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CURRENT RESEARCH TRENDS IN MOUNTAIN BIODIVERSITY IN NW EUROPE

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SUMMARY.- Focusing on four themes in relation to biodiversity (vegetation science, keystone grazers, long-term studies and protected areas), a synthesis of current research in the mountain areas of Fennoscandia, Iceland and Scotland is presented. Recent relevant advances in vegetation science include classifications of mountain habitats which together with species distribution maps offer new possibilities for analysis. Generalisations emerging from comparisons of the ecology and ecophysiology of plants between different mountain areas are greatly needed. Further studies on the ecological impacts of keystone grazers are urgently required because of the alarming rate of degradation of montane habitats. The topics highlighted from northern Fennoscandia include (i) the effect of overgrazing by reindeer on the cover of foliose lichens and on the regeneration of mountain birch, (ii) the ecological interactions between the autumnal moth and mountain birch, and (iii) the effect of rodents on vegetation. Long-term studies of slow processes to capture rare but important events are needed to better understand the functioning of mountain ecosystems. Examples of such studies are presented for (i) the moss Racomitrium lanuginosum *as an indicator of airborne nitrogen pollution, (ii) research based on cyclic oscillations of vole numbers, and (iii) the application of breeding birds in environmental assessment. The conservation of appropriate areas is important for mountain biodiversity. Mountain habitats have been protected extensively in northern Europe. The evaluation of how representative the existing areas are and how to use them for research need international co-ordination.*

RÉSUMÉ.- On présente une synthèse de la recherche actuelle dans les régions de montagne de la Scandinavie, l'Islande et l'Ecosse, centrée sur quatre sujets autour de la biodiversité (science de la végétation, herbivores principaux, études à long terme et zones protégées). Les résultats récents d'importance en science de la végétation portent sur la classification des habitats de montagne, qui, avec les cartes de répartition des espèces, offrent des nouvelles possibilités pour l'analyse. On a fortement bésoin de généralisations tirées de la comparaison entre l'écologie et l'écophysiologie des plantes dans différentes zones de montagne. Il nous manque aussi

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des études sur les impacts écologiques des principaux herbivores étant donné l'alarmant taux de dégradation des habitats de montagne. Les sujets soulignés dans la Scandinavie du Nord touchent (1) l'effet du surpaturage des rennes sur la couverture des liquens foliacés et sur la régéneration du bouleau nain, (2) les interactions écologiques entre la mite d'automne et ce même bouleau, et (3) l'effet des rongeurs sur la végétation. Il nous semble indispensable de réaliser les études à long terme sur les processus à faible vitesse; elles conduiront à saisir des événements rares mais importants; cela permettra de mieux comprendre le fonctionnement des écosystèmes de montagne. Des exemples de telles études sont ici présentés pour (1) la mousse Racomitrium lanuginosum *comme indicateur de la pollution aérienne par l'azote, (2) la recherche basée sur les oscillations périodiques du nombre de campagnols, et (3) l'utilisation des oiseaux nicheurs pour l'évaluation de l'environnement. La conservation de zones appropriées est importante pour la biodiversité de la montagne. Les habitats de montagne sont largement protégés dans l'Europe du Nord. Cependant, l'évaluation de la représentativité des zones actuellement protégées ainsi que leur usage pour la recherche auraient besoin d'une coordination internationale.*

RESUMEN.- Sintetizamos aquí las investigaciones actuales que se desarrollan en las zonas de montaña de Escandinavia, Islandia y Escocia. Recientemente, los avances destacados en el estudio de la vegetación que clasifican los hábitats de montaña, junto con los mapas de distribución de las especies, permiten nuevos enfoques científicos. Se hace necesario comparar la ecología y la ecofisiología de las plantas entre diferentes áreas montañosas y luego extraer generalizaciones. Igualmente resultan urgentes nuevos estudios sobre los impactos de los herbívoros principales, teniendo en cuenta la rápida degradación de los hábitats de montaña. Los temas tratados para el N de Escandinavia son (1) el efecto del sobrepastoreo de los renos en la cobertura de los líquenes foliáceos y en la regeneración del abedul, (2) las interacciones ecológicas entre la polilla de otoño y el abedul, y (3) el efecto de los roedores en la vegetación. Parece indispensable desarrollar estudios a largo plazo sobre procesos lentos con el fin de aprehender fenómenos raros pero importantes y atisbar el funcionamiento de los ecosistemas de montaña. Comentamos algunos ejemplos de tales estudios para: 1) el musgo Racomitrium lanuginosum *como indicador de la contaminación del aire por nitrógeno; 2) investigaciones sobre las oscilaciones periódicas del número de topillos, y 3) aplicación de las aves nidificantes a la evaluación ambiental. Es muy importante la conservación de determinadas áreas para la biodiversidad de la montaña. En este sentido, cabe considerar que los hábitats de montaña se han conservado ampliamente en el N de Europa. Sin embargo, la evaluación de la representatividad de esas zonas protegidas y su consiguiente uso para la investigación necesita una coordinación internacional.*

Keywords: Mountain biodiversity, research topics, Northwestern Europe.

1. Introduction

Some of the largest and most valuable near-pristine areas in Europe are found in Northern mountains. According to climatic models a decrease in the biodiversity of northern mountains can be expected. The models predict that

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the concentration of CO_2 will double in the next 50 years and the average temperature in Nordic latitudes will rise by several degrees, probably more in winter than in summer. For various scenarios see SÆLTHUM (1995). Accordingly, some mountain habitats may become wooded or change to moorlands or peatlands during the next few centuries. In the meantime, the Arctic ozone hole is predicted to reach the state that now prevails in the Antarctic (AUSTIN *et al.*, 1992), which would expose organisms to increased UV-radiation.

Biological processes in relation to long-term atmospheric changes have been intensively studied in northern alpine and arctic environments (HOLTEN *et al.*, 1993; GUISAN *et al.*, 1995; KARLSSON & CALLAGHAN, 1996). Biological interactions are complex, however, and further difficulties arise from the uncertainty of how precipitation, growing season length, cloudiness and UV-B radiation levels will change on a regional scale (CALLAGHAN & JONASSON, 1995).

The most imminent threat to biodiversity in the northern mountains is grazing pressure, which often acts in combination with other types of man-made agents deleterious to nature, including nitrogen deposition and acidification. The complex nature of the problem is clear and some of the components will be discussed in turn. After briefly outlining the physiography of the NW European mountains and presenting some recent results in plant community ecology and geobotany, I will concentrate on ecological interactions between major consumers and plants. Finally, I will discuss the importance of long-term studies in understanding the functioning of northern montane ecosystems, and of the value of protected mountain areas.

The ecology of mountain and arctic tundra have much in common in the north (WIELGOLASKI, 1975; 1997; HOLTEN *et al.*, 1993; CHAPIN & KÖRNER, 1995; GUISAN *et al.*, 1995). Accordingly, I will also present some relevant results from low-lying areas which bear a resemblance to tundra and from some boreal forests. The review on the ecosystems of the Caledonian Mountains (SONESSON & MOLAU, 1998) complements some of my themes.

2. Physiography

The majority of the alpine heaths of north-western Europe is situated on the Fennoscandian ridge, where they form a patchy network of about 1800 km long and from 150 to 300 km wide, running in a NE direction (Figure 1). This ridge is divided into two parts by the mainly forested lowlands in Central Fennoscandia, but both south and north of it we find well-developed montane and alpine life zones from mountain birch *Betula pubescens* ssp.

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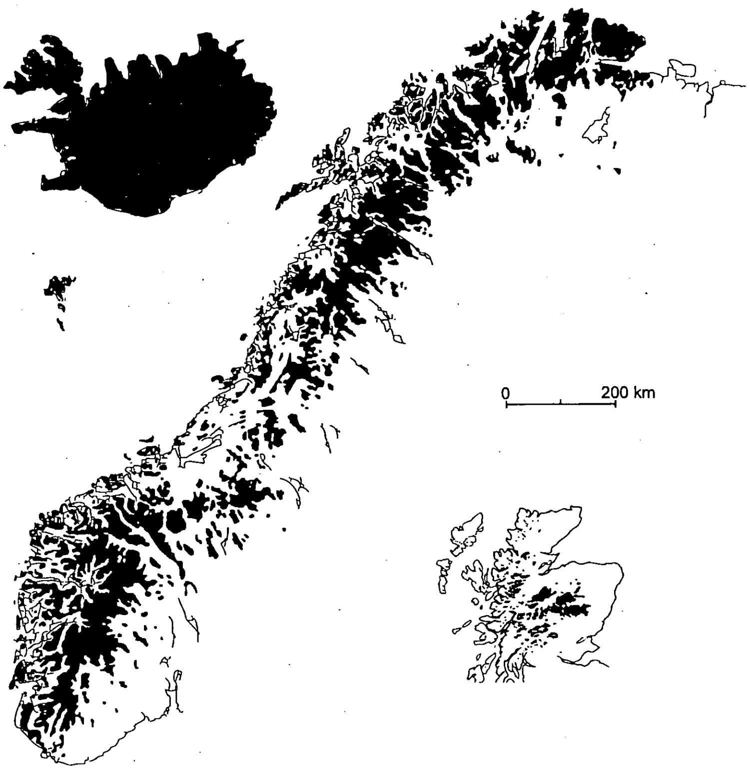

Figure 1. Mountain heaths and glaciers in Iceland (including tundra habitat), the Faeroe Islands, Fennoscandia and Scotland (from THOMPSON & BROWN, 1992 and BERNES, 1993).

czerepanovii (N.I. Orlova) Hämet-Ahti forest to the low, middle and high alpine zones. The predominance of birch in Fennoscandian mountain forests is caused by the combined effects of high-latitude and oceanicity. Oceanicity decreases strongly from west to east and especially towards the central north. Alpine and arctic elements intermingle in Fennoscandia, where the northernmost mountain areas geobotanically mostly belong to the hemiarctic zone (Figure 2). The inclusion of the Northern Kola Peninsula contributes some tundra-like elements to Fennoscandia, which, however, is separated by the White Sea from the tundra proper.

The second mountain area is in Scotland extending about 200 km from south to north and 100-150 km from west to east (Figure 1). In terms of post-glacial distribution, the specialist core of the alpine fauna and flora of Fennoscandia and Scotland may represent the oldest elements in northern

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Europe which invaded the area from about 10000 years ago. On an evolutionary time scale it is a short period, thus endemic species are few in the northern mountains (RATCLIFFE & THOMPSON, 1988). The Scottish Highlands, which together with the Alps are the best studied among European mountains, are extreme in many respects. The climate is hyper-oceanic and a strong human impact has much upset the typical sequence of altitudinal zones found in other European mountains (THOMPSON & BROWN, 1992). The montane area is small, but about 8000-9000 years ago when temperatures were approximately 2 °C above present it was probably even smaller. Thus these mountains have experienced notable bottleneck phases that have resulted in their impoverished arctic-alpine biodiversity.

The third large upland and mountain area of NW Europe is in Iceland, isolated by sea by about 1000 km from Norway and 800 km from Scotland. Iceland is covered by a coherent collection of semi-natural or natural alpine heaths in an area of about 250 km in N-S and 350 km in E-W directions

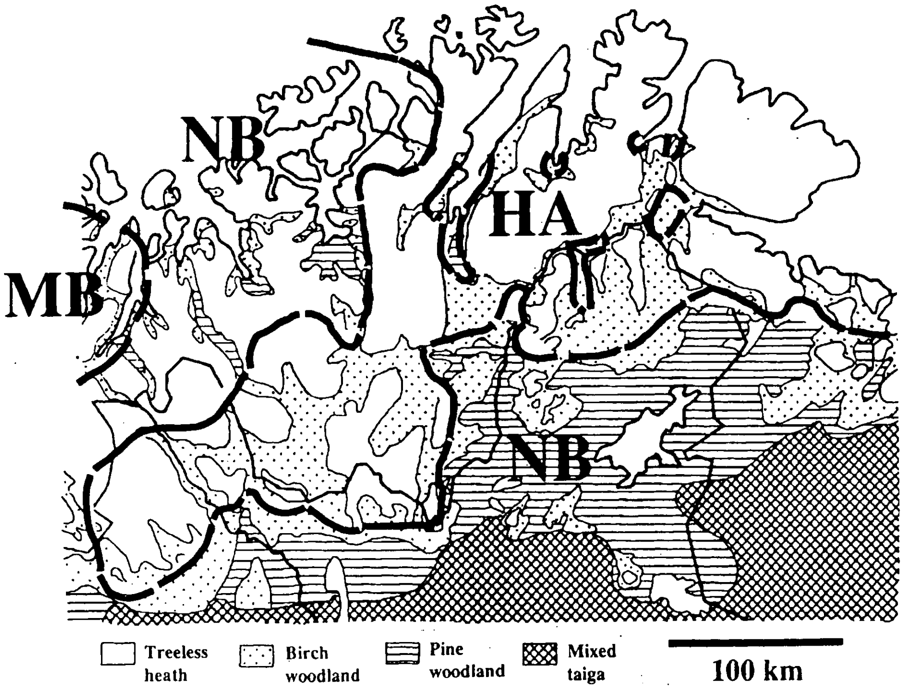

Figure 2. Geobotanical zones of northern Fennoscandia. HA, hemiarctic, NB, northern boreal and MB, middle boreal zone (from OKSANEN & VIRTANEN, 1995).

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(Figure 1). Although many features of this volcanic, strongly glaciated and sparsely vegetated subarctic land are those of the tundra (THÓRHALLSDÓTTIR, 1997), it has still interest for a study on the biodiversity in European mountains. Iceland has no endemic species in spite of its being an island for at least 15 million years. It was extensively glaciated during the last Ice Age and probably received most of its biota on ice rafts and in flood debris from Fennoscandia during the earliest Holocene. Its arctic-alpine elements suffered a further impoverishment during the post-glacial climatic fluctuations (BUCKLAND & DUGMORE, 1991).

The main arctic mountains of Europe are in Spitsbergen (Svalbard) and in the Urals. Spitsbergen is a highland area about 700 km north of Norway. The shore terraces of West Spitsbergen are several hundred thousand years old and have not experienced glaciation (MILLER, 1982). Thus this archipelago has offered potential refugia for arctic plants and animals over several glacial ages and possibly during the whole Pleistocene (for discussions of the nunatak theory see DAHL, 1990; 1998 and BIRKS, 1993).

The Urals (IGOSHINA, 1969; GORCHAKOVSKY & BOLSHAKOV, 1978; ALEKSANDROVA, 1980) are outside the scope of this review mainly because of the scarcity of recent literature in languages other than Russian. One must stress, however, the value of the Urals in the context of European mountain biodiversity. This 3300 km long mountain chain (Phai-Koy Mountains and Novaya Zemlya included) which is, on average, only 60-80 km wide, set deep in the Eurasian continent crosses a great variety of climatic zones from south to north. Its southern parts are heavily affected by the clearing of mountain forests, radioactive dumping and air pollution caused by heavy industry. However, north of latitude 60° there still exists rich and fairly pristine montane nature.

3. Some recent advances in plant community ecology, geobotany and ecophysiology

Vegetation and plant biogeographical studies have provided a basic framework for understanding the biodiversity of the vast area of northern European mountains. Studies of organism groups other than plants have traditionally used the classification units of vegetation science as reference points. Recent biogeographical classifications including an overview of earlier literature are available for Fennoscandia (HAAPASAARI, 1988; OKSANEN & VIRTANEN, 1995), Scotland (BROWN *et al.*, 1993a, b), Iceland (GUNNLAUGSDÓTTIR, 1985; BJARNASON, 1991) and Spitsbergen (VIRTANEN & EUROLA, 1997).

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The classifications of north Fennoscandian mountain heaths (OKSANEN & VIRTANEN, 1995) and Scottish upland sites (BROWN *et al.*, 1993a) have covered the most important elements in their areas and extracted much new information from existing data sets. The plant communities appear to be differentiated in relation to edaphic factors in the mountains of northern Fennoscandia as opposed to the arctic Spitsbergen, where the distribution of communities mainly reflects climatic differences among the three regions (inner fjord, W-SW coast and *Dryas*) studied by VIRTANEN & EUROLA (1997). In Scotland the biogeographical patterns of upland plant assemblages have been explained by three factors: oceanity (indicating temperature range), precipitation and altitude, with relatively minor influence by geology (BROWN *et al.*, 1993b).

Generalisations emerging from analyses at a broad geographical scale such as the recent comparison of the vegetation among Spitsbergen, Fennoscandia and the Alps by OKSANEN & VIRTANEN (1995) are of particular value. In an analysis of the distribution of different plant morphological characters, they found that over the whole of Fennoscandia, montane vegetation at the highest elevations was more similar to the vegetation of polar deserts than to the vegetation of high alpine habitats in the Alps. HAVSTRÖM *et al.* (1993) have shown that the growth of a typical representative of the arctic flora, the dwarf-shrub *Cassiope tetragona* (L.) L. Don reacted differently to manipulations of nutrients, temperature and shade in Spitsbergen compared with low and high subarctic sites in Fennoscandia. Competition for nutrients and light were the main limiting factors for growth near the low altitude distribution limit. Temperature was the main limiting factor in the northern parts of its range, and at high altitudes in the southern parts of its range. Thus the species may be expected to respond in different ways to future climatic change in various parts of its range.

JONASSON (1995) has elucidated the ecophysiological factors that account for some of the differences between Fennoscandian mountains and the Alps with regard to elevation, atmospheric partial CO_2 pressure, amount of UV-radiation, diurnal light conditions and the contrast between day and night temperatures. Biogeographical, physiological and ecological differences between arctic and alpine environments and their relevance to invertebrates, which with the exception of butterflies and spiders belong to taxa largely neglected in montane research, have recently been discussed by HASLETT (1995).

In modelling the distribution of mountain species in relation to climatic information from 456 meteorological stations in Norway, SÆTERSDAL & BIRKS (1997) have opened interesting possibilities for the analysis of species distribution data. A logistic regression analysis of the distribution of 107

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vascular plants and their biological properties revealed, for example, that most species tolerated a surprisingly broad amplitude of mean July and January temperatures. Thus the increase of temperature itself may not have a dramatic effect on the majority of common alpine species. Instead, the habitat specialists with a small geographic range will be the most vulnerable.

On the other hand, alpine plants are sensitive to competition by species from lower altitudes and of more temperate latitudes. Future climatic warming has been predicted to cause the advancement of the latter group northwards and uphill so that the total increase in species richness would be greatest in alpine/boreal regions in Fennoscandia (SÆTERSDAL *et al.*, 1998). Northern and alpine species would lose out in this process. For example, the distribution of a typical arctic-alpine plant *Silene acaulis* (L.) Jacq. has been simulated to decline notably in Europe (HUNTLEY *et al.*, 1995).

Based on comparisons between the maximum summer temperatures and the distribution of plant species, DAHL (1998) has defined the arctic and the alpine elements among north European plants. The latter group of species being composed of high, mid and low sub-elements. The hypothesis that overheating on hot summer days (protein coagulation at lethal temperatures between 43 °C and 53 °C) would cause the death of plants has been tested and proposed as the most important ecophysiological mechanism responsible for these groups (DAHL, 1951; 1992; 1998).

4. The effects of grazing on mountain biodiversity

Grazing by reindeer *Rangifer tarandus* L., sheep, goat and microtine rodents (voles and lemmings) are of primary importance in influencing vegetation in alpine and oroarctic areas in Fennoscandia. It is evident that natural grazing pressure has always been high in the northern mountains and has contributed to their species richness by disrupting uniform carpets of competitively superior plant species (OKSANEN & VIRTANEN, 1995; OKSANEN *et al.*, 1995). Moderate grazing and trampling by semi-domestic reindeer, for example, seems to be mainly positive in nutrient-rich mountain areas, and probably helps the rarities of the Fennoscandian mountain flora persist. In the barren mountains, if stocking density is low and the rotation between summer and winter pastures is well organised damage to the vegetation is low.

On the other hand, degradation due to trampling has reached high levels in the continental lichen-dominated highlands, where large reindeer herds are kept during the summer. In Iceland at the time of settlement, 1100 years ago, the overall vegetation cover was about 65% (ARNALDS, 1987).

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Overgrazing by sheep has facilitated erosion by wind and water of the fragile volcanic soils and half the once vegetated area has been changed into a subarctic desert (DUGMORE & BUCKLAND, 1991; BERNES, 1993; 1996). Grazing still persists and increasing tourist traffic by cross-terrain vehicles and horses are also contributing to serious erosion of the soil. The mountains of Scotland have experienced a change in their vegetation due to intensive grazing by sheep and locally trampling and browsing by large herds of red deer (*Cervus elaphus* L.) are problematic, as is the spread of footpaths and other recreational traffic (THOMPSON & BROWN, 1992; SCOTTISH NATURAL HERITAGE, 1995; GORDON *et al.*, 1998; THOMPSON & HORSFIELD, 1997).

Environmental effects of overgrazing were found to be important in a project that studied pollution around Monchegorsk in 1990-1994 (TIKKANEN & NIEMELÄ, 1995). Although most of the research was made in northern boreal forest, its results on vegetation changes in the field and ground layers and in soil microbiology are relevant to considering the effects of grazing and pollution on mountain biodiversity.

The environs of Nickel and Monchegorsk in the Kola Peninsula, bordering the Fennoscandian mountains in the NE, is one of the eight most seriously polluted areas of the former Soviet Union. Nickel and copper smelters have been operating there since 1939 and polluted an area of about 10 000 km^2, the largest of this kind in northern Europe. In the environs of Monchegorsk pollution (SO_2, dust, Ni and Cu) had destroyed the undergrowth in the boreal forest and initiated erosion within a radius of about 10 km from the source of emissions. Only remnants of dwarf-shrubs, *Deschampsia flexuosa* (L.) Trin. and certain tolerant lichens were left of the original vegetation and tolerant crustose lichens such as *Trapeliopsis granulosa* (Hoffm.) Lumbsch, *Placynthiella oligotropa* (J.R. Laundon) Coppins & P. James and *P. uliginosa* (Schrad.) Coppins & P. James have increased (VÄRE & OHTONEN, 1995). The effect of pollution could be observed within a radius of about 40-km from Monchegorsk. The Monchegorsk mountains are within that radius and some of the abruptness of pollution impacts on the vegetation could partly be explained by the sheltering effects of the mountains in more westerly areas. Outside the polluted range in the absence of grazing by reindeer uniform carpets of the reindeer lichen (*Cladonia stellaris* (Opiz) Pouzar & Vêzda) dominated (65% cover; mosses and dwarf-shrubs covered the rest). This was in sharp contrast with that across the Finnish border where heavy overgrazing by reindeer had caused a patchy ground cover with c. 30% bare ground and dwarf-shrub and mainly bryophytes dominated (OKSANEN, 1995; VÄRE *et al.*, 1995).

A comparison among grazed sites, ungrazed exclosures established 30 to 50 years ago and the heavily polluted sites around Monchegorsk has shown

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that soil microbial activity was similar between the grazed and the polluted sites (OKSANEN, 1995). It has been concluded that on the grazed sites the decomposition of detritus had decreased and energy flow through the ecosystem had been disturbed. The absence of a *Cladonia* carpet had accentuated variations in humidity and temperature and the buffering capacity of the vegetation against air pollutants had decreased.

Large herds of reindeer are kept to make the cost of supplementary winter-feeding and the heavy machinery used in modern husbandry economical. HELLE (1989) has estimated that in the southernmost parts of its range in Finnish Lapland there may be ten times too many reindeer in relation to the carrying capacity of the vegetation. Because of the supplementary feeding of hay in wintertime density-dependent limitation (available amount of lichen during the winter) no longer applies (KUMPULA *et al.*, 1998). In earlier decades reindeer numbers collapsed in hard winters, when ice layers in the snow made the digging of lichens impossible for the reindeer.

Overgrazing and trampling effects are not so heavy in mountains, but reliable estimates of stocking densities are lacking. Before the national borders were drawn the reindeer moved seasonally between inland winter and coastal summer ranges (OKSANEN *et al.*, 1995). Access to the Norwegian coastal areas has gradually become impossible for the Mountain Lapps of Sweden from 1751 and of Finland from 1852. Since then serious local overgrazing incidences by reindeer have been observed in the continental mountains. The only realistic sustainable alternative to solve the problem is to decrease reindeer numbers.

Species-poor northern montane ecosystems fluctuate strongly and the role of keystone species is important for their functioning. The model in Figure 3 is based largely on studies made around Abisko in Swedish Lapland, where the impact of the reindeer is small (EMANUELSSON, 1987). Several of the keystone grazers belong to arvicoline rodents. The dominant consumer is the grey-sided vole (*Clethrionomys rufocanus* Sundevall), which by periodically reducing the dwarf-shrub cover during winter influences their interspecific interactions (EMANUELSSON, 1984). In chionophilous sites of Fennoscandian mountains the Norwegian lemming (*Lemmus lemmus* L.) has an even stronger impact (not shown in Figure 3) by periodically removing mosses. In the absence of lemmings the increasing moss layer would virtually eliminate vascular plants from snow-bed sites (SÖYRINKI, 1939; MOEN *et al.*, 1993). During mass outbreaks, which occur at intervals just over 30 years in northern Fennoscandia (HENTTONEN & KAIKUSALO, 1993), lemmings have a drastic impact on large tracts of alpine vegetation and they also affect boreal forests.

Although over 55 insect species feed on leaves of the mountain birch (KOPONEN, 1983), two outbreaking geometrid moths can have an especially

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large impact. In coastal areas the winter moth (*Operophtera brumata* L.) while in inland areas the autumnal moth (*Epirrita autumnata* Borkhausen) are important (Figure 3). Although the latter is a holarctic polyphagous species, outbreaks have been noticed only in the mountain birch forests of NW Europe, where they occur at about 10-year intervals (TENOW, 1972; 1975; HAUKIOJA *et al.*, 1988; RUOHOMÄKI, 1991; BYLUND, 1995). For example in 1964-1966 the larvae defoliated about 5000 km^2 of birch forests in Finnish Lapland, of which about 1500 km^2 did not recover and now forms new alpine heath (KALLIO & LEHTONEN, 1975).

Generally mountain birch regenerates effectively from seeds or from sprouts of basal dormant buds. Newly emerged leaves of the mountain birch are a preferred food for grazers (HAUKIOJA *et al.*, 1985). Reindeer grazing is an especially important limiting ecological factor in the regeneration of mountain birch in Finnish Lapland at present (LEHTONEN & HEIKKINEN, 1995). The situation is different around Abisko, because reindeer numbers are lower there. After defoliation the trees rejuvenate there from basal sprouts and a mosaic of stands of different age-structure is generated (BYLUND, 1995). Although several herbivorous insects have been found to benefit from moderate air pollution, it has not been shown to stimulate the ability of the autumnal moth to attack the mountain birch (RUOHOMÄKI *et al.*, 1996).

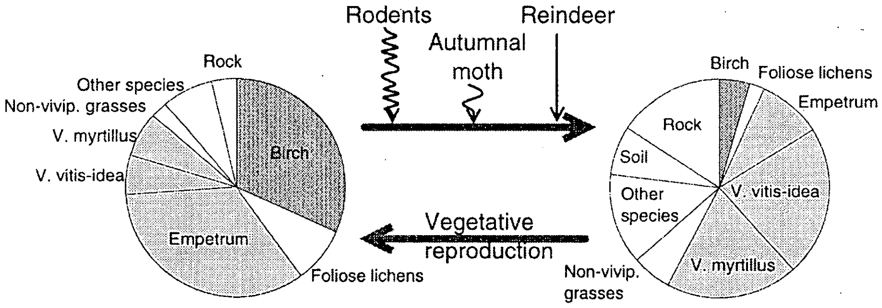

Figure 3. Model of the effect of grazing on alpine heath vegetation in Swedish Lapland. Vegetative growth increases the cover of the dwarf shrub *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher, foliose lichens (particularly species of *Cladonia*) and that of the mountain birch. Of the major grazers, the effect of the reindeer is annually stable; it consumes foliose lichens and through trampling increases the proportion of bare ground. The grey-sided vole *Clethrionomys rufocanus* Sundevall, and other rodents reach peak density every 4 to 5 years. Winter grazing by voles decreases the cover of *Empetrum* and the faster growing *Vaccinium vitis-idaea* L. and *V. myrtillus* L. fill the released space. Larvae of the autumnal moth defoliate the mountain birch about every ten years and cause a patchy distribution of the trees. (Modified from Figure 7 of CALLAGHAN & EMANUELSSON, 1985).

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Relationships between the mountain birch and its consumers are now understood fairly well in northern mountains (Figure 4), but the same does not apply to interactions between plants and their grazers in general. Future studies could, for example, analyse the grazing effects in mountains from satellite information (KUMPULA *et al.* 1998), permitting progress in several mountain areas simultaneously, apply exclosures and other types of manipulation and develop models of optimal grazing strategy in relation to biodiversity.

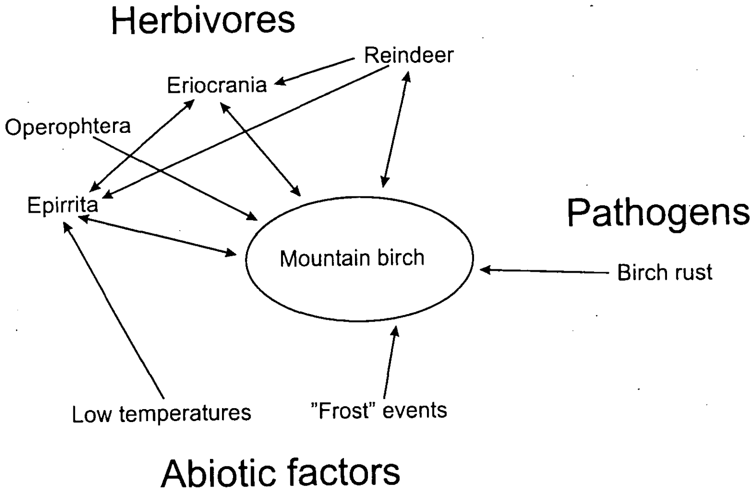

Figure 4. Some interactions and abiotic perturbations in the mountain birch-folivore system at Abisko, Swedish Lapland. Extreme winter cold kills the eggs of *Epirrita*; arrows from reindeer to insects indicate unintentional «predation» in the sprout stratum. (From TENOW, 1996).

5. The value of long-term studies on mountain biodiversity

Our ability to predict trends on the basis of pure biological theory is very limited. Long-term studies of biodiversity are needed to collect data on slow processes, which are often cumulative and non-linear, and to observe rare but important, often unexpected events. Surveillance will detect trends and events, however, their understanding often requires more detailed studies. I will present in this section some results of long-term studies of biodiversity in the northern mountains, using a moss species, voles and birds as examples.

In the primary succession on the lava fields of Iceland, the most characteristic plant is the moss *Racomitrium lanuginosum* (Hedw.) Brid., which

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covers vast areas by forming carpets up to 30-40 cm thick (BJARNASON, 1991). This moss is also common but grows smaller on rocks elsewhere in the northern mountains and is most prominent in oceanic montane heaths and on drier parts of ombrotrophic mires. The *Racomitrium lanuginosum - Carex bigelowii* community is the most extensive near-natural alpine plant community in Scotland (THOMPSON & BROWN, 1992).

Racomitrium is an important indicator of the emission and deposition of nitrogen compounds. These emissions are a potentially acute environmental threat for montane ecosystems, which consist of species adapted to low nitrogen supply (BADDELEY *et al.*, 1994). Particularly worrying in this respect is that although levels of SO_2, another serious air pollutant have fallen, No_x emissions are still rising. In Britain, monitoring of montane *Racomitrium* heaths has revealed their deterioration during the last 50 years (RATCLIFFE, 1977; RATCLIFFE & THOMPSON, 1988; BADDELEY *et al.*, 1994), which is considered to be one of the more serious conservation issues in the British uplands (THOMPSON & BROWN, 1992; THOMPSON & HORSFIELD, 1997). The increase in nitrogen contents of the moss has been strongest near urban centres, which supply the major proportion of airborne nitrogen oxides (Figure 5). Transplant studies between sites representing different levels of pollution and their comparisons with historical *Racomitrium* samples from herbaria were used to document the importance of atmospheric deposition in the enrichment of nitrogen to the moss (BADDELEY *et al.*, 1994).

In Fennoscandia, the oscillations of vole numbers are an important phenomenon for population ecology and have consequences for vegetation dynamics. Annual variation in rodent numbers has been followed at several field stations over Fennoscandia (STENSETH & IMS, 1993; HENTTONEN & HANSKI, 1999). The longest series comes from Kilpisjärvi in Finnish Lapland (Figure 6), where the voles of the genera *Clethrionomys* and *Microtus* oscillate with a periodicity of 4 to 5 years.

Explanations for these fluctuations have long been sought extensively. A common view nowadays is that these cycles are generated in a strongly seasonal environment, where deep and tight snow cover effectively isolates wintering microtines from their generalist predators. Seasonality directs the rapid reproduction of the voles to summer season, when food is abundant. In these circumstances delayed density dependent predation by specialist predators acts as a destabilising force. The mathematical models offered by the study groups of Hanski (HANSKI *et al.*, 1991; 1993) and Oksanen (OKSANEN, 1990; OKSANEN & OKSANEN, 1992) both start from this starting point, but else differ notably logistically and result in different outcomes (fluctuating vs. chaotic).

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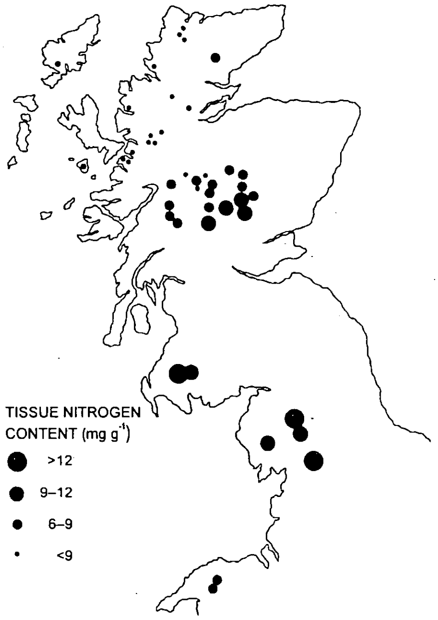

Figure 5. Nitrogen concentration (mg g^{-1} d. w.) in *Racomitrium lanuginosum* from mountain summit sites in NW Britain (from BADDELEY *et al.*, 1994).

When the voles are taken as two «species», *Clethrionomys* (bank vole) and *Microtus* (field vole), a predator-prey model parameterised for voles and predatory weasels *Mustela erminea* L. and *M. nivalis* L. explains the cyclic patterns of vole numbers (HANSKI *et al.*, 1993; HANSKI & HENTTONEN, 1996; HENTTONEN & HANSKI, 1999). Hanski's model matches the occurrence of small rodent peaks from the year 1871 onwards in Norway (STEEN *et al.*, 1990).

During most of the years the dynamics appeared distinctly cyclic, with the exception of about 20 years at the beginning of the 20th century, when the cyclic pattern temporarily disappeared. A probable explanation for this may be the dynamics of multi-species predator-prey assemblages. The disappearance of cycles represents a special chaotic case, when numbers of either one or the other vole «species» have a long-term low.

A study in Finnish Lapland which has followed vole numbers since the early 1980s found that a large reduction in the number of the most numerous species of the field voles (*Microtus agrestis* L.) caused the bank voles to become more abundant. They also became distinctly more stable i.e. the multiannual cycles disappeared (Figure 6) (HANSKI & HENTTONEN, 1996).

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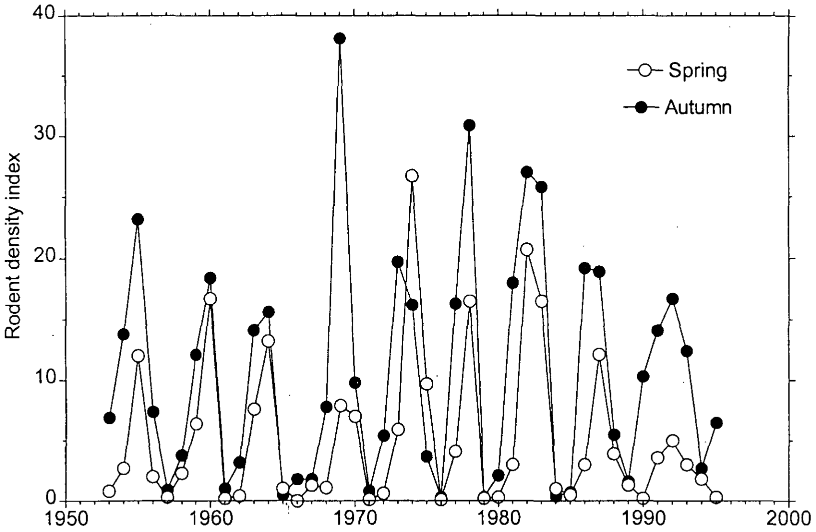

Figure 6. Long-term rodent dynamics in northern Fennoscandia at Kilpisjärvi (pooled density of five vole species, with the grey-sided vole dominating at 60-90% in most years). Open symbols denote spring densities and filled symbols autumn densities (data by H. Henttonen). One of the most characteristic features of the cycles in northern Fennoscandia is the synchronous crashes of all rodent species (HANSON & HENTTONEN, 1985).

The advantages of using the numbers of breeding birds in environmental studies are that sampling is relatively inexpensive and it covers many, ecologically versatile species, with a well known ecology (TUCKER & EVANS, 1997). Bird data are especially efficient in reflecting broad-scale habitat changes, but difficulties easily arise due to the great mobility of birds. In northern montane environments this factor is especially critical, because nearly all breeding bird species are migratory.

Rigorous censuses of breeding birds have been made in alpine habitats and mountain birch forest in the Luvre area in Swedish Lapland for decades (ENEMAR *et al.*, 1984; SVENSSON *et al.*, 1984). These studies revealed the large year to year instability of montane bird assemblages (see also JÄRVINEN, 1979), explained, in the main, by climatic reasons. Of special value is the information on the alarming decrease of several mountain birds that have emerged from various long-term censuses. For example, the population of the formerly frequent shore lark (*Eremophila alpestris* L.) has crashed in northern Fennoscandia during the last 50 years so that the species is now endangered in Finland (<10 breeding pairs) and vulnerable in Sweden (about 500 pairs) (NORDISKA MINISTERRÅDET, 1995; AHLEN &

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TJERNBERG, 1996; VÄISÄNEN *et al.*, 1998). The reasons for this trend are not known. The lesser white-fronted goose (*Anser erythropus* L.) is endangered due to former over-hunting, which perhaps still continues in its eastern wintering areas. It may become extinct in the Nordic countries in the near future, despite costly attempts at saving it. The dotterel (*Charadrius morinellus* L.) numbers have heavily decreased in the Finnish mountains since the 1880s and the downward trend was especially pronounced during the 1970s (Figure 7). European dotterels have obviously suffered from over-hunting and the use of pesticides in their wintering range in North Africa (review in SAARI, 1995), but may also be susceptible to grazing and predation in breeding areas (e. g. THOMPSON & BROWN, 1992; THOMPSON & WHITFIELD, 1993).

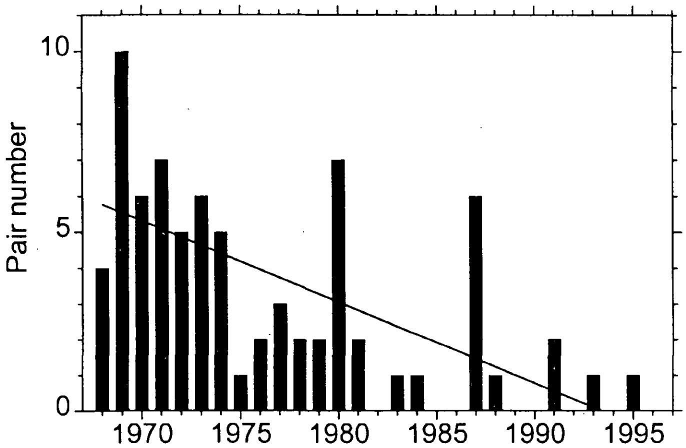

Figure 7. Annual totals for number of nests and broods of the dotterel, *Charadrius morinellus* L. on an alpine study plot of 58 hectares at Värriötunturi fell, NE Finnish Lapland (from PULLIAINEN *et al.*, 1992 and SAARI, 1995; and L. SAARI, *pers. comm.*).

Waders are of special value in northern mountains, because of their species richness (JÄRVINEN & VÄISÄNEN, 1978). The dotterel in Scotland has been included as an indicator of the condition of montane environments (THOMPSON & WHITFIELD, 1993). Mountain areas where the dotterel has had poor breeding during the last 30 years have been identified and changes in management are sought to reduce grazing pressure by sheep and deer in those areas. The implications of overgrazing for dotterel are an increased frequency of trampled clutches and the transformation of its favoured mossy mountain heaths into less optimal grassy pastures. Recently, BYRKJEDAL & THOMPSON (1998) have discussed trends in the distribution and density of Eurasian golden plovers, which are susceptible to predation and habitat change.

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Some questions regarding long-term studies remain open. What other long-term studies are going on in the northern mountains (review of monitoring methods for arctic-alpine areas in OLSEN, 1995; see also GRÖNLUND & MELANDER, 1995)? Have we enough, diverse and exact data from the various mountain habitats for monitoring? What could be the role of voluntary assistants in collecting bird (and perhaps vascular plant and lepidoptera) data? How could the costs of data treatment and publishing of such projects be recovered? Would funding be available for long-term monitoring of mountain biodiversity made by professionals on keystone species?

6. The importance of protected areas for mountain biodiversity

Montane areas in the Nordic countries have been protected better than any other major biome (BERNES, 1993; 1996), mainly because the protection of barren land owned by the state has been «cheap». The network of protected mountain heaths covers relatively well the range of types and environmental variation (Figure 8). In Iceland these account for 9% (9400 km^2) of the land area and in Sweden one-third (17 000 km^2) of the mountain areas. In Norway, where the majority of the Nordic mountains are situated, about 10% have been protected. In Spitsbergen the three national parks cover 9500 km^2 (15%). In Finland mountain areas are few, but almost all have had some form of protection. Large mountain regions, which are protected by their remoteness from roads, are in a fairly pristine state in the Nordic countries (Figure 8).

There are problems facing the conservation of montane biodiversity in the northern mountains. The status of a protected area may be overturned in favour of mining, hydro-power industry or recreation interests. In practice, the maintenance or restoration of the natural state of the protected areas alone may be difficult to achieve. The status of the reindeer is particularly problematic in Finland. They can freely (over)graze and cause large disturbances in almost all protected areas. Natural food chains with top predators cannot be formed, because the killing of predators such as the wolf (*Canis lupus* L.) and the wolverine (*Gulo gulo* L.) by reindeer keepers is commonplace (Figure 9) and it probably happens in protected areas, also.

The reproduction rates of the arctic fox (*Alopex lagopus* L.) fluctuate widely with the abundance of microtines, but winter populations are also highly dependent on reindeer carcasses (ANGERBJÖRN *et al.*, 1995; KAIKUSALO & ANGERBJÖRN, 1995). The arctic fox has been declining probably due to competition from the immigrating red fox (*Vulpes vulpes* L.) and also because

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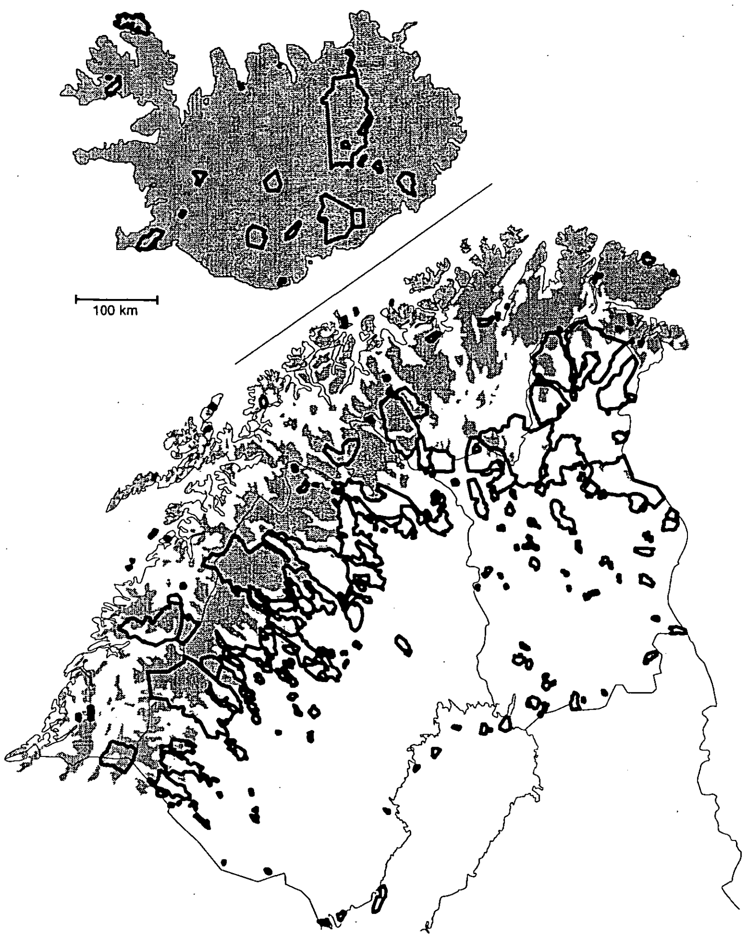

Figure 8. Protected areas of the Fennoscandian mountains (bold borders) cover notable proportion of mountain heaths (shaded areas) in N Fennoscandia and Iceland (*cf.* Figure 1) (from BERNES, 1993; 1996).

the larger predators are no longer supplying ungulate carcasses for the arctic fox (KAIKUSALO & ANGERBJÖRN, 1995).

In the future use of protected areas for the study of biodiversity, we need to establish how representative they are within each European mountain area. Furthermore, a set of minimum requirements, which the protected mountains are to fulfill, should be determined so that the original conservation objectives are met. Finally, priorities for studies of biodiversity

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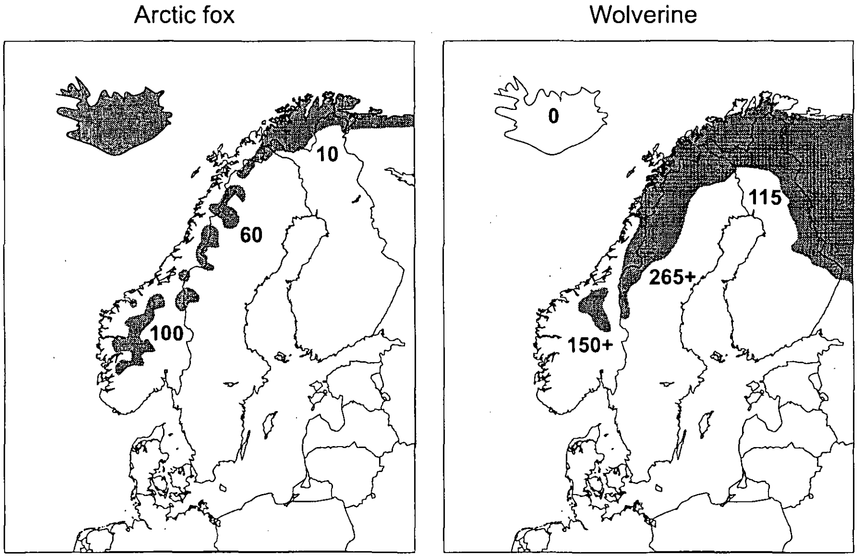

Figure 9. Present distribution and numbers of the arctic fox (left) and the wolverine (right) in Nordic countries (The arctic fox distribution from BERNES, 1993; population size H. Henttonen, *pers. comm.*; wolverine distribution from LANDA *et al.*, 1999; population size, I. KOJOLA, *pers. comm.*).

in each area are needed. Although the practical details are for national authorities to work out, broad guidelines for planning a science policy of mountain conservation could be formulated by an international workshop.

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