



Sensitivity to environmental change of the treeline ecotone and its associated biodiversity in European mountains

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ABSTRACT: Transition zones between mountain forests and treeless tundra, i.e. treeline ecotones, are characterized by great regional variety. In this paper, we discuss the biodiversity in various trophic levels in treeline ecotones throughout Europe, with particular focus on recent changes in land use and climate in northern and central mountains. In northernmost Europe, mountain birch prevails, while conifers (spruce, pine, larch) are the dominating species further south. While at continent-wide to global scales, the ecotone position is largely controlled by heat deficiency, it depends on a multitude of partly interacting abiotic and biotic factors other than climate at smaller scales. Climate change is a driving factor in treeline ecotone change, including physiognomic structure and biodiversity, although the effects of climate and other factors often overlap. Historical legacy plays an important role in this respect, and human impacts are particularly important. The recent decline in pastoral use of many European treeline areas often strongly influences plant diversity and re-growth of trees and other woody species. Climate change together with changing tree cover may influence snow cover, moisture regime, and nutrient conditions. Subsequently changed site conditions influence plant–plant interactions, favoring some species and disfavoring others, and plant–animal interactions. Native animals may cause widespread or local disturbances in treeline ecotone areas. Mass outbreaks of leaf-eating insects, for example, usually affect comparatively large forested areas whereas mammalian herbivores and birds have more local impact. However, high numbers of wild or domestic mammalian herbivores may challenge the carrying capacity of treeline ecotone areas at the same time as they preserve an open pasture character. This calls for cross-disciplinary study approaches, addressing the complexity of the ecotone regarding both causal background and biogeographic diversity.

KEY WORDS: Treeline ecotone · Ecotone change · Land use change · Climate change · Animal impact

1. INTRODUCTION

Transition zones between mountain forests and treeless tundra, i.e. treeline ecotones, are characterized by great regional variety regarding abiotic and biotic components structuring the zone. Accordingly, due to environmental change and treeline shift, bio-

diversity has been changing in the subalpine and lower alpine zone in many European mountains. In this paper, we discuss the biodiversity in various trophic levels in treeline ecotones throughout Europe, with particular focus on recent changes in land use and climate in northern and central mountains.

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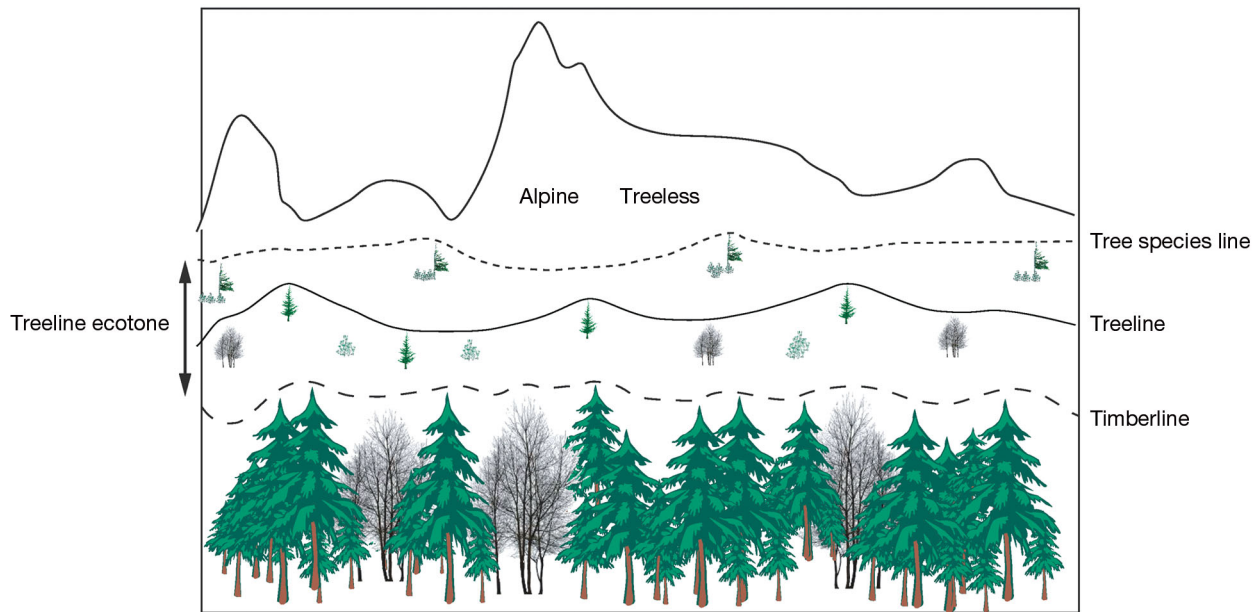


Fig. 1. Characteristics of the treeline ecotone

1.1. Treeline ecotone

The treeline ecotone spans the transition in decreased tree cover and tree height from the upper closed mountain forest to the treeless tundra. This transition boundary includes a number of tree status delineations (e.g. timberline, treeline, and tree species line; Fig. 1) used in studies of treeline ecotone dynamics. The definition of the ecotone and included lines may vary in the published literature (Callaghan et al. 2002a, Holtmeier 2009, Körner 2012, Irl et al. 2016, Holtmeier & Broll 2017, this Special), but are commonly classified regarding causal background, to climatically, topographically, or anthropogenically defined ecotones and lines. The climatic treeline ecotone generally decreases in altitude from southern to northern mountains in Europe and is found from above 2000 m above sea level (a.s.l.) in southern Europe to close to sea level in the northernmost subarctic parts (Cudlín et al. 2017, this Special). The ecotone may be abrupt (e.g. in steep or heavily grazed areas), but is normally a relatively wide boundary, and may thus regionally cover a considerable area of the lower and most productive part of the alpine zone. The vastness of the treeline ecotone, and its conspicuous transition from tree-covered to treeless areas, makes it an important biogeographic component of region-wide ecological, climatic, and socioeconomic relevance (Callaghan et al. 2002b).

In northern Europe, both the alpine and arctic treeline ecotones are normally formed by mountain birch

Betula pubescens subsp. *tortuosa* (Ledeb.) Nyman (Wielgolaski 2001, 2005), but may regionally also include Norway spruce *Picea abies* L. and Scots pine *Pinus sylvestris* L. In mountains further south, the ecotone is normally formed by conifers such as spruce, pine (e.g. *Pinus sylvestris*, *P. cembra* L., *P. uncinata* Ramond ex DC.) and larch *Larix decidua* L., but regionally also beech *Fagus sylvatica* L. (Wilmanns 1989, Nagy et al. 2003, Holtmeier 2009 for ample references). In the upper part of the ecotone, trees become progressively more stunted and may form extensive areas with scattered individual krummholz or krummholz groups. In some mountain areas of Europe, the 'true krummholz' mountain pine *Pinus mugo* Turra, the usually prostrate and gnarled growth of which is genetically predetermined, dominates above the high-stemmed mountain forests (Holtmeier 1981, 2009).

Historically, extensive changes in the elevation of the treeline ecotone have occurred throughout Europe. For example, in both the Scandes and mountains further south, pollen analyses and radiocarbon dating of tree remains found in mires, alpine sediments, and at retreating glacier fronts have revealed that trees grew at much higher elevation during the early to mid-Holocene than today (Holtmeier 1974, 1993, 2009, Kullman 1995, 2004, Tinner et al. 1996, Allen & Huntley 1999, Kullman & Källgren 2000, Aas & Faarlund 2001, Tinner & Theurillat 2003, Heiri et al. 2006). During the late Holocene and until termination of the Little Ice Age (Grove 1988), treeline eco-

tone retreat was the dominating trend in many European mountains (Karlén 1976, Shiyatov 1993, Kullman 1995). Later, the trend has reversed in response to both the release from the long-term climatic suppression during the Little Ice Age and the more recent climate warming (Kullman 1986, 2003, Gervais & MacDonald 2000, Shiyatov 2003, Camarero & Gutiérrez 2004, Motta et al. 2006). However, although an advancing trend is dominating, non-advancing trends occur across European mountains (Harsch et al. 2009, Van Bogaert et al. 2011, Dinca et al. 2017, this Special).

In general, thermal deficiency during the growing season is a main factor limiting tree growth and development at high elevation, which has been well known since the beginning of treeline research. However, although southern slopes usually provide favorable thermal conditions, the treeline ecotone may be at a relatively low elevation due to moisture deficiency, as is the case in many summer-dry Mediterranean mountains (e.g. Brandes & Ise 2007, González de Andrés et al. 2015). Insufficient moisture supply as a result of summer drought also occurs at the treeline in Central Europe, as for example, in the Sudetes, where it affects tree seedling establishment on southern exposures (Tremel & Chuman 2015, Tremel et al. 2016). Extreme winds, snow cover, wildfires, etc. may also influence tree growth in European treeline areas (Holtmeier & Broll 2017). In addition, low-elevation ecotones may be due to historical and/or ongoing human activities, e.g. logging and pastoral use, creating anthropogenic elevation of the treeline ecotone. When landscape controlling pressures (e.g. human activities) cease or lessen, the response might be seen as a swift reforestation (Hofgaard 1997a, Bolli et al. 2007, Batllori & Gutiérrez 2008, Bryn 2008). However, summer drought periods or other disturbances may affect tree growth and prevent or delay natural reforestation considerably (Hofgaard 1997a,b, Brandes & Ise 2007, Grunewald & Scheithauer 2008, González de Andrés et al. 2015), due to the multitude of abiotic and biotic factors controlling changes in both structure and location of the treeline ecotone (Holtmeier & Broll 2005, Hofgaard et al. 2012, Weisberg et al. 2013, Kulakowski et al. 2016).

The altitude of the treeline ecotone location decreases from central parts of mountain massifs to coastal areas. Central areas have a more continental climate due to protection from cool and moisture-carrying air masses, and thus, normally have higher daytime temperatures during the growing season, compared to heavily dissected and maritime mountain ranges. The 'mass elevation effect' (De Quervain

1904) often overlaps with the influence of the continental climate (Brockmann-Jerosch 1919, Turner 1961, 1970, Holtmeier 2009, Kašpar & Tremel 2016). In addition to the north–south and coast–inland gradients, mountain topography strongly influences ecotone elevation and spatial patterns at smaller scales (Holtmeier 2009, Holtmeier & Broll 2010, 2012). This is most evident for steep slopes, where recurrent avalanches often prevent tree establishment and cause topographically defined ecotone location.

1.2. Biodiversity

Transition zones between 2 major biomes generally have high biodiversity. This also applies to the treeline ecotone compared to the forest at lower elevation and the treeless tundra at higher elevation (Hofgaard & Wilmann 2002). High biodiversity in ecotones is mainly caused by an overlapping distribution of species originally belonging to the 2 adjoining biomes. In addition, as mountains are often characterized by a highly varying and rugged topography, the biological richness is high with strong differences occurring at short distances (Huston 1994). Further, a mix of vegetation-covered ground and open patches with high light intensity at the ground is characteristic of the treeline ecotone. Taken together, this provides a wide range of temperature- and moisture-defined microhabitats favorable to high species diversity (Körner 2003, Nagy & Grabherr 2009).

Species richness across European treeline ecotones decreases with latitude, but depends on a large number of abiotic and biotic factors, such as human activities and soil conditions (Callaghan et al. 2004, Vittoz et al. 2010). However, the general trend with decreasing species diversity towards high latitudes or altitudes makes the ecotone an indistinct species boundary. A general decrease in species diversity is accompanied by a strong nutrient and productivity gradient (Callaghan et al. 2004), but there is a lack of evidence for a causal connection between latitudinal decrease in species diversity and productivity (Rohde 1992). This is evidenced by some species groups with a high frequency in the treeline ecotone showing a reversed latitudinal trend, such as willows, wasps, sawflies, aphids, and peatland birds, which has been related to habitat heterogeneity (Kouki 1999).

Scenarios for biodiversity change caused by human activity indicate land use as the most important driver for biodiversity changes in terrestrial ecosystems (Sala et al. 2000), which has strong relevance to

the treeline ecotone. Changes in biodiversity affect the functioning of ecosystems, and thereby also society through many ecosystem services (Garcia-Ruiz et al. 1996, Cardinale et al. 2012; this Special: Sarkki et al. 2017a,b, Kyriazopoulos et al. 2017, Fleischer et al. 2017, Nijnik et al. 2017).

2. CHANGES IN PLANT DISTRIBUTION

Although changes in temperature and precipitation (including snow cover) surely alter treeline ecotone locations and species diversity, as apparent from the Holocene period and recent history (Kullman 1995, 2003, Aas & Faarlund 1996, 2001, Körner 2003, Shiyatov 2003, Hofgaard et al. 2013, Mathisen et al. 2014, Schwörer et al. 2014), it has also been shown that land use changes may have stronger impact than climate change (Motta et al. 2006, Gehrig-Fasel et al. 2007, Aune et al. 2011, Callaghan et al. 2013, Grytnes et al. 2014, Strebel & Bühler 2015). This is also indicated in reports from the present SENSFOR study (Sarkki et al. 2016, Cudlín et al. 2017, Kyriazopoulos et al. 2017).

In many parts of Europe, there is a long tradition of grazing cattle, sheep, and goats at and above the treeline. This allows forage around the farms at low elevation to be saved for the winter season (Holtmeier 1974, 1987, 2009, Bryn & Daugstad 2001). In northern Europe, semi-domestic reindeer are similarly moved between alpine summer grazing areas and lower elevation winter grazing areas. Through time, this European-wide practice has created non-climatic ecotone locations and diversity characteristics. Many different human activities has contributed to this throughout history (Emanuelsson 1987, Bryn & Daugstad 2001, Gehrig-Fasel et al. 2007) and in more recent times, tourism and recreation has impacted the treeline ecotone vegetation to an increasing degree (Wielgolaski 1998, Körner 2003, Forbes et al. 2005, Törn et al. 2009, Rixen & Rolando 2013, Sato et al. 2013, Tolvanen & Kangas 2016, Ylisirniö & Allén 2016). Activities with an impact across or directly below the treeline ecotones are, or have been, tree clearing for space, fire wood, fencing, and building purposes, and harvesting of young twigs and leaf material, particularly from deciduous trees, as additional fodder. Litter has been used for bedding in the cattle sheds. The magnitude of an impact is dependent on both direct human activities (e.g. cutting) and on grazer diversity and density (Fig. 2), and in addition, on the duration of summer grazing throughout history (Austrheim et al. 2008, Speed et al. 2010,



Fig. 2. Pasture husbandry may differ widely between European mountains. In southern and central Europe, sheep are generally kept in dense herds controlled by herders (upper panel), and gathered in fenced areas for the night to avoid carnivore predation (middle panel). In the Scandinavian mountains, a non-herding system is practiced which allows sheep to disperse over the landscape in small groups (lower panel) under occasional monitoring by owners. Upper panel: Pyrenees, Spain. Photography by J. Inkeröinen. Middle and lower panels: Rodnei Mountains, Carpathians, Romania and Dovre mountains, Norway. Photography by A. Hofgaard

2012). In some treeline areas, natural pastures have been cultivated, fertilized and sown with grass of non-alpine origin to increase the amount of the fodder (Fig. 3). These pasture management methods



Fig. 3. Summer farm with grass production using non-alpine grass species and artificial fertilizers. Flåmsætrin, Central Norway. Photography by A. Hofgaard

have strongly influenced the natural vegetation. Lowland species, including anthropocores, brought to the treeline ecotone areas by these cultivation practices might cause an anomalous increase in species diversity in an area, at least locally and for a short period (Cudlín et al. 2017). However, these non-alpine species could linger in the area and become invasive in future favorable environmental conditions (Crooks & Soulé 1999). As to novel competitive interactions, it may be essential to accurately predict plant species' responses to e.g. climate change (Hofgaard 1999, Alexander et al. 2015). The presence of potentially invasive species make any prediction difficult or impossible (Mooney & Hofgaard 1999, Petitpierre et al. 2016).

During the last 50 to 100 yr, summer farming practice has become strongly reduced both in northern and more southern European mountain areas (Bryn & Daugstad 2001, Tasser & Tappeiner 2002, Camarero & Gutiérrez 2007, Chauchard et al. 2007, Tasser et al. 2007, Batllori & Gutiérrez 2008, Ameztegui et al. 2010, Treml et al. 2016). One reason is the increased importance of imported fodder due to its low cost, while at the same time, the labor-demanding traditional summer farming has become too costly. In some European mountains, however, such as the Alps, farmers are paid by the authorities (Fischer et al. 2008) to continue the traditional pastoral use of elevated mountain areas. This is intended to maintain the character and biodiversity of the cultural landscape that the alpine zone represents. However, in many European mountain areas, grazing by e.g. sheep, is still a normal land use form (Fig. 2), and in others, traditional land use is being replaced by use linked to winter and/or summer tourism (Fig. 4).



Fig. 4. In downhill ski areas, the upper part of the mountain forest and corridors through the forest are managed as open woodlands to favor ski tourism (upper panel: Klosters, Switzerland), and preservation of pastures in the treeline ecotone creates attractive areas for hiking tourism (lower panel: Jaman, Switzerland). Photography by A. Hofgaard

Abandonment or reduction of traditional pastoralism in treeline ecotone areas is normally followed by strong and very fast recolonization and growth of trees, shrubs, and other plant species palatable to domestic and semi-domestic animals. Biodiversity

may increase at the early stages of recolonization of former alpine pasture (Strebel & Bühler 2015, Cudlín et al. 2017), but then decrease at later stages due to growing tree and shrub populations outcompeting alpine pasture species (Holtmeier & Broll 2017) (Fig. 5). This basically land use-driven process is evident both in the Scandes, where mountain birch quickly colonizes abandoned alpine pasture fields (Bryn 2008, Bryn & Hemsing 2012, Bryn et al. 2013) (Fig. 6), and in more southern European mountains (Dirnböck et al. 2003, Gehrig-Fasel et al. 2007, Sitko & Troll 2008), where e.g. mountain pine is an efficient colonizer (Fig. 7). However, in northern Fennoscandia, where reindeer husbandry prevails, temperature also appears to be an important factor directly (Karlsen et al. 2017, this Special). In addition, recent increased precipitation in northern regions (Hanssen-Bauer et al. 2015) might also have influenced mountain birch growth (Mathisen et al. 2014), as this species is favored by precipitation (Wielgolaski 2001, 2003, Wielgolaski & Karlsen 2007). The increased growth observed in mountain birch in the Scandes might also indicate increased nutrient supply as a consequence of increased precipitation and temperature, and subsequent increased decomposition (Wielgolaski & Nilsen 2001, Wielgolaski & Karlsen 2007). Similarly, expansion of green alder *Alnus viridis* Chaix in the Alps as a result of reduced land management has an important influence on nitrogen conditions in former nitrogen-poor montane grasslands (Bühlmann et al. 2016). However, as observed in Swiss mountain grasslands, nitrogen deposition might be negatively related to species richness due



Fig. 5. Recruitment and spread of coniferous shrub (*Pinus mugo*, lower left) and tree (*P. cembra*, right) populations outcompeting alpine pasture species. Rodnei Mountains in the northern Carpathians, Romania. Photography by A. Hofgaard

to increased competition among vascular plants and bryophytes (Roth et al. 2013). Increased nutrient availability in the soil, either through artificial fertilization or increased decomposition, will change the species composition. In particular, the cover and frequency of lichen and bryophyte species are reduced, while graminoids and some deciduous shrubs are generally favored (Klanderud 2008, Olsen & Klanderud 2014). This change in species composition most often results in reduced biodiversity.

Reforestation of husbandry-related grazing lands and other tree colonization in alpine areas requires viable seed production and dispersal from the forest at lower elevation. However, although viable seeds are generally available and easily dispersed by wind



Fig. 6. Re-growth of young birch *Betula pubescens* after abandoned summer grazing practice. The previously open meadows with scattered old birch is now dominated by a dense layer of birch saplings (dark green). Røldal, southern Norway. Photography by N. Eide



Fig. 7. Mountain pine *Pinus mugo* quickly colonize abandoned herding areas (right hand side of the ridge) and form a dense shrub cover. In areas with continued herding (left side), the alpine flora prevails. Rodnei Mountains in the northern Carpathians, Romania. Photography by A. Hofgaard

or birds across the treeline ecotone and beyond, this might not necessarily result in recruitment of tree seedlings surviving to sapling and tree size (Aune et al. 2011). Temporal and transitory seedling cohorts are often characteristic of the upper part of the tree-line ecotone (Juntunen et al. 2002, Kullman 2002, Aune et al. 2011) making the tree species line (cf. Fig. 1) very dynamic. Survival and growth to sapling and tree size in the open exposed alpine area requires long-term favorable site conditions with regard to a large number of abiotic and biotic factors, such as topography, snow cover and duration, soil, wind, temperature, moisture, plant density, and herbivory, and the interplay between these factors (Cairns & Moen 2004, Holtmeier & Broll 2005, Batllori et al. 2010, Hofgaard et al. 2010). In addition, the importance of these factors is species-specific and varies through time (Holtmeier & Broll 2005, Hofgaard et al. 2012, Wielgolaski & Inouye 2013), and the response is also sensitive to the current ecotone structure (Camarero et al. 2017). Consequently, disentangling the causes and predicting treeline ecotone responses to environmental changes are challenging (Sveinbjörnsson et al. 2002), although the most common determinants for treeline ecotone location are temperature and land use (see Section 1.1. above).

Tree advance is initially associated with a change in height growth of previously established saplings (Kullman 2002, Hofgaard et al. 2009) causing densification of the current scattered tree layer (Batllori & Gutiérrez 2008, Mathisen et al. 2014) and movement of the treeline location (Kullman & Öberg 2009). Further densification and relocation is dependent on new establishment and survival in the ecotone and beyond the current upper sapling cohort (Kullman 2002, Hofgaard et al. 2009). The increased abundance of trees and tree saplings changes the structure of the ecotone, including enhanced snow trapping during winter, and thus further promotes tree growth and establishment through, for example, reducing wind destruction of leading shoots. During the winter season, soil temperatures under a deep snowpack do not drop much below zero. Soil moisture is increased in the early growing season by the meltwater (Sveinbjörnsson et al. 2002, Dalen & Hofgaard 2005, Holtmeier 2009).

As trees and forest advance to higher altitudes and latitudes, increasingly more of the former low-alpine or low-arctic area disappears, leaving less space for tundra species (Dirnböck et al. 2003, Gottfried et al. 2012). Knowledge of the rate of this process is important for predictions of tundra disappearance and

associated threats to alpine biodiversity and climate feedbacks (Callaghan et al. 2002b, Pearson et al. 2013). Expansion of forest or shrub cover to areas beyond the current forest at high elevation and high latitude has contrasting climate feedbacks through carbon sequestration (cooling) and reduced surface reflectance (warming) (Bala et al. 2007, Pearson et al. 2013, te Beest et al. 2016). According to estimates for Scandinavian mountain forests, the warming effect is considerably stronger than the cooling, because of the typically low density in mountain forests and the large changes in surface reflectance of snow-covered tundra areas (de Wit et al. 2014). However, the change in reflectance caused by vegetation is a slow process, as the rate of forest migration is low due to the multitude of interacting and counteracting abiotic and biotic environmental factors. The typical advance rate for the warming periods since the late 19th century has been less than 1 m yr^{-1} altitudinally (Kullman & Öberg 2009, Kharuk et al. 2010, Mathisen et al. 2014, Cudlín et al. 2017) and some 10 s m yr^{-1} latitudinally (Hofgaard et al. 2013). These empirically based rate estimates represents less than one-tenth of model-based rate estimates (Hofgaard et al. 2013), and it is essential to consider this mismatch when discussing magnitude and time frame of potential threats to alpine biodiversity.

3. ANIMAL IMPACT IN TREELINE AREAS

In addition to domestic animals, wild fauna depend on, interact with, and change the structure and location of the treeline ecotone. This fauna represents a large number of species of mammals, birds, insects, and other vertebrates and invertebrates. Herbivore activities will have a direct impact through both consumption of biomass (browsing, grazing, seed feeding) and other regular or life history related activities such as trampling, digging, gnawing, and girdling. Animal activities also have indirect impact in treeline areas through e.g. carnivore–herbivore interactions and subsequent animal population dynamics (Hambäck et al. 2004), and through decomposition of dead organic matter by soil-dwelling invertebrates. Quantification of animal impact in treeline areas is not straightforward due to the structural heterogeneity of the ecotone and biogeographic differences throughout Europe. The heterogeneity provides diverse macro- and microhabitats supporting a variety of organisms from soil microorganisms that specialize in particular habitats to animals with large ranges that require different habitats for forage and shelter.

Further, animals typically associated with forested areas, such as some corvids, deer, wolverine, and red fox, frequently use treeline areas and the above tundra to search for food and occasionally for breeding. Animals associated with tundra, such as lemmings and reindeer, periodically or annually forage in the ecotone (Fig. 8) (Post et al. 2009, Killengreen et al. 2012). In addition, as discussed in Section 2, the structure and quality of present treeline ecotone habitats have often been, and still are, strongly influenced by human activities. As the type and extent of human influences vary regionally and locally, the possibility of generalization is limited. In the following paragraphs, we outline some examples of animal impact in treeline areas.

In the central European mountains, increased numbers of ungulates such as red deer *Cervus elaphus* have locally suppressed tree regeneration and impaired self-maintenance of tree stands in treeline areas (Loison et al. 2003, Kiffner et al. 2008, Holtmeier 2012). Similarly, but to a lesser extent, chamois *Rupicapra rupicapra* and ibex *Capra ibex* herbivory affect saplings and trees across the ecotone (ten Houte de Lange 1978, Senn 2000). In addition, high ungulate densities may cause severe soil erosion both in the treeline ecotone and in the adjacent alpine tundra (Holtmeier 1967, 2012, 2015). In most cases, habitat fragmentation and inadequate game management are major causes of 'over-sized' ungulate populations.

In the north, reindeer (semi-domesticated and wild) occur regionally in large populations, and throughout history, have profoundly affected the vegetation in their foraging range, including the treeline ecotone vegetation (Oksanen et al. 1995, Kashulina et al. 1997, Mårell et al. 2002, Colpaert et al. 2003, Helle & Kojola 2006, Olofsson et al. 2009). Reindeer grazing may inhibit tree seedling survival and prevent vegetative regeneration from basal shoots of mountain birch (Kaitaniemi et al. 1999, Holtmeier 2002, Cairns & Moen 2004, Neuvonen & Wielgolaski 2005, Solberg et al. 2005), and under high reindeer densities, the grazing areas might become increasingly degraded with regard to species diversity and productivity (Kullman 2005, Holtmeier & Broll 2006, Broll et al. 2007, Käyhkö 2007, Anschlag et al. 2008, Tømmervik et al. 2009). This is particularly evident in winter grazing areas where the main food for reindeer is slow-growing reindeer lichens (Gaare & Skogland 1975). Lichen ground cover has been strongly reduced both by high grazing pressure and by climate change. In addition to reindeer, increasing north Scandinavian populations



Fig. 8. Winter grazing by semi-domestic reindeer in the treeline ecotone of northern Fennoscandia. Photography by K. Laine

of moose *Alces alces* are affecting height growth and survival of young Scots pine in treeline areas (Stöcklin & Körner 1999, Holtmeier & Broll 2011) and in afforestation areas at lower elevation. These impacts by reindeer and moose on tree recruitment may locally or regionally overrule the influence of changing climate (Stöcklin & Körner 1999, Aune et al. 2011, Holtmeier 2012), and in the case of reindeer, the carrying capacity of the landscape has sometimes been questioned (Neuvonen & Wielgolaski 2005, Solberg et al. 2005).

In addition to large mammals, rodents, chiefly microtine rodents, may have a large impact on treeline ecotone vegetation, particularly in north European mountains. In this region, massive population peaks of lemmings *Lemmus lemmus* and voles, e.g. *Microtus agrestis*, are well-known biotic characteristics with a return cycle of approximately 4 yr (Andersson & Jonasson 1986, Henttonen & Wallgren 2001, Ims & Fuglei 2005). The grazing and gnawing during population peak periods reduce moss and dwarf shrub cover locally and over large regions (Olofsson et al. 2012, Kaarlejärvi et al. 2015). This fragmentation of the bottom and field layer might facilitate establishment of new mountain birch seedlings. However, lemmings and voles also damage and feed on birch seedlings, and in general, rodents adversely affect young trees and shrubs (Fig. 9) rather than promoting successful seedling establishment. Thus, field vole feeding may hasten birch decline, in combination with outbreaks of defoliating geometrid moths and subsequent reindeer grazing (see below). Further, but not of large scale



Fig. 9. Lemming and microtine vole forage damage of mountain birch and surrounding woody plants (upper panel) and willow shrubs (*Salix* sp.) (lower panel). The gnawing activity occurred in winter below the snow surface. Upper panel: Tärnafjällen in the Central Scandes Mountains, Sweden. Lower panel: Abisko in the Northern Scandes Mountains, Sweden. Photography by A. Hofgaard

importance, mountain hares *Lepus timidus* reduce growth of mountain birch saplings by heavy browsing and damage trees by gnawing off the bark (Rao et al. 2003, Holtmeier 2012).

In northern mountain birch-dominated ecotones and adjacent forest areas, the natural dynamics are driven by cyclic and abrupt population increases of defoliating insects such as the autumnal moth *Epirrita autumnata* and winter moth *Operophtera brumata* (Tenow 1972, Tenow et al. 2007). The frequency and intensity of these insect outbreaks are linked to the climate at local to regional scales. They can cause large scale stand mortality and former forest might be turned into tundra (Tenow & Nilssen 1990, Neuvonen et al. 2005, Tenow et al. 2007). This tundra

produced by defoliators, together with the lowered treeline ecotone, might become a long-term state due to intensified reindeer grazing in the newly deforested areas (Kallio & Lehtonen 1975, Oksanen et al. 1995, Holtmeier et al. 2003, Lempa et al. 2005, Neuvonen & Wielgolaski 2005, Neuvonen et al. 2005, Holtmeier & Broll 2006). In a warming climate, expansion of the outbreak range of defoliating insects is likely (Jepsen et al. 2011), and will include higher altitudes and latitudes (Skre et al. 2017, this Special). This might hinder or counteract climate-driven advance of treeline ecotones (Olofsson et al. 2009, Aune et al. 2011, Hofgaard et al. 2013). A parallel to the autumnal moth outbreaks in northern Europe are the cyclic outbreaks of the larch-bud moth *Zeiraphera diniana* in the European Alps. However, larch stands at treeline ecotone elevations are generally not affected due to the low density of trees. At lower elevations, increased cyclic outbreaks are probably due to human-induced expansion of pure larch forests. In cases of severe defoliation, growth and seed production are reduced (Holtmeier 1974, 2015).

Soil-dwelling invertebrates (e.g. earthworms, enchytraeids, collembola, spiders, tardigrades, woodlice, snails, millipedes, nematodes, dipteran larvae, and ants) play an important role through breaking down dead organic matter, mineral-rich (nitrogen, phosphorous) excretory products, and bioturbation, thus influencing nutrient turnover and plant communities (Broll 1998, Holtmeier 2015). In general, taxa, abundance, biomass, and species richness of soil-dwelling invertebrates decrease with altitude. In the treeline ecotone, however, they are controlled by often sharply contrasting site conditions (geological substrate, soils, microclimates, moisture, vegetation) overlapping with historical human impact (Holtmeier 2009). However, in contrast to mass outbreaks of leaf-eating insects, soil invertebrates do not significantly influence treeline spatial and temporal structures, whereas reforestation of abandoned alpine pastures will probably bring about major changes influencing soil invertebrate fauna and also aboveground insects and ground beetles (*Carabidae*) in the long-term. Predicting possible feedbacks on the treeline, however, is difficult because of the often inscrutable interactions of the numerous environmental factors and their relative implications (Holtmeier 2009, 2015).

Among birds, the Eurasian nutcracker *Nucifraga caryocatactes* is a highly effective agent influencing the tree distribution pattern of stone pine *Pinus cembra* and the dynamics of treeline ecotones in central and eastern European mountain areas due to its

seed-caching activities (Zong et al. 2010, Holtmeier 2012, 2015). Surplus stored seeds (i.e. seeds not consumed during the winter) may germinate and result in the establishment of trees in new areas and at higher elevation. This bird-mediated sowing has contributed to the re-establishment of stone pine over large areas formerly cleared by man. Further, without the nutcracker, natural upward advancement of trees in response to climatic warming would be impossible. Birds other than nutcrackers, e.g. grouse and ptarmigan species, and seed-eating birds, usually have a low impact on the treeline ecotone. However, grouse and ptarmigan species might locally limit growth, particularly of young trees, by consuming or destroying buds and terminal shoots (Holtmeier 2012, 2015), and in addition, pastoral abandonment may lead to an overall increase in avian diversity (Laiolo et al. 2004) due to increased shrub and tree cover.

4. CASCADING EFFECTS OF LAND USE AND CLIMATE CHANGES: A SCENARIO EXAMPLE FROM THE NORTH

The outcome of combined pressure on the natural environment by intense land use and climate changes might be difficult to quantitatively and qualitatively forecast. However, it is necessary to consider the matter for sustainable management reasons. A commonly discussed example is the semi-domestic reindeer herding system in northern Scandinavia. The long history of the herding system has shaped the distribution and abundance of species and thus formed the current cultural landscape. However, the herding system is not static and has to adapt to modern socioeconomic changes and requirements, at the same time as the climate is both highly variable and changing. Here we outline some of the biological complexities involved (see also Sections 2 & 3 above). While reindeer owners may wish to increase their income by allowing more animals within a given area, this of course will result in increased grazing pressure. The new grazing regime might or might not initially affect both summer (herb-dominated) and winter (lichen-dominated) grazing grounds, but winter areas are common bottlenecks in the annual migration practice. Lichens are a major reindeer food source in the winter, and accessibility varies widely between individual winters due to snow quality. Warm winters with rain and icing events force reindeer to use a lot of energy digging for lichens. Due to the very slow growth rate of lichens, considerable

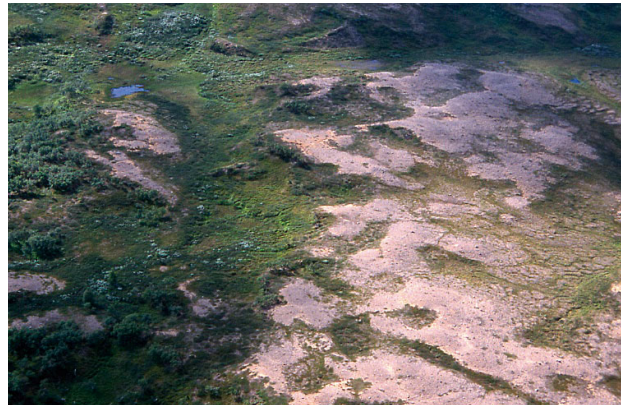


Fig. 10. Wind-eroded convex topography on Koahppeloarvi (northernmost Finnish Lapland). The substrate is rapidly draining sandy-skeletal glacial till. Erosion was initiated by reindeer winter-grazing activities that destroyed the dwarf shrub–lichen vegetation and made the substrate susceptible to deflation. Moisture deficiency is characteristic of such sites and adversely affects tree seedling establishment. The photograph was taken from approximately 250 to 300 m above ground. Photography by F. K. Holtmeier

time is needed for vegetation recovery following excess removal of lichens by e.g. too high grazing pressure. At the same time, digging for lichens by the reindeer population cause patches of open soil, which facilitate establishment of higher plants, e.g. mountain birch. Birch is further facilitated by the ongoing increased temperature and precipitation in the region, although on well drained substrates exposed by reindeer scraping and trampling, moisture deficiency affects or prevents birch seedling establishment (Fig. 10). Increased temperature and moisture availability may also increase decomposition rate and mineralization of organic material. In these ways, nutrient-demanding plant species may outcompete the slow-growing lichens. Because of diminishing lichen cover, the reindeer population has to adjust its diet to include vascular plant parts such as the young shoots of birch saplings. However, at increased temperatures in winter, the survival rate of the eggs of defoliating insects using birch as host species will increase along with arrival of new defoliating species in the area. Increased frequency of defoliators and increased spatiotemporal outbreak occurrence may transform birch-dominated areas to treeless tundra. The quality of these areas as winter grazing areas is thus further diminished, and the reindeer owners will have to reduce the number of animals using the area or keep the herds in summer grazing areas for prolonged periods. This will, however, cause other cascading effects.

5. CONCLUDING REMARKS AND PERSPECTIVES

While from a continent-wide view, thermal deficiency increasing with elevation and latitude controls treeline ecotone structure and position, many other climatic and biotic factors are involved at regional and smaller scales. Not least, the after effects of historical human impact are often of major importance and may overrule the influence of natural factors. Therefore, assessment of treeline ecotone variety and causation needs a cross-disciplinary complex approach combining natural and socio-economic sciences. Climate change, reduced pastoral use, and increased tourism and other human uses are the main driving factors of current changes across the treeline ecotone. The role of animals (wild and domestic or semi-domestic ungulates, rodents, birds, and insects) in the treeline ecotone needs to be studied in more detail, in particular regarding possible cascading effects such as the presented mountain birch–reindeer scenario. Treeline ecotone change will have far-reaching implications for biodiversity, plant and animal communities, and also for the relative effects of microtopography on site conditions (microclimates, soil ecological conditions) and ecosystem services (e.g. protection from destructive avalanches, prevention/reduction of soil erosion).

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