and II show that cliffs in the boreo-nemoral forested landscape are largely dominated by generalist bryophytes, and contained considerably lower proportions of obligate cliff species, while the cliffs in the sub-arctic alpine valley in Paper I shared very few bryophyte species with the surrounding landscape. This provides an additional argument for the importance of cliff habitats in subarctic alpine regions in terms of biodiversity on the landscape level.

Previous studies on cliff vegetation have shown a positive correlation between heterogeneity of cliff microtopography and species richness of bryophytes (Weibull and Rydin 2005; Kuntz and Larson 2006a; Hespánhol et al. 2011), vascular plants (Davis 1951; Bunce 1968; Kuntz and Larson 2006a). In my studies, this was found in some cases, but not consistently. Feature index was positively correlated with species density (of bryophytes in Paper III and vascular plants in Paper I). In Paper II the size of features was negatively related to species richness, but the density of features was not significant. The mechanism for this is not clear.

Cliffs are heterogeneous habitats, and sampling these communities in a optimal way was a challenging task (not only in terms of their inaccessibility) since vegetation is sparse and spatially variable. Previous studies on cliff vegetation have used different sampling methods, and my results show that different methods may give very different results in terms of the number of individuals included in the survey. I used both randomly placed point frames on the cliff face (Papers I and III) and plot-less individual-based methods (the Point-centered quarter method in Paper II). Results show that the later method (PCQM) is preferred when investigating the sparsely vegetated cliff face habitat, since it included more individuals and consequently is likely to give a more accurate view of the community composition and richness (Figure 12). Direct comparisons between species richness from studies using different methods should be avoided.

Table 1. Overview of the location, dominating vegetation at the investigated sites, organism groups investigated and main topics of the four Papers included in this thesis.

Paper	I	II	III	IV
<i>Location</i>	Northern Sweden	South-west Sweden	South-west Sweden	Northern Sweden
<i>Vegetation type</i>	Cliffs in a sub-arctic alpine valley	Cliffs in boreo-nemoral forest	Cliffs in boreo-nemoral forest	Heaths/meadows in a sub-arctic alpine valley
<i>Organism group(s)</i>	Vascular plants, bryophytes and lichens	Bryophytes	Bryophytes and lichens	Vascular plants
<i>Main topic</i>	Diversity and environmental conditions	Diversity and environmental conditions versus dispersal ability	Diversity and disturbance from climbers	Diversity and nurse plants/facilitation

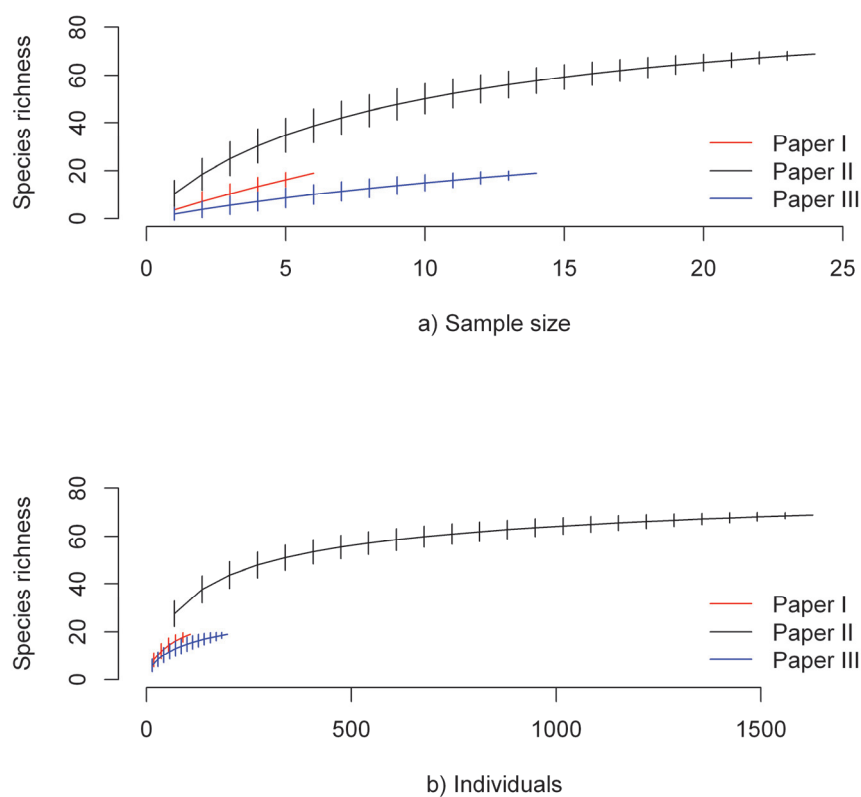


Figure 12. Accumulation curves of the total cumulative species richness over all sites in the bryophyte cliff communities for Paper I (red), Paper II (black) and Paper III (blue). Paper II used plot-less individual-based sampling, which seems to be advantageous in these heterogeneous habitats and give a more complete estimate of the sampled communities. In Papers I and III, the asymptote of the curve was not reached, and comparisons between studies using different sampling methods should be avoided.

4. CONCLUSIONS

1. Cliff habitats are important for biodiversity in sub-arctic alpine landscapes. They contain a distinct vegetation type including some rare species. Cliffs in this region have previously been largely overlooked in ecological studies and in order to capture the full species diversity in alpine areas it is important to include cliff habitats in assessments of biodiversity. Different organism groups responded differently to the environmental conditions in cliffs and hence should be separated when investigating drivers of both community composition and species density/richness.
2. Distribution of obligate cliff bryophytes is indicated to be limited by dispersal. This demonstrates the importance of maintaining high connectivity in the landscape also for species with small propagules, and is important for conservation of cryptogams with high substrate specificity. Dispersal ability is likely to be a limiting factor for bryophytes with low frequency of spore production. We did not find the size of cliffs to be important for species richness on cliffs, which has been reported in some previous studies.
3. In our investigated area, we could not find convincing evidence that climbing was significantly reducing species richness nor having a significant impact on the composition of cliff cryptogam communities. Environmental variables were better predictors of community structure. In order to separate the potential negative impact from rock climbers, environmental conditions should be included in the analyses. Not doing so implies a risk of interpreting communities with low species richness as an effect of disturbance from rock climbing when it may be that these environments were less species rich also prior to climbing started, but are preferably selected by climbers.

4. *Silene acaulis* is acting as a nurse-plant in cold-stressed communities at the investigated sub-arctic alpine tundra site. As stress increases along the elevational gradient (along which also temperature and nutrient availability decreases), interspecific interactions shift from competition to facilitation. At higher elevation, presence of *Silene acaulis* enhances local biodiversity.

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