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Prof. Dr. Friedrich-Karl Holtmeier (retired)
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Impact of wild herbivorous mammals and birds on the altitudinal and northern treeline ecotones

Friedrich-Karl Holtmeier

Institute of Landscape Ecology, University of Münster,

Robert-Koch-Straße 28, D-48149 Münster, Germany,

fkholtmeier@arcor.de

Abstract

Wild herbivorous mammals may damage treeline vegetation an cause soil erosion at a local scale. In many high mountain areas of Europe and North America, large numbers of red deer have become a threat to the maintenance of high-elevation forests and attempts to restore the climatic treeline. In northern Fennoscandia, overgrazing by reindeer in combination with mass outbreaks of the autumnal moth are influencing treeline dynamics. Moose are also increasingly involved damaging treeline forest. In the Alps, the re-introduction of ibex is causing local damage to subalpine forests and tree establishment above the forest limit as well as aggravating soil erosion. High-elevation forests and treeline in Europe are susceptible to the deleterious impact of wild ungulate populations because of former extensive pastoral use. Rodents may damage tree seedlings and saplings by girdling, root cutting, bark stripping and burrowing. Hares damage young trees by gnawing. Large numbers of small rodents may occasionally impede tree regeneration by depleting the seed sources. Rodents do not contribute to forest expansion beyond the current treeline. Among birds, nutcrackers are highly effective in influencing tree distribution patterns and treeline dynamics. Without the nutcracker caching of stone pine seeds any upward advance of the trees in response to climatic warming would be impossible. Some bird species such as black grouse, willow grouse and ptarmigan can impair tree growth by feeding on buds, catkins and fresh terminal shoots.

Keywords:

Browsing, over-grazing, trampling, wallowing, burrowing, seed dispersal,

treeline dynamics, treeline spatial pattern

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1 Introduction

In the global view, the location of the altitudinal and polar treelines is controlled mainly by thermal deficiency. At the landscape and smaller scales, however, many other factors are involved, such as depth and duration of the winter snow cover, soil conditions, forest fires, competition, succession, human impact, and, not least, animals (Fig. 1; Holtmeier 2009; Holtmeier and Broll 2010). The influence of most of these factors on the position and spatial-temporal structures of the treelines has been and still is intensively investigated.

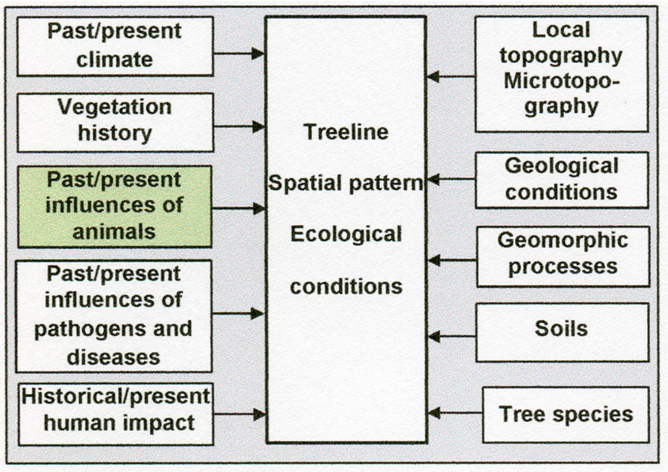

Figure 1: Factors influencing treeline spatial pattern, physiognomy and ecological conditions (modified from Holtmeier 2009).

With a few exceptions, comparatively little attention has been paid, however, to the effects of wild animals (e.g., Holtmeier 1966, 1967a, 1967b , 1974, 2002, 2009; Mattes 1978, 1982; Miller et al. 1982; French et al. 1997; Schütz 1998, 2005; Mellmann-Brown 2002, 2005; Cairns and Moen 2004; Moens et. al 2008; Hofgaard et al. 2010; Aune et al. 2011).

Mammalian herbivores and birds may influence tree growth, physiognomy, regeneration as well as seed dispersal, soils, distribution pattern of trees and treeline dynamics (Holtmeier 2002, 2009). The magnitude of animal effects is related to numerous factors. These include herbivore population density, habitat structure and availability as well as quality of forage (palatability, digestibility). Ecologically the different tree species at the treeline vary in their susceptibility and responses to animal injury. Any attempts at generalisation of treeline responses to climate variation and physical and biological disturbance in particular must include caveats (for review see Gill 1992a, 1992b). The main problem is the multitude of interacting factors and their great local variation. The ecological interrelationships are often inscrutable. Moreover, damage caused to the trees is differently considered (e.g., by forest owners, foresters, ecologists or nature conservationists). Not least, comparable studies are relatively rare.

Disturbance by animals may occur on landscape and local scales. Mass outbreaks of leaf-eating insects or pine beetles, for example, (for ample references see Holtmeier 2002, 2009) usually affect large forested areas on a landscape scale. By contrast, mammalian herbivores and birds influence the treeline usually at the local and microscale where their effects on seedlings and saplings may overrule the influence of changing climate (e.g., Holtmeier 2009; Holtmeier and Broll 2011a; Aune et al. 2011). This is demonstrated in the following by examples from Europe and North America. The impact of animals and their effects on treeline have to be considered in the landscape context. This is particularly the case where the structures and quality of habitats have often been, and still are being, strongly influenced by human activities (e.g., pastoral use, forestry, outdoor recreation, tourism). Therefore, the possibility of arriving at generalizations of the interactions between animals and their habitats in the treeline landscape is limited.

2 Ungulates

In the past virgin forests of Central Europe, wild ungulate populations were probably about ten times lower than at present, although numbers fluctuated considerably due to natural factors and increasing human influence (Widmann 1991; Danilkin 1996; Wotschikowsky et al. 2010). As prehistoric numbers of ungulates have been deduced from pollen and plant macrofossils as well as from identifiable bones and teeth (e.g., Martin 1973; Bradshaw et al. 2003) they are rather speculative and might be underestimated. Written sources (e.g., archives, hunting laws, reports on hunting bags) may occasionally give some more reliable evidence of historic game densities. During historical times some wild ungulate species almost became extinct. They, however, regularly recovered when hunting pressure decreased. In recent decades, the populations of many wild ungulates, particularly of cervids, have been higher than ever before during historical times (e.g., Gill 1990; Bradshaw et al. 2003). Current numbers often exceed the carrying capacity of the fragmented habitats.

Damage caused to trees by browsing and bark-stripping, for example, is usually related to wild ungulate population density, and the availability of forage, in particular during winter, and vulnerability of the tree species. Wild ungulates usually affect tree seedlings and saplings more than mature trees. High-altitude forests, reforestation areas and natural young growth in the altitudinal and northern treeline ecotones are particularly susceptible to browsing for two principal reasons: First, trees growing close to their climatic limit suffer from permanent climatic stress. Any additional damage may reduce their vitality or even prove fatal. Secondly, due to slow growth young trees at the treeline are usually exposed to browsing for a longer period compared to young growth at lower elevation (e.g., Bodenmann and Eiberle 1967; Holtmeier 1974, 2002; Eiberle 1980; Lavsund 1987; Kennel 1998; Holtmeier and Broll 2011). Thus, large mammalian herbivores at high densities may impede natural regeneration of tree stands at the altitudinal and northern treelines, in particular as production of viable seeds rarely occurs in these sites (e.g., Barclay and Crawford 1984; Holtmeier 1993, 2009; Smith et al. 1993; Lescop-Sinclair and Payette 1995; Hessl and Baker 1997; Luckman and Kavanagh 1998). However, seed production may change due to climatic warming (e.g. Holtmeier 2009; Holtmeier and Broll 2010a).

All treeline tree species are vulnerable to damage by wild ungulates. These large herbivores usually prefer the palatable species and switch to the less palatable after having depleted the palatable ones (Motta 1996; Gill 1992, 2000). Susceptibility to browsing also differs between tree species (Holtmeier 1974, 2002: Eiberle 1975, 1978). If heavily browsed, however, they will all produce distorted low growth forms. The ultimate form of herbivorous injury comes from complete bark girdling, which kills the trees. Impacts on trees also differ by ungulate species. Red deer (*Cervus elaphus*), for example, often cause serious damage, whereas direct impact by both bighorn sheep (*Ovis canadensis*) and mountain goats (*Oreamnos americanus*) on treeline conifers appears to be unimportant. Both species prefer grasses and herbs and occasionally browse shrubs (eg., *Salix* spp., *Betula glandulosa*, rabbitbrush, *Chrysothamnus* spp., *Ribes* spp., etc.) (Brandborg 1955; Hibbs 1967; Laundré 1994; Von Elsner-Schack 1994; Beachman et al. 2007). In winter, when forage is limited, mountain goats also eat twigs of coniferous trees (Adams and Smith 1988; Fox and Smith 1988). Significant browsing impact on treeline has not been reported however.

Wild ungulates also influence treeline ecological conditions by trampling, wallowing, and bedding (e.g., Butler 1993, 1995; Noss et al. 2000; Holtmeier 1968, 1969, 1976, 2002). Such effects are usually localized. Trampling and wallowing do not only affect tree seedlings directly but may also initiate soil erosion and thus cause moisture and nutrient deficiencies. On the other hand, trampling and wallowing by ungulates may create niches suitable for tree regeneration (e.g., Miles and Kinnaird 1979; Bichler 1997; Chadwick 1983; Butler et al. 2004), because wind-blown tree seeds may reach a seedbed in exposed mineral soil more easily than in dense dwarf shrub or grass vegetation. Moisture and nutrient deficiency may, however, impair seedling establishment in wind-eroded sites (Holtmeier et al. 2003, 2004). This effect can be mitigated by deposition of urine and excrement by ungulates frequenting such places (e.g., Holland and Detling 1990; Holland et al. 1992; Molvar et al. 1993; Hobbs 1996; Persson et al. 2000).

Although endozoochoric and epizoochoric dispersal of seeds of grasses, herbs and shrubs by wild mammalian herbivores is very common, dispersal of tree seeds by wild ungulates does not significantly influence the treeline.

2.1. Red deer

Red deer affect trees by browsing fresh annual shoots, terminal buds and twigs as well as by bark stripping. Bark-stripping occurs mainly in winter when deep snowpack makes foraging more difficult and thus increases expenditure of energy. Severe stress may cause a tenfold increase of energy expenditure compared to energy demand at rest (Fig. 2; Onderschenka 1985; Esslinger 1988). Consequently, browsing pressure will increase considerably. Young trees with smooth bark are often severely affected. In winter, the proportion of conifer forage in ungulate diet increases considerably

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(Schröder 1977), with evergreen species being more susceptible, because they retain reserves (carbohydrates and nutrients) in their needles. Needle loss reduces productivity. By contrast, deciduous trees store reserves in stems and roots (Ericsson et al. 1985; Kozlowski et al. 1991). There is therefore a seasonal dimension as to when damage is most likely to take place (Eiberle 1978; Miller et al. 1982; Gill 1992b). During the rutting season, stags are very aggressive. They often destroy the bark by beating their antlers against the tree trunks. Stags also cause damage to trees when rubbing the stems with the antlers to remove the velvet. Injured stems then become susceptible to fungus infection.

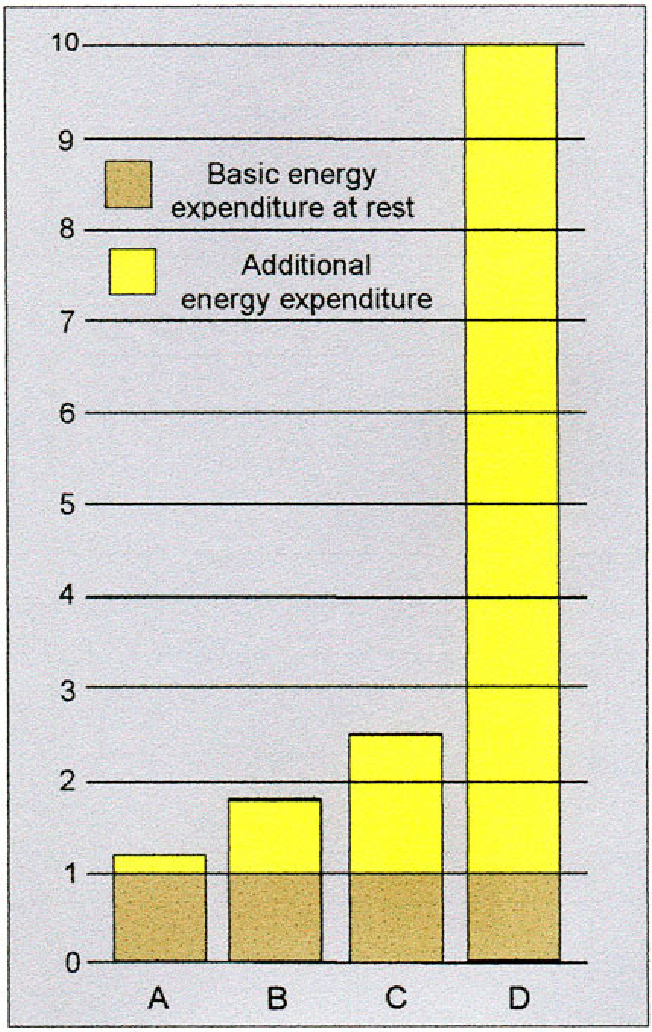

Figure 2: Relative increase of energy expenditure by red deer moving on snow-free and snow-covered ground at different speeds (modified from Esslinger 1988). A – Standing, B – Walking (1 km on level snow-free ground), C – Browsing when walking on snow-covered ground, D – Fleeing on snow-covered ground.

During snow-rich winters, red deer, if not supported by supplemental feeding within the mountain forest at lower elevation, frequent the treeline ecotone and the alpine zone where strong winds remove the snow from exposed terrain thus making food more accessible. Seedlings and young growth that became established in such sites may be damaged or even destroyed by browsing and trampling. Very windy conditions, however, make red deer retreat to the shelter of upper forest stands (Schmidt 1993), where they may affect young growth in the understorey and in forest gaps.

In the European Alps, red deer (and also chamois, *Rupicapra rupicapra*) affect high-altitude reforestation more than natural young growth in the treeline ecotone (Schönenberger et al. 1990; Senn 1999). In the northern Alps, losses of more than 70% of young trees occurred in high-altitude afforested areas (Löw and Mettin 1977). In many high elevation spruce, larch and stone pine forests, red deer have locally suppressed tree regeneration and thus supported the expansion of tall grasses such as woolly reed grass (*Calamagrostis villosa*). As a result of reduced surface roughness, snow slides can become more frequent, affecting in turn occasional young growth of trees and development of sound stand structures (e.g., Gampe 1989; Ott et al. 1997).

Large numbers of red deer may interfere with maintaining healthy mountain forests. These forests often have a protective function, preventing avalanches, soil erosion and landslides (Fig. 3). Thus, there is probably no alternative to reducing red deer density (e.g., Bavier 1976; Schönenberger 1986; Pfister et al. 1987). However, despite rigorous culling significant damage can still take place as red deer habitats are progressively shrinking due to increasing disturbances from outdoor recreation (cf. Fig. 3; Reimoser et al. 1987; Reimoser 1999; 2003). Increased energy demands from permanent stress and constant movement to escape disturbances (Onderschenka 1985; Esslinger 1988; Petrak 1988; Herbold et al. 1992) have to be compensated by forage uptake (cf. Fig 2). As a result, grazing and browsing impacts in the remaining habitats increase (cf. Fig. 3). Not least, many high elevation forests are particularly sensitive to deer damage because they have been grazed by cattle for centuries and often were already overaged before red deer density increased (Holtmeier 1967b). Although open patches created by trampling may provide suitable seed beds for wind-blown seeds (e.g., larch, spruce, mountain pine) browsing impedes successful seeding establishment and growth. Thus, red deer in great numbers may delay or even prevent natural invasion of trees into abandoned alpine pastures and the advance of the mountain forest to greater elevation in response to climatic warming. On the other hand, species diversity would be higher in a relatively open subalpine/alpine landscape as if mountain forests exdanded closed up the potentially available habitats (e.g., Grabherr and Pauli 1994; Theurillat et al. 1998; Luckman and Kavanagh 2000; Grace 2002; Theurillat and Guisan 2001; Tinner and Kaltenrieder 2005; Malanson et al. 2007; Sundquist et al. 2008; Holtmeier 2009; Nagy and Grabherr 2009; Pauchard et al. 2009).

In some Rocky Mountain national parks (e.g. Rocky Mountain National Park, Colorado, Yellowstone Park, Wyoming, Montana), it was mainly park policy that led elk populations (American elk or Wapiti, *Cervus canadensis*) to grow to excessive numbers and cause severe disturbances to the park ecosystems (Chase 1987; Wagner et al. 1995 for detailed review).

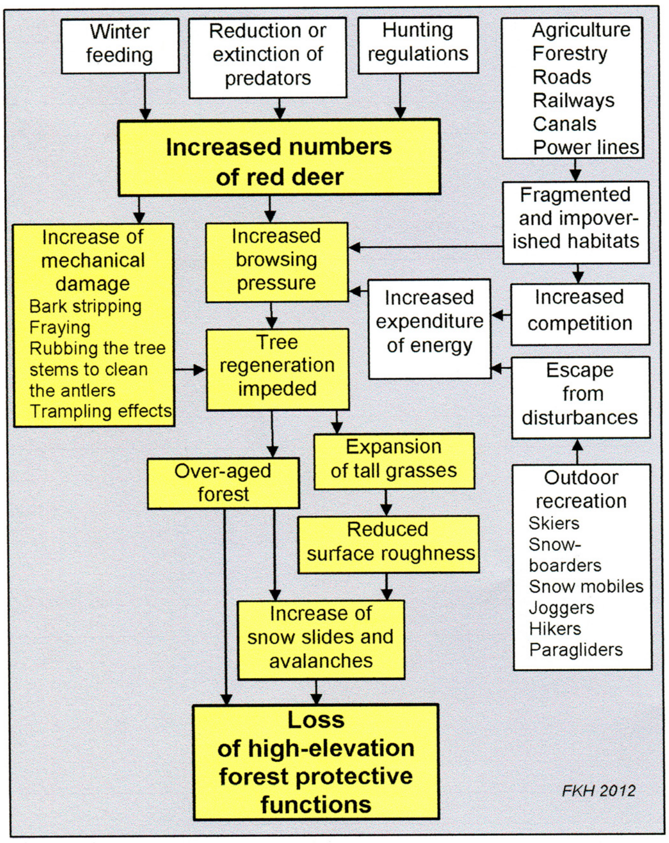

Figure 3: Causes (white boxes) and consequences (yellow boxes) of over-sized red deer populations and their impact on the protective functions of high-elevation forests.

Elk are destroying willows (*Salix glauca*, *Salix brachycarpa*), which are widespread within and above the treeline ecotone (Stevens 1980; personal observations in many areas of the Colorado Front Range). The decline of willows is then harmful to ptarmigan (*Lagopus leucurus*) which rely on willow buds as an essential food source, particularly during spring and autumn (Clarke and Johnson 2005). In Yellowstone, decline of woody browse species began after eradication of wolves in the 1920s (Ripple and Beschta 2003). After reintroduction of wolves 70 years later, recovery of suppressed browse plants (willows, aspen) was locally observed (Vucetich et al. 2005; Vucetich at al. 2002; Smith et al. 2003; Ripple and Beschta 2003; Beschta and Ripple 2010; Estes et al. 2011). Wolves have rapidly increased in numbers. In 2011, about 10 wolf packs (about 100 wolves in total) were living in Yellowstone. Elk numbers have decreased almost linearly in relation to growing wolf numbers. One may ascribe elk decline mainly to wolf predation. However, natural elk population control may be more complex as other large predators (Black bear, *Ursus americanus*; Grizzly bear, *Ursus arctos*; mountain lion, *Felis concolor*) and, in particular, climate (drought, severe snow-rich winters) are also involved (Kauffman et al., 2010). Thus, the effectiveness of wolf predation as regulating factor might be overestimated. On the other hand, wolf predation is influencing elk population permanently, whereas periods of extreme drought or snow-rich winters usually occur at irregular intervals. Extreme climatic events, although usually being short-lived, may, however, have long-lasting effects.

2.2 Reindeer and moose

In many areas of northern Eurasia, the semi-domesticated reindeer population (*Rangifer tarandus*) has grown beyond the natural habitat carrying capacity (Holtmeier 1974, 2002; Heikkinen and Kalliola 1989; Evans 1995; Helle 2001; Lempa et al. 2005a, 2005b) for several reasons (Fig. 4).

In northern Finland, the reindeer population has more than doubled since the mid-1970s (Kumpula and Nieminen 1992; Burgess 1999). The highest density was reached in the 1990s (Oksanen et al. 1995; Danell et al. 1999; Helle and Kojola 2006) Reindeer density is much higher in Finland as compared to Norway or Sweden.

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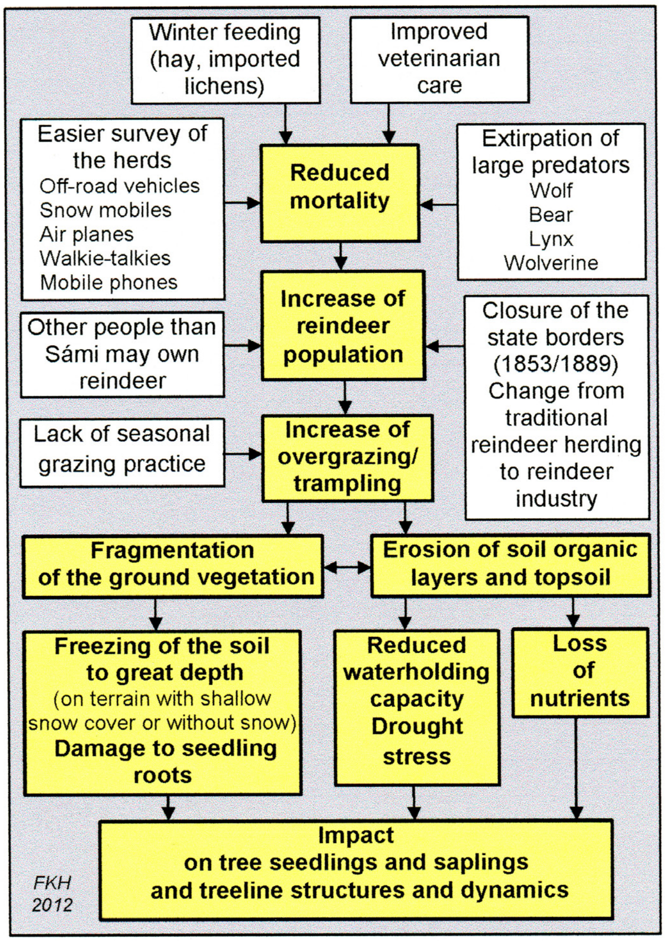


Figure 4: Causes (white boxes) of oversized reindeer population and its impact (yellow boxes) on treeline in northernmost subarctic Finland.

In addition to high numbers of reindeer the abandonment of traditional seasonal grazing practices has caused excessive summer grazing pressure on the ranges that were not grazed during summer before (Käyhkö et al. 1994).

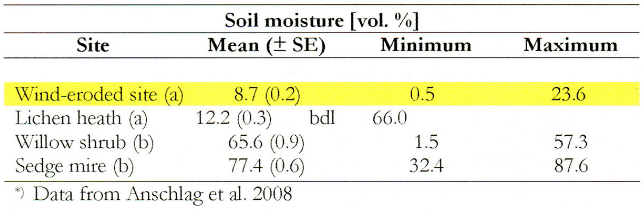
In the treeline ecotone, reindeer cause damage mainly to seedlings and young growth of the mountain birch (*Betula pubescens* ssp. *czerepanovii*), willow shrubs and dwarf shrub-lichen heath by browsing leaves and by trampling. In addition, over-browsing on willow shrubs and fragmentation of willow stands affect grouse-habitat quality and may contribute to the reduction of grouse populations (e.g., den Herder et al. 2008; Henden et al. 2011), as described above for American elk and ptarmigan (a species of grouse). Willow thickets provide food, breeding habitat and shelter from predators, and their destruction is a further serious diminution of the treeline habitat (Watson and Moss 2008).

Wind-exposed (mostly convex) topography is particularly prone to reindeer impact. When snow crusts form in early spring, reindeer visit the wind-exposed terrain where snowpack is shallow or absent and lichens are easily accessible (Helle and Tarvainen 1984). In summer, reindeer also frequent wind-swept terrain to escape harassment by insects (Hagemoen and Reimers 2004). In particular, dry lichen cover (Skuncke 1969; Holtmeier et al. 2003; Kumpula et al. 2011) as well as thin 'biological crusts' formed by algae, fungi and mosses (Belnap 2001; Belnap et al. 2001) are vulnerable to trampling. In intensely grazed areas, the original lichen cover is almost completely destroyed, and only small patches of mat-like dwarf shrub vegetation and cushion plants remain, interspersed with exposed mineral soil (e.g., Broll et al. 2007; Anschlag et al. 2008; Fig 5).

Figure 5: Wind-eroded convex site in the birch-treeline ecotone on the N-facing slope of Koahppeloaivi (northern Finnish Lapland) at about 320 m elevation. Wind from the west (left hand side) prevails. The substrate is rapidly draining sandy-skeletal till. Wind-erosion was triggered by reindeer grazing and trampling. Where drifting snow accumulates, the original dwarf shrub cover (mainly *Empetrum hermaphroditum* and *Betula nana*) still exists. Photo taken by the author, 6 July 1998.

Wind rapidly erodes dry sand and coarser loose material (up to 2cm, Seppälä 2004; Butler et al. 2009). Once the organic layers are removed, the nutrient supply and the water-holdingcapacity of the soil decrease (Table 1; Holtmeier et al. 2003; Holtmeier et al. 2004; Holtmeier and Broll 2005). Nutrients contained in urine and pellets may have a mitigating effect. However, they are unlikely to compensate completely for nutrient loss in such places.

Table 1 Soil moisture (topmost 6 cm) at different microsites in the birch-treeline ecotone, northernmost Finnish Lapland Number of measurements: (a) n = 500; (b) n = 300; bdl = below detection limit *)



Site	Soil moisture [vol. %] Mean (± SE)	Minimum	Maximum
Wind-eroded site (a)	8.7 (0.2)	0.5	23.6
Lichen heath (a)	12.2 (0.3)	bdl	66.0
Willow shrub (b)	65.6 (0.9)	1.5	57.3
Sedge mire (b)	77.4 (0.6)	32.4	87.6

*) Data from Anschlag et al. 2008

As exposed soil freezes to great depth in such places (Fig. 6), damage to fine seedling roots is likely. Roots are much less frost tolerant than plant tissue projecting above the snowpack (e.g., Larcher 1980; Coleman et al. 1992; Sutinen et al. 1997, Ryyppö et al. 1998; Repo et al. 2001). In exposed fine soils, frequent frost-heave may push tree seedlings out of the ground.

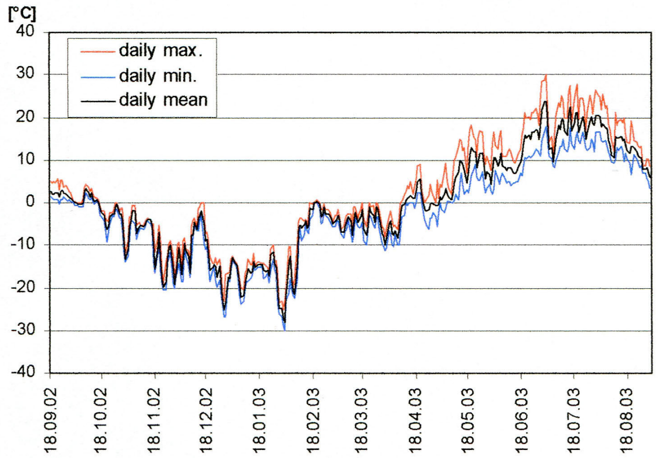


Fig. 6. Soil temperatures at 2.5 cm depth (18 September 2002 - 1 September 2003) on wind-eroded convex terrain at about 267 m (Staloskaidi, Finnish Lapland). In this place, winter snowpack does usually not last longer than a few days. The diurnal amplitude is very narrow in winter and increases considerably during summer. Data provided by K. Anschlag (Institute for Geography, University of Bonn).

These effects and drought stress, typical of sandy substrate, usually override possible positive effects of relatively high soil temperatures during summer (Holtmeier et al. 2004; Holtmeier 2009). While birch seedlings are usually rare or even absent in such treeline sites, seedling density may be very high on open patches created by reindeer within the birch forest (reduced competition; Lehtonen 1987; Suominen and Olofsson 2000; Holtmeier et al. 2003). In our study areas the area of open patches with mineral substrate exposed by reindeer and subsequent erosion in the treeline ecotone and above is still expanding (Holtmeier et al. 2003; Holtmeier et al. 2004; Holtmeier and Broll 2006; Broll et al. 2007; Käyhkö 2007; Anschlag et al. 2008). Similar observations have been made in the southern Swedish Scandes (Kullman 2005) and in northern Norway (Evans 1995). There, large-scale landscape degradation combined with overgrazing by reindeer has caused a depression of the altitudinal belts and birch forest upper limit together with soil erosion (Löffler 2005).

Although reindeer do not browse conifers, they may severely damage conifer saplings (*Pinus sylvestris*, *Picea abies*) while cleaning their antlers. Conifer saplings less than 150 cm in height are particularly at risk of being affected by reindeer (Holtmeier and Broll 2011b). Moreover, seedlings may be severely damaged by trampling. In addition, reindeer may scrape or dislodge pine seedlings buried under the snowpack when pawing through the snow for lichens (e.g., Aalborg 1955; Skuncke 1969; Holtmeier and Broll 2011a). Within closed pine forest stands, these effects are minimal (Helle 1966) as long as seedlings regularly become established in sufficient numbers. At the upper distribution limits of pine, where seedlings are rare, reindeer impact may prevent successful pine regeneration (Holtmeier and Broll 2011a).

At the upper distribution limit of Scots pine in northernmost Finnish Lapland, we found more than 80% of young pines (total 155) with disturbed growth forms caused by climatic influences, reindeer, moose and ptarmigan (Holtmeier and Broll 2010a). In nearly 50% of these pines, the terminal leaders were clipped by moose, willow grouse (*Lagopus lagopus*) and ptarmigan (*Lagopus mutus*), which can be deduced from the clearly visible bites. In addition, lateral shoots were often broken or torn off (moose, reindeer), and the bark of the stems was stripped off (snow hare, moose).

The greatest threat by animals to the treeline birch stands, however, may be the combined effect of overgrazing by reindeer and defoliation during episodic mass outbreaks of the autumnal moth (*Epirrita autumnata*; Kallio and Lehtonen 1975; Oksanen et al. 1995; Helle 2001; Holtmeier et al. 2003; Lempa et al. 2005a; Neuvonen et al. 2005; Holtmeier and Broll 2006). Relatively densely spaced peaty hummocks (10 - 30 cm; Fig. 7), which commonly occur on the presently treeless terrain within the birch-treeline ecotone, indicate former birch sites (Holtmeier and Broll 2006). These birches probably died due to climatic cooling (Koutaniemi 1990) between the 1940s and 1990. Mass outbreaks of the autumnal moth and subsequent very cold summers combined with increased reindeer impact probably hastened, birch decline (Holtmeier and Broll 2006), as did voles feeding on birch seedlings (e.g., Kallio and Kärenlampi 1970). Birches may recover from such injuries by forming stump sprouts. However, this new growth often dies from rot. Root rot, expanding from the root stock, infects the new sprouts before they have become independent (Lehtonen and Heikkinen 1995; Holtmeier 2009).

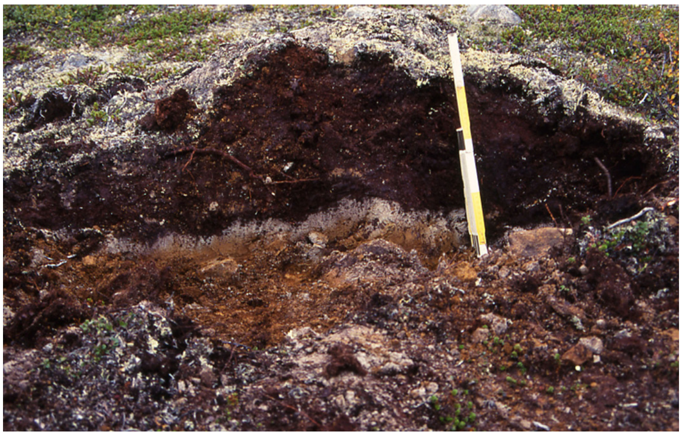


Figure 7: Organic (peaty) hummock overlying a Podzol (Staloskaidi, northern Finnish Lapland) at about 340 m elevation. The hummock developed from litter accumulating around the stem base of a polycormic mountain birch. We conclude that this birch died due to defoliation during episodic mass-outbreaks of the autumnal moth (*Epirrita autumnata*) and subsequent very cold summers combined with increased reindeer impact. Photo taken by the author, September 2000.

In general, tree seedlings and saplings have only a low probability of surviving on heavily grazed terrain (e.g., Holtmeier 1974; Holtmeier et al. 2004; Anschlag et al. 2008; Olofsson et al. 2004; Hofgaard et al. 2010; Aune et al. 2011).

In Sweden and Finland, moose (*Alces alces*) numbers have rapidly increased since the 1960s and 1970s (e.g. Nygren 1987; Bergström and Hjeljord 1987; Persson et al. 2000; Lavsund et al. 2003; Kouki et al. 2004). Luxuriant secondary vegetation (grasses, herbs, and deciduous trees) that followed clear cutting and land abandonment as well as recent afforestation has considerably improved the forage for moose (e.g. Strandgaard 1982). Moreover, hunting practices (harvesting mainly males) and also lack of predators have led to increased moose populations. While the effects of growing moose populations on boreal forest have been intensively studied, reports on moose impact on treeline are rare. However, severe damage caused by moose to young pines near the northern treeline has been reported from northern Sweden (Åbisko area) for example (Stöcklin and Körner 1999).

Moose impact is reflected in deformed growth forms in most trees that have started projecting beyond the winter snowpack (≈ 40-50 cm). In northernmost Finland (Utsjoki), moose have been invading at great numbers from northern Norway during the last three decades (communication Seppo Neuvonen, Finnish Forest Research Institute (METLA), Joensuu, Finland). They may be attracted by extensive pine afforestation along the Tenojoki (Tana River) and increasing regeneration within the old pine forests on the river terraces and lower slopes during the second half of the 20th century (Holtmeier 1974; Holtmeier and Broll 2011) as well as by pastures and meadows (hay making, silage) along the Tenojoki (Fig. 8). Though moose prefer deciduous trees, pine foliage is an important winter diet (Histøl and Hjeljord 1993; Heikkilä and Härkönen 1996; Löyttyniemi 1985; Nikula 1992; Stöcklin and Körner 1999). Afforestation is most seriously affected (Lavsund 1987; Niemelä et al 1989). Trees less than 250 cm in height are under the constant risk of being damaged by moose (Bjørneraas et al. 2012). On the mountains, moose have possibly delayed already climatically-driven establishment of new Scots pines beyond the current altitudinal limit of old-growth pines (Holtmeier and Broll 2011).

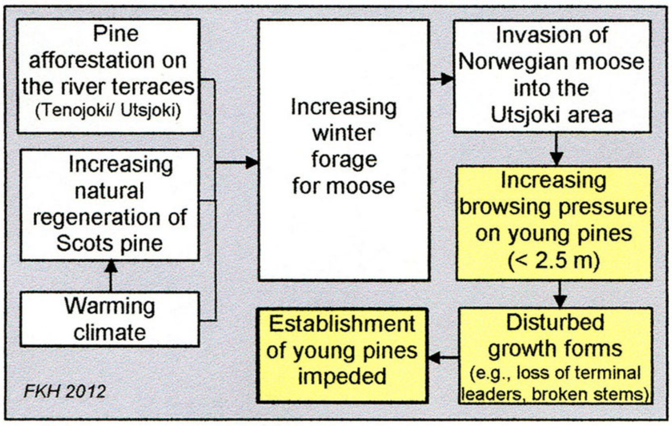


Figure 8: Probable causes (white boxes) of increasing moose population and its impact (yellow boxes) on Scots pine establishment above the present upper limit of mature pines in Utsjoki, northern Finnish Lapland.

2.3 Ibex

The impact of ibex (*Capra ibex*) on subalpine forests, high elevation reforestation and the treeline in the European Alps is only of local importance. However, the current effects of large ibex populations on the treeline and alpine vegetation illustrate the complexities of problems surrounding the re-introduction of a native wild mammalian herbivore species. Ibex have come into conflict with efforts to prevent natural hazards (avalanches, mass-wasting) using reforestation and artificial barricades above the existing forest limit.

After near-extirpation, ibex were re-introduced to many of their original alpine habitats – for example, to the mountains (2,600 m – 3,200 m) towering above Pontresina village (1820 m; Fig. 9) in the Upper Engadine (Grison, Switzerland). Ibex were re-introduced to this area in the early 1920s (Holtmeier 1969; 1987a, 2002; Feuerstein 1997) and quickly became a tourist attraction.

Figure 9: View (to the east) of the central section of the ibex reserve on the SW-facing slope (on the left) above Pontresina village. The terrain above the forest was grazed by sheep and cattle for centuries. Photo taken by the author, beginning of October 1973.

Optimal habitat conditions and prohibition of hunting were the main factors that favoured rapid growth of the ibex population (Fig. 10). Moreover, predators had been eradicated with the exception of the golden eagle (*Aquila chrysaetos*), which occasionally preys on ibex kids (Haller 1996).

On the steep avalanche-prone slopes above Pontresina, reforestation has been carried out up to an altitude of 2,500 m in order to reduce the danger of avalanches. Afforestation started in 1897 (Bisaz 1968). By the late 1940s the first damage caused by ibex to the subalpine forest and high-altitude reforestation above the anthropogenic forest limit was apparent (Campell 1958; Bisaz 19968). Ibex frequent the reforestation areas and the natural mountain forest mainly during winter. They damage the trees by rubbing and banging their horns against the tree stems and also by browsing and bark stripping (Fig. 11). Young trees are most affected. Their elastic stems, bouncing back under the ibex attacks, probably stimulate ibex aggressiveness. During severe winters, stem injuries increase (Feuerstein 1997) and render the trees more vulnerable to the harsh treeline climate and expose them to pathogens. In addition, trampling intensifies soil erosion in the alpine grassland (Fig. 12). Once the mineral soil has been exposed, frequent needle ice formation (Fig. 13) and resultant geli-solifluction (sensu Troll 1973) enhance erosion. Runoff and wind remove loose mineral material and organic matter lying on the surface. The bare mineral soil is exposed to high solar radiation loads and drains rapidly due to the lack of an organic layer. Under these circumstances, natural establishment of tree stands beyond the forest limit is unlikely.

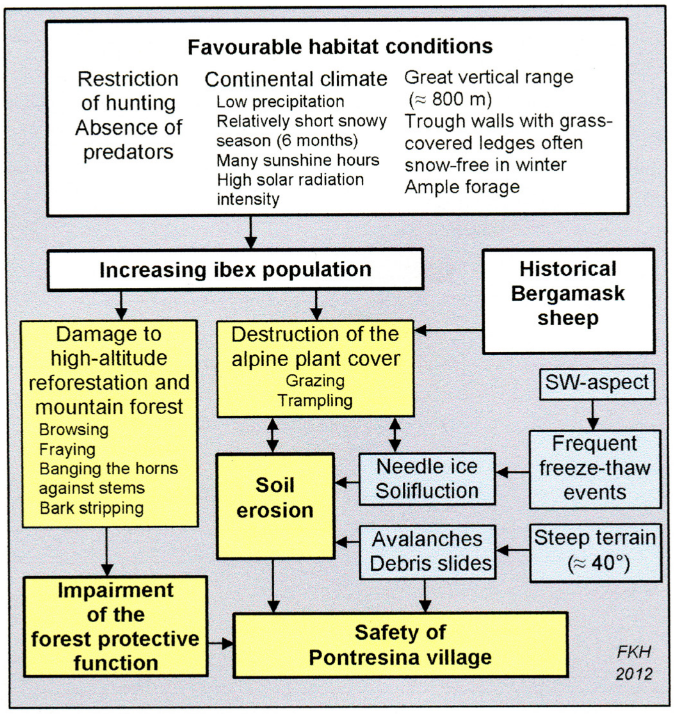


Figure 10: Large ibex numbers and after-effects of historical seasonally migrating (transhumance) Bergamask sheep herds (white boxes) affect high-altitude reforestation and subalpine forest and increase soil erosion in the ibex reserve (yellow boxes). Soil erosion is enforced by natural physical factors (blue boxes). This situation may threaten the safety of Pontresina village.

Soil erosion is also common within the forest, particularly on the steep southwest-facing trough wall (Fig. 14; Nievergelt 1966; Holtmeier 1987a, 2002), where it occurs in sheltered places frequented by ibex in winter and during bad weather (Holtmeier 1968, 1969, 1987a, 2002; Ten Houte de Lange 1978). Damage to tree stems inside the forest is also caused primarily by ibex even though red deer contribute (Feuerstein 1997).

The severe soil erosion in this region began with historical pastoral usage. For centuries, large herds of Bergamask sheep had regularly used the extensive alpine pastures above Pontresina during summer until 1904 when the Bergamask shepherds were forbidden to graze their sheep in the Upper Engadine to avoid spreading foot-and mouth-disease (cf. Fig.10).

However, almost simultaneously ibex were re-introduced to Munt da la Bês-cha (Munt da la Bês-cha = 'Sheep Mountain') and Piz Albris. They continued the destruction of alpine vegetation and caused soil erosion (Holtmeier 1968, 1969, 1976).

Fig. 11: Swiss stone pine (*Pinus cembra*, three meters high) damaged by ibex on Munt da la Bês-cha above Pontresina village at 2340 m. Photo taken by the author, 17 September 1967.

Fig. 12: Soil erosion on the mountain above Pontresina village at about 2600 m. Several ibex are in the middle of the picture. Establishment of trees as a result of climatic warming is unlikely in such sites (see also Fig. 13). Photo taken by the author, 8 October 1967.

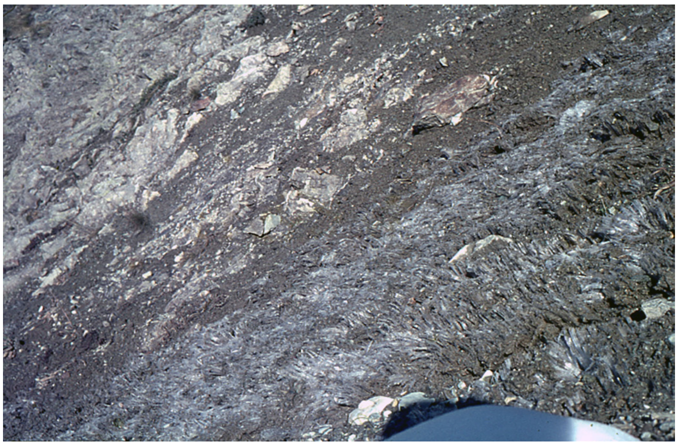


Fig. 13: Needle ice on the SW-exposed slope at 2,345 m above Pontresina village where historical Bergamask sheep and re-introduced ibex destroyed the plant cover. Needle ice (length 4 - 5 cm) formed on exposed mineral soil after several days of rain followed by night temperatures of -6 °C. When the melting ice needles fall over, uplifted loose soil particles will be translocated downslope. Water-saturation of loose material causes solifluction or mudflow. Photo taken by the author, 6 October 1967, 11h.

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Fig. 14: Trampling effects in a sheltered site within the subalpine forest (*Larix decidua*, *Pinus cembra*) on the steep SW-facing slope above Pontresina village. Photo taken the author, 1967

Ongoing culling, trapping, decreasing reproduction, accidents, and harsh winters temporarily reduced ibex numbers to nearly 600 individuals. However, ibex population regularly recovered and peaked at more than 1200 individuals between the late 1980s and early 1990s. In the following years, ibex numbers ranged below 1000 individuals (Fig. 15).

Against all expectations hunting has had only a moderate effect. In the beginning of the present century, very severe winters (1999 and 2001) caused a drastic decline to nearly 600 animals (communication 'Amt für Jagd und Fischerei Graubünden' 2011). After the population peak in 2008, the following severe winter claimed many ibexes. However, even if such recurrent extremes prevented ibex from growing to the natural carrying capacity of the habitat, even the lower numbers would be too high with regard to the safety of Pontresina village. Thus, additional control is needed to keep ibex numbers at a tolerable level, which is probably around 600 individuals. The regular recovery of the ibex population (cf. Fig. 15) shows that control operations together with extreme winters have not been a threat to the continued existence of ibex in this area. Thus, regular reduction of ibex numbers would not put this important tourist attraction at risk.

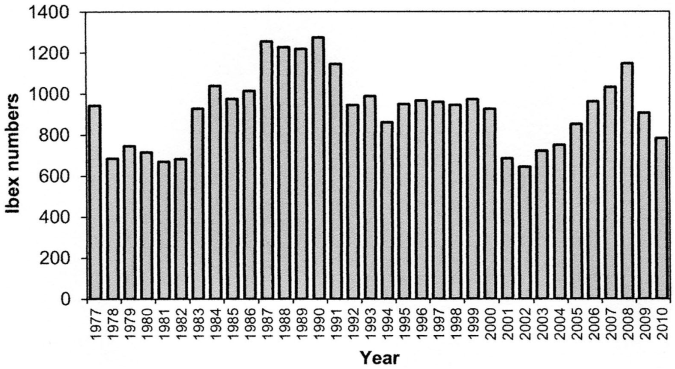

Figure 15: Fluctuations in numbers of the ibex population on Munt da la Bês-cha (including Val Chamuera). Data gratefully received from 'Amt für Jagd- und Fischerei Graubünden', 2011.

3 Hares and small rodents

Hares (*Lepus timidus*, *Lepus americanus*) browse young trees and gnaw the bark of stems projecting beyond the winter snowpack (Fig.16; Holtmeier 1971, 1974, 2005a). In winter, the main food of hares is birch and willow even though pine is also used. Hares often completely girdle stems and twigs of saplings above the snowpack completely girdled. Increasing snowpack enable hares to feed on parts of trees and shrubs at a height that would have been out of their reach from bare ground. Sometimes a distinct 'browsing line' is obvious in the sapling stems. The extent of the damage caused to trees and shrubs during winter by hares probably relates to the shortage of alternative forage (grasses, forbs and other ground vegetation) in winter (Rao et al. 2003).

Many small rodent species such as voles (e.g., *Microtus* spp., *Clethrionomys* spp; *Lemmus lemmus*) and northern pocket gophers (*Thomomys talpoides*, Geomyidae) are active under the winter snowpack. In the treeline ecotone, they prefer places where drifting snow accumulates. The snowpack provides shelter from

Figure 16. Scots pine 'krummholz' (*Pinus sylvestris*; Ø 13cm, >100 years old) of which the bark on the upper stem side projecting above the winter snowpack has been gnawed off by mountain hare (*Lepus timidus*). Jesnalvarri (northern Finland) at 325 m. Photo taken by the author, 15 August 2003.

cold air temperatures (Marchand, 1987) and from the numerous predators (Formozov, 1946; Vose and Dunlap, 1968; Pruitt, 1970). Voles and pocket gophers may attack tree seedlings and parts of saplings encased in the snow by girdling, bark stripping and root cutting (e.g., Buckner 1977; Holtmeier 1982, 1987 b, 2002; Teipner et al. 1983; Rousi 1988). Damage caused by digging of pocket gophers, for example, along the root systems might affect young trees as suggested by Schütz (2005). Below-ground damage, so far has not sufficiently been studied.

Direct injury to seedlings and saplings caused by small rodents is probably less important than damage due to intense burrowing activities. Burrowing rodents such as ground squirrels (e.g., *Spermophilus columbianus*) and northern pocket gophers may damage tree seedlings, pushing them out of the ground or covering them with excavated soil (e.g., Holtmeier 1987b, 2009).

In this respect, the pocket gophers` activities are most impressive. Pocket gophers not only accumulate excavated soil on the surface, thus creating mounds similar to those produced by moles, but they also construct extended tunnel systems inside the snowpack where they can move with relative safety from their many predators. Gophers also use their snow tunnels to dump excavated soil (Thorn, C. 1978; Teipner et al. 1983). After snowmelt, these filled tunnels form a net of tube-like 'eskers' (winter casts; Fig. 17) lying on the ground (Holtmeier 1982, 1987b, 2002; ; DeLella Benedict 1991; Schütz 1998, 2005). Up to 50% of a pocket gopher habitat may be covered by 'mounds' and 'eskers' (Buckner 1977; Holtmeier 1982). As a result, tree seedlings are often killed. On the other hand, such open patches may facilitate the establishment of seedlings (e.g., Kallio and Lehtonen 1973; Holtmeier 1974; Butler et al. 2004). Nevertheless, many other factors such as other animals (e.g., American elk, *Cervus canadensis*; mule deer, *Odocoileus hemionus*), climatic injuries, short growing seasons, snow fungus infection (e.g., *Herpotrichia juniperi*; *Phacidium infestans*), lack of moisture and downslope translocation of excavated soil by heavy rainfall and needle ice solifluction (Hall et al. 1999) may ultimately kill tree seedlings. Regardless, the number of open microsites caused by burrowing rodents appears to be insufficient to explain the much higher number of seedlings that have become established above the mountain forest Butler et al. 2004), and it would appear the climate warming is the driving factor.

Figure 17. Pocket gopher 'eskers' (snow tunnel fillings) in the treeline ecotone, Colorado Front Range at about 3350 m. Photo taken by F.-K. Holtmeier, 25 July 1989.

Consumption of large quantities of tree seeds and, in particular, destruction of seedlings by tree squirrels (*Sciurus* spp., *Tamasciurus* spp.), ground squirrels (*Spermophilus* spp.), chipmunks (*Tamias* spp.) and other small rodents may temporarily impede forest regeneration inside high mountain forests. In a Bavarian mixed mountain forest (*Picea abies* and *Fagus sylvatica* with a few deciduous species admixed), large populations of the northern red-back vole (*Clethrionomys rutilus*) and the yellow-necked field mouse (*Apodemus flavicollis*), for example, almost prevented any regeneration of trees, after both rodents had reproduced in large numbers under the winter snowpack in response to a rich seed supply during the previous year (Bäumler and Hohenadl 1980). Generally, small rodents adversely affect tree regeneration rather than promoting successful seedling establishment (Vander Wall 1990, and references therein). There are exceptions, however. Tree seed dispersal by rodents as a driver of forest expansion into open areas and beyond the treeline is unlikely (Mattes 1978, 1982; see also Hutchins 1994).

4 Birds

Some tree species at the treeline depend mainly on animals for seed dispersal such as mountain ash (*Sorbus aucuparia*, *Sorbus microphylla*), beech (*Fagus* sp.), juniper (*Juniperus* sp.) and many pine species (*Pinus*) that have heavy wingless seeds.

4.1 Nutcrackers

Undoubtedly, dispersal and hoarding of heavy wingless seeds of stone pines by nutcrackers (*Nucifraga caryocatactes* and subspecies in Eurasia; *Nucifraga columbiana* in North America) are the most predominant influence of birds on the treeline ecotone. Between nutcrackers and stone pines a true mutualism has evolved (Mattes 1978, 1985; Vander Wall and Balda 1981; Tomback and Linhart 1990; Lanner 1996; Tomback 2001). Lanner (1996) described this interdependence briefly as 'Tree feeds bird, bird plants tree'.

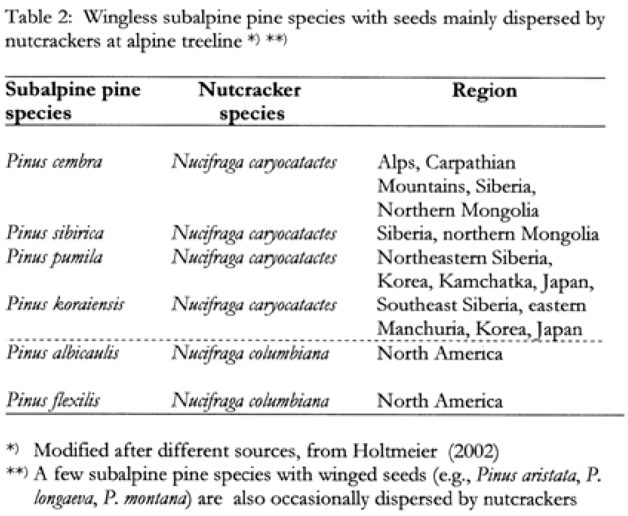

Table 2: Wingless subalpine pine species with seeds mainly dispersed by nutcrackers at alpine treeline *) **)

Subalpine pine species	Nutcracker species	Region
Pinus cembra	*Nucifraga caryocatactes*	Alps, Carpathian Mountains, Siberia, Northern Mongolia
Pinus sibirica	*Nucifraga caryocatactes*	Siberia, northern Mongolia
Pinus pumila	*Nucifraga caryocatactes*	Northeastern Siberia, Korea, Kamchatka, Japan,
Pinus koraiensis	*Nucifraga caryocatactes*	Southeast Siberia, eastern Manchuria, Korea, Japan
Pinus albicaulis	*Nucifraga columbiana*	North America
Pinus flexilis	*Nucifraga columbiana*	North America

*) Modified after different sources, from Holtmeier (2002)
**) A few subalpine pine species with winged seeds (e.g., *Pinus aristata*, *P. longaeva*, *P. montana*) are also occasionally dispersed by nutcrackers

The seeds of stone pines (Tab. 2) are the most important food of nutcrackers, although these birds also take seeds of other pines, as well as hazel nuts, berries, insects and even small mammals (e.g., Crocq 1978; Giuntoli and Mewaldt 1978; Mattes 1978; Tomback 1978, 1998; Glutz von Blotzheim 1993).

Nutcrackers scatter-hoard stone pine seeds by burying seed caches within the forest, in the treeline ecotone, and in the alpine zone. One nutcracker may cache between 30,000 to more than 100,000 seeds per season, depending on annually varying seed availability (Kuznezov 1959; Reijmers 1959; Mezhennyi 1964; Vander Wall and Balda 1977; Mattes 1978, 1982; Tomback 1982; Vander Wall 1990). Nutcrackers rely on the hoarded seeds for food in winter and to feed their nestlings in early spring when other food is scarce (e.g., Campell 1950, 1955; Oswald 1956; Holtmeier 1966; Tomback 1977, 1980; Mattes 1978, 1982; Hutchins and Lanner 1982; Lanner 1982, 1990; Vander Wall and Hutchins 1983). Nutcrackers` retrieval rates range from 50% (Lanner 1996) to >80% (Mattes 1978, 1982; Conrads and Balda 1979; Tomback 1980; Glutz von Blotzheim 1993). At times of poor seed production nutcrackers, together with other seed harvesting animals (e.g., squirrels, woodpeckers, jays), may almost deplete the seed sources. However, enough seeds will usually be left to guarantee natural regeneration.

Compared to wind-mediated seed dispersal, seed dispersal by nutcrackers is advantageous to tree establishment for several reasons. While dwarf shrub and grass cover may prevent wind-borne seeds from reaching a suitable seedbed, nutcrackers place the seeds in the soil at two to four centimeters depth (depending on the quality of the substrate), in the litter layer, in moss cushions, rotting fallen tree trunks and stumps where the seeds are protected from high temperatures and drought that may impair germination. Moreover, the seeds are not visible to seed predators (e.g., other nutcrackers, jays, mice, voles, squirrels, chipmunks; e.g. Mattes 1878, 1979; Hutchins 1994). These animals may, however, accidentally encounter nutcrackers` seed caches. Great numbers of wind-borne seeds (e.g., spruce, larch, Scots pine), which lie on the surface, are lost to rodents. Not least, the cached seeds are usually of good quality because nutcrackers harvest seeds mainly below the treeline and also test seed quality by 'bill clicking' before filling their sublingual pouch

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(Vander Wall and Balda 1977; Mattes 1978, 1982; Tomback 1978).

Unretrieved caches may give rise to solitary pine seedlings and seedling clusters (e.g., Campell 1950; Oswald 1956; Holtmeier 1966, 1967a, 1967b, 2002, 2009; Tomback 1977, 1982; Mattes 1978, 1982; Furnier et al. 1987; Hiller et al. 2002). As stone pine seeds may remain viable in the seed cache for several years (e.g., Askawa 1957; Tomback et al. 1993; McCaughey 1994, Kajimoto et al. 1998; Tomback et al. 2001), regeneration does not depend so much on annually varying seed production. Due to varying degrees of dormancy the individual trees within a stone pine cluster that originated from one seed cache may be of different ages (Tomback et al. 1993; Tomback 2005). Root competition cannot be excluded as a negative factor in densely grouped stone pine seedlings and saplings (Holtmeier 1986). In contrast to Swiss stone pine and whitebark pine, tree clusters are less common in Siberian stone pine (*Pinus sibirica*) and Korean stone pine (*Pinus koraiensis*) for example (Hutchins et al. 1996; Tomback 2005).

It is not only seed dispersal and seed hoarding that makes nutcrackers effective agents in treeline dynamics. Selection of seed caching sites is equally important. In contrast to distribution of stone pine seedlings, seedling distribution of larch and other anemochorous tree species has a tendency to be accidental. The nutcrackers prefer convex landforms for establishing seed caches. This is particularly obvious in intensively sculptured terrain (Fig. 18, whereas seed caching is more irregular on uniform topography (Fig. 19; Holtmeier 1993, 2009; Mellmann-Brown 2005).

Figure 18: Swiss stone pines that were 'planted' by the European nutcracker (*Caryocatactes caryocatactes*) on convex topography at about 2270 m (Piz Rosatsch, Upper Engadine, Switzerland). Photo taken by the author, 23 September 1968.

Figure 19: Irregular distribution pattern of limber pines (*Pinus flexilis*) that originated from seed caches of the Clark´s nutcracker (*Caryocatactes columbiana*) on relatively uniform terrain of Bald Mountain (Colorado Front Range) at about 3420 m. Photo taken by the author, 15 July 1994.

During extensive fieldwork on treeline in the Alps, the author observed hundreds of seed caching nutcrackers. Only a few were caching seeds in concave terrain. However, the reasons for the specific site selections are still obscure (cf. Holtmeier 1974, 2002). Convex sites probably act as landmarks primarily, that help the nutcrackers to retrieve their seed caches (Mattes 1982; Vander Wall 1982; Kamil and Balda 1985). Survival of seedlings is better on convex landforms compared to snow-rich sites, although damage by climatic injury is common (Holtmeier 1974, 2005b). In snow-rich sites, creeping and settling snow (abrasion and breakage) and white snowblight (*Phacidium infestans*) usually impede seedling establishment.

On wind-swept topography, nutcrackers often cache seeds also at the leeside of boulders and tree islands where snow drifts accumulate during winter (Marr 1977; Holtmeier 1978; Holtmeier and Broll 1992; Mellmann-Brown 2002, 2005: Resler 2004; Resler and Tomback 2008). Snow drifts provide shelter from wind and excessive direct solar radiation. Particularly in dry climates, melt-water released from the snow drift may also be beneficial to the seedlings although it keeps soil temperature low until early summer (Buckner 1977; Holtmeier 1981, 1987b, 1996, 2005b; Hättenschwiler and Smith 1999). As most seed-caching sites are sufficiently covered with snow, they are relatively favorable for tree establishment. This would also explain the high concentration of whitebark pine seedlings and clusters in shallow depressions with snow lingering until midsummer found by Mellmann-Brown (2002, 2005) on relatively uniform terrain in the treeline ecotone on Beartooth Plateau (Wyoming/ Montana). At sites with deep and extremely late lying snow (e.g., gullies, depressions) seeds may germinate but seedlings will not survive. Nevertheless, local conditions may change due to feedbacks from the trees (Fig 20; Donaubaur 1963; Holtmeier 1965, 1967a, 1985, 1986; Holtmeier and Broll 2010a).

In the European Alps, nutcrackers are an important agent driving natural reforestation of former alpine pastures and expansion of Swiss stone pine beyond the uppermost seed trees (Holtmeier 1966, 1967, 2009; Mütherthies 2002). Seed dispersal by small rodents appears to have little influence (Mattes 1982). Without seed dispersal by the European nutcracker an advance of Swiss stone pine to greater altitude in response to climate warming will not be possible (Holtmeier 1966, 1967a, 1967b, 1974, 2002). The same holds true for the Siberian stone pine, Siberian dwarf pine (*Pinus pumila*) and Korean stone pine (*Pinus koraiensis*) in Asia. In the Rocky Mountains and other mountain ranges in the American west, Clark´s nutcracker is the only agent distributing seeds of whitebark pine (*Pinus albicaulis*) and limber pine (*Pinus flexilis*) at large quantities within and beyond the treeline ecotone (Tomback 1977, 1978, 1982, 2001, 2005; Holtmeier 2002, 2009). There, whitebark pines, often acting as 'pioneer trees', may facilitate the establishment of other tree species such as subalpine fir or Engelmann spruce in their immediate neighbourhood (Franklin and Dyrness 1973; Resler and Tomback 2008).

In the past, the European nutcrackers were systematically destroyed as they often ripped off unripe cones and prevented harvest of sufficient quantities of stone pine seeds needed for afforestation. Even the decline of Swiss stone pine was attributed to seed predation by nutcrackers (e.g., Hess 1916). The main reason for the stone pine decline was, however, human impact (e.g., Holtmeier 1967b, 1974, 2009). Swiss stone pine was affected more than larch by pastoral activity and forest fires. Not least, stone pine seeds were a favourite food of the mountain people. Thus, the nutcracker was considered a competitor for food and killed whenever possible. Nowadays the public attitude has completely changed, although foresters occasionally complain of 'too many' nutcrackers, which cause damage to tree nurseries by digging for recently sown stone pine seeds and pulling plantules out of the ground to get the attached seed.


Fig. 20: Swiss stone pine cluster (*Pinus cembra*) 'planted' by the European nutcracker (*Caryocatactes caryocatactes*) on the northwest-facing slope of the Upper Engadine main valley at about 2200 m. The taller and older trees gradually increased snow deposition. They became infected by white snowblight (*Phacidium infestans*) and lost all their needles encased in the winter snowpack. The younger pines were completely destroyed. Photo taken by the author, September 1968.

4.2 Other birds

At the treeline, birds other than nutcrackers usually do harm to the trees, in particular to young growth. Grey-headed juncos (*Junco caniceps*, a Rocky Mountain species), for example, occasionally feed on very young spruce seedlings and increase first-season mortality (Noble and Shepperd 1973). Black grouse (*Lyrurus tetrix*), willow grouse, ptarmigan and white-tailed ptarmigan clip buds, staminate catkins, and fresh shoots projecting beyond the snowpack (e.g., Pulliainen and Iivanainen 1981), in locations with shallow snowpack in winter. Willow grouse lives mainly in the birch treeline ecotone and in the birch forest, whereas ptarmigan are largely restricted to the alpine zone. However, after snowfall, flocks of ptarmigan occasionally move from the alpine zone to lower elevations (treeline ecotone, green alder thickets, *Alnus viridis*) (Eiberle 1974; Ratcliff 1990).

Black grouse have profited from historical human impact on high elevation forests, which left wide open areas covered with dwarf shrub vegetation and alpine grassland, scattered trees and krummholz (Holtmeier 1965, 1974; Holtmeier and Broll 2005). These areas provide optimal habitat structures for black grouse (leks, shelter and food). Black grouse live in the treeline landscape all year round. In winter they occasionally move to lower elevations (Mattes et al. 2005). Clipping of fresh terminal shoots up to 4 mm in diameter is typical for grouse, and may cause forked or dwarfed growth forms in trees (e.g., Hustich 1940; Blüthgen 1942; Holtmeier 1974). Such impact usually is only of local importance. It may become critical, however, in the long-term for high-altitude reforestation (Schönenberger et al. 1990).

Although endozoochoric dispersal of tree seeds is less effective as compared with seed caching by nutcrackers, the occurrences of mountain ash up to the tree limit in the Alps, in the Scandinavian mountains (Kullman 1986), in Scotland or in the dry Himalayas presumably originates from seeds defecated by fruit-eating birds such as fieldfares (*Turdus pilaris*), ring ouzels (*Turdus torquatus*) (e.g., Mattes et al. 2005), and white-backed thrushes (*Turdus kessleri*, Himalayas; Mauersberger 1995). The same holds true for juniper trees growing on rocky sites at high elevation in the dry regions of the Himalayas and in southern Tibet (Miehe and Miehe 2000). In addition to thrushes, jackdaws (*Corvus monedula*) and choughs (*Pyrrhocorax* spp.) are dispersers of ripe juniper berries (Schickhoff 1993, 2005). However, the seeds often are destroyed or lose their germination capacity when passing through the digestive track. Defecated viable seeds that have reached a suitable seedbed may germinate. When using rock outcrops for feeding on berries the birds usually defecate some seeds that fall into rock crevices. Shelter from excess direct solar radiation (reduced evaporation and photooxidative stress) and fine mineral and organic matter that accumulates in such places increase soil moisture conditions, and nutrients may facilitate germination and seedling establishment.

5 Conclusions

- In contrast to mass outbreaks of leaf-eating insects or bark beetles that usually affect forests at the landscape scale, wild mammalian herbivores and birds influence the treeline usually at the local or microscale.

- In some areas, treeline pattern and dynamics cannot be explained without considering effects of wild ungulates, small mammals and birds.

- Wild herbivorous mammals in great numbers may prevent natural regeneration in high-elevation forests and natural reforestation above the current forest limit regardless of favourable climatic conditions. Birds (grouse) do harm to young growth in the treeline ecotone.

- The severity of damage caused to the trees is related to their vulnerability. In the harsh treeline environment vulnerability is generally high but differs between tree species.

- The magnitude of the effects of wild ungulates depends not only on ungulate population densities but also on changes in the treeline environment due to human impact. In the Alps, the negative effects on mountain forests and treeline by deer have been increasing due to increasing scarcity of undisturbed habitats. In Rocky Mountain National Parks, the impact of overgrazing by American elk must be attributed to historical loss of large predators and inadequate park policy. The impact of reindeer on treeline is related mainly to increased reindeer populations and change of the traditional herding practices.

- Compared to the effects of red deer, American elk and reindeer, the impact of ibex on reforestation, natural tree regeneration and soil erosion is only of local importance. Bighorn sheep and mountain goats locally influence treeline landscape mainly through trampling.

- In contrast to the effects of increased ungulate populations the impact by hares and small burrowing rodents probably has remained the same over time. Squirrels at population peaks may act as effective seed predators within the forests. Predation on tree seeds and seedlings by voles and mice rapidly decreases above closed forest. Pocket gophers, on the other

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hand, influence establishment of seedlings particularly in open treeline sites.

- Nutcrackers are the only animals driving the expansion of stone pines into formerly grazed areas and altitudinal advancement of the tree line up to the physiological limit of tree growth. The pine clusters 'planted' by nutcrackers may facilitate establishment of other conifer species by providing shelter to them from the harsh high-elevation climate. Thus, the nutcrackers may influence treeline landscape pattern and dynamics considerably.

- Discussion of local altitudinal treeline advancement in response to climate warming should he influences of wild-living animals that may confound some predictions, at least at the local scale.

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7 References

Aalborg, T. 1955. Skador på tallplantor inom ett starkt renbetat område i Hedesocken. Norrlands Skogsförbubds tidskrift 4

Adams, L. G. and C. A. Smith 1988. Winter forages of mountain goats on central Colorado. Journal of Wildlife Management 47, 1237-1243

Anschlag, K., Broll, G. & F.-K. Holtmeier, F.-K. 2008. Mountain birch seedlings in the treeline ecotone, Subarctic Finland: Variation above- and below-ground growth depending on microtopography. – Arctic, Antarctic, and Alpine Research 40 (4), 609-616

Askawa, S. 1957. Studies on hastening of seeds of five-leaved pines (Japanese, Emglish summary). Bulletin Governmental Forest Experimental Station Tokyo 10, 41-54

Aune, S., Hofgaard, A. & L. Söderström 2011. Contrasting climate and land-use driven tree encroachment pattern of subarctic tundra in northern Norway and the Kola Peninsula. Canadian Journal of Forest Research 41, 437-449

Bäumler, W. and W. Hohenadl 1980. Über den Einfluß alpiner Kleinsäuger auf die Verjüngung in einem Bergmischwald der Chiemgauer Alpen. Forstwissenschaftliches Centralblatt 99, 207-221

Barclay, A. M. & R. M. M. Crawford 1984. Seedling emergence in the rowan (Sorbus aucuparia from an altitudinal gradient. Journal of Ecology 72, 627-636

Bavier, G. 1976. Graubündens Waldwirtschaft. Ein Vergleich und Ausblick. Bündner Wald 29 (6), 220-248

Beachman, J. J., Cameron, P., Collins, M. S. and T. D. Reynolds 2007. Rocky Mountain bighorn sheep (Ovis Canadensis): A technical conservation assessment. USDA Forest Service, Rocky Mountain Region. http://www.fs.fed.us/r2/projects/scp/assessessments/rockymountainbighornsheep.pdf

Bekker, M., Clark, J. T. & M. W. Jackson 2009. Landscape metrics indicate differences in patterns and dominant controls of ribbon forests in the Rocky Mountains, USA. Applied Vegetation Science 12: 237-249

Belnap, J. 2001. Biological crusts and wind erosion. In: Belnap, J.& O. Lange (eds.), Biological crusts: structure, function and management, Ecological Studies 150, 340-347

Belnap, J., Büdel, B. & O. Lange 2001. Biological crusts: characteristics and distribution. In: Belnap, J. & O. Lange (eds.), Biological crusts: structure, function and management, Ecological Studies 150, 1-30

Bergström, R. & O. Hjeljord, O. 1987. Moose and vegetation interactions in northwestern Europe and Poland. Swedish Wildlife Research Supplement 1, 213-228

Beschta, R. L. and W. J. Ripple 2010. Recovering riparian plant communities with wolves in Northern Yellowstone, U.S.A. Restoration Ecology 18 (3): 380-389

Bichler, C. 1997. Auswirkungen von Huftieren auf die Wiederbewaldungsdynamik auf drei subalpinen Weiden im Schweizerischen Nationalpark. Diplomarbeit, Abteilung Biologie, Eidgenössische Technische Hochschule Zürich

Bisaz, O. 1968. Das Lawinenverbauungs- und Aufforstungsprojekt "Munt da la Bês-cha" (Schafberg) der Gemeinde Pontresina. Bündnerwald 21 (5), 201-207

Bjørneraas, K., Herfindal, I., Solberg, E. J., Sæther, B. E., Van Moorter, B. & Rolandsen, C. M. 2012. Habitat quality influences population distribution, individual space use, and functional responses in habitat selection by a large herbivore. Oecologia 168: 231-243

Blüthgen, J. 1942. Die polare Baumgrenze. Veröffentlichungen des Deutschen Wissenschaftlichen Instituts Kopenhagen, Reihe 1, Arktis 10

Bodenmann, A. & K. Eiberle 1967. Über die Auswirkungen des Verbisses der Gemse im Aletschwald. – Schweizerische Zeitschrift für Forstwesen 7, 461-470

Bradshaw, R. H. W., Hannon, G. E. & A. M. Lister 2003. A long-term perspective on ungulate-vegetation interactions. Forest Ecology and Management 181: 267-280

Brandborg, S. M. 1955. Life history and management of mountain goats in Idaho. Idaho Wildlife Bulletin 1, 1-42

Broll, G., Holtmeier, F.-K., Anschlag, K., Brauckmann, H.-J., Wald, S. & Drees, B. 2007. Landscape mosaic in the treeline ecotone on Mt Rodjanoaivi, Subarctic Finland. Fennia 185 (2), 88-105

Buckner, D. L. 1977. Ribbon forest development and maintenance in the central Rocky Mountains of Colorado. Dissertation, University of Colorado at Boulder

Burgess, P. 1999. Human environmental interactions in Upper Lapland, Finland. Arctic Centre Reports 27, Artic Centre, University of Lapland, Rovaniemi

Butler, D. R. 1993. The impact of mountain goat migration on unconsolidated slopes in Glacier National Park, Montana. Geographical Bulletin 35, 98-106

Butler, D. R. 1995. Zoogeomorphology. Animals as geomorphic agents. Cambridge University Press

Butler, D. R., Malanson, G. P. & L. M. Resler 2004. Turf-banked terrace treads and risers, turf exfoliation and possible relationships with advancing treeline. Catena 58: 529-274

Butler, D. R., Malanson, G. P., Resler, L. M., Walsh, S. J., Wilkerson, F. D., Schmidt, G. L. & C. F. Sawyer (2009. Geomorphic patterns and processes at alpine treeline. In: Butler, D. R., Malanson, G. P., Walsh, S. J. & D. B. Fagre (eds.), The changing alpine treeline: The example of Glacier National Park, MT, USA. Developments in Earth Surface Processes 12, 163-184, Elsevier, Amsterdam

Cairns, D. and J. Moen 2004. Herbivory influences tree lines. Journal of Ecology 92, 1019-1024

Campell, E. 1944. Der Wald des Oberengadins im Wandel der Zeiten. Festschrift zur Jahresversammlung der Schweizerischen Naturforschenden Gesellschaft 124, 93-102

Campell, E. 1950. Der Tannen-oder Nußhäher und die Arvenverbreitung. Bündner Wald, Beiheft 4 (1), 3-7

Campell, E. 1955. Der Lärchen-Arvenwald. Bündner Wald, Beiheft 5, 14-26

Campell, E. 1958. Steinwild im Engadin. Bündner Wald 11, 287-24

Chadwick, D. H. 1983. A beast the color of winter. The mountain goat observed. Sierra Club Books, San Francisco

Chase, A. 1987. Playing God in Yellowstone. The destruction of America`s first national park. Harvest Book, San Diego, New York, London

Clarke, J. A. & R. E. Johnson, R. E. 2005. Comparisons and contrasts between the foraging behaviors of two white-tailed ptarmigan (Lagopus leucurus) populations, Rocky Mountains, Colorado, and Sierra Nevada, California, U.S.A. Arctic, Antarctic, and Alpine Research 37 (2), 191-176

Coleman, M. D., Hinckley T. M., McNaughton, G. & B. A. Smit 1992. Root cold hardiness and native distribution of subalpine conifers. Canadian Journal of Forest Research 22, 932-938

Conrads, K. and Balda, R. P. 1979. Überwinterungschancen Sibirischer Tannenhäher (Nucifra caryocatactes macrorhyncos) im Invasionsgebiet. Bericht des Naturwissenschaftlichen Vereins, Bielefeld 24, 115-137

Crocq, C. 1978. Écologie du Casse-noix (Nucifraga caryocatactes L.) dans les Alpes francaises due sud; ses relations avec l`Arolle (Pinus cembra L.). Dissertation, L`Université du Droit d` Économie et de Sciences D` Áix-Marseille, France

Danell, Ö., Staatland, H. & M. Nieminen 1999. Rennäring i Nordvest Europa. – In Dahle, H. K., Danell, Ö., Gaare, E. and Nieminen, M. (eds.), Reindrift i Nordvest Europa i 1998 – biologiske muligheter og begrensninger, 19-30, Nordisk ministeråd, Køvenhavn

Danilkin, A. 1996. Behavioural ecology of Siberian and European roe deer. London, Glasgow, Weinheim, New York, Tokyo, Melbourne, Madras

den Herder, M., Virtanen, R. & H. Roininen 2008. Reindeer herbivory reduces willow growth and grouse forage in a forest-tundra ecotone. Basic and Applied Ecology 9, 324-331

DeLella-Benedict, A. 1991. The Southern Rockies. The Rocky Moutain regions of southern Wyoming, Colorado, and Northern New Mexico. A Sierra Club Naturalists`s Guide. Sierra Club Books, San Francisco

Donaubaur, E. 1963: Über die Schneeschütte-Krankheit (Phacidium infestands Karst.) der Zirbe (Pinus cembra L.) und einige Begleitpilze. Mitteilungen der Forstlichen Bundse-Versuchsanstalt Mariabrunn 60,575-600

Eiberle, K. 1974: Waldkundliche Aspekte der Forschung an Rauhfußhühnern. Schweizerische Zeitschrift für Forstwesen 125 (3), 147-170

Eiberle, K. 1975. Results of simulations if game damage by cutting the shoots. Schweizerische Zeitschrift für Forstwesen 126, 821-839

Eiberle, K. 1978. The consequential effects of simulated deer browsing damage on the development of young forest trees. Schweizerische Zeitschrift für Forstwesen 129, 757-768

Eiberle, K. 1980. Methodische Möglichkeiten zum Verständnis der waldbaulich tragbaren Verbissbelastung. Schweizerische Zeitschrift für Forstwesen 131 (4), 311-326

Ericsson, A., Hellquist, C., Langstrom, B., Larsson, S. & O. Tenow 1985. Effects on growth of simulated and induced shoot pruning by Tomicus piniperda as related to carbohydrate and nitrogen dynamics in Scots pine. Journal of Applied Ecology 22, 105-124

Esslinger, H. 1988. Ski-Heil. ARD Sendereihe Globus, Beiheft 1 zur Sendung vom 10. Januar 1988

Estes; J. A., Terborgh, J., Brashares, J. S., Power, M. E., Berger, J., Bond, W. J., Carpenter, S. R., Essington, T. E., Holt, R. D., Jackson, J. B., Marquis, R. J., Oksanen, L., Oksanen, T., Paine, R. T., Pikitch, E. K., Ripple, W. J., Sandin, S. A., Scheffer, M., Schoener, T. W., Shurin, J. B., Sinclair, A. R. E., Soulé, M. E., Virtanen, R. and D. A.Wardle, D. A. 2011. Trophic downgrading of Planet Earth. Science 333: 301-306

Evans, R. 1995. Impacts of reindeer grazing on soils and vegetation in Finnmark. NORUT informasjonsteknologi, Tromsø

Feuerstein, G. C. 1997. Analyse von Stammverletzungen durch den Alpensteinbock (Capra i. ibex) in einem subalpinen Lärchen-Arvenwald. Diplomarbeit, Abteilung für Forstwissenschaft (VI), ETH Zürich, Samedan

Formozov, A. N. 1946. The covering of snow as an integral factor of the environment and its importance in the ecology of mammals and birds (in Russian with French summary). Material for Fauna and Flora of U.S.S.R., New Series, Zoology 5, 1-152

Fox, J. L. & Smith C. A. 1988. Winter mountain goat diets in southeast Alaska. Journal of Wildlife Management 52, 362-365

Franklin, J. F. & C. T. Dyrness 1973. Natural vegetation of Oregon and Washington. – USDA Forest Service, General Technical Report PNW-8

French, D. D., Miller, G. R. and R. P. Cummins 1997. Recent development of high-altitude Pinus sylvestris in the northern Cairngorm Mountains, Scotland. Biological Conservation 79, 133-144

Furnier, G. R., Knowles, P., Clyde, M. A. and Dancik, B. P. 1987. Effects of avian seed dispersal on the genetic structure of whitebark pine populations. Evolution 41 (3), 607-612

Gampe, S. 1989. Über Sanierungsaufforstungen in den Bayerischen Alpen. Mitteilungen aus der Staatsforstverwaltung Bayerns 44

Gill, R. M. A. 1990. Monitoring the status of European and North American cervids. GEMS Information Series 8.Global Environmental Monitoring System. United Nations Environment Programme, Nairobi, Kenya

Gill, R. M. A. 1992a. A review of damage by mammals in northern temperate forests: 1. Deer. Forestry 65 (2), 145-169

Gill, R. M. A. 1992b. A review of damage by mammals in north temperate forests: 3. Impact on trees and forests. Forestry 65 (4, 363-388

Gill, R. 2000. The impact of deer on woodland biodiversity. Forestry Commission, August 2000, 1-6

Gill, R. M. A. & V. Beardall 2001. The impact of deer on woodlands: the effect of browsing and seed dispersal on vegetation structure and composition. Forestry 74 (3), 209- 218

Glutz von Blotzheim, U. N. (ed.) 1993. Handbuch der Vögel Mitteleuropas, Vol 13 Passeriformes. Aula-Verlag, Wiesbaden

Grabherr, G. & H. Pauli 1994. Climate effects on mountain plants. Nature 369: 448

Grace, J., Berninger, F. & L. Nagy 2002. Impacts of climate change on the tree line. Annals of Botany 90, 537-544

Hagemoen, R. I.M. & E. Reimers 2004. Reindeer summer activity pattern in relation to weather and insect harassment. Journal of Ecology 71, 883-892

Hall, K., Boelhouwers, J, and K. Driscoll 1999. Animals as erosion agents in the alpine zone: Some data and observations from Canada, Lesotho, and Tibet. Arctic, Antarctic, and Alpine Research 31(4), 436-446

Haller, H. 1996. Prädation und Unfälle beim Steinbock Capra ibex im Engadin. Zeitschrift für Jagdwissenschaft 42, 26-35

Hättenschiler, S. & W. K. Smith 1999. Natural seedling occurence in treeline conifers: A case study from the Central Rocky Mountains, U.S.A. Acta Oecologica 20, 219-224

Heikkilä, R. & S. Härkönen 1996. Moose browsing in young Scots pine stands in relation to forest management. Forest Ecology Management 88, 179-186

Heikkinen, R. K. & R. Kalliola 1989. Vegetation types and map of the Kevo nature reserve, northernmost Finland. Reports from the Kevo Subarctic Research Station 11, 22-35

Helle, T. 1966. An investigation on reindeer husbandry in Finland. Fennia 95 (4)

Helle, T. 2001. Mountain birch forests and reindeer husbandry. In: Wielgolaski, F. E. (ed.), Nordic mountain birch ecosystems. Man and the Biosphere Series 27, New York, London, 279-291

Helle, T. & I. Kojola 2006. Population trends of semi-domesticated reindeer in Fennoscandia – evaluation of explanations. In Forbes, B., Bölter, C., Müller-Wille, L., Hukkinen, J., Müller, F., Gunslay, N. & Y. Konstantino (eds.), Reindeer management in northernmost Europe: linking practical and scientific knowledge in socio-ecological systems. Springer, Berlin, 319-339

Helle, T. & I. Tarvainen 1984. Determination of the winter digging period of semi-domestic reindeer in relation to snow conditions and food resources. Reports from the Kevo Subarctic Research Station 19, 49-56

Henden, J.-A., Ims, R. A., Yoccoz, N. G. & S. T. Killengreen 2011. Declining willow ptarmigan populations: The role of habitat structure and community dynamics. Basic and Applied Ecology 12, 413-422

Herbold, H., Suchentrunk, F., Wagner, S. & R. Willing 1992. Einfluss anthropogener Störreize auf die Herzfrequenz von Rotwild (Cervus elaphus) und Rehwild (Capreolus capreolus). Zeitschrift für Jadgwissenschaft 38: 145-159

Hess, A. 1916. Der Tannenhäher in forstwirtschaftlicher Bedeutung. Schweizerische Zeitschrift für Forstwesen 67

Hessl, A. E. and L. Baker 1997. Spruce and fir regeneration in the forest tundra ecotone of Rocky Mountain National Park, Colorado, U.S.A. Arctic and Alpine Research 29, 173-183

Hibbs, L. D. 1967. Food habits of the mountain goats in Colorado. Journal of Mammalogy 48, 242-248

Hiller, B., Müterthies, A., Holtmeier, F.-K. & G. Broll 2002. Investigations on spatial heterogeneity of humus forms and natural regeneration of larch (Larix decidua Mill.) and Swiss stone pine (Pinus cembra L.) in an alpine timberline ecotone (Upper Engadine, Central Alps, Switzerland). Geographica Helvetica 2: 81-90

Histøl, T. & O. Hjeljord 1993. Winter feeding strategies of migrating and nonmigrating moose. Canadian Journal of Zoology 71, 1421-1428

Hofgaard, A., Løkken, J. O., Dalen, L. & H. Hytteborn 2010. Comparing warming and grazing effects on birch growth in an alpine environment - a 10-year experiment. Plant Ecology and Diversity 3 (1), 19-27

Hobbs, N. T. 1996. Modification of ecosystems by ungulates. Journal of Wildlife Management 60 (4), 695-713

Holland, E. A. & J. K. Detling 1990. Plant response to herbivory and below-ground nitrogencycling. Ecology 71, 1040-1049

Holtmeier, F.-K. 1965. Die Waldgrenze im Oberengadin in ihrer physiognomischen und ökologischen Differenzierung. Dissertation Mathematisch-Naturwissenschaftliche Fakultät, Rheinische Friedrich-Wilhelms-Universität Bonn

Holtmeier, F.-K. 1966. Die ökologische Funktion des Tannenhähers im Zirben-Lärchenwald und an der Waldgrenze im Oberengadin. Journal für Ornithologie 4, 337-345

Holtmeier, F.-K. 1967a. Zur natürlichen Wiederbewaldung aufgelassener Alpen im Oberengadin. Wetter und Leben 19: 195-202

Holtmeier, F.-K. 1967b. Die Verbreitung der Holzarten im Oberengadin unter dem Einfluß des Menschen und des Lokalklimas. Erdkunde 21 (4), 249-258

Holtmeier, F.-K. 1968. Ergänzende Beobachtungen in der Steinwildkolonie am Schafberg und Piz Albris bei Pontresina. Bündnerwald 21, 244-249

Holtmeier, F.-K. 1969. Das Steinwild in der Landschaft von Pontresina. Natur und Museum 99 (1), 15-24

Holtmeier, F.-K. 1971. Waldgrenzstudien im nördlichen Finnisch-Lappland und angrenzenden Nordnorwegen. Reports from the Kevo Subarctic Research Station 8, 53-62

Holtmeier, F.-K. 1974. Geoökologische Beobachtungen und Studien an der subarktischen und alpinen Waldgrenze in vergleichender Sicht (nördliches Fennoskandien/Zentralalpen). Erdwissenschaftliche Forschung VIII, Franz Steiner Verlag, Wiesbaden.

Holtmeier, F.-K. 1976. Pontresina - landschaftliche Bindung und aktuelle Probleme einer Oberengadiner Gemeinde. Westfälische Geographische Studien 33, 329-349

Holtmeier, F.-K. 1978. Die bodennahen Winde in den Hochlagen der Indian Peaks Section, Colorado Front Range. Münstersche Geographische Arbeiten 3, 3-47

Holtmeier, F.-K. 1979. Die polare Waldgrenze (forest-tundra-ecotone) in geoökologischer Sicht. In: Müller-Wille, L. and H. Schroeder-Lanz (eds.), Kanada und das Nordpolargebiet. Trierer Geographische Arbeiten, Sonderheft 2, 230-252

Holtmeier, F.-K. 1981. Einige Besonderheiten des Krummholzgürtels in der Colorado Front Range. Wetter und Leben 33, 150-160

Holtmeier, F.-K. 1982. „Ribbon-forest“ und „Hecken“ - streifenartige Verbreitungsmuster des Baumwuchses an der oberen Waldgrenze in den Rocky Mountains. Erdkunde 36, 142-153

Holtmeier, F.-K. 1985. Climatic stress influencing the physiognomy of trees at the lpolar and mountain timberline. In Turner H. and W. Tranquillini (eds.), Establishment and tending of subalpine forest: Research and management. Proceedings 3rd International Workshop IUFRO Project Group P 1.07-00 Ecology of Subalpine Zones1984, Eidgenössische Anstalt für das forstliche Versuchswesen, Bericht 270, 31-40

Holtmeier, F.-K. 1986. Über Bauminseln (Kollektive) an der klimatischen Waldgrenze – unter besonderer Berücksichtigung von Beobachtungen in den verschiedenen Hochgebirgen Nordamerikas. Wetter und Leben 38: 121-139

Holtmeier, F.-K. 1987a: Biber und Steinwild. Ökologische Aspekte der Wiederansiedlung von Tieren in ihren ehemaligen Lebensräumen. Münstersche Geographische Arbeiten 26, 99-117

Holtmeier, F.-K. 1987b. Beobachtungen und Untersuchungen über den Ausaperungsverlauf und einige Folgeerscheinungen in „ribbon-forests“ an der oberen Waldgrenze in der Front Range, Colorado. Phytocoenologia 15 (23), 373-396

Holtmeier, F.-K. 1993. Der Einfluss der generativen und vegetativen Verjüngung auf das Verbreitungsmuster der Bäume und die ökologische Dynamik im Waldgrenzbereich. Beobachtungen und Untersuchungen in Hochgebirgen Nordamerikas und in den Alpen. Geoökodynamik 14, 153-182

Holtmeier, F.-K. 1996. Der Wind als landschaftsökologischer Faktor in der subalpinen und alpinen Stufe der Front Range, Colorado. Arbeiten aus dem Institut für Landschaftsökologie 1, 19-45

Holtmeier, F.-K. 2002. Tiere in der Landschaft. Einfluss und ökologische Bedeutung. UTB 8230, Stuttgart

Holtmeier, F.-K. 2005a. Change in the timberline ecotone in northern Finnish Lapland during the last 35 years. Reports from the Kevo Subarctic Research Station 23, 97-113

Holtmeier, F.-K. (2005b): Relocation of snow and its effects in the treeline ecotone – with special regard to the Rocky Mountains, the Alps and Northern Europe. – Die Erde 136 (4): 343-373

Holtmeier, F.-K. 2009. Mountain timberlines. Ecology, patchiness, and dynamics. – Advances in Global Change Research 36, Springer+Business Media B. V., Dordrecht, Boston, London

Holtmeier, F.-K. & Broll, G. 1992. The influence of tree islands on microtopography and pedoecological conditions in the forest-alpine tundra ecotone on Niwot Ridge, Colorado Front Range, U.S.A. Arctic and Alpine Research 24 (3), 216-228

Holtmeier, F.-K., Broll, G., Müterthies, A. & K. Anschlag, K. 2003. Regeneration of trees in the treeline ecotone: northern Finnish Lapland. Fennia 181 (2), 103-128

Holtmeier, F.-K., Broll, G. & K. Anschlag 2004. Winderosion und ihre Folgen im Waldgrenzbereich und in der alpinen Stufe einiger nordfinnischer Fjelle. GeoÖko 25, 203-224

Holtmeier, F.-K. & G. Broll 2005. Sensitivity and response or northern hemisphere altitudinal and polar treelines to global environmental change at landscape and local scales. Global Ecoloy and Biogeography 14, 395-410

Holtmeier, F.-K. & G. Broll, G. 2006. Radiocarbon-dated peat and wood remains from the Finnish Subarctic: evidence of treeline and landscape history. The Holocene 16 (5), 743.751

Holtmeier, F.-K. & G. Broll 2010a. Altitudinal and polar treelines in the Northern Hemisphere - causes and response to climate change. Polarforschung 79 (3), 139-153

Holtmeier, F.-K. & G. Broll 2010b. Wind as an ecological agent at treelines in North America, the Alps, and in the European Subarctic. Physical Geography 31 (3), 2030233

Holtmeier, F.-K. & G. Broll 2011. Response of scots pine (Pinus sylvestris) at its altitudinal limit in northernmost subarctic Finland to warming climate. Arctic 64 (3), 269-280

Hustich, I. 1940. Pflanzengeographische Studien im Gebiet der niederen Fjelden im westlichen Finnisch Lappland II. Über die horizontale Verbreitung der alpinen und alpiken Arten sowie einige Angaben über die winterlichen Naturverhältnisse auf den Fjelden; Artenverzeichnis. Acta Botanica Fennica 27, Helsingfors

Hutchins, H. E. 1994. Role of various animals in dispersal and establishment of whitebark pine in the Rocky Mountains, U.S.A. In: Schmidt, W. C. and F.-K. Holtmeier (compilers), Proceedings - International Workshop on Subalpine Stone Pines and Their Environment: the Status of Our

Knowledge, St. Moritz, Switzerland, September 5-11, 1992. USDA Forest Service, Intermountain Research Station, General Technical Report INT-GTR-309, 163-171

Hutchins, H. E. & R. Lanner 1982. The central role of Clark´s Nutcracker in the dispersal and establishment whitebark pine. Oecologia 55, 195-201

Hutchins, H. E., Hutchins, S. A. & B. W. Liu 1996. The role of birds and mammals in Korean pine (Pinus koraiensis) regeneration dynamics. Oecologia 107, 120-130

Kajimoto, T., Onodera, H. Daimaru, H. & T. Teki 1998. Seedling establishment of subalpine stone pine (Pinus pumila) by nutcracker (Nucifraga) seed dispersal on Mt. Yumori, Northern Japan. Arctic and Alpine Research 30 (4), 408-417

Kallio, P. & L. Kärenlampi 1970, A review of the stage reached in the Kevo IBP in 1970. International Biological Programme, Tundra Biome, Working Meeting on Analysis of Ecosystems, Kevo Finland, September 1970, 79-91

Kallio, P. & J. Lehtonen 1973, Birch forest damage caused by Oporinia autumnata (Bkh.) in 1965-1966 in Utsjoki, N-Finalnd. Reports from the Kevo Subarctic Research Station 10, 55-69

Kallio, P. & J. Lehtonen 1975. On the ecoctastrophe of birch forests caused by Oporinia autumnata (BKH.) and the problem of reforestation. In: Fennoscandian tundra ecosystems, Part 2 (Wielgolaski, F. E., ed.), Ecological Studies 17, 174-180

Kamil, A, C. and Balda, S. B. 1985. Cache recovery and spatial memory in Clark`s nutcracker (Nucifraga Columbiana). Journal of Experimental Psychology: Animal Behavior Processes 11: 95-11

Kauffman, M.J., Brodie, J. F. and E. S. Jules 2010. Are wolves saving Yellowstone`s aspen? A landscape-level test of a behaviorally mediated trophic cascade. Ecology 91 (9): 2742-2755

Käyhkö, J. 2007. Aeolian blowout dynamics in subarctic Lapland based on decadal levelling investigations. Geografiska Annaler 89A (1), 65-81

Käyhkö, J. & P. Pellikka 1994. Remote sensing of the impact of reindeer grazing on vegetation in northern Fennoscandia using SPOT XS data. Polar Research 13, 115-124

Kennel, E. 1998. Was kann das Vegetationsverhalten zum nachhaltigen Management eines waldverträglichen Schalenwildbestandes leisten? Vorschlag zur Bewertung von Verbissbefunden. Berichte der Bayerischen Akademie für Naturschutz und Landschaftspflege 22, 51-58

Kouki, J., Arnold, K. & P. Martikainen 2004. Long-term persistence of aspen - a key host for many threatened species - is endangered in old-growth conservation areas in Finland. Journal for Nature Conservation 12, 41-52

Koutaniemi, L. 1990. Suomen lämpö- ja sadeoljen viimeaikaisin kehitys. Terra 104, 275-283

Kozlowski, T. T., Kramer, P. J. & S. G. Pallardy 1991. The physiological ecology of woody plants. Academic Press, London

Kullman, L. 1986. Temporal and spatial aspects of subalpine populations of Sorbus aucuparia in Sweden. Annales Botanic Fennici 23, 215-275

Kullman, L.(2005. Wind-conditioned 20th century decline of birch treeline vegetation in the Swedish Scandes. Arctic 58 (3), 286-294

Kumpula, J. & M. Nieminen 1992. The inventory of reindeer pastures in Finland by satellite imagery. In: Extended abstracts. Symposium on the state of the environment and environmental monitoring in Northern Fennoscandia and Kola Peninsula, 6-8 October, Rovaniemi, Finland 1992 (Tikkanen, E., Varmola, M. & T. Katermaa, (eds.), 294-296

Kumpula, J., Stark, S. & and Ø. Holand 2011. Seasonal grazing effects by semi-domesticated reindeer on subarctic mountain birch forests. Polar Biology 34, 441-453

Kuznezov, N. I. 1959. On the ecology of the nutcracker Nucifraga caryocatactes in the Mid Urals. Bjull. Moip. SSSR 64, 132-133

Lanner, R. M. 1982. Adaptations of whitebark pine for seed dispersal by Clark`s Nutcracker. Canadian Journal of Forest Research 12, 391-402

Lanner, R. M. 1990. Biology, taxonomy, evolution and geography of stone pines of the world. Proceeding Symposium Whitebark Pine Ecosystems: Ecology and management of a high-mountain resource. USDA Forest Service, Intermountain Research Station, General Technical Report INT-270, 14-24

Lanner, R. M. 1996. Made for each other. A symbiosis of birds and pines. New York, Oxford

Larcher, W. 1980. Ökologie der Pflanzen auf pyhsiologischer Grundlage. (3rd edition). Stuttgart

Laundré, J. W. 1994. Resource overlap between mountain goats and bighorn sheep. Great Basin Naturalist 54, 114-1221

Lavsund, S. 1987. Moose relationships to forestry in Finland, Norway and Sweden. – Proceedings of the 2nd International Moose Symposium. 1 Viltrevy, Supplement 1: 229-246, Stockholm

Lavsund, S., Nygren, T. & E. J. Solberg, E. J. 2003. Status of moose populations and challenges to moose management in Fennoscandia. Alces 39, 109-130

Lehtonen, J. 1987. Recovery and development of birch forests damaged by Epirrita autumnata in Utsjoki area. Reports from the Kevo Subarctic Rsearch Station 20, 35-39

Lehtonen, J. & R. K. Heikkinen 1995. On the recovery of mountain birch after Epirrita damage in Finnish Lapland, with a particular emphasis on reindeer grazing. Ecoscience 2, 349-356

Lempa, K., Neuvonen, S. & H. Tømmervik, H. 2005a. Effects of reindeer grazing on pastures . a necessary basis for sutainable reindeer herding. In: Plant ecology, herbivory, and human impact in Nordic mountain birch forests (Wielgolaski, F. E., ed), Ecological Studies 180, 159-164

Lempa, K., Neuvonen, S. & H. Tømmervik, H. 2005b. Sustainable reindeer herding in mountain birch ecosystem. – In: Wielgolaski, F. E.(ed.), Plant ecology, herbivory, and human impact in Nordic mountain birch forests, Ecological Studies 180, 269-272

Lescop-Sinclair, K. & S. Payette 1995. Recent advance of the arctic treeline along the eastern coast of Hudson Bay. Journal of Ecology 83, 929-936

Löffler, J. 2005. Reindeer grazing impact in artic-alpine landscapes in western Greenland, and central and northern Norway. Geoöko 26, 1-18

Löyttyniemi, K. 1985. On repeated browsing of Scots pine saplings by moose Alces alces. Silva Fennica 19, 387-391

Löw, H. & C. Mettin 1977. Der Hochlagenwald im Werdenfelser Land. Forstwissenschaftliches Centralblatt 96, 108-120

Luckman, B. H. & T. A. Kavanagh 1998. Documenting the effects of recent climate change at treeline in the Canadian Rockies. In: Beniston, M. & J. K. Innes (eds.), Impact of climate variability on forests), 121-144, Heidelberg

Luckman, B. H. & T. A. Kavanagh 2000, Impact of climatic fluctuations on mountain environments in the Canadian Rocky Mountains. Ambio 29, 271-280

Malanson, G. P., Butler D. R., Fagre, D. B., Walsh, S. J., Tomback, D. F., Daniels, L. D., Resler, L., Smith, W. K., Weiss, D. J., Peterson, D. L., Bunn, A. G., Hiemstra, C. A., Liptzin, D., Bourgeron, P. S., Shen, Z. & C. I. Millar 2007. Alpine treelines of western North America: Linking organism-to-landscape dynamics. Physical Geography 28, 378-396

Marchand, P. J. 1987. Life in the cold. An introduction to winter ecology. University Press of New England, Hannover/London

Marr, J. W. 1977. The development and movement of the tree islands near the upper limit of tree growth in the Southern Rocky Mountains. Ecology 58, 1159-1164

Martin, P. S. 1973. The discovery of America. Science 1979, 969-979

Mattes, H. 1978. Der Tannenhäher im Engadin. Studien zur Ökologie und Funktion im Arvenwald. Münstersche Geographische Arbeiten 2

Mattes, H. 1982. Die Lebensgemeinschaft von Tannenhäher und Arve. Eidgenössische Anstalt für das forstliche Versuchswesen, Berichte 241

Mattes, H. (1985): The role of animals in cembran pine forest regeneration. In: Establishment and tending of subalpine forests: Research and management. Proceedings 3rd IUFRO workshop P 1.07-00 1984 (Turner, H. and Tranquillini, W., editors). – Eidgenössische Anstalt für das forstliche

Versuchwesen, Berichte 270: 195-205

Mattes, H., Maurizio, R. & W. Bürkli 2005. Die Vogelwelt im Oberengadin, Bergell und Puschlav. Schweizerische Vogelwarte, Sempach

Mauersberger, G. 1995. Vögel. Urania Tierreich, Leipzig, Jena, Berlin

McCaughey, W. W. 1994. The regeneration process of whitebark pine. In: Schmidt, W. & F.-K. Holtmeier (compilers), Proceedings of the International Workshop on Subalpine Stone Pines and Their Environment: The status of our knowledge, St. Moritz, Switzerland, September 5-11, 1992. USDA Forest Service, Intermountain Research Station, General Technical Report, INT-GTR 309, 179-187

Mellmann-Brown, S. 2002. The regeneration of whitebark pine in the timberline ecotone on Beartooth Plateau, Montana and Wyoming. Dissertation, Mathematisch-Naturwissenschaftliche Fakultät, Westfälische Wilhelms-Universität, Münster

Mellmann-Brown, S. 2005. Regeneration of whitebark pine in the timberline ecotone of the Beartoorth Plateau, U.S.A.: Spatial distribution and responsible agents. In: Broll G. & B. Keplin (eds.), Mountain Ecosystems. Studies in treeline ecology, Springer, Berlin, Heidelberg, New York, 97-115

Mezhennyi, A. A. 1964. Biology of the nutcracker Nucifraga caryocatactes macrorhynchos on South Yakutia. Zoll. Žurnal 43, 1679-1687

Miehe; G. & S. Miehe 2000, Comparative high mountain research on the treeline ecotone under human impact. Erdkunde 54, 34-50

Miles, J. & J. W. Kinnaird 1979. Grazing: With particular reference to birch, juniper and Scots pine in the Scottish Highlands. Scottish Forestry 33, 280-289

Miller, G. R., Kinnaird, J. W. & R. P. Cummins 1982. Liability of saplings to browsing on a red deer range in the Scottish Highlands. Journal of Applied Ecology 19, 941-951

Moens, J., Cairns, D. M. & C. W. Lafon 2008. Factors structuring the treeline in Fennoscandia. Plant Ecology and Diversity 1, 77-97

Molvar, E. M., Bowyer, R. T. & V. Van Ballenberghe 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. Oecologia 94, 472-479

Motta, R. 1996. Impact of wild ungulates on forest regeneration and tree composition of mountain forests in the Western Italian Alps. Forest Ecology and Management 88, 93-98

Müterthies, A. 2002. Struktur und Dynamik der oberen Grenze des Lärchen-Arvenwaldes im Bereich aufgelassener Alpweiden im Oberengadin. Arbeiten aus dem Institut für Landschaftsökologie 11, Westfälische Wilhelms-Universität, Münster

Nagy, L. & G. Grabherr 2009. The biology of alpine habitats. The Biology of Habitats Series, Oxford University Press

Neuvonen, S. & F. E. Wielgolaksi 2005. Herbivory in northern birch forests. In: Wielgolaski, F. E. (ed.), Plant ecology, herbivory, and human impact in Nordic mountain birch forests, 183-189, Springer, Berlin, Heidelberg

Neuvonen, S., Bylund, H. & H. Tømmervik 2005. Forest defoliation risks in birch forest by insects under different climate and land use scenarios in northern Europe. In: Wielgolaski. F. E., (ed.), Plant ecology, herbivory, and human impact in Nordic mountain birch forests, Ecological Studies 180, 125-138

Niemelä, P., Hagman; M. & K. Lehtilä 1989. Relationships between Pinus sylvestris L. origin and browsing preference by moose in Finland. Scandinavian Journal of Forest Research 4, 239-246

Nievergelt, B. 1966. Der Alpensteinbock (Capra ibex L.) in seinem Lebensraum. – Mammalia depicta, Verlag Paul Parey, Berlin

Nikula, A. 1992. Animals as forest pests in Finnish-Lapland. Finnish Forest Research Institute, Research papers 451, 22-29

Noble, D. L. & W. D. Shepperd 1973. Gray-headed juncos important to first season mortality of spruce. Journal of Forestry 71, 763-765

Noss, R. F., Graham, R., McCullough, D. R., Ramsey, F. L., Seavey, J., Whitlock, C. and M. P. Williams 2000. Review for scientific material relevant to the occurrence, ecosystem role, and tested management options for mountain goats in Olympic National Park. Conservation Biology Institute, Corvallis

Nygren, T. 1987. The history of moose in Finland. Swedish Wildlife Research, Suppl. 1, 49-54

Oksanen, L., Moen, J. & T. Helle 1995. Timberline patterns in northernmost Fennoscandia. Relative importance of climate and grazing. Acta Botanica Fennica 153, 93-107

Olofsson, J., Hulme, P. E., Oksanen, L. & O. Suominen 2004. Importance of large and small mammalian herbivores for the plant community structure in the forest tundra ecotone. Oikos 106, 324-334

Onderschenka, K. 1985. Auswirkungen der Umweltveränderungen auf das Rot-, Reh- und Gamswild. Allgemeine Forstzeitung 10, 255-256

Oswald, H. 1956. Beobachtungen über die Samenverbreitung bei der Zirbe (Pinus cembra). Allgemeine Forstzeitung 67, 200-202.

Ott, E., Frehner, M., Frey, H. U. & P. Lüscher 1997. Gebirgsnadelwälder. Ein praxisorientierter Leitfaden für eine standortgerechte Waldbehandlung. Verlag Paul Haupt, Bern, Stuttgart, Wien

Pauchard, A., Kueffer, C., Dietz, H., Daehler, C. C., Alexander, J., Edwards, P. J., Arevalo, J. R., Cavieres, L. A., Guisan, A., Haider, S., Jacobs, G., McDougall, K., Millar, C. I., Naylor, B. J., Parks, C. G., Rew, L. J. & T. Seipl 2009. Ain`t no mountains high enough: plant invasions reaching new elevations. Frontiers in Ecology and the Environment 7 (9), 479-486

Persson, I.-L., Danell, K. & R. Bergström 2000. Disturbance by large herbivores in boreal forests with special reference to moose. Annales Zoologici Fennici 37, 251-263

Petrak, M. 1988. Skilanglauf und Rothirsch (Cervus elaphus Linné, 1758) in der Eifel. Bilanz des Konzeptes zur Lebensraumberuhigung im Wintersportgebiet Monschau. Zeitschrift für Jagdwissenschaft 34, 104-114

Pfister, F., Walther, H., Erni, V. & M. Candrian 1987. Walderhaltung und Schutzaufgaben im Berggebiet. EAFV Berichte 294

Pruitt, W. O. Jr. 1970. Some ecological aspects of snow. In: Ecology of the Subarctic regions. Proceedings of the Helsinki Symposium. Ecology and Conservation 1, Paris, 83-99

Pulliainen, E. & J. Iivanainen 1981. Winter nutrition of the willow grouse (Lagopus lagopus L.) in the extreme north of Finland. Annales Zoologici Fennici 18, 263-269

Rao, S. K., Iason, G. R., Hulbert, I. A. R., Elston, D. A. & P. A. Pracey 2003. The effect of sapling density, heather height and season of browsing by mountain hares on birch. Journal of Ecology 40, 626-638

Ratcliff, D. A. 1990. Bird life of mountain and upland. Cambridge University Press, Cambridge

Reimoser, F. 1999. Schalenwild und Wintersport. Laufener Seminarbeiträge 6, 39-45

Reimoser, F. 2003. Steering the impacts of ungulates on temperate forests. Journal of Nature Conservation 10, 243-252

Reimoser, F., Mayer, H. Holzinger, A. & J. Zandl 1987. Einfluss von Sommer- und Wintertourismus auf Waldschäden durch Schalenwild im Angertal (Bad Gastein). Centralblatt für das gesamte Forstwesen 104, 95-118

Reijmers, F. F. 1959. Birds of the cedar pine forests of South-Central Siberia and their role in the life of cedar pine. Trudy Biologischeskogo Instituta, Sibirskogo, Otdelenie . Akad. Nauk. USSR 5, 121-166

Repo, T., Nilsson, J.-E., Rikala, R., Ryyppö, A. & M.-L. Sutinen 2001.: Cold hardiness of Scots pine (Pinus sylverstris). – In: Bigras, F. J. & S. J. Colombo (eds.), Conifer cold hardiness. Tree Physiology 1: 463-493, Kluwer, Dordrecht, Boston, London, 463-493

Resler, L. M. 2004. Conifer establishment sites at the alpine treeline ecotone, Glacier National Park, Montana. Dissertation, Department of Geography, Texas State University, San Marcos

Resler, L. M. & D. F. Tomback 2008. Blister rust prevalence in krummholz whitebark pine: Implications for treeline dynamics, Northern Rocky Mountains, Montana, U.S.A. Arctic, Antarctic, and Alpine Research 40 (1), 161-170

Ripple, W. J. and R. L. Beschta 2003. Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecology and Management 184, 299-313

Rousi, M. 1988. Susceptibility of winter-dormant Pinus sylvestris families to vole damage. Scandinavian Journal of Forest Research 4, 149-161

Ryyppö, A., Repo, T. & E. Vappaavuori 1998. Development of freezing tolerance in roots and shoots of scots pine seedlings at non-freezing temperatures. Canadian Journal of Forestry 28, 557V-265V

Schickhoff, U. 1993. Das Kaghan-Tal im Westhimalaya (Pakistan). Bonner Geographische Abhandlungen 87

Schmidt, K. 1993. Winter ecology of nonmigratory Alpine red deer. Oecologia 95 (2), 226-233

Schickhoff, U. 2005. The upper timberline in the Himalayas, Hindu Kush and Karakorum; a review of geographical and ecological aspects. – In: Broll, G. & B. Keplin, B. (eds.), Mountain ecosystems. Studies in treeline ecology, 275-354

Schönenberger, W. (1986): Wiederaufforstung eines Bergwaldes. – Neue Zürcher Zeitung 38: 35-36

Schönenberger, W., Frey, W. & F. Leuenberger 1990. Ökologie und Technik der Aufforstung im Gebirge. Anregung für die Praxis. Eidgenössische Anstalt für das forstliche Versuchswesen, Berichte 325

Schröder, W. 1977. Räumliche Verteilung und Nahrungswahl von Gams und Rotwild im Hochgebirge. Forstwissenschaftliches Centralblatt 96, 94-99

Schütz, H.-U. 1998. Untersuchungen zur Ökologie von „ribbon forests“ der Colorado Front Range (Rocky Mountains, U.S.A.) unter besonderer Berücksichtigung von Thomomys talpoides (Geomyidae). Dissertation Mathematisch-Naturwissenschaftliche Fakultät, Westfälische Wilhelms-Universität, Münster

Schütz, H.-U. 2005. Pocket gopher – actor under the stage. Studies on Niwot Ridge, Colorado Front Range, U.S.A. In: Broll, G. & B. Keplin (eds.), Mountain ecosystems. Studies in treeline ecology, 153-180

Senn, J. 1999. Tree mortality caused by Gremmeniella abietina in a subalpine afforestation in the central Alps and its relationship with duration of snow cover. – European Journal of Forest pathology 29, 65-74

Seppäla, M. 2004. Wind as a geomorphic agent in cold climates. Studies in Polar Research. Cambridge University Press, Cambridge

Skuncke, F. 1969. Reindeer ecology and management in Sweden. Ecological Papers of the University of Alaska 8, Fairbanks, University of Alaska

Smith, D. W., Peterson, R. O. and D. B. Houston 2003. Yellowstone after wolves. BioScience 53, 330-340

Smith, W. K., Germino, M. J., Hancock, T. E. & D. M. Johnson 2003. Another perspective on altitudinal limits of alpine timberlines. Tree Physiology 23, 1101-1112

Stevens, D. R. 1980. The deer and elk of Rocky Mountain National Park: a ten-year study. National Park Service, Rocky Mountain National Park, Estes Park, Colorado, ROMO-N-13r.

Stöcklin, J. & C. Körner 1999. Recruitment and mortality of Pinus sylvestris near the Nordic treeline: the role of climatic change and herbivory. In: Hofgarard, A., Ball, J. P., Danell, K. and T. V. Callaghan (eds.), Animal response to global change in the north. Ecological Bulletins 47, 168-177

Strandgaard, S. 1982. Factors affecting the moose population in Sweden during the 20th century with special attention to silviculture. Swedish University of Agricultural Sciences, Department of Wildlife Ecology, Report 8

Sundqvist, M. K., Björk, R. G. & U. Molau 2008. Establishment of boreal forest species in alpine-dwarf shrub heath in subarctic Sweden. Plant Ecology and Diversity 1, 67-75

Suominen, O. & J. Olofsson 2000. Impacts of semi-domestic reindeer on structure of tundra and forest communities in Fennoscandia: A review. Annales Zoologici Fennici 37, 233-249

Sutinen, M.-L., Ritari, A., Holapppa, T. & K. Kujala 1997. Seasonal changes in soil temperature and in the frost hardiness of Scots pine under subarctic conditions. In: Islander, I. K., Wright, E. A., Radke, J. K., Shmatt, B. S., Groenvelt, O. H. & L. B.

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Hinzman, L. B. (eds.), International symposium on physics, chemistry and ecology of seasonally frozen soils, June 10-12, 1997; Fairbanks, AK, Cold Regions Research and Engineering Laboratory Special Report 97-10, 513-517, Hanover, New Hampshire

Teipner, C., L., Garton, E. O. & L. Nelson Jr. 1983. Pocket gophers in forest ecosystems. USDA Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah, General Technical Report INT-154

Ten Houte de Lange, S. M. 1978. Zur Futterwahl des Steinbocks (Capra ibex L.). Eine Untersuchung an der Steinbockkolonie am Piz Albris bei Pontresina. Zeitschrift für Jagdwissenschaft 24, 113-138

Theurillat, J.-P., Felber, F., Geissler, P., Gobat, J.-M., Fierz, M., Fischlin, A., Küpfer, P. Schussel, A., Velutti, C. & G.-F. Zhao 1998. Sensitivity of plant and ecosystems of the Alps to climate change. In: Cebon, P., Dahinden, U., Davies, H. C., Imboden, D. & C. C. Jaeger (eds.), Views from the Alps: Regional perspectives on climate change, 225-308, MIT Press, Cambridge, MA.

Theurillat, J.-P. & A. Guisan 2001. Potential impact of climate change on vegetation in the European Alps: a review. Climate Change 50, 77-109

Thorn, C. 1978. A preliminary assessment of the geomorphic role of pocket gophers in the alpine zone of the Colorado Front Range. Geografiska Annaler 60 A (3-4), 181-187

Tinner, W. & P. Kaltenrieder 2005. Rapid responses of high-mountain vegetation to early Holocene environmental changes in the Swiss Alps. Journal of Ecology 93, 936-947

Tomback, D. F. 1977. The behavioural ecology of Clark´s Nutcracker (Nucifraga columbiana) in the eastern Sierra Nevada. Ph. D. thesis, University of California, Santa Barbara

Tomback, D. F. 1978. Foraging strategies of Clark´s nutcracker. The Living Bird 16, 123-161

Tomback, D. F. 1980. How nutcrackers find their seed stores. Condor 82, 1-19

Tomback, D. F. 1982. Dispersal of white bark pine seeds by Clark´s nutcracker. A mutualism hypothesis. Journal of Animal Ecology 51, 451-467

Tomback, D. F. 1998. Clark`s nutcracker. The birds of North America, no. 331, 1-23

Tomback, D. F. 2001. Clark´s nutcracker: agent of regeneration. In: Tomback, D. F., Arno S. F. and R. E. Keane (eds.), Whitebark pine communities. Ecology and Restoration, 88-104. Island Press, Washington, Covelo, London

Tomback, D. – F. 2005. The impact of seed dispersal by Clark´s nutcracker on whitebark pine: Multi-scale perspective on a high mountain mutualism. – In: Broll, G. & B. Keplin, B. (eds.), Mountain ecosystems. Studies in treeline ecology, 181-201, Springer Berlin, Heidelberg, New York

Tomback, D. F., Anderies, A. J., Carsey, K. S. and Mellmann-Brown, S. (2001): Delayed seed germination in whitebark pine and regeneration patterns following the Yellowstone fires. Ecology 82, 2587-2600

Tomback, D. F. and Y. B. Linhart 1990. The evolution of of bird-dispersed pines. Evolutionary Ecology 4, 185-219

Tomback, D. F., Sund, S. K. & L. Hoffmann 1993. Post-fire regeneration of Pinus albicaulis: Height-age relationships, age structure, and microsite characteristics. – Canadian Journal of Forest Research 23, 113-119

Troll, C. 1973. Rasenabschälung (turf exfoliation) als periglaziales Phänomen der subpolaren Zonen und der Hochgebirge. Zeitschrift für Geomorphologie, Neue Folge, Supplement Vol. 17, 1-32

Vander Wall, S. B. 1982. An experimental analysis of cache recovery in Clark`s nutcracker. Animal Behavior 30: 84-94

Vander Wall, S. B. 1990. Food hoarding in animals. The University of Chicago Press, Chicago and London

Vander Wall, S. B. and Balda, R. P., 1977. Co-adaptations of the Clark´s Nutcracker and the Piñon Pine for efficient seed harvest and dispersal. Ecological Monographs 47, 89-11

Vander Wall, S. B. 1981. Ecology and evolution of food-storage behavior in conifer-seed-caching corvids. Zeitschrift für Tierpsychologie 56, 217-241

Vander Wall, S. B. and Hutchins, H. E. 1983. Depencence of Clark`s nutcracker (Nucifraga Columbiana) on conifer seeds during the post-fledging period. Canadiaan Field Naturalist 97, 208-214

Von Elsner-Schack, I. 1986; Habitat use by mountain goats, Oreamnos americanus, on the eastern slopes of the Rocky Mountains at Mount Hamell, Alberta. Canadian Field-Naturalist 100, 319-324

Vose, R. N. and D. G. Dunlap 1968. Wind as factor in the local distribution of small mammals. Ecology 49 (3), 381.386

Vucetich, J. A., Smith, D. and D. R. Strahler 2005. Influence of harvest, climate and wolf predation on Yellowstone elk, 1961-2004. Oikos 111, 259-270

Vucetich, J. A., Peterson, R. O. and O. L. Schaefer 2002. The effect of prey and predator densities on wolf predation. Ecology 83, 3003-3012

Wagner, F. H., Foresta, R., Gill, R. B., McCullough, D. R., Pelton, M. R., Porter, W. F. and H. Salwasser 1995. Wildlife policies in the U. S. National Parks. Island Press, Washington D. C:

Watson, A. & R. Moss 2008. Grouse: The natural history of British and Irish species. London, UK, Harper Collins

Widmann, P. 1991. Zur Synökologie von Wild und Waldvegetation. Allgemeine Forstzeitung 8, 382-384

Wotschikowsky, U., Simon, O., Elmauer, K. & S. Herzig 2010. Leitbild Rotwild. Wege für ein forschrittliches Management (2nd actualized edition), Deutsche Wildtier Stiftung, Hamburg