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Treelines—Approaches at Different Scales

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Abstract: Scales in treeline research depend on the objectives and must match the underlying natural processes. Factors and processes at one scale may not be as important at another scale. In the global view, the number of factors influencing climatic treeline position can be reduced to the effects of heat deficiency. Emphasis, however, should be laid on differentiation of the treeline by their regionally and locally varying physiognomy, diversity, spatial and temporal features, and heterogeneity. An assessment of the relative importance of the factors shaping regional/local treeline physiognomy, spatial patterns, and dynamics should have priority. This can be achieved only by syndisciplinary research. Such studies are indispensable for assessing treeline response to climate change at the regional and landscape scales.

Keywords: scales; treeline heterogeneity; climate change; treeline dynamics; human impact; treeline history; animals' impact

1. Introduction

Altitudinal and polar treelines are very heterogeneous and show a great physiognomic, genetic, and ecological variety due to their geographical position (climatic zone or region, climate character), tree species and history of vegetation, climate, and landscape (e.g., steep or gentle mountain slopes, gently rolling landscape). However, treeline researchers have been operating and are operating on their common object with different objectives and methods and at different spatial (global/zonal, regional, landscape, local, micro) and temporal scales (short-term, medium-term, long-term). Factors and processes at one scale may not be as important at another scale. This has probably been, and still is, the main problem for treeline researchers from different disciplines in understanding better the complex nature of their common research object and in comprehending each other's arguments.

It is not a question of whether or not treeline research has to be carried out at large or fine scales, but the scale depends on the objectives and must match the underlying processes [1,2]. The focus may be, for example, on the physiological responses of trees to heat deficiency or insufficient moisture and nutrient supply at the treeline in general or on regional and local treeline spatial patterns and dynamics under the influence of numerous mostly interacting factors. Both approaches are justified.

Heterogeneity of treeline and spatial pattern and ecological variety increases from the global/zonal to finer scales (Figure 1). Temporal scales—short-term ($\leq$1 year), medium-term (some years to several decades), and long-term (several decades, hundred years, or more) also play an important role. The timing and intensity of Holocene climatic fluctuations and treeline response vary geographically (e.g., [3–6]).

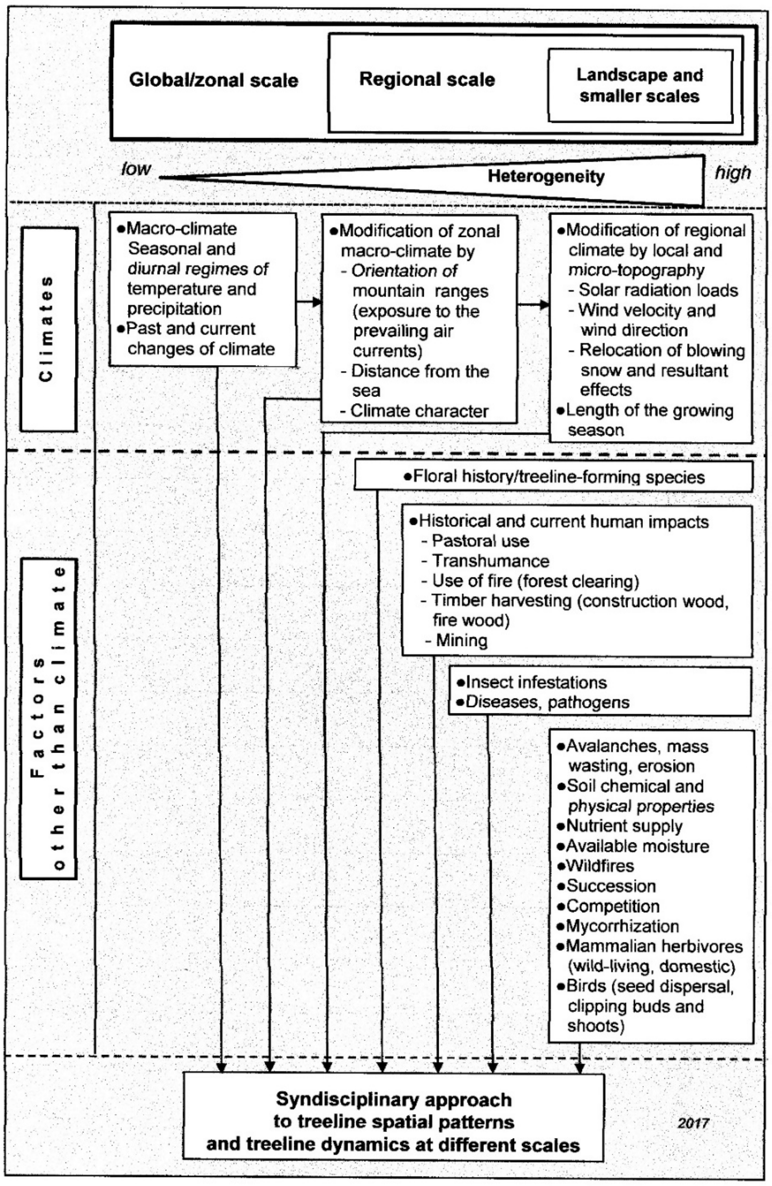


Figure 1. Treeline heterogeneity and complexity at different scales need a syndisciplinary approach. Coarse scale constraints are also inherent in physical and biological processes at finer scales. Their influence, however, may be disguised by the local factors. Modified from Holtmeier and Broll [4].

The relative importance of the regionally, locally, and temporally varying factors and processes has increasingly attracted interest in treeline research [4,7–16]. Treeline is usually defined as a theoretical “line” connecting the uppermost or northernmost trees exceeding a certain minimum height. A minimum tree height of ≥2 m is internationally well accepted, although there many alternatives (see [5] for discussion). In the present article, the term “treeline” is applied to the transitional zone (ecotone), extending from the altitudinal or northern limit of closed forest to the uppermost and northernmost often stunted individuals (krummholz, scrub) of the forest-forming tree species (i.e., the physiological limit of tree growth). The minimum tree height is disregarded.

The aim of the present article is to explain the need for treeline studies to combine the results from different disciplines, including sufficient flexibility to switch between scales of consideration, and to meet the complexity of the combined effects of the numerous partly interacting factors that control treeline position and treeline spatial patterns and dynamics. This article is concerned with treelines outside the tropics.

2. Traits and Causation of Treeline at Coarse (Global/Zonal) Scales

In a global view, treeline is usually handled as a "line" presumed to be approximately in balance with thermal conditions. Early research already explored coincidences of altitudinal and polar treelines and certain isotherms (mean air temperature) that roughly indicate the thermal control of treeline at the global and regional scales (see [5,16]). Modeling the influences of abiotic factors on treeline position in New Zealand at different scales [11] showed that 82% of coarse scale (regional) variation in treeline elevation is associated with thermal conditions, while these explained only 44–52% of variation at finer scales (Figure 1).

The debate on the complex mechanism of heat deficiency underlying worldwide control of treeline position has repeatedly been resumed with special emphasis on the role of low soil temperature [17–19]. While temperatures of foliage tissue may considerably differ from ambient air temperature (e.g., [20–23]), the mean soil temperature in the rooting zone and the root temperature at similar depths usually match. Hence, the rooting zone temperatures may better correlate than air temperatures with worldwide treeline position (see also [24]). The limit of tree growth in the world's humid mountains, for example, has been found to correlate best with a mean 5.5–7.5 °C soil temperature at a 10 cm depth during the growing season or year-round, as in the tropics [18]. Such criticalisotherms may serve as a reference line. Thus, treelines positioned below such an isotherm should be explained by climatic fluctuations or other, regionally and locally varying factors (e.g., permanent strong winds, drought), which may prevent trees from reaching their altitudinal and northern limits set by heat deficiency (e.g., [5,25,26]).

In addition to the latitudinal decrease of treeline, the decrease in tree stature (Figure 2) is common at altitudinal and polar treelines, and reflects the control of tree growth by heat deficiency. As wind velocity increases with elevation, wind (turbulent mixing, evapotranspiration, mechanical damage) plays an important role at the treeline, at least at mid-latitudes (global, zonal scales), where strong (upper-air) westerly winds prevail. Strong and cold polar winds will probably also influence the northern treeline.

Figure 2. Decrease of tree stature at treeline (about 3480 m) on Tumbstone Ridge (Rocky Mountain National Park, Colorado). Both the wedge- and mat-like growth forms (right) and the high-stemmed tree islands below (left) are formed by the same species (*Picea engelmannii* and *Abies lasiocarpa*). Photo by F.-K. Holtmeier, 13 July 1994.

Approaching the tree limit, height growth is generally more impaired than diameter growth. Thus, compact growth forms, particularly in mature trees, are very common (e.g., [27–29]) (Figure 3). The uppermost krummholz, however, often displays mat-like growth. Like chamaephytes (dwarf shrubs), low mats profit from the relatively warm, calm microclimate near the ground and are largely protected from climatic injury in winter by the snowpack, facts that have been well known since the beginning of the systematic treeline research (e.g., [30–32]).

Figure 3. Compact bristlecone pine (*Pinus aristata*) in an open tree stand on Goliath mountain over 1000 years old, Mt. Evans (Colorado) at 3500 m. Photo by F.-K. Holtmeier, 7 July 1979.

The ability of certain tree species to persist even for centuries as suppressed growth forms plays an important role, as the trees may buffer adverse periods that inhibit height growth (Figure 4). After site conditions improve, "suppressed" trees may recover and assume normal vertical growth, usually by the release of erect branches (phenotypic plasticity) (Figure 5) (e.g., [5,33–37]). In case conditions, dieback may worsen. Phenotypic plasticity varies in the different treeline tree species. In any case, it is advantageous for tree survival at the altitudinal and polar treeline.

Figure 4. Suppressed vertical growth in mature bristlecone pines (*Pinus aristata*) on extremely wind-swept terrain at 3360 m (Kingston Peak, Colorado Front Range). Photo by F.-K. Holtmeier, 1 August 1991.

Figure 5. Wind-shaped subalpine fir "krummholz" (*Abies lasiocarpa*) that released vertical stems after a long time of suppressed growth. Dieback due to blowing snow/ice occurred at the wind-exposed edge (left), while snow fungus infection (*Herpotrichia juniperi*) caused needle loss at the downwind end (right) of this clonal group, where blowing snow accumulates in winter. Niwot Ridge (Colorado Front Range) at 3450 m. Photo by F.-K. Holtmeier, 7 July 1997.

3. Treeline at Landscape (Regional), Local, and Microscales

The great physiognomic and ecological variety of treeline are closely related to the regional and local conditions (regional climates, microclimates, geomorphology, tree species, soils, human impact [4,5,38–40] (cf. Figure 1). For example, treelines may be formed by conifers or deciduous trees or by both. Moreover, a treeline may be interrupted by a "line" formed by trees several meters high. In other places, the high-stemmed mountain forest gradually merges into dense scrub ("krummholz," the same species as that in the forest; cf. Figures 4 and 5) that borders the alpine zone. In some mountains, the high-stemmed forest gives way to a belt of "true krummholz" (other species as in the forest; e.g., *Pinus mugo, Pinus pumila, Alnus viridis*, and *Alnus sitchensis*) bordering the alpine zone [33,41].

A deeper insight into the varying spatial treeline patterns, causes and dynamics can only be achieved by regional and local studies within different climatic regions (climate character, temperature, and precipitation regimes) and linking the results of treeline research at different spatial (cf. Figure 1) and temporal scales (see also, [13,42–48]).

The effects of an underlying topographic pattern on site conditions (cf. Figure 1) are key factors controlling spatial and temporal treeline structures at the landscape and finer scales, (e.g., [4,5,7,48–56]). Microclimates, distribution of soil temperatures and soil moisture, relocation of snow, depth, and duration of the winter snowpack, avalanches, and runoff all depend on microtopography (length and width $\leq$10 m, area 10–100 m^2). These effects locally overrule the direct influence of general thermal altitudinal gradients (see below), at least as long as the terrain is only sparsely covered with trees. Comparable effects have been documented for the alpine zone [57]. Atmospheric pressure is the only climatic factor that is not influenced by microsite conditions [58].

Microtopography also influences pedogenesis and the distribution of soil types. While soils in the treeline ecotone and in the adjacent lower alpine zone (i.e., potential treeline) have developed with the limits set by the general elevational gradients of temperature and precipitation, they vary considerably depending on the local parent material, substrate (physical and chemical properties), vegetation, and on climate history (e.g., [51,59–62]). Thus, a locally varying mosaic of soils (soil types) is typical of the treeline ecotone, whereas no real treeline-specific soils exist [5].

At coarse scales (global, zonal, and regional), the influence of soils on the treeline position (mature trees) can be widely ignored, except for increasing paludification due to thawing permafrost in wide areas at the northern treeline (e.g., [63,64]). Extended boulder fields (saprolite) may also be important. At the local scale and microscales, however, soil conditions may play an important role, particularly at the seedling stage and, thus, for treeline dynamics and high-altitude afforestation as well. Soil temperature, for example, moisture, and nutrient supply are often critical factors in this context.

In addition to the effects of local landforms and microtopography on the ecological conditions at treeline, the feedbacks of trees and tree groups on their immediate environment may be of major importance. For example, depth, spatial pattern, and duration of the winter snowpack and resultant side effects often must be attributed to trees' feedbacks (e.g., [65,66]). Moreover, compact trees shading the ground reduce soil temperature (e.g., [17,59,66,67]) and, thus, create a cold root zone. However, even age-old trees and suppressed compact krummholz in the treeline ecotone have been growing for many decades, centuries, or even thousands of years and are still producing growth rings, even though shading by the tree canopy has been keeping growing season soil temperature low all the time. Remarkably, many suppressed ancient trees have promptly responded to decreasing climatic stress by the release of vertical stems several meters high (phenotypic plasticity, cf. Figure 5) even though their rooting zone has not warmed up. Thus, the role of soil temperature in treeline dynamics needs further study.

Nevertheless, tree roots spreading into treeless sunlit gaps as well as tree seedlings would benefit from the warmer conditions, provided no other adverse factors, such as intense solar radiation loads, moisture deficiency, and wind impact outweighed the advantage of wider spacing (e.g., [68–70]). Thus, widely spaced trees are more exposed to climatic injuries than those within tree stands, as is reflected in an abrupt increase of climatically shaped growth forms above the closed forest. At sites with no or only little snow in winter, severe frosts may destroy fine roots in the topsoil [68,71–73]. Root disruption increases seedling mortality and the loss of fine roots impairs efficient nutrient uptake. In the end, the supposed positive effect of wide-spacing-mechanism (sensu [17]) would not explain the existence of abrupt climatic treelines.

Moreover, the ecological properties and requirements of the tree species represented at treeline and their sensitivity to physical and biological disturbances (e.g., [74]) as well as regeneration (seed-based or layering, root suckers; [75]), mycorrhization, and, not least, the species' competitive ability (e.g., [27,76–79]) must be taken into consideration at small scales (cf. Figure 1). The susceptibility of trees to different environmental factors may be different at different life stages [80]. Diseases, pathogens, insect calamities, and wildlife are factors that may lastingly affect trees and other vegetation at treeline at the regional and local scales and must not be disregarded [81]. Last but not least, postglacial landscape history and site history often have considerably influenced treeline spatial structures and dynamics (Figure 6).

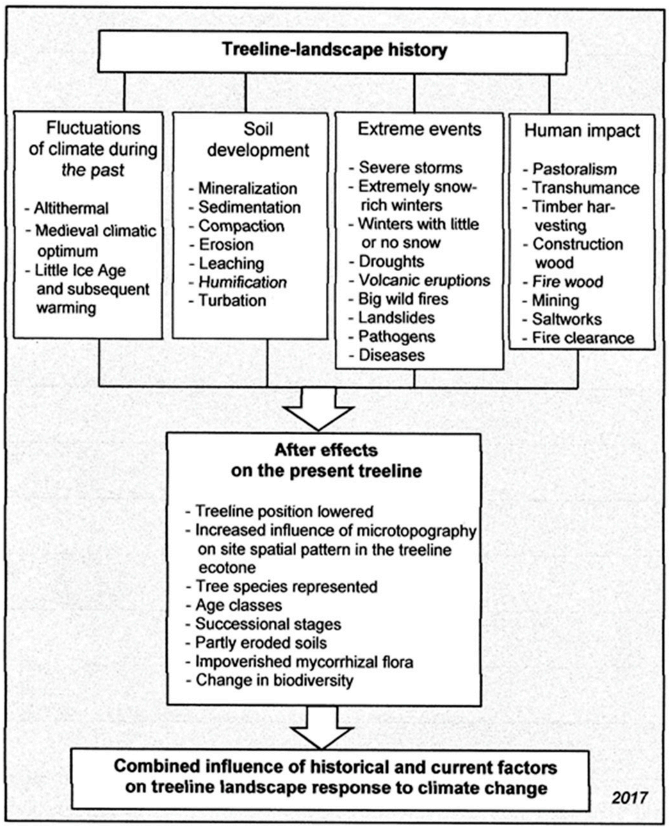


Figure 6. Present treeline under the influence of treeline-landscape history.

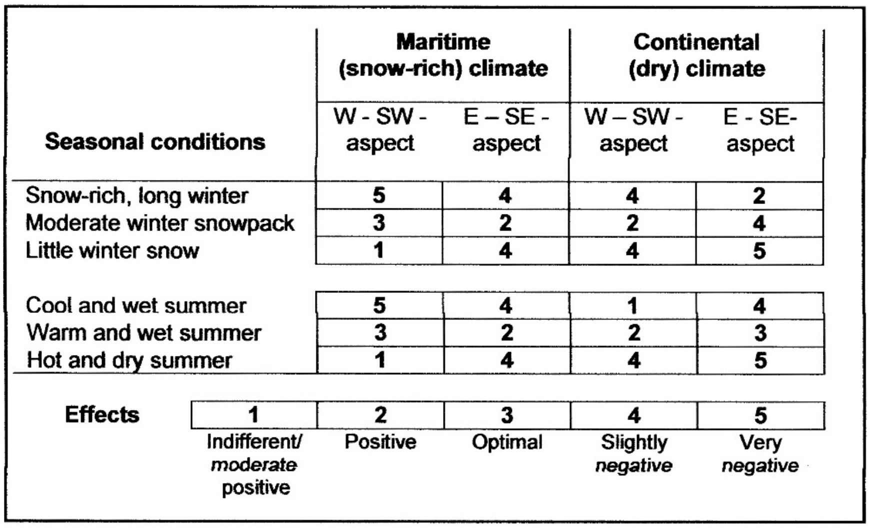
4. Treeline Dynamics at Different Spatial and Temporal Scales

At the coarse scale (global, zonal), the magnitude of treeline advancement can be roughly predicted by the calculated shift of whatever isotherm that would set a limit to tree growth. According to a model presented by Paulsen and Körner [82], for example, treeline would be located at an elevation where the minimum length of the growing season is 94 days, with a daily minimum temperature just above zero (0.9 °C) and a mean of 6.4 °C during all these days. The extent of treeline advancement to greater elevations and more northerly latitudes, however, varies regionally, locally, and temporally as well as by tree species (e.g., [8,29,43,63,83–89]). The direct influence of heat deficiency on tree establishment is often overruled by other abiotic and biotic factors (e.g., permanent strong winds and recurrent periods of drought). They can prevent tree establishment already below their thermal limit. Moreover, the establishment of new tree generations (reproductive success and succession) and feedbacks on site conditions in the treeline ecotone usually respond to climate change with a time lag.

At local and finer (micro) scales, the multiple interactions of trees and site conditions (microclimate, soils, moisture, snowpack, etc.) are of primary importance. Thus, the distance from the seed source, the way of seed dispersal (anemochoric, zoochoric), the overlying of seeds, the availability of viable seeds, seed predation, and the availability of favorable seed beds (e.g., [5,85,87,88,90–93]) are relevant factors that need further examination. However, discussion of whether reduced availability of viable seeds are playing a major role or not is controversial (e.g., [3,5,17,19,45,87,90,93–97]). In any case, the performance of "new" trees that survived the seedling stage and became a sapling appears to be the most important factor for treeline advance in the medium and long term.

Monitoring treeline at the landscape and smaller scales (e.g., tree coverage, successional stages, tree species, tree height, growth forms, age classes, seedling establishment, and survival rate, in particular, as related to site conditions, etc.) is fundamental for assessing the relative importance of the factors in the regional and local context and for looking ahead to the regional and local treeline response to global climate change [44,46,54].

Thus, the relative effects of seasonal conditions (snow cover, temperature, and humidity) modified by the exposure of local topography to incident solar radiation and the prevailing winds (season, direction, and velocity) on tree seedlings at the treeline are different in maritime mountains compared to continental mountains (Figure 7). Strongest contrasts in exposure to solar radiation and its effects on the length of the snowfree season, moisture conditions, temperature, and vegetation can be expected in continental high-mountain areas (regional scale).



Seasonal conditions	Maritime (snow-rich) climate W - SW - aspect	Maritime (snow-rich) climate E – SE - aspect	Continental (dry) climate W – SW - aspect	Continental (dry) climate E - SE- aspect
Snow-rich, long winter	5	4	4	2
Moderate winter snowpack	3	2	2	4
Little winter snow	1	4	4	5
Cool and wet summer	5	4	1	4
Warm and wet summer	3	2	2	3
Hot and dry summer	1	4	4	5

Effects	1	2	3	4	5
	Indifferent/ *moderate* positive	Positive	Optimal	Slightly *negative*	Very *negative*

Figure 7. Possible effects (schematic) of seasonal conditions on tree seedlings invading west-southwest and east-southeast exposures of local topography in maritime and continental climates of the temperate zone in the northern hemisphere. Prevailing winds from western directions.

Lack of available moisture during the growing season may be more critical for tree establishment and alpine plant communities in general than heat deficiency, as for example in some semi-arid or arid inland mountain areas, in the Mediterranean, and on several subtropical islands, where the position and local pattern of the treeline often depend on low precipitation above the trade wind inversion, (e.g., [52,98–106]).

At the treeline on Tenerife, summer drought turned out to be critical for the survival of *Pinus canariensis* seedlings, whereas these suffer from frost in winter due to the absence of a protective snow cover [101]. In Greek high mountains protected from advective moisture-carrying air masses, tree growth appears to be affected more by frequent insufficient plant-available moisture than by low growing season temperature [103]. In the central Himalayas, for example, where precipitation decreases with increasing elevation above 2000–3000 m, birch (*Betula utilis*), which forms the treeline (3900–4150 m), appears to be limited by a low amount of moisture during the pre-monsoon season rather than by thermal deficiency [107].

However, the lack of moisture during the growing season also occurs at the treeline in the temperate and boreal zone. Thus, in the Colorado Front Range, the increase in droughts has led to high mortality in conifers in subalpine forests since the 1980s [108]. In the same place, artificial warming increases the productivity and competitive ability of plant communities in the alpine zone only if soil moisture is sufficient [109]. Long-lasting winter snowpack on the Sun-exposed leeside of local topography may prevent moisture stress until early summer, when moisture in the earlier snow-free sites is already exhausted [59,110]. In central Sierra Nevada (California), warm and dry conditions reduce diameter growth in treeline conifers, while deep snowpack mitigates drought effects. On the other hand, lasting snowpack can limit the growth of species that are usually restricted to snowrich terrain, such as mountain hemlock (*Tsuga mertensiana*) [111]. At the treeline in eastern Quebec, the expansion of black spruce (*Picea mariana*) driven by climate warming has slowed down probably due to drought and drying seedbeds on tundra soils [112]. In the southern Swedish Scandes, mountain birch has been declining in response to summer droughts, while Scots pine expansion will probably continue [3]. In the Sudetes Mountains (Central Europe), seedling establishment was found to be adversely affected by summer warming causing drought, especially in the upper part of the treeline ecotone and on south-facing slopes [96]. Drought effects, as a result of low regional precipitation, may be locally enforced by the lack of plant available moisture resulting from a low water-holding capacity (coarse texture, low humus content) or a high capillary tension on certain sites (e.g., loamy soils) in the treeline ecotone. Thus, at the mountain birch treeline in northern Finland, for example, low soil moisture is probably critical for the establishment of seedlings on permeable wind-eroded soils (e.g., [68,113]). Normally, seedlings are more affected by a lack of available moisture than deep-rooted mature trees.

Moreover, climate change and its side effects, such as the increase of insect attacks and wild fires, will not influence different tree species in the same way. Larch (*Larix* sp.), for example, protected by a thick cork-like bark and renewing needle foliage every year, is relatively tolerant to fire in contrast to, for example, spruce (*Picea* sp.), subalpine fir (*Abies lasiocarpa*), and Swiss stone pine (*Pinus cembra*).

The temporal scale of consideration plays a major role in this respect. Thus, in the long term, for example, the increase in drought-tolerant tree species such as Douglas fir (*Pseudotsuga menziesii*) and seral non-host aspen stands (*Populus tremuloides*) at the cost of subalpine fir (*Abies lasiocarpa*) and increasing populations of young trees, may reduce the susceptibility of weakened tree stands to bark beetle attacks (e.g., [114]). Bark beetles kill more thick trees than thin ones because trees with a larger diameter have a thicker phloem, which the beetles need for oviposition.

Not least, many treelines are not natural and many natural climatic treelines are not in balance with the current climate (e.g., [5,11,27,69,83,115–117]). The after-effects of postglacial treeline history (cf. Figure 6) appear to be important factors in this respect, at least in high-mountain areas of Europe and Asia, that were already settled in prehistoric times and where human impact (pastoral use, forest clearing, fire, mining, etc.) on the treeline is almost omnipresent ([5]). Yet, land-use history, both intensity and longevity, vary locally and regionally and, thus, can be assessed at regional/local scales only (e.g., [47,85,118,119]).

Past climates as well as natural and anthropogenic disturbances have produced a spatial-temporal mosaic of patches at different successional stages (cf. Figure 6) that responds differently to climate change. Modern change in economic structure, particularly decreases or cessations of grazing alpine pastures, probably supported by warming climate, has resulted in the invasion of many former alpine pastures by trees (e.g., [5,27,83,89,96,120–124]).

The regionally varying response of the altitudinal and northern treelines to the warming periods from the 1920s to the 1940s and since the late 1980s (e.g., [5,39,118,125–127]) and long-term dendrochronological studies (e.g., [80]) suggest that a more differentiating view is needed. In many areas, the treeline responds to climate warming by the transformation of suppressed existing growth forms rather than by the establishment of new trees at increasingly higher elevations (e.g., [6,35,36,45]).

Trees that can establish themselves beyond the current treeline are usually exposed to a much windier climate than at lower elevation (e.g., [3,49]), regardless of whether the treeline is natural or anthropogenic. Thus, the anthropogenic treeline is often climatically shaped like a natural climatic treeline [27,128]. The feedbacks of increasing tree population and alpine scrub (e.g., willows) may facilitate or affect seedling establishment in the remaining open patches and influence treeline dynamics profoundly (e.g., [65,113,129]). It is often difficult, however, to unambiguously distinguish the overlapping effects of a warming macro climate (global and zonal) and local conditions being modified by the feedbacks of tree vegetation. Thus, research on these feedbacks and the response of seedlings and saplings rather than of mature trees to their current treeline environment should be intensified (see also [9,129–131]).

Comparatively little attention has been paid so far to the effects of mammalian herbivores, birds, and insects on treeline ecotones, with a few exceptions (e.g., [5,94,132–139]). Animals may lastingly influence tree growth and physiognomy, regeneration, seed dispersal, soils, distribution pattern of trees, and treeline dynamics at the landscape and smaller scales (cf. Figure 1). The expansion of stone pines (e.g., *Pinus cembra*, *P. sibirica*, *P. albicaulis*, *P. koraiensis*; five-needled fascicles, wingless seeds, cones that remain closed at maturity) into, say, formerly grazed areas and the advancement to a potential climatic tree limit can be mediated only by seed dispersal and seed caching through nutcrackers (*Nucifraga caryocatatces*, *Nucifraga macrorhyncos*, Eurasia; *Nucifraga columbiana*, North America) [5,94].

On the other hand, animals' adverse effects (e.g., herbivory and trampling) on seedlings and saplings may locally overrule the influence of a warming climate that drives a treeline to a higher elevation and a more northerly position. Mass outbreaks of leaf-eating insects and bark beetles, for example, usually affect large forested areas at the regional (and landscape) scales, whereas wild and domestic mammalian herbivores and birds influence treelines usually at the local and microscale. Soil material excavated by burrowing rodents and displaced over the ground surface may lastingly influence site conditions (e.g., [94,134,140,141]). Animals' effects, in particular on seedlings and saplings, should be more intensively studied [5,94,138].

The change of treeline biodiversity in response to changing treeline patterns can be expected at all scales. Biodiversity may increase during the early successional stage of tree advancement into the open tundra and alpine zone. Later, however, treeline diversity might decline parallel due to increasing tree cover (e.g., [65,142]). As biodiversity is mainly the result of the regional and local history of the biocoenoses and ecosystems and of the present environmental conditions (cf. Figures 1 and 7), it must primarily be assessed at regional and finer scales. On low elevations, for example, suitable habitats for alpine plant communities might shrink considerably or completely disappear, whereas on high mountain massifs a relatively broad alpine zone will be left (Figure 8). The discussion on this issue is controversial (e.g., [3]). The regional and local variations are much more difficult to foresee than global advance of treeline driven by global warming (see also [142]).

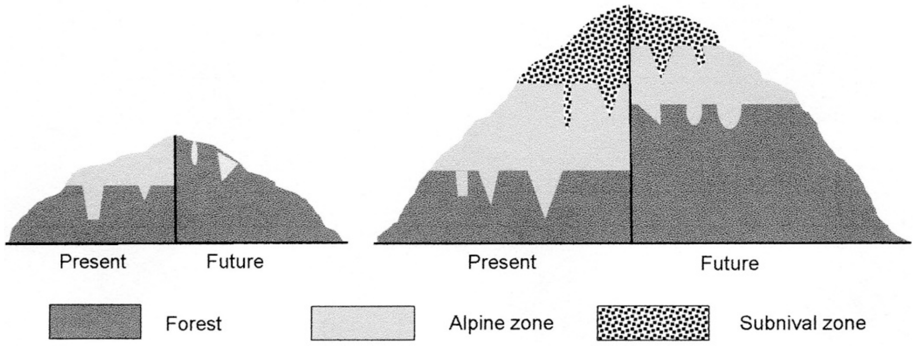


Figure 8. Possible effect of mountain forest expansion to higher elevation on relatively low mountains (**left**) and large mountain massifs (**right**).

Similar topographic structures within and beyond the present treeline ecotones usually cause similar "treeline types". The patchiness of a treeline on a gentle mountain slope, for example, differs from a treeline on heavily dissected high-mountain terrain or on a smoothly rolling land surface. Thus, local treeline types characterized by a distribution pattern of trees, the nature of the prevailing damage, and tree physiognomy and reproduction, as related to local landforms and their effects on site conditions, could help to differentiate treeline ecologically [4,54]. The feedbacks of an expanding forest (increasing tree densities) on the environment will reduce the regional landscape albedo and increase surface roughness of the present treeless tundra. Consequently, more sensible and—to a lesser extent—latent heat (evapotranspiration) will be released into the lower atmosphere and warm it up above that in high albedo areas (e.g., [143–145]). In the long term, the heating effect will probably increase, mainly due to the infilling of the present forest–tundra ecotone with trees. In northern Siberia, where evergreen conifers will probably expand at the costs of deciduous species, the change in albedo might be particularly notable [146].

In contrast, in rugged high mountains, a noteworthy heating of the lower atmosphere is less likely because on steep slopes the lower alpine area to become covered with forest and tree stands appears to be too small (Figure 9; [39,147]) if compared to rolling subarctic/arctic landscapes where the forest may expand northward hundreds of kilometers [143,148].

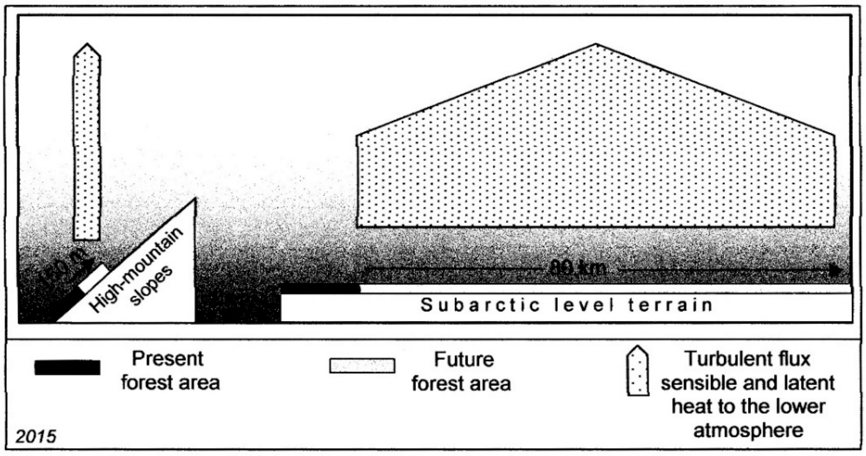


Figure 9. Influence of forest advancement to greater elevation on steep mountains and into presently treeless subarctic areas on heat transfer to the lower atmosphere. On steep high-mountain slopes, a forest advance of 150 m on a 2-km wide transect would increase the area of reduced albedo by 3 km^2, while on level subarctic terrain, a comparable rise of temperature would be associated with a northward shift of the boreal forest by 80 km. As a result, the area (width 2 km) of reduced albedo would increase by 160 km^2.

On the other hand, positive feedbacks of expanding mountain birch forest on warming as an effect of lower albedo and reduced snow cover were found in southcentral Norway [149]. In high mountains, such as the Swiss Alps, the upward shift of the climatic snowline is also expected to cause significant heating due to the comparatively low albedo of the exposed ground and prolonged snow-free season [150].

Satellite images or other remote sensing techniques allow for the exploration of treelines even in almost unknown and often inaccessible areas, thus providing an unprecedented broad database for monitoring treelines and treeline shifts (e.g., [42,117,151–157]). Spatial resolutions approximately at a 1-m scale are possible [13,158,159]. Light-weighted unmanned aerial vehicles (e.g., octocopters) may support field mapping of, for example, fine-scale treeline spatial patterns (canopy structures, clustering, ground vegetation) or of the local snow pattern and snowmelt by repeat photography. Ground-based repeat photography has been successfully used for the detection of treeline landscape change over decadal time scales (e.g., [29,45,144,160,161]). Remote sensing data combined with as many ground truths and laboratory experimental studies as possible appear to be the appropriate way to assess treeline variety, diversity, and change at all scales. The more details, such as reproduction, mortality, physiological adaptation, feedbacks of trees, human impact, wildfires, etc., that are added to the models, the more effectively they can be applied at landscape and regional scales.

5. Conclusions

There is neither a special scale nor a specific scientific method with which treelines can be approached. Scales and methods depend on the objectives of the studies and must match the underlying processes.

In a global view, the position of the altitudinal and northern climatic treelines is closely related to heat deficiency. At the regional and smaller scales, however, geology, local, and microtopography, substrate, historical and present human impact, diseases, pathogens, and animals' influence usually determine treeline position and spatial pattern and successional stages often overlap with the direct effects of the macroclimate and may prevent trees from reaching their climatic (thermal) limit. The great regional physiognomic, biological, and ecological diversity of the altitudinal and polar treelines turns out to be an outstanding common trait in the global treeline pattern. Thus, treeline research should focus more on the regional and local peculiarities rather than on generalizations and assess the relative importance of the treeline influencing factors along the world's climatic treelines. To grasp treeline ecological heterogeneity, the complexity and variety of a syndisciplinary approach at different scales is needed.

An assessment of the relative importance of the relevant treeline factors in regional and local contexts is also fundamental for looking ahead to the regional (and local) treeline response to global climate change. This would also provide a sound base for sustainable ecological management as well as for the restoration and maintenance of protected high elevation forests in treeline areas under the influence of changing macroclimates (global, zonal, or regional). Additional attempts to find better worldwide coincidences between certain mean air or soil temperatures—or of both—and tree growth at the climatic treeline are really not very promising, as they will only confirm the well-known fact that heat deficiency is the globally dominating constraint in treeline causation. The regional and local variations are much more difficult to foresee than the global advance of treelines driven by climate warming.Treeline types characterized by the distribution pattern of trees, the nature of the prevailing damage, and tree physiognomy, and reproduction, as related to local landforms and their effects on site conditions, could help to differentiate treeline advancement.

As for modeling treeline dynamics at the regional and smaller scales, downscaling of statistical relationships existing between treeline position and one or two environmental (usually temperature and precipitation) factors found at the global or zonal scale produces simplistic scenarios that will not go beyond general statements and hardly contribute to a better causal (functional) understanding. Researchers studying the upscaling of local soil conditions, for example, and tree growth at the treeline must consider the topographical context.

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