Impact of wild herbivorous mammals and birds on the altitudinal and northern treeline ecotones

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Abstract

Wild herbivorous mammals may damage treeline vegetation and 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
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.


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; Lavsdun 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 Payne 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 (e.g., 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.
(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.

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 understory 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 extended 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).

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 et 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 (Kaufmann 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.
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-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).

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-holding capacity 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.
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.

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., Alborg 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,

![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).](image)

![Table 1. Soil moisture (topmost 6 cm) at different microsites in the birch-treeline ecotone, northernmost Finnish Lapland. Number of measurements: (a) n = 505; (b) n = 300; bdl = below detection limit.](image)
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, birth 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 (Stälso, 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; Lavssund 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 (Äbiskö 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 (Lavssund 1987; Niemelä et al 1989). Trees less than 250 cm in height are under the constant risk of being damaged by moose (Bjørnraas 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).

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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 Bès-cha (Munt da la Bès-cha = ‘Sheep Mountain’) and Piz Albris. They continued the destruction of alpine vegetation and caused soil erosion (Holtmeier 1968, 1969, 1976).

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.

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

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.

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...
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, 1987b, 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.
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>
<thead>
<tr>
<th>Subalpine pine species</th>
<th>Nutcracker species</th>
<th>Region</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Pinus cembra</em></td>
<td><em>Nucifraga caryocatactes</em></td>
<td>Alps, Carpathian Mountains, Siberia, Northern Mongolia</td>
</tr>
<tr>
<td><em>Pinus sibirica</em></td>
<td><em>Nucifraga caryocatactes</em></td>
<td>Siberia, northern Mongolia</td>
</tr>
<tr>
<td><em>Pinus pumila</em></td>
<td><em>Nucifraga caryocatactes</em></td>
<td>Northeastern Siberia, Korea, Kamchatka, Japan</td>
</tr>
<tr>
<td><em>Pinus koraiensis</em></td>
<td><em>Nucifraga caryocatactes</em></td>
<td>Southeast Siberia, eastern Manchuria, Korea, Japan</td>
</tr>
<tr>
<td><em>Pinus albicaulis</em></td>
<td><em>Nucifraga columbiana</em></td>
<td>North America</td>
</tr>
<tr>
<td><em>Pinus flexilis</em></td>
<td><em>Nucifraga columbiana</em></td>
<td>North America</td>
</tr>
</tbody>
</table>

* Modified after different sources, from Holtmeier (2002)
** A few subalpine pine species with winged seeds (e.g., *Pinus aristata, P. lambertiana, 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 1992, 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., squirrels, 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.
Wild herbivorous mammals and birds

Unretrieved caches may give rise to solitary pine seedlings and seedling clusters (e.g., Campell 1950; Oswald 1956; Holtmeier 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).

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; Mühtherthies 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 (Tombback 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 Tombback 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.

At the treeline, birds other than nutcrackers usually do harm to the trees, in particular to young growth. Grey-headed junco (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
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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