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Review and synthesis

A global framework for linking alpine-treeline ecotone patterns to underlying processes

Maaïke Y. Bader, Luis D. Llambí, Bradley S. Case, Hannah L. Buckley, Johanna M. Toivonen, J. Julio Camarero, David M. Cairns, Carissa D. Brown, Thorsten Wiegand and Lynn M. Resler

M. Y. Bader (<https://orcid.org/0000-0003-4300-7598>) ✉ (maaïke.bader@uni-marburg.de), Univ. of Marburg, Faculty of Geography, Ecological Plant Geography, Marburg, Germany. – L. D. Llambí, Univ. de Los Andes, Facultad de Ciencias, Inst. de Ciencias Ambientales y Ecológicas, Mérida, Venezuela. – B. S. Case (<https://orcid.org/0000-0002-4360-335X>) and H. L. Buckley (<https://orcid.org/0000-0002-4170-080X>), Auckland Univ. of Technology, School of Science, Auckland, New Zealand. – J. M. Toivonen (<https://orcid.org/0000-0002-0539-039X>), Univ. of Turku, Biodiversity Unit, Turku, Finland. – J. J. Camarero (<https://orcid.org/0000-0003-2436-2922>), Inst. Pirenaico de Ecología (IPE-CSIC), Zaragoza, Spain. – D. M. Cairns (<https://orcid.org/0000-0003-4110-196X>), Texas A&M Univ., Dept of Geography, College Station, TX, USA. – C. D. Brown (<https://orcid.org/0000-0002-1587-6641>), Memorial Univ., Dept of Geography, St. John's, Canada. – T. Wiegand (<https://orcid.org/0000-0002-3721-2248>), Helmholtz Centre for Environmental Research – UFZ, Dept of Ecological Modelling, Leipzig, Germany. – L. M. Resler (<https://orcid.org/0000-0002-5135-1797>), Virginia Tech, Dept of Geography, Blacksburg, VA, USA.

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Globally, treeline ecotones vary from abrupt lines to extended zones of increasingly small, stunted and/or dispersed trees. These spatial patterns contain information about the processes that control treeline dynamics. Describing these patterns consistently along ecologically meaningful dimensions is needed for generalizing hypotheses and knowledge about controlling processes and expected treeline shifts globally. However, existing spatial categorizations of treelines are very loosely defined, leading to ambiguities in their use and interpretation. To help better understand treeline-forming processes, we present a new framework for describing alpine treeline ecotones, focusing on hillside-scale patterns, using pattern dimensions with distinct indicative values: 1) the spatial pattern in the x-y plane: a) decline in tree cover, and b) change in the level of clustering. Variation along these dimensions results in more or less ‘discrete’ or ‘diffuse’ treelines with or without islands. These patterns mainly indicate demographic processes: establishment and mortality. 2) Changes in tree stature: a) decline in tree height, and b) change in tree shape. Variation along these dimensions results in more or less ‘abrupt’ or ‘gradual’ treelines with or without the formation of environmental krummholz. These patterns mainly indicate growth and dieback processes.

Additionally, tree population structure can help distinguish alternative hypotheses about pattern formation, while analysing the functional composition of the ecotonal vegetation is essential to understand community-level processes, controlled by species-specific demographic processes.

Our graphical representation of this framework can be used to place any treeline pattern in the proposed multi-dimensional space to guide hypotheses on underlying processes and associated dynamics. To quantify the dimensions and facilitate comparative research, we advocate a joint effort in gathering and analysing spatial patterns from treelines globally. The improved recognition of treeline patterns should allow more effective comparative research and monitoring and advance our understanding of treeline-forming processes and vegetation dynamics in response to climate warming.

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Introduction

Why is a globally consistent description of treelines useful and needed?

Recognizing globally recurrent vegetation physiognomies has organized our perception of the natural world and has facilitated communication among ecologists and biogeographers at least since the times of Alexander von Humboldt (von Humboldt and Bonpland 1807). It has enabled the formulation of globally-applicable hypotheses about the factors and processes determining vegetation cover and has facilitated meaningful extrapolations of research findings across continents. Recognizing recurrent patterns in vegetation transitions or ecotones should provide similar advantages (Brown et al. 1996, Strayer et al. 2003). At vegetation boundaries, such as alpine treeline ecotones, spatial patterns may be a key to understanding the dynamic processes that determine the current and future distribution of species and ecosystems (Harsch and Bader 2011).

The spatial patterns of treeline ecotones vary greatly and, to some extent, every treeline ecotone is unique, reflecting ecological processes produced by particular combinations of climatic conditions, the topographic template, species composition and disturbance history (Brockmann-Jerosch 1919, Holtmeier 2009). However, some broad treeline ecotone patterns are repeated globally. In this context, it is important to distinguish the treeline ecotone from the potential treeline, i.e. the highest elevation at which tree growth is possible in a region before thermal conditions become unsuitable. Due to different combinations of stochastic, ecological and climatic processes, the space downslope of the potential treeline is rarely filled completely with trees. The realized treeline, a line connecting the uppermost trees of a certain size (sizes reviewed in Holtmeier 2009), is located somewhere within the transition zone between forest and low-stature alpine vegetation, i.e. the treeline ecotone. This transition zone (also referred to here as 'treeline' for simplicity) is the focus of this paper.

At the global scale, the predictability of treeline elevation has long been recognized (von Humboldt and Bonpland 1807, Brockmann-Jerosch 1919, Hermes 1955) and can be captured well by the mean growing-season temperature and a minimum growing-season length (Körner and Paulsen 2004). The global pattern in potential treeline elevation is therefore well explained by latitude and regional thermal modifiers such as mountain mass, continentality and cloudiness (Paulsen and Körner 2014, Karger et al. 2019). We postulate here that spatial patterns of treeline ecotones may also be predictable globally, even if requiring more predictors than potential treeline elevation does. The reason we expect this predictability is that these patterns reflect a limited set of

fundamental ecological processes that are repeated at treelines around the world. However, although some geographic patterns in treeline ecotone structure have been recognized (Wardle 1965, 2008, Holtmeier 2009), the global distribution of these patterns is incompletely known and has not been systematically described, let alone explained. Mapping this distribution is useful, however, as it can form the basis for formulating hypotheses about controlling processes and for predicting treeline shifts once these hypotheses are sufficiently tested.

Pattern–process relationships

Despite the large variation in treeline ecosystems, which occur in many different climate zones and biogeographic regions, treeline spatial pattern at the hillslope scale, or 'treeline form', exhibits globally recurrent characteristics that should be indicative of controlling processes and thus of expected dynamics under climate change (Harsch and Bader 2011, Trembl and Veblen 2017). In individual-based models at this local scale, distinct treeline patterns (such as abrupt versus gradual) emerged only under certain combinations of processes and parameters (Wiegand et al. 2006, Martinez et al. 2011). The assumption is that these pattern–process dependencies in modelled ecotones reflect similar dependencies in real ecotones.

A meta-analysis of published studies suggested that treeline advance due to climate change differed among treelines with different spatial patterns, with abrupt treelines having advanced less than more gradual types (Harsch and Bader 2011). This difference can be explained theoretically by stabilizing positive feedback processes maintaining the abrupt boundaries (Armand 1992, Wilson and Agnew 1992, Bader et al. 2008), although other processes, like natural (Cairns and Moen 2004, Butler et al. 2009a) and anthropogenic (Miehe and Miehe 1994, Batllori and Gutierrez 2008) disturbances, offer alternative explanations. Such feedback processes are likely to also lead to temporal abruptness, i.e. stability potentially followed by fast changes (Armand 1992, Wilson and Agnew 1992, Bader et al. 2008). The abruptness is thus not the cause of the stability, but an indication of characteristic processes that lead to spatial abruptness (e.g. positive feedback in spatial patterns of mortality). This indicative value is the main topic of this paper, while in some cases the spatial patterns can additionally be a cause of specific dynamics, e.g. dispersed trees serving as seed sources and thus facilitating further tree establishment (Trembl and Chuman 2015), or tree islands affecting snow redistribution and hence seedlings establishment (Hättenschwiler and Smith 1999).

One important impediment to drawing clearer connections between patterns and processes is the inconsistency in the descriptions of spatial patterns in the literature and the lack of clear definitions of treeline forms (e.g. gradual versus abrupt treelines). As a result, any grouping of treelines based on these descriptions is highly uncertain. To overcome this problem, we here propose a standardized description of treeline-ecotone spatial patterns at the hillslope scale based

on clearly identifiable axes (dimensions) of variation in spatial topology that allows for consistent identification of treeline types and their transitions. We then propose how these patterns could be linked to basic growth and demographic processes as hypotheses that can be further explored via modelling and experimental research. We do not aim to force treelines into discrete categories (although the extreme exemplary treeline forms are of value for verbal description) but rather propose to capture different aspects of the spatial pattern along continuous axes that allows to place each treeline into a multi-dimensional 'pattern' space. Additionally, we propose a standardized terminology to avoid confusion about the meaning of terms like 'abrupt', 'gradual', 'diffuse', etc.

Once we can consistently describe treeline patterns and link them to the proposed hypotheses about underlying processes, causal links to specific mechanisms can be elaborated in subsequent research (Brown et al. 1996). Once we understand in more detail how specific spatial patterns relate to underlying processes, we will be better able to interpret changes in spatial patterns as changes in controlling factors or processes (Martinez et al. 2011), and to use our process knowledge to predict treeline dynamics in accordance to their spatial pattern.

What efforts have already been made to describe treeline form?

Although the origin of different spatial treeline patterns has been discussed for over 100 yr (Ellenberg 1966, Frankhauser 1901 and Schröter 1926 in Tranquillini 1979, references for Russian research in Armand 1992), these patterns remain only loosely defined. This discrepancy is probably due to the great variety of patterns found in different parts of the world, making one overarching descriptive framework a difficult, but worthwhile endeavor.

Holtmeier (2009), on the basis of extensive research on treeline physiognomy and landscape patterns in different parts of the world, distinguished four types of treeline, based on their spatial structure: abrupt forest limit, transition zone (ecotone), 'true krummholz belt' and gradual transition from high-stemmed forest to crippled trees of the same species. Thereby, 'true krummholz' is used for genetic krummholz, i.e. species that can grow only as shrubs. This is in contrast to the more common definition of krummholz as environmentally-induced stunted and crippled trees, which we will use here. To avoid confusion, we suggest referring to genetic krummholz as shrubs, as already practiced in recent literature (Mayr et al. 2019, Treml et al. 2019). Holtmeier (2009, p. 17) does not further differentiate the ecotonal treeline type but describes it as 'characterized by a mosaic of tree clumps, scattered groves, isolated, more or less deformed tree individuals and treeless patches covered by low shrubs, herbs and grasses'.

In Harsch et al. (2009) and Harsch and Bader (2011), ecotonal treelines are differentiated into diffuse and island forms, i.e. those with predominantly isolated tree individuals and those with tree clumps and groves. Apart from these two

types, abrupt and krummholz treelines were distinguished. A main disadvantage of this classification into four treeline forms (abrupt, diffuse, island and krummholz) is that 'diffuse' is defined as a mixture of gradual decrease in tree cover and a decrease in tree size, leading to ambiguous predictions about the importance of growth responses and population processes such as establishment and mortality (Harsch and Bader 2011, Treml and Veblen 2017). Additionally, the krummholz in 'krummholz treelines' has been interpreted both as environmentally-induced and as genetic krummholz, again leading to confusion about the processes related to these forms (Schickhoff et al. 2015, Treml and Veblen 2017). A third disadvantage lies in the suggested discreteness and simplicity of the classification, when in fact treeline forms are very variable and differ along more dimensions than can be captured by four classes. For this reason, we here promote the idea of capturing different aspects of the spatial pattern along continuous axes, each quantifying a different ecologically meaningful dimension of the treeline pattern.

Wiegand et al. (2006) described treeline spatial patterns along three dimensions: tree height, adult tree density and tree age. The pattern was defined by the abruptness of changes along the ecotone according to these dimensions, which could be either 'abrupt' or 'smooth', with the goal of comparing them to patterns emerging in different parameterizations of an individual-based model. Only certain combinations of processes allowed for the emergence of different treeline types, suggesting a clear signal in treeline pattern that allows for inference of the underlying processes. Wiegand et al. (2006) illustrate well why defining patterns in a meaningful way is necessary for studying pattern-process relationships at treelines, a concept we here develop further.

Objectives

We propose a standardized, globally-applicable description of spatial patterns occurring at alpine treelines at the hillslope scale (i.e. treeline form *sensu* Harsch and Bader 2011) that is based on the main dimensions of pattern indicative of underlying processes and that allows adequately analyzing the spatio-temporal dynamics of these patterns. Specifically, we aim to: 1) propose a framework for describing alpine treelines based on different dimensions of their spatial patterns, 2) propose a standardized terminology for these patterns and 3) develop hypotheses for the general mechanisms behind these patterns.

The recognition of spatial similarities within the wide physiognomic variety exhibited by treeline ecotones worldwide is essential for addressing generalised hypotheses about the functioning and local dynamics of this fascinating global phenomenon.

Pattern dimensions

Here, we present a framework for describing different dimensions of treeline spatial patterns, at the hillslope scale, that are informative of underlying processes and should thus allow for

a comparison of treeline sites that may show similar dynamics at a particular point in time. A given treeline can take any position along these dimensions, although some combinations are not possible. We provide labels for the far ends of the spectra to facilitate communication and we use these as examples to discuss the processes underlying the patterns (in general below, with examples in Box A).

We define the hillslope scale as an area a person would see when walking from the closed forest up into the alpine zone on a regular slope in moderately foggy conditions (sight of about 30 m). At this scale, the spacing of individual trees is of interest, and observable patterns include those related to surface microtopography, like trees established in the shelter of rocks (Resler et al. 2005), as well as self-organized patterns (Alftine and Malanson 2004, Bader et al. 2008, Zeng et al. 2007). One scale level higher we will refer to as the 'landscape scale', i.e. the course of the ecotone through the topography (see below). At this scale, patterns like local north-south differences and the effect of terrain concavity and convexity on ecotone elevation and form are described, as well as larger topography-related forest patches.

Two sets of pattern dimensions

The following scheme describes two types of pattern, each consisting of two pattern dimensions (axes in Fig. 1c, 2b), that describe treeline-ecotone form.

- 1) The spatial pattern of tree cover as seen from above (2-D in the x-y plane along the slope, Fig. 1). These patterns mainly indicate the demographic processes establishment and mortality (see below: demographic processes'). They can be described in the following two pattern dimensions:
 - a) Rate of change in tree density or cover from forest to alpine vegetation (Fig. 1c, x-axis): fastest if canopy cover does not decrease up to the tree-species line, i.e. the forest approaches the alpine in a closed front, so the treeline is discrete; slower if the canopy opens up into sparse cover at the tree-species line. Whether density (number of trees per area) or cover is evaluated will depend on the type of data available: remotely-sensed data will give a better image of tree cover, while field surveys often will be based on stem positions or numbers per area (i.e. densities). Both measures are valid for evaluating this dimension, but the interrelatedness of the two with tree size needs to be considered. If trees become smaller, the ratio between tree cover and stem density will decrease. Therefore, to maintain a stable tree cover, the stem density will need to increase.
 - b) If the canopy opens up towards the tree-species line, the level of clumping or dispersion of the trees (Fig. 1c, y-axis) may stay similar to that in the forest (i.e. the treeline is diffuse) or trees may increasingly clump into islands (tree-islands or krummholz-islands).
- 2) Changes in tree stature and physiognomy (in a vertical cross-section across the ecotone, Fig. 2). These patterns

mainly indicate growth and canopy dieback processes (see below). They can be described along the following two pattern dimensions:

- a) Abruptness of the decline in maximum woody-plant height across the ecotone (Fig. 2b, x-axis): most abrupt if tall trees change directly to low-stature alpine vegetation or krummholz, most gradual if woody plants slowly decrease in size across the ecotone.
- b) Deformation of the tree shape (Fig. 2b, y-axis): none if trees only get shorter, intermediate for e.g. multi-stemmed or flagged upright trees, strong if tree species form environmental krummholz (Pereg and Payette 1998). A species turnover into shrubs does not constitute deformation, but if a belt of tall shrub species exists that changes into small prostrate shrubs (i.e. krummholz) of the same species, as seen sometimes in e.g. *Pinus mugo* or *Rhododendron*, this does constitute deformation and this second transition should be noted.

For each of the dimensions we can quantify associated detailed measures and therefore formally place each treeline unambiguously into a multi-dimensional state space. Additionally, it is useful to attach to each treeline a name based on a simplified nomenclature (Table 1). For naming we suggest to use discrete and gradual as defaults, considering gradual discrete treelines (Fig. 3a) as our null model. We can thus distinguish gradual (gradual height and implied discrete density change; Fig. 3a), diffuse (implied gradual height and diffuse density change; Fig. 3b), abrupt diffuse (abrupt height and diffuse density change; Fig. 3e), abrupt (abrupt height and implied discrete density change; Fig. 3d), as well as e.g. tree-island treelines (implied gradual height change and tree islands; Fig. 3c), and abrupt krummholz-island treelines (abrupt height change with krummholz islands; Fig. 3l).

In many cases, treelines will not belong to the far ends of the pattern dimensions but will represent intermediate or mixed forms. These can be verbally described using the same terms, for example 'diffuse with some islands', or more precisely, e.g. 'predominantly diffuse treeline with about 20% of trees clustered into islands (intermediate form) and with abrupt sections along ca 30% of its length (mixed form)'. The level of mixing will depend on the length of treeline that is described, e.g. one line transect along the slope (no mixtures, but intermediate forms possible) or a wider section of the treeline across a slope (mixtures and intermediate forms possible). With time, treeline form may also shift dynamically along the axes defined here from one form to another as the treeline-shaping processes change in relative importance due to population development or environmental change.

A simple theoretical framework for causes of treeline form

Treeline spatial pattern constitutes a snapshot in a potentially dynamic system and cannot replace a detailed monitoring of population processes and their drivers to fully understand

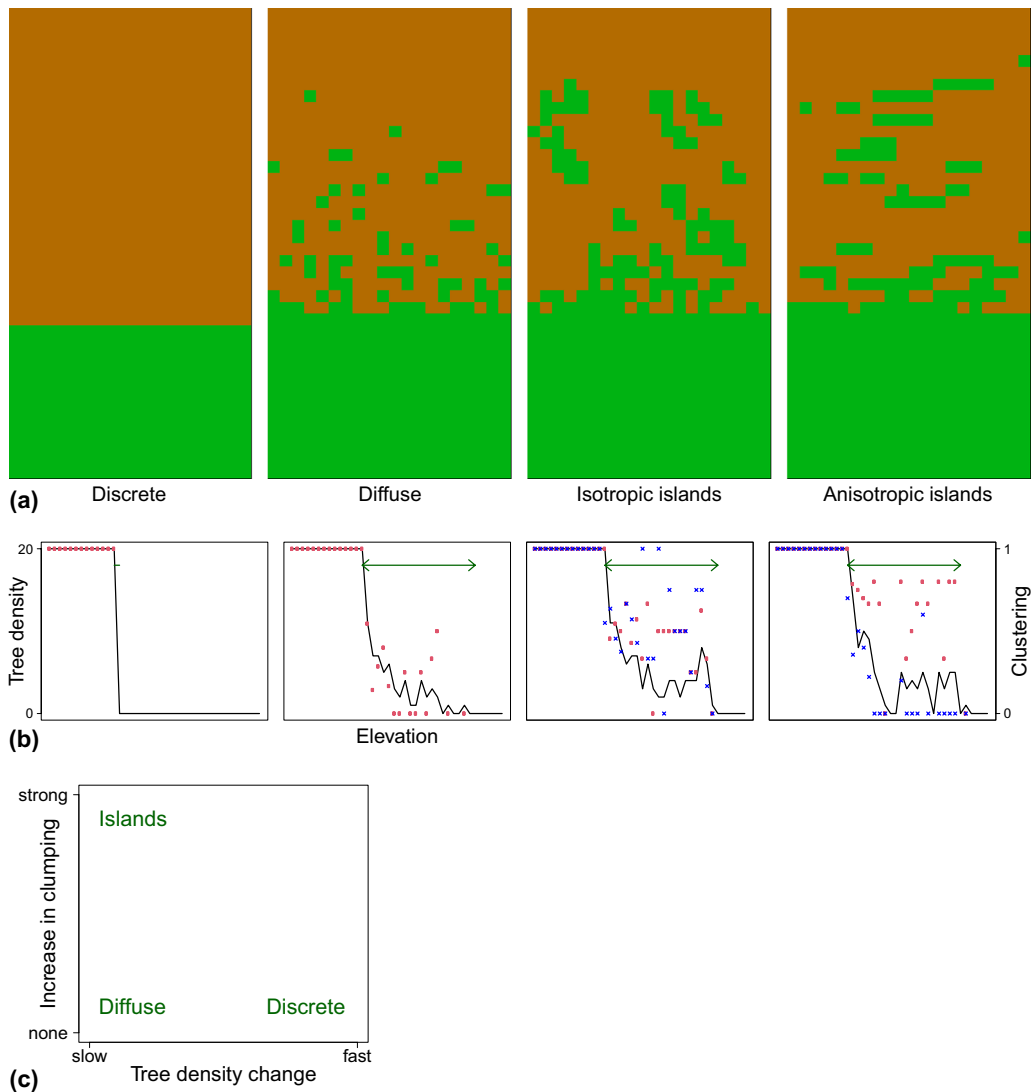


Figure 1. First set of dimensions of treeline spatial pattern: the 2-D pattern as seen from above. (a) Examples of treeline ecotone patterns as seen along elevational transects. (b) Changes in tree cover (black line) and the fraction of tree pixels with another tree pixel directly to their right (as a simple measure of clustering in the x direction; red dots) or to their top (clustering in the y-direction; blue crosses) across the ecotones shown in (a). The dark green arrows indicate the extent of the ecotones, which approaches a length of zero in the discrete treeline (left). (c) The two dimensions (axes) that define the 2-D pattern. The terms in the graphs denote the position of different treeline types at the far ends of the axes. The combination of a discrete treeline with increased clumping (top right of the graph) is not expected to exist.

how a treeline develops. However, patterns can be a powerful and efficient proxy for inferring the ecological processes that control treeline dynamics. We here follow the hypothesis of Harsch and Bader (2011) that variation in treeline form is essentially driven by three general processes: growth limitation, dieback (aboveground biomass loss) and mortality (including establishment failure). Each treeline spatial pattern dimension is indicative of particular spatial gradients of these three ‘first-level’ processes (Fig. 4, Table 1), while a more detailed analysis of the patterns, combined with further empirical evidence, may reveal what underlying (‘second-level’) processes cause these gradients. ‘Third-level’ processes include species interactions modifying the second-level processes, e.g. through sheltering or shading (Harsch and Bader 2011).

In terms of first-level processes, spatial patterns of all forest borders will indicate the same processes. Our framework is thus potentially more widely applicable than at alpine treelines alone. For example, very abrupt boundaries are found between forest and grassland in the Indian Ghats (Joshi et al. 2019) and in fragmented Brazilian Atlantic forest (Silva and Anand 2011), indicating high tree mortality outside established forest, with the second-level processes varying from frost damage to fire.

Second-level processes, on the other hand, can vary widely among ecotones with similar spatial patterns. These processes can be physiological or mechanical, brought about by different environmental factors, like frost or fire in the example above, both leading to abrupt treelines. At this level, there is thus no

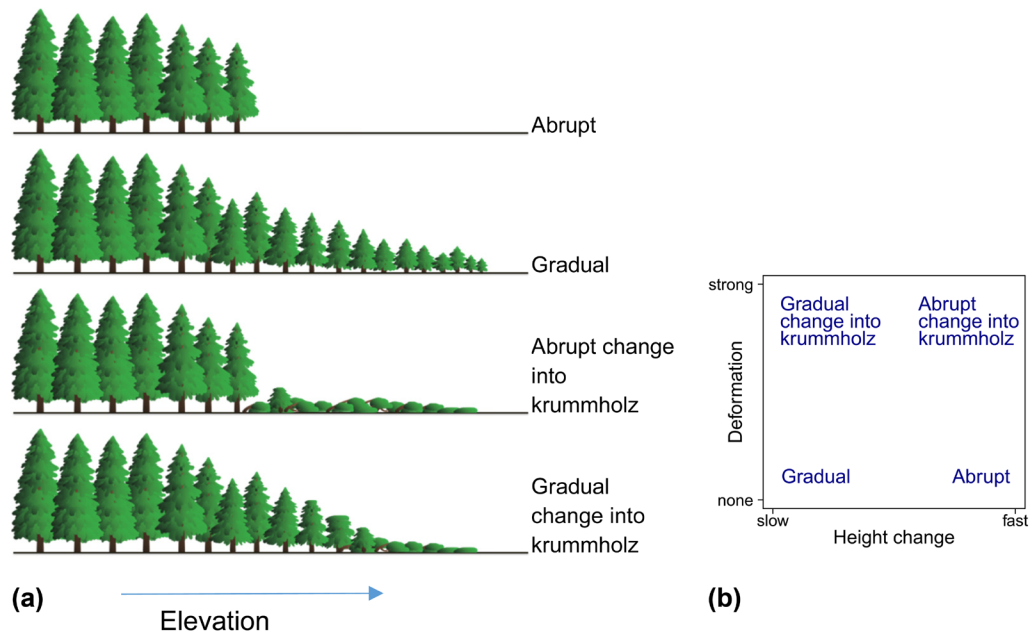


Figure 2. Second set of dimensions of treeline spatial pattern: changes in tree stature. (a) Examples of treeline ecotone patterns in the vertical cross section. All treelines shown here are discrete in terms of their 2-D pattern (Fig. 1) and vary in their tree stature pattern only. (b) The two dimensions (axes) that define the cross-section pattern of tree stature. The terms in the graphs denote the position of different treeline types at the far ends of the axes.

one-to-one relationship between ecotone patterns, at the scale and level of detail we defined them here, and underlying processes, but these patterns can certainly guide the search for the controlling second-level processes. In alpine treeline ecotones, typical second-level processes include, for example, reduced cell formation (due to a lack of warmth or nutrients), loss of foliage (due to e.g. frost or wind), snow moulds (under a long-laying snow pack), desiccation (due to frozen soils or summer drought), fire damage (due to forest fires or alpine-vegetation burning), dispersal limitation (due to poor seed production or an absence of vectors) and germination failure (due to various stressors). Many of these processes and their controlling factors

are not specific to treeline, but they are nonetheless important determinants of past and future dynamics. Although different second-level processes can result in similar spatial patterns, in many cases they will also leave specific spatial signatures. For example, if dieback due to wind damage is important, longitudinal krummholz islands may be formed (Alftine and Malanson 2004) and exposed sites will have stronger krummholz formation than sheltered sites (Holtmeier and Broll 2010). In contrast, if dieback is caused by snow moulds (Barbeito et al. 2013), trees will be more stunted in sites that accumulate snow due to their topographic position or due to neighboring vegetation (Holtmeier 2005).

Table 1. Summary of the framework, with the terms (in bold) proposed for the far ends of the four dimensions that describe spatial patterns of alpine treeline ecotones, and a summary of the processes which they may indicate to be important. As seen here, the framework is hierarchical, with options for the type of change depending on the rate of change.

	a) Rate of change	b) Type of change	Controlling processes (first-level)	Controlling processes (second- and third-level)
2-D pattern	Discrete		Mortality above but not in the ecotone	Any type of damage or stress. If gradual, growth limitation above the ecotone
	Ecotone	Diffuse	Mortality within the ecotone	Environmental heterogeneity or stochasticity. And/or ongoing seed-limited colonization
		Island	Mortality within the ecotone	Environmental heterogeneity, clustered seed dispersal, clonal reproduction, or positive feedback tree cover – microclimate via wind and snow redistribution (abrasion, snow moulds, short growing-season)
Tree stature	Abrupt	Into alpine	Seedling mortality	Overheating, desiccation, photoinhibition, freezing damage, soil limitations
	Gradual	Into krummholz	Dieback	Winter desiccation, snow moulds, browsing, abrasion
		No krummholz	Growth	Tissue formation (limited by a lack of heat)
		Into krummholz	Growth and dieback	Tissue formation + winter desiccation, snow moulds, browsing, abrasion

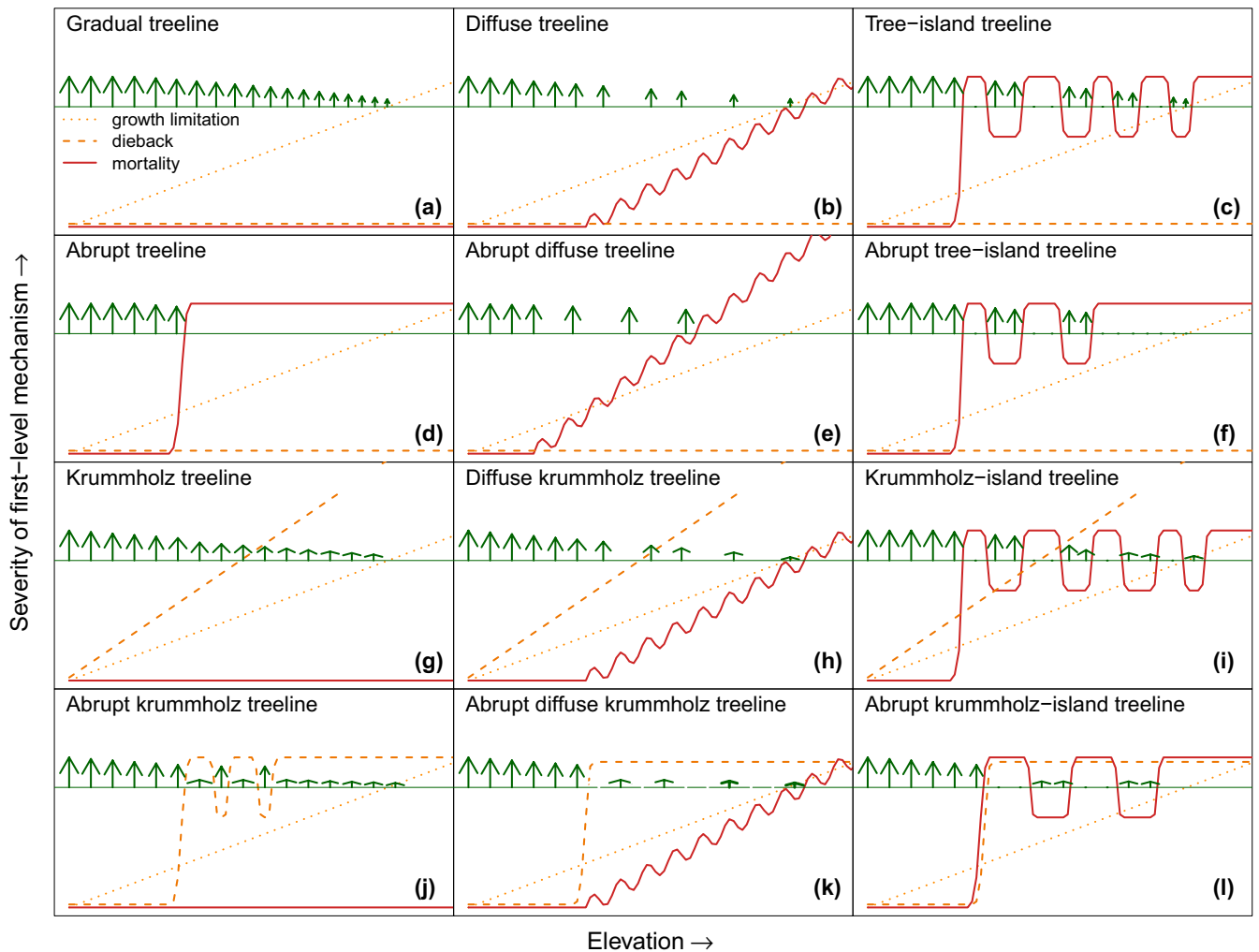


Figure 3. Variation in treeline form according to the dimensions presented in Fig. 1, 2: the 2-D spatial pattern (columns) and changes in tree size and shape (rows). The graphs show the hypothesized gradients in the first-level processes growth limitation (dotted orange), dieback (dashed orange) and mortality (including establishment failure, red line) leading to these patterns. Shown are simplified gradients and minimal models, i.e. if a process is not needed to create the pattern, it is set to stay constant. Growth limitation is assumed to always occur, although sometimes it does not affect the pattern much (e.g. in d). The upper line indicates the most limiting process at any point along the elevational gradient. Sudden shifts in the stress severity (c, d, f, i–l) are due to positive feedback of the vegetation on environmental conditions: forest or krummholz ameliorating conditions for establishment (c, d, f, i, l) or trees escaping damaging conditions near the ground (j–l). Sinusoid lines (panels b, e, h, k) indicate environmental heterogeneity independent of the vegetation itself. The diffuse patterns in these panels could be caused by patchy environmental conditions or, especially in expanding populations, spatial and temporal stochasticity in seed rain and mortality. This is a modification of the scheme in Harsch and Bader (2011), expanding it from four spatial types (abrupt, diffuse, island and krummholz) to twelve examples representing the extreme ends in a continuous space of pattern dimensions.

Seed rain and clonal reproduction are other important examples of second-level processes and can be strong drivers of spatial pattern. Although not technically a form of mortality (in contrast to e.g. seed predation and germination failure, Crofts and Brown 2020), a lack of seed rain or clonal dispersal is, at the very general first level, an alternative form of ‘mortality’, because both lead to an absence of trees. Many seed-dispersal types lead to spatial patterns that cannot be unequivocally distinguished from patterns caused by early-stage mortality. For example, a decreasing tree density with distance above the forest line, indicating reduced establishment success, can be caused by either a dispersal gradient

or an environmental gradient causing a survival gradient. As another example, tight clumps of trees, if not related to topography, can indicate either seed caching by nutcrackers (Holtmeier 1966), layering (Laberge et al. 2000) or positive feedback between trees and their environment, all leading to a higher establishment in the clump and establishment failure outside of it. However, some specific spatial patterns almost certainly indicate an inhomogeneous seed distribution or clonal reproduction by layering or rhizomes, e.g. loose clustering of small trees around a larger focal tree indicating local seed dispersal or dispersal via rhizomes (Kullman 2007). For most tree species, the reproductive strategies are



(a)



(b)

Figure 4. Functional diversity patterns. (a) Example of a two-species treeline, with a deciduous and an evergreen conifer tree species (*Larix decidua* and *Picea abies*), both able to colonize open space, in a grassland and dwarf-shrub matrix in the Swiss Alps (photo: Matthias Jochner). (b) Example of a multi-species treeline with a gradual species turnover: transition from mixed podocarp-broadleaved forest with, amongst others, the trees *Halocarpus biformis* and *Libocedrus bidwillii* to the transition zone with, amongst others, the small trees/shrubs *Dracophyllum* spp. and *Olearia* spp. (Wardle 2008), and then increasingly small shrubs and tussock grassland on the western slopes of the southern Alps of New Zealand (photo: M. Y. Bader).

sufficiently known to distinguish seed-based from clonal processes, although care should be taken with assumptions (e.g. assumed clonal tree islands turned out to be non-clonal after genetic analysis, and even local seed dispersal seemed to play a small role, so that the patterns may have been due to microclimate-based positive feedback, Johnson et al. 2017). However, to distinguish the importance of dispersal limitation from that of other processes leading to establishment failure, spatial patterns are not sufficient and more detailed experiments are needed (Crofts and Brown 2020).

Identifying spatial patterns according to the suggested four dimensions, and inferring spatial gradients in the first-level processes from these patterns, is the first step to understanding

the drivers of treeline dynamics (Wiegand et al. 2006, Martinez et al. 2011). For addressing site-specific hypotheses about the underlying second-level processes and controlling environmental factors, a more detailed analysis of spatial patterns at particular treelines will be needed. A strong aid to such pattern analyses is the age distribution of the trees, which can be obtained using dendrochronological methods based on dating tree-rings or based on growth scars for younger individuals (Hagedorn et al. 2014, Camarero et al. 2015, Liang et al. 2016, Vitali et al. 2017). Although laborious to obtain (and impossible for regions lacking seasonal climate variation), such information is invaluable for reconstructing the population dynamics within an ecotone, thereby providing important additional indications about the processes that control it. Even stronger patterns can be obtained if such data are combined with tree-ring-based data on growth responses to climate (Elliott 2011, Liang et al. 2016, Jochner et al. 2017b).

The following sections are intended to help the interpretation of observed patterns, along the two pairs of pattern dimensions, in terms of the underlying first-level processes growth limitation, dieback and mortality (Fig. 3). Further examples are given in Box A.

Change in tree cover (discrete–diffuse–islands): demographic processes

The horizontal 2-D spatial pattern (the treeline as viewed from above) is mostly determined by the presence and absence of trees across space. The absence of trees indicates that establishment has failed (e.g. due to a lack of viable seeds or safe sites) or trees have died and disappeared. In other words, mortality (including establishment failure) is a major determinant of these patterns (Fig. 3). In contrast, growth and canopy dieback should have stronger effects on the pattern of tree stature change and are less likely to be important for the 2-D spatial pattern, except where they interact with mortality (see below). Indeed, a recent test of climate responses in different treeline forms showed that treelines defined by either a diffuse or discrete 2-D pattern did not differ much in their growth response to warming. Instead, the diffuse treelines were controlled mostly by population processes. In contrast, treelines defined by the formation of krummholz (dimension 2b: deformation) had a stronger growth response than non-krummholz forms (Trembl and Veblen 2017).

a) If there is no decline in tree cover with elevation, i.e. if the treeline is a discrete, closed boundary between forest and alpine vegetation (formed either by tall trees or with trees gradually getting shorter, either with a closed or more open canopy, but without changing canopy cover with elevation), this indicates that establishment of trees up to the tree-species line is possible and not increasingly limited with elevation (Fig. 3a, d, g, j, left column). When gradual (see below), such treelines are caused either by increasing growth reduction with tree size, or additionally by dieback limiting tree stature, indicated by a decline in tree height with or without deformation (Fig. 3a, g, j, see below). When abrupt, such treelines are caused by a recent disturbance or by establishment

failure outside existing tree cover (in abrupt discrete treelines, Fig. 3d). Such an abrupt change in establishment chances is unlikely to be caused by underlying environmental gradients but more likely by a positive feedback between the vegetation and the microenvironment, which may include soil and microclimatic factors (Wilson and Agnew 1992).

Conversely, a decline in tree cover, be it into a diffuse or clumped (island) pattern, indicates that trees have not established everywhere below the tree-species line or have been removed. Formulating this very basic interpretation is the first step towards explaining it. The following, not mutually exclusive, reasons may apply:

- 1) The treeline is advancing: the established trees are outposts and establishment is seed limited. If the number of dispersed seeds or the frequency of years in which establishment is possible is low, such an 'advancing' state can last very long.
- 2) Establishment is limited by the number of safe sites, which decreases with elevation and is related to: a) microtopographic features; or b) existing vegetation cover.
- 3) The established trees are remnants: the treeline has been opened up by disturbances, especially land use or the surrounding trees have died due to climate deterioration.

These three reasons may result in superficially similar patterns, but in a pure case of reason 1, the spatial pattern should be random or explainable by non-random seed rain patterns, the tree ages (not just sizes) should clearly decrease with elevation, and outpost trees should be relatively young (Batllori and Gutierrez 2008, Elliott 2012). If outpost individuals do not reproductively mature, local establishment in the upper ecotone remains dependent on long-distance seed dispersal from lower-elevation source populations, slowing advance and maintaining this outpost-based diffuse pattern over long time periods (though long-distance dispersal appears to be common at some treelines Johnson et al. 2017). Such long-lasting 'advance' patterns may also occur if, on top of limited seed availability, the number of years with climatic conditions allowing establishment is very low. In these two cases, outpost populations may be evenly or unevenly aged, depending on whether propagule dispersal upslope is sporadic or continuous, and on the frequency of favorable years for establishment.

If reason 2 (also) applies, it should be evident that establishment patterns are associated to local vegetation cover (e.g. local cover of alpine shrubs facilitating establishment of woody species, Llambí et al. 2013, Bueno and Llambí 2015), to topographic shelter (Batllori et al. 2009, Astudillo-Sánchez et al. 2019), or to other, regionally-specific, types of microsites (Johnson and Yeakley 2019). In practice, these associations are not always easy to detect, as topography may become covered and vegetation replaced by developing trees. Reason 1 implies temporal heterogeneity combined with stochasticity, while reason 2 implies spatial heterogeneity. In any case, of all spatial patterns, diffuse treelines are most characterized by heterogeneity and stochastic processes.

The third reason may be suspected if the first two do not apply, i.e. if outpost trees are of high and well-distributed

ages and if the soil and topography appear homogenous, and particularly if livestock grazing is apparent in the region (Ellenberg 1966). In many cases, an opening up due to land use will be accompanied by a recolonization (Vitali et al. 2019). Similarly, current climate warming may lead to recolonization around climatic relict trees (Kullman 2007). In both cases current diffuseness would thus be due to a mix of reasons 1 and 3.

b) If the tree cover declines, trees can either thin out randomly, over-disperse or cluster together. Random patterns or associations with microtopographic features indicate that safe sites (or seed rain patterns) are topographic or caused by interactions with alpine vegetation (Fig. 3b, e, h, k, middle column). In contrast, both over-dispersion and clustering indicate that, additionally, feedback processes involving existing tree cover shape and maintain these patterns, indicating negative and positive feedback respectively (Malanson 1997, Bader et al. 2008).

Over-dispersion could indicate that trees compete with each-other (e.g. for water), or otherwise negatively affect each other. Körner (1998) suggested that cooler soils under closely-spaced trees suppresses tree root growth, which would explain why isolated trees can be found at higher elevations than closed forest. Such shading could thus cause a negative feedback that could lead to over-dispersion. However, this mechanism appears to affect tree spacing only in permafrost soils, so at some boreal treelines (Crawford 2008, Körner 2012). At alpine treeline, soil cooling in the shade of trees does not appear to restrict tree root growth (Kubisch et al. 2017). Other negative effects of soil cooling on tree establishment, e.g. via nutrient availability, might still lead to a negative feedback, but there is currently no evidence that such feedback affects tree spacing at alpine treelines. As far as we are aware, over-dispersed tree cover at alpine treeline can be observed only in arid mountains (Lauer 1978, Hoch and Körner 2005), indicating underground competition for water. However, here it is not specific to the treeline. If trees are already over-dispersed in the forest, such a treeline would only be considered diffuse if the cover of trees decreases further towards the treeline, which could then be due either to increased competition (if there is an elevational gradient in precipitation or soil properties) or to decreased microsite availability. However, in a recent study at moisture-limited treelines in the Himalayas the opposite was observed: young trees at treeline tended to cluster together, and most strongly so in the drier sites (Sigdel et al. 2020).

Such clustering into rounded or elongated tree or krummholz islands likely indicates facilitative interactions (Germino et al. 2002, Batllori et al. 2009) among trees or krummholz (Fig. 3c, f, i, l, right column). This phenomenon has been extensively described, in particular in the literature from North America (Alftine and Malanson 2004, Bekker 2005, Resler 2006, Zeng and Malanson 2006). Islands indicate that conditions outside are unfavorable for tree establishment, while the islands themselves ameliorate the conditions, resulting in positive feedback. Stabilizing positive feedback is particularly strong if the islands negatively

affect the conditions around the islands, which can occur if they redistribute wind or snow (Hättenschwiler and Smith 1999). Clonal reproduction, e.g. via layering, can also play an important role in the formation and dynamics of tree and krummholz islands (Marr 1977, Benedict 1984). This, and local seed dispersal, are also processes with positive feedback, the presence of parent trees having a strong positive effect on the emergence of more stems.

Tree island shapes can range from rounded (isotropic) to strongly elongated (anisotropic), even forming 'ribbons' or 'fingers' (Holtmeier 1982, Baker and Weisberg 1995, Allen and Walsh 1996, Bekker and Malanson 2008). Such more specific forms can help to identify second-level processes. For example, clustering into longitudinal krummholz islands has been attributed to direct wind effects (Marr 1977, Benedict 1984, Alftine and Malanson 2004, Bekker 2005), while forest ribbons may be formed due to the redistribution of snow, resulting in snow cover that is too shallow or too deep on the windward and leeward side, respectively, of the ribbons (Holtmeier 1982, Hättenschwiler and Smith 1999).

Changes in tree stature (abrupt–gradual–krummholz): growth and dieback

a) Changes in tree stature can, of course, only occur where trees are present. If trees disappear before important decreases in tree stature take place, i.e. if the treeline consists of an abrupt change from tall trees to low-stature alpine vegetation, mortality must be more limiting than other first-level processes (Fig. 3d–f). If tree height declines gradually, this can be due to growth limitation or dieback, or a combination of both (Holtmeier 1985, Holtmeier 2009). Gradual treelines without signs of dieback can be considered the null-model of treeline form: growth is the only limiting factor. With elevation, growth must be increasingly limited by tree height (i.e. with coupling to the atmosphere), i.e. growth must cease at a certain tree size and this size must decrease with elevation, to produce a stable gradual treeline in which trees do not eventually, even if very slowly, grow tall. Alternatively, a size-independent decrease in growth rate could also lead to a stable gradual treeline if tree longevity is limited. However, there are indications that trees near treeline can grow extremely old (LaMarche 1979, Laberge et al. 2000, Holtmeier 2009, Morales et al. 2012), although elevational trends in maximum tree ages are not known for most treelines and in species with enough data the oldest trees are not necessarily forming part of the treeline (Galvan et al. 2014). This may be due to a more recent establishment or a younger maximum age due to persistent stress or very frequent dieback. In practice, some level of dieback nearly always accompanies a strong growth decline, even if not necessarily leading to krummholz formation. Additionally, a gradual decline in tree height could be caused by species turnover across the treeline ecotone from tall tree species to small trees and treeline shrubs (see below).

b) If there is an abrupt change from tall trees to krummholz (environmental krummholz only, a change into shrub species implies very different mechanisms), this, in turn, indicates that mortality is not the most important process, but frequent

dieback of shoots keeps trees crippled, unless they have managed to grow beyond a critical height, after which growth is not a mayor limitation (Fig. 3j–l). These mechanisms may function at the level of forest versus a krummholz belt above (e.g. as individuals or islands, Fig. 3k–l), or at the level of individual trees, where single upright trees and krummholz may occur mixed throughout the ecotone (Fig. 3j).

Abrupt height declines from tall forest into alpine vegetation or krummholz indicate that positive feedback occurs, either between tree presence and seedling survival or between tree size and biomass maintenance. In the first case, this implies a positive feedback switch (Wilson and Agnew 1992) and a high temporal stability of the treeline (Armand 1992, Bader et al. 2008), while in the second case the escape of krummholz to upright trees is much more likely to occur and can lead to a fast treeline change through a rapid vertical growth of already established individuals (Pereg and Payette 1998, Gamache and Payette 2004, Holtmeier and Broll 2005, Devi et al. 2008, Kullman and Oberg 2009).

Similar to island shape, the directionality (anisotropy) of deformations can be an indication of the causal (second-level) processes. An obvious example is wind deformation, but slope processes and radiation-related processes (e.g. winter desiccation) can also cause directional damage patterns. In most cases, a detailed analysis of damage and regrowth patterns, including not only directionality but also e.g. the heights above the ground where damage starts and ends (possibly related to e.g. snow-depths or the reach of local browsers), will give strong indications of the second-level processes at hand (Pereg and Payette 1998).

Applying the approach

Natural versus anthropogenic treelines

Do patterns indicate the same processes if a treeline form has an anthropogenic origin? We suggest here that the interpretation of patterns in terms of first-level processes is independent of the second-level causes. Still, in this framework, undisturbed and disturbed treelines should be clearly distinguished to facilitate the interpretation of patterns in terms of second-level processes, which of course is of interest. For example, abrupt treelines indicate a dominant role of mortality. In many cases this will be caused by anthropogenic influences such as fires or agricultural disturbance in tropical mountains (Miehe and Miehe 1994, González et al. 2011, Bueno and Llambí 2015), but it can also be due to, or maintained by, natural processes such as seedling mortality due to frost or radiation intolerance (Bader et al. 2007b, Wardle 2008) (Box A). Likewise, gradual diffuse treelines can indicate that a treeline is advancing (i.e. trees are smaller because they are younger and the forest does not form a closed front because not all sites have been colonized yet, Batllori and Gutierrez 2008) and/or that there has been inhomogeneous mortality combined with a lack of warmth for growth. Again, this mortality might have happened naturally, most likely in

the establishment phase, or may have been caused by harvesting or fire. The latter has been offered as an interpretation for some gradual diffuse treelines, e.g. in southern Andes or the Alps (Ellenberg 1966, Tranquillini 1979).

For predicting future treeline shifts based on spatial pattern, understanding the land use history is certainly relevant. Historical reasons do not change the basic interpretation of the pattern in terms of primary causes, but with very recent anthropogenic disturbance, the current pattern will not give much information about future dynamics, unless disturbances are continued. However, the recovery of patterns after disturbance is informative (Vitali et al. 2019). If no re-invasion of deforested land at treeline takes place, the treeline will thus still be abrupt after many years, indicating that it is also less likely to respond to climatic change (González et al. 2011). A diffuse re-invasion indicates that the harsh alpine conditions outside the forest do not prevent tree establishment so that treeline shifts can be fast. The distinction of re-invasion from the presence of remnant trees requires estimations of tree ages.

Multi-species treelines

Many treelines are formed by just one or two tree species (Fig. 4a), but some can be quite diverse, with 40 or more tree species at some tropical cloud-forest treelines (Ramírez et al. 2009, Peters et al. 2014). Diverse treelines include those on the western slopes of the southern Alps of New Zealand and cloud forest treelines in the northern Andes (Fig. 4b, Bader et al. 2007a, Wardle 2008, Ramírez et al. 2009, Peters et al. 2014, Sarmiento Pinzón and León Moya 2015). The causes of diversity patterns are related to large-scale biogeographic processes that are outside the scope of this paper. Still, considering diversity patterns is important when describing treeline patterns, because through species-specific demographic and growth processes they determine community-level processes that may have important implications for treeline dynamics. Two important diversity aspects are the functional diversity in tree species and the type of non-tree vegetation in and above the ecotone. Among trees, particular relevance lies in the presence of colonizer tree species, resistant to alpine conditions, which could facilitate the subsequent establishment of other species. Such facilitation is seen, for example, at some treelines where whitebark pine is present (Resler and Tomback 2008, Pyatt et al. 2016, Tomback et al. 2016) and is expected between radiation-tolerant and shade-demanding species at tropical treelines (Bader et al. 2007b, Llambí et al. 2013).

The non-tree vegetation matrix can have both positive and negative effects on tree establishment in the ecotone, depending on its stature and cover (Akhalkatsi et al. 2006, Llambí et al. 2013, Dial et al. 2016, Liang et al. 2016, Loranger et al. 2017). Whereas low-stature vegetation is important mainly at the seedlings stage (Loranger et al. 2017, Frei et al. 2018), tall non-tree vegetation can affect trees much longer. Where present, small tree and large shrub species may take over the habitat above the closed forest, fundamentally altering the processes that prevent trees from establishing

above their current elevational limit. Whereas environmental krummholz indicates that dieback is the dominant process preventing the establishment of upright trees, shrubs do not have to indicate this at all. It also does not preclude it, however. Shrubs can, in turn, become stunted and sometimes environmental krummholz can be found among the shrubs (Okitsu and Ito 1989).

Useful information about the species composition includes the richness in tree species and the presence of functional groups among trees. In the context of treeline dynamics, an important functional distinction is between pioneers/colonizers/stress-tolerant/light-demanding versus late-successional/shade-tolerant species. Other important properties are deciduousness, the ability for layering and seed dispersal mode. Describing the presence of such functional traits can be of great relevance for understanding treeline dynamics. Not only tree traits, but also the composition and structure of the non-tree ecotonal vegetation can affect the processes shaping the treeline ecotone. This can be summarized into vegetation types, e.g. lichen tundra, tussock grassland or tall shrub thicket, while additionally the presence, cover, height and spatial arrangement of functional groups (e.g. lichens, herbs, lawn grasses, tussock grasses, dwarf shrubs, tall shrubs) are of interest, as they can strongly affect the establishment chances for trees (Lett et al. 2016, Loranger et al. 2017) and can also point to changes in limiting abiotic conditions across the treeline (Arzac et al. 2019).

Additionally, functional groups of other biota, including seed predators, seed dispersers, browsers, pathogens and decomposers, may strongly affect some ecological processes and thereby control or modify treeline dynamics and spatial patterns (Holtmeier 1966, 2009, Hagedorn et al. 2019). Although not in focus in most treeline research projects, information about the distribution, diversity and activity of such groups is useful auxiliary information for understanding the vegetation patterns.

The landscape scale

At most treelines, except those on homogenous slopes, recognizing the described patterns in the field is a challenge because different patterns may occur at a site due to variation in local topography and disturbance history. Although it may be confusing, such heterogeneity is also an opportunity, because it provides a 'natural experiment', indicating that different processes are important to a different degree at different landscape positions, with implications for expected dynamics (Allen and Walsh 1996, Elliott and Kipfmüller 2010, Holtmeier and Broll 2012, Greenwood et al. 2014, Bourgeron et al. 2016). Therefore, depending on the specific research questions, two good options are to map only the dominant treeline type in the area (noting what proportion of the landscape actually shows this pattern) or to map the patterns within relatively narrow vertical belt transects and to relate the patterns to landscape positions.

In particular in diffuse and gradual treelines, where patterns of mortality and growth, respectively, should depend

most directly on climatic gradients (Fig. 3), steep slopes are likely to have narrower ecotones than gentle slopes. Of course, the ecotone width should thus be interpreted with respect to the slope angle. However, we suspect that there is no qualitative difference in the processes that cause medium-wide and very-wide diffuse, gradual or island ecotones, although differences in ecotone width may indicate that the processes vary in intensity. Accounting for slope angles is therefore mainly important when comparing treeline patterns quantitatively, e.g. among regions or with respect to model output (Martinez et al. 2011).

Another scale-related question is how to interpret tree islands, or forest outposts, that are associated with specific topographic positions, e.g. depressions. This is a question not only of scale but also of the mechanisms that allow these islands to exist. Most tree islands are probably started in the protection of some topographic feature, even if it is just a small rock or topographic depression (Resler et al. 2005, Resler 2006, Llambí et al. 2013). For many islands, the forest patch can then expand from the protected site and maintain itself due to the protection it provides to establishing trees. This would thus be a true self-maintained island, even if it becomes rather large. If, however, the forest is restricted to topographic microsites without proliferating out of the abiotic protection zone, the outpost is unlikely to be indicative of treeline-forming processes and should not be considered a tree island. Instead, it may be interpreted as part of a landscape-scale pattern.

Landscape-scale patterns offer an additional window for gaining insights into treeline-controlling processes, ideally to be interpreted in conjunction with treeline form (Tremblay and Chuman 2015). The existence of recurrent patterns indicating controlling processes is suggested by comparative research by, for example, Friedrich-Karl Holtmeier (1973, 2005, 2009, Holtmeier and Broll 2017), several North-American geographers (Butler et al. 2009b), Peter Wardle (Wardle 1965, Wardle et al. 2001, Wardle 2008) and Georg Miede (Miede and Miede 1994, 2000). A systematic analysis of described landscape patterns, accompanied by a GIS-based analysis of remotely-sensed patterns in tree cover in treeline landscapes globally, would likely reveal additional dimensions defining treeline types in terms of landscape-scale controlling processes (Case and Hale 2015).

Data collection and analysis strategies

For some of the pattern dimensions, in particular the patterns in deformation and species composition, field knowledge is indispensable and transects along the slope are the most appropriate sampling method. To also allow an analysis of population structure and spatial point patterns, such transects should be wide enough (at least 30 m, as a rule of thumb, to assure including enough trees also at the uppermost low-tree-density end of the ecotone) and long enough to capture the entire ecotone width (Camarero and Gutiérrez 2004, Liang et al. 2011, Wang et al. 2016, Vitali et al. 2017, Sigdel et al. 2020). Thereby, it may be necessary to

restrict seedling counts to smaller subplots, if regeneration is very prolific. Ideally, tree-ring-based growth and age patterns would also be collected along such transects, at least in non-tropical regions where most tree and shrub species form annual rings. However, for characterizing growth forms, tree height changes and species compositions only, narrower transects or smaller plots in sequence along the ecotone can be sufficient and may be preferable under budget or time constraints. Other patterns, like spatial clumping in the x–y plane, may be described more efficiently using remotely sensed data (Chhetri and Thai 2019). Because of the small-scale patterns addressed, high-resolution (< 1-m resolution) aerial or satellite-based images are best suited. Such images are available for an increasing portion of Earth's surface, including remote treeline areas, although data availability may still be limited for very cloudy or very remote sites. Additional very promising technologies include Airborne Laser Scanning (Coops et al. 2013, Hauglin and Næsset 2016, Bolton et al. 2018) and drone-based stereo-photography (Jochner et al. 2017a), both allowing the creation of surface models that may allow determining the height of even relatively small trees, depending on the alpine vegetation matrix. A combination of field and remote-sensing methods, focusing precious field-work time on those pattern dimensions that cannot be obtained remotely, may be the most efficient method to obtain information on all pattern dimensions needed to fully characterize a site. Importantly, even if not all patterns can be fully mapped, e.g. in remote areas, detecting at least some dimensions of the patterns can allow inferences about the associated processes, which can be an important improvement in site-specific knowledge, allowing better predictions.

The observed patterns indicate what processes have acted upon the ecotone in the past, up to the present date and our best-informed prediction is therefore for these processes to continue to act in the future. However, treeline ecotones are dynamic systems. Some are more dynamic than others, as indicated by their spatial pattern, but this may also change, in particular in times of environmental and land-use change. Multi-temporal datasets could allow analyzing the dynamics of the patterns and mapping these dynamics using the conceptual diagrams proposed here (e.g. trajectories from abrupt to gradual or discrete to diffuse treelines). Re-evaluation of spatial patterns can serve to validate previous assumptions and model predictions about pattern–process relationships and to detect changes in controlling processes.

Therefore, it is strongly recommended to revisit treelines regularly, the frequency depending on the expected dynamics and the purpose of monitoring the treeline. If the purpose is a detailed monitoring of population processes, yearly revisits with a resampling of population parameters can be very useful (Kullman 2007), though at very stable treelines like the abrupt *Nothofagus* treelines in New Zealand, resampling every ten years may be sufficient to capture any dynamics (Harsch et al. 2012). If the purpose is to validate predictions of treeline dynamics, revisits can be more widely spaced, though preferably not by more than ca five years, to not miss out on unexpected changes (e.g. abrupt treelines turning

diffuse and shifting upwards due to sudden tree establishment after passing a climatic threshold – Danby and Hik 2007a, Elliott 2012, Camarero et al 2015 – or after a change in land use – Vitali et al. 2017). Thereby, revisits do not need to imply resampling, or even field visits, but could also be based on high-resolution remote-sensing (aerial or ground-based) images, including images from the past (Danby and Hik 2007b, Lutz et al. 2013, Greenwood et al. 2014, Travers-Smith and Lantz 2020).

Having mapped the tree and forest cover, a next step is a visual interpretation of the spatial pattern based on the examples and descriptions provided in this paper. For height decline and deformation gradients we recommend a manual interpretation, as automated edge detection and description algorithms consistently perform worse than the human brain (Bader et al. 2007a). However, for the 2-D cover patterns we recommend a quantitative interpretation, describing gradients in cover intensity and the level of clustering. For this type of analysis, spatial statistics can be applied. Depending on the data type, a point-pattern analysis, which represents trees as points (x–y coordinates) with associated variables as tree size or age (care should be taken to not confuse stem density and cover), could be applicable. In such an analysis, the pattern dimensions can be described using the measures intensity and clumping, complemented with measures like anisotropy (Camarero et al. 2000, 2005, Illian et al. 2007, Wiegand and Moloney 2013). A second interesting option is an analysis of tree cover based on patch-based metrics, e.g. using FRAGSTATS (Allen and Walsh 1996, Alftine and Malanson 2004, McGarigal et al. 2012).

The conceptual framework presented here, in which contrasting treeline forms or patterns are predicted to occur as a result of different first-level processes, could be formalized via individual based models in which these pattern–process links can be explicitly explored (Wiegand et al. 2006, Martinez et al. 2011), and the outputs of these models tested against empirical data derived from different treelines. Models could also be elaborated to include second-level processes and their environmental drivers. As different processes can result in similar patterns, this approach will require a multi-pattern evaluation of the results (i.e. using pattern-oriented modeling, Wiegand et al. 2003). Thereby, the more patterns (spatial, temporal, demographic and compositional) the model can correctly predict, the more likely is it a realistic representation of the processes involved. Such models could also be used as a framework to explore the dynamics of treeline spatial patterns (e.g. island formation and expansion, shifts from abrupt to gradual treelines, etc.) as a result of changes in the underlying drivers. However, it should also be clear that spatial patterns cannot tell us everything, and in some cases pattern analysis will need to be complemented by further experimental or observational studies evaluating the role of specific processes and mechanisms (e.g. ecophysiological constraints, dispersal patterns, neighbor interactions).

Conclusions

Alpine treeline ecotones can exhibit many different spatial patterns, but within this variation there is order that can help to recognize treelines with similar controlling processes and expected dynamics. Important dimensions to describe these patterns are the rate of change in tree cover and the strength and shape of clustering of this cover, and changes in tree height and tree shape. These pattern dimensions could be complemented by additional information about tree age distributions, the functional composition of the ecotone vegetation and environmental conditions to distinguish second-level processes in more detail. Describing and ordering the variation in the four main pattern dimensions systematically should help to maximize the use of the information gained in treeline studies beyond the particular sites studied. Stratifying treeline research and monitoring efforts according to spatial types should also help to cover the full range of dynamics expected at different treeline types. These advantages should allow us to more efficiently gain the necessary understanding to predict treeline shifts in response to climate and land-use changes. We encourage all treeline researchers to try to quantify the dimensions presented here and to work towards validating this qualitative scheme with a quantification of patterns and model- and field-based tests of pattern-process relationships.

Invitation

Discussing and sharing spatial data and pattern descriptions is possible via the following website: <www.alpine-treelines.net>, one of its aims being the creation of a world map of treeline spatial patterns, the other to provide a network environment for treeline researchers interested in these issues. Treeline pattern detection, analysis and classification tools will be made available on this website as they are developed.

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References

- Akhalkatsi, M. et al. 2006. Facilitation of seedling microsites by *Rhododendron caucasicum* extends the *Betula litwinowii* alpine treeline, Caucasus Mountains, Republic of Georgia. – Arctic Antarct. Alp. Res. 38: 481–488.
- Alftine, K. J. and Malanson, G. P. 2004. Directional positive feedback and pattern at an alpine tree line. – J. Veg. Sci. 15: 3–12.
- Allen, T. R. and Walsh, S. J. 1996. Spatial and compositional pattern of alpine treeline, Glacier National Park, Montana. – Photogram. Eng. Remote Sens. 62: 1261–1268.
- Armand, A. D. 1992. Sharp and gradual mountain timberlines as a result of species interaction. – In: Hansen, A. J. and di Castri, F. (eds), Landscape boundaries: consequences for biotic diversity and ecological flows. Springer, pp. 360–378.
- Arzac, A. et al. 2019. Modelling the effect of temperature changes on plant life-form distribution across a treeline ecotone in the tropical Andes. – Plant Ecol. Divers. 12: 619–631.
- Astudillo-Sánchez, C. C. et al. 2019. Recruitment and facilitation in *Pinus hartwegii*, a Mexican alpine treeline ecotone, with potential responses to climate warming. – Trees 33: 1087–1100.
- Bader, M. Y. et al. 2007a. Vegetation structure and temperature regimes of tropical alpine treelines. – Arctic Antarct. Alp. Res. 39: 353–364.
- Bader, M. Y. et al. 2007b. High solar radiation hinders tree regeneration above the alpine treeline in northern Ecuador. – Plant Ecol. 191: 33–45.
- Bader, M. Y. et al. 2008. A simple spatial model exploring positive feedbacks at tropical alpine treelines. – Arctic Antarct. Alp. Res. 40: 269–278.
- Baker, W. L. and Weisberg, P. J. 1995. Landscape analysis of the forest-tundra ecotone in Rocky Mountain National Park, Colorado. – Profess. Geogr. 47: 361–375.
- Barbeito, I. et al. 2013. Snow fungi-induced mortality of *Pinus cembra* at the Alpine treeline: evidence from plantations. – Arctic Antarct. Alp. Res. 45: 455–470.
- Batliori, E. and Gutierrez, E. 2008. Regional tree line dynamics in response to global change in the Pyrenees. – J. Ecol. 96: 1275–1288.
- Batliori, E. et al. 2009. Seedling recruitment, survival and facilitation in alpine *Pinus uncinata* tree line ecotones. Implications and potential responses to climate warming. – Global Ecol. Biogeogr. 18: 460–472.
- Bekker, M. F. 2005. Positive feedback between tree establishment and patterns of subalpine forest advancement, Glacier National Park, Montana, U.S.A. – Arctic Antarct. Alp. Res. 37: 97–107.
- Bekker, M. F. and Malanson, G. P. 2008. Linear forest patterns in subalpine environments. – Prog. Phys. Geogr. 32: 635–653.
- Benedict, J. B. 1984. Rates of tree-island migration, Colorado Rocky Mountains, USA. – Ecology 65: 820–823.
- Bolton, D. K. et al. 2018. Evidence of vegetation greening at alpine treeline ecotones: three decades of Landsat spectral trends informed by lidar-derived vertical structure. – Environ. Res. Lett. 13: 084022.
- Bonanomi, G. et al. 2018. Anthropogenic and environmental factors affect the tree line position of *Fagus sylvatica* along the Apennines (Italy). – J. Biogeogr. 45: 2595–2608.
- Bourgeron, P. S. et al. 2016. The forest–alpine ecotone: a multi-scale approach to spatial and temporal dynamics of treeline change at Niwot Ridge. – Plant Ecol. Divers. 8: 763–779.
- Brockmann-Jerosch, H. 1919. Baumgrenze und Klimacharakter. – Rascher & Cie.
- Brown, J. H. et al. 1996. The geographic range: size, shape, boundaries and internal structure. – Annu. Rev. Ecol. Syst. 27: 597–623.
- Bueno, A. and Llambí, L. D. 2015. Facilitation and edge effects influence vegetation regeneration in old-fields at the tropical Andean forest line. – Appl. Veg. Sci. 18: 613–623.
- Butler, D. R. et al. 2009a. Geomorphic patterns and processes at alpine treeline. – In: Butler, D. R. et al. (eds), The changing Alpine treeline, the example of Glacier National Park, MT, USA. Elsevier, pp. 63–84.
- Butler, D. R. et al. 2009b. The changing Alpine treeline, the example of Glacier National Park, MT, USA. – Elsevier.
- Cairns, D. M. and Moen, J. 2004. Herbivory influences tree lines. – J. Ecol. 92: 1019–1024.
- Camarero, J. J. and Gutierrez, E. 1999. Structure and recent recruitment at alpine forest–pasture ecotones in the Spanish central Pyrenees. – Ecoscience 6: 451–464.
- Camarero, J. J. and Gutiérrez, E. 2004. Pace and pattern of recent treeline dynamics: response of ecotones to climatic variability in the Spanish Pyrenees. – Clim. Change 63: 181–200.
- Camarero, J. J. et al. 2000. Spatial pattern of subalpine forest–alpine grassland ecotones in the Spanish central Pyrenees. – For. Ecol. Manage. 134: 1–16.
- Camarero, J. J. et al. 2005. Spatial patterns of tree recruitment in a relict population of *Pinus uncinata*: forest expansion through stratified diffusion. – J. Biogeogr. 32: 1979–1992.
- Camarero, J. J. et al. 2015. Recent and intense dynamics in a formerly static Pyrenean treeline. – Arctic Antarct. Alp. Res. 47: 773–783.
- Case, B. S. and Hale, R. J. 2015. Using novel metrics to assess biogeographic patterns of abrupt treelines in relation to abiotic influences. – Progr. Phys. Geogr. 39: 310–336.
- Chhetri, P. K. and Thai, E. 2019. Remote sensing and geographic information systems techniques in studies on treeline ecotone dynamics. – J. For. Res. 30: 1543–1553.
- Coops, N. C. et al. 2013. Characterization of an alpine tree line using airborne LiDAR data and physiological modeling. – Global Change Biol. 19: 3808–3821.
- Crawford, R. M. M. 2008. Plants at the margin: ecological limits and climate change. – Cambridge Univ. Press.
- Crofts, A. L. and Brown, C. D. 2020. The importance of biotic filtering on boreal conifer recruitment at alpine treeline. – Ecography 43: 914–929.
- Cuevas, J. G. 2000. Tree recruitment at the *Nothofagus pumilio* alpine timberline in Tierra del Fuego, Chile. – J. Ecol. 88: 840–855.
- Danby, R. K. and Hik, D. S. 2007a. Variability, contingency and rapid change in recent subarctic alpine tree line dynamics. – J. Ecol. 95: 352–363.
- Danby, R. K. and Hik, D. S. 2007b. Evidence of recent treeline dynamics in southwest Yukon from aerial photographs. – Arctic 60: 411–420.
- Devi, N. et al. 2008. Expanding forests and changing growth forms of Siberian larch at the Polar Urals treeline during the 20th century. – Global Change Biol. 14: 1581–1591.
- Dial, R. J. et al. 2016. Shrubline but not treeline advance matches climate velocity in montane ecosystems of south-central Alaska. – Global Change Biol. 22: 1841–1856.
- Ellenberg, H. 1966. Leben und Kampf an den Baumgrenzen der Erde. – Naturwissenschaftliche Rundschau 4: 133–139.
- Elliott, G. P. 2011. Influences of 20th-century warming at the upper tree line contingent on local-scale interactions: evidence

- from a latitudinal gradient in the Rocky Mountains, USA. – *Global Ecol. Biogeogr.* 20: 46–57.
- Elliott, G. P. 2012. Extrinsic regime shifts drive abrupt changes in regeneration dynamics at upper treeline in the Rocky Mountains, USA. – *Ecology* 93: 1614–1625.
- Elliott, G. P. and Kipfmüller, K. E. 2010. Multi-scale influences of slope aspect and spatial pattern on ecotonal dynamics at upper treeline in the southern Rocky Mountains, USA. – *Arctic Antarct. Alp. Res.* 42: 45–56.
- Frei, E. R. et al. 2018. Biotic and abiotic drivers of tree seedling recruitment across an alpine treeline ecotone. – *Sci. Rep.* 8: 10894.
- Galvan, J. D. et al. 2014. Seeing the trees for the forest: drivers of individual growth responses to climate in *Pinus uncinata* mountain forests. – *J. Ecol.* 102: 1244–1257.
- Gamache, I. and Payette, S. 2004. Height growth response of tree line black spruce to recent climate warming across the forest-tundra of eastern Canada. – *J. Ecol.* 92: 835–845.
- Germino, M. J. and Smith, W. K. 1999. Sky exposure, crown architecture and low-temperature photoinhibition in conifer seedlings at alpine treeline. – *Plant Cell Environ.* 22: 407–415.
- Germino, M. J. et al. 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. – *Plant Ecol.* 162: 157–168.
- González, W. et al. 2011. Successional dynamics of the tree component in the forest-paramo transition belt in the tropical Andes. – *Ecotrópicos* 24: 60–79.
- Greenwood, S. et al. 2014. Strong topographic sheltering effects lead to spatially complex treeline advance and increased forest density in a subtropical mountain region. – *Global Change Biol.* 20: 3756–3766.
- Hagedorn, F. et al. 2014. Treeline advances along the Urals mountain range – driven by improved winter conditions? – *Global Change Biol.* 20: 3530–3543.
- Hagedorn, F. et al. 2019. Above- and belowground linkages shape responses of mountain vegetation to climate change. – *Science* 365: 1119–1123.
- Harsch, M. A. and Bader, M. Y. 2011. Treeline form – a potential key to understanding treeline dynamics. – *Global Ecol. Biogeogr.* 20: 582–596.
- Harsch, M. A. et al. 2009. Are treelines advancing? A global meta-analysis of treeline response to climate warming. – *Ecol. Lett.* 12: 1040–1049.
- Harsch, M. A. et al. 2012. Causes of tree line stability: stem growth, recruitment and mortality rates over 15 years at New Zealand *Nothofagus* tree lines. – *J. Biogeogr.* 39: 2061–2071.
- Hättenschwiler, S. and Smith, W. K. 1999. Seedling occurrence in alpine treeline conifers: a case study from the central Rocky Mountains, USA. – *Acta Oecol.* 20: 219–224.
- Hauglin, M. and Næsset, E. 2016. Detection and segmentation of small trees in the forest-tundra ecotone using airborne laser scanning. – *Remote Sens.* 8: 407.
- Heenan, P. B. and Smissen, R. D. 2013. Revised circumscription of *Nothofagus* and recognition of the segregate genera *Fuscopora*, *Lophozonia* and *Trisyngyne* (Nothofagaceae). – *Phytotaxa* 146: 1–31.
- Hermes, K. 1955. Die Lage der oberen Waldgrenze in den Gebirgen der Erde und ihr Abstand zur Schneegrenze. – Selbstverlag des Geographischen Inst. der Univ. Köln.
- Hoch, G. and Körner, C. 2005. Growth, demography and carbon relations of *Polylepis* trees at the world's highest treeline. – *Funct. Ecol.* 19: 941–951.
- Holtmeier, F. K. 1966. Die ökologische Funktion des Tannenhähers im Zirben-Lärchenwald und an der Waldgrenze des Oberengadins. – *J. Ornithol.* 107: 345.
- Holtmeier, F. K. 1973. Geocological aspects of timberlines in northern and central Europe. – *Arctic Alp. Res.* 5: A45–A54.
- Holtmeier, F. K. 1982. 'Ribbon-forest' und 'Hecken': Streifenartige Verbreitungsmuster des Baumwuchses an der oberen Waldgrenze in den Rocky Mountains. – *Erdkunde* 36: 142–153.
- Holtmeier, F. K. 1985. Climatic stress influencing the physiognomy of trees at the polar and mountain timberline. – In: Turner, H. and Tranquillini, W. (eds), Establishment and tending of sub-alpine forest: research and management. IUFRO project group P1.07-00, pp. 31–40.
- Holtmeier, F. K. 2005. Relocation of snow and its effects in the treeline ecotone – with special regard to the Rocky Mountains, the Alps and northern Europe. – *Erde* 136: 343–373.
- Holtmeier, F. K. 2009. Mountain timberlines. Ecology, patchiness and dynamics. – Springer.
- Holtmeier, F. K. and Broll, G. 2005. Sensitivity and response of northern hemisphere altitudinal and polar treelines to environmental change at landscape and local scales. – *Global Ecol. Biogeogr.* 14: 395–410.
- Holtmeier, F.-K. and Broll, G. 2010. Wind as an ecological agent at treelines in North America, the Alps and the European Subarctic. – *Phys. Geogr.* 31: 203–233.
- Holtmeier, F. K. and Broll, G. 2012. Landform influences on treeline patchiness and dynamics in a changing climate. – *Phys. Geogr.* 33: 403–437.
- Holtmeier, F. K. and Broll, G. 2017. Treelines – approaches at different scales. – *Sustainability* 9: 808.
- Illian, J. et al. 2007. Statistical analysis and modelling of spatial point patterns. – Wiley.
- Jochner, M. et al. 2017a. Among-tree variability and feedback effects result in different growth responses to climate change at the upper treeline in the Swiss Alps. – *Ecol. Evol.* 7: 7937–7953.
- Jochner, M. et al. 2017b. Tree growth responses to changing temperatures across space and time: a fine-scale analysis at the tree-line in the Swiss Alps. – *Trees* 32: 645–660.
- Johnson, A. C. and Yeakley, J. A. 2019. Microsites and climate zones: seedling regeneration in the alpine treeline ecotone worldwide. – *Forests* 10: 864.
- Johnson, J. S. et al. 2017. Seed dispersal at alpine treeline: an assessment of seed movement within the alpine treeline ecotone. – *Ecosphere* 8: e01649.
- Joshi, A. A. et al. 2019. Frost maintains forests and grasslands as alternate states in a montane tropical forest–grassland mosaic; but alien tree invasion and warming can disrupt this balance. – *J. Ecol.* 108: 122–132.
- Karger, D. N. et al. 2019. Why tree lines are lower on islands-climatic and biogeographic effects hold the answer. – *Global Ecol. Biogeogr.* 28: 839–850.
- Körner, C. 1998. A re-assessment of high elevation treeline positions and their explanation. – *Oecologia* 115: 445–459.
- Körner, C. 2012. Alpine treelines. Functional ecology of the global high elevation tree limits. – Springer.
- Körner, C. and Paulsen, J. 2004. A world-wide study of high altitude treeline temperatures. – *J. Biogeogr.* 31: 713–732.
- Kubisch, P. et al. 2017. Fine root abundance and dynamics of stone pine (*Pinus cembra*) at the alpine treeline is not impaired by self-shading. – *Front. Plant Sci.* 8: 602.

- Kullman, L. 2007. Tree line population monitoring of *Pinus sylvestris* in the Swedish Scandes, 1973–2005: implications for tree line theory and climate change ecology. – *J. Ecol.* 95: 41–52.
- Kullman, L. and Oberg, L. 2009. Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: a landscape ecological perspective. – *J. Ecol.* 97: 415–429.
- Laberge, M. J. et al. 2000. Life span and biomass allocation of stunted black spruce clones in the subarctic environment. – *J. Ecol.* 88: 584–593.
- LaMarche Jr., V. C. 1979. Environment in relation to age of bristlecone pines. – *Ecology* 50: 53–59.
- Lauer, W. 1978. Timberline studies in central Mexico. – *Arctic Alp. Res.* 10: 383–396.
- Lett, S. et al. 2016. Bryophyte traits explain climate-warming effects on tree seedling establishment. – *J. Ecol.* 32: 1666–1680.
- Leuschner, C. 1996. Timberline and alpine vegetation on the tropical and warm-temperate oceanic islands of the world: elevation, structure and floristics. – *Vegetatio* 123: 193–206.
- Liang, E. et al. 2011. Little change in the fir tree-line position on the southeastern Tibetan Plateau after 200 years of warming. – *New Phytol.* 190: 760–769.
- Liang, E. et al. 2016. Species interactions slow warming-induced upward shifts of treelines on the Tibetan Plateau. – *Proc. Natl Acad. Sci. USA* 113: 4380–5.
- Llambí, L. D. et al. 2013. Spatial relations and population structure of a dominant tree along a treeline ecotone in the Tropical Andes: interactions at gradient and plant–neighbourhood scales. – *Plant Ecol. Divers.* 6: 343–353.
- Loranger, H. et al. 2017. Competitor or facilitator? The ambiguous role of alpine grassland for the early establishment of tree seedlings at treeline. – *Oikos* 126: 1625–1636.
- Lutz, D. A. et al. 2013. Four decades of andean timberline migration and implications for biodiversity loss with climate change. – *PLoS One* 8: e74496.
- Malanson, G. P. 1997. Effects of feedbacks and seed rain on ecotone patterns. – *Landscape Ecol.* 12: 27–38.
- Marr, J. W. 1977. The development and movement of tree islands near the upper limit of tree growth in the southern Rocky Mountains. – *Ecology* 58: 1159–1164.
- Martinez, I. et al. 2011. Disentangling the formation of contrasting tree-line physiognomies combining model selection and Bayesian parameterization for simulation models. – *Am. Nat.* 177: E136–E152.
- Mayr, S. et al. 2019. Winter embolism and recovery in the conifer shrub *Pinus mugo* L. – *Forests* 10: 941.
- McGarigal, K. et al. 2012. FRAGSTATS v4: spatial pattern analysis program for categorical and continuous maps. – Computer software program produced by the authors at the Univ. of Massachusetts, Amherst, <www.umass.edu/landeco/research/fragstats/fragstats.html>.
- McGlone, M. 2004. Timberline and climate change. – *Te Taiao* 2004: 8–9.
- McIntire, E. J. B. et al. 2016. Wind exposure and light exposure, more than elevation-related temperature, limit tree line seedling abundance on three continents. – *J. Ecol.* 104: 1379–1390.
- Miehe, G. and Miehe, S. 1994. Zur oberen Waldgrenze in tropischen Gebirge. – *Phytocoenologia* 24: 53–110.
- Miehe, G. and Miehe, S. 2000. Comparative high mountain research on the treeline ecotone under human impact. Carl Troll's 'Asymmetrical zonation of the humid vegetation types of the World' of 1948 reconsidered. – *Erdkunde* 54: 34–50.
- Miehe, G. et al. 2015. Vegetation ecology. – In: Miehe, G. and Pendry, C. (eds), *Nepal. An introduction to the natural history, ecology and human environment of the Himalayas*. Royal Botanic Garden Edinburgh, pp. 385–472.
- Morales, M. S. et al. 2012. Precipitation changes in the South American Altiplano since 1300 AD reconstructed by tree-rings. – *Clim. Past* 8: 653–666.
- Norton, D. A. and Schönenberger, W. 1984. The growth forms and ecology of *Nothofagus solandri* at the alpine timberline, Craigieburn Range, New Zealand. – *Arctic Alp. Res.* 16: 361–370.
- Okitsu, S. and Ito, K. 1989. Conditions for the development of the *Pinus pumila* zone of Hokkaido, northern Japan. – *Vegetatio* 84: 127–132.
- Paulsen, J. and Körner, C. 2014. A climate-based model to predict potential treeline position around the globe. – *Alp. Bot.* 124: 1–12.
- Pereg, D. and Payette, S. 1998. Development of black spruce growth forms at treeline. – *Plant Ecol.* 138: 137–147.
- Peters, T. et al. 2014. An ecological paradox: high species diversity and low position of the upper forest line in the Andean Depression. – *Ecol. Evol.* 4: 2134–2145.
- Pyatt, J. C. et al. 2016. The importance of conifers for facilitation at treeline: comparing biophysical characteristics of leeward microsites in whitebark pine communities. – *Arctic Antarct. Alp. Res.* 48: 427–444.
- Ramírez, L. et al. 2009. Vegetation structure along the forest-páramo transition belt in the Sierra Nevada de Mérida: implications for understanding treeline dynamics. – *Ecotrópicos* 22: 83–98.
- Rehm, E. M. and Feeley, K. J. 2015. The inability of tropical cloud forest species to invade grasslands above treeline during climate change: potential explanations and consequences. – *Ecography* 38: 1167–1175.
- Resler, L. M. 2006. Geomorphic controls of spatial pattern and process at alpine treeline. – *Profess. Geogr.* 58: 124–138.
- Resler, L. M. and Tomback, D. F. 2008. Blister rust prevalence in krummholz whitebark pine: implications for treeline dynamics, northern Rocky Mountains, Montana, USA. – *Arctic Antarct. Alp. Res.* 40: 161–170.
- Resler, L. M. et al. 2005. Topographic shelter and conifer establishment and mortality in an alpine environment, Glacier National Park, Montana. – *Phys. Geogr.* 26: 112–125.
- Robles-Gutiérrez, C. A. et al. 2016. Probability of mortality by fire damage of young *Pinus hartwegii* Lindl. trees in the Izta-Popo National Park. – *Revista Chapíngo Serie Ciencias Forestales y del Ambiente XXII*: 165–178.
- Sarmiento Pinzón, C. E. and León Moya, O. A. 2015. Transición bosque-páramo. Bases conceptuales y métodos para su identificación en los Andes colombianos. – *Inst. de Investigación de Recursos Biológicos Alexander von Humboldt*.
- Schickhoff, U. 2005. The upper timberline in the Himalayas, Hindu Kush and Karakorum: a review of geographical and ecological aspects. – In: Broll, G. and Keplin, B. (eds), *Mountain ecosystems: studies in treeline ecology*. Springer, pp. 275–354.
- Schickhoff, U. et al. 2015. Do Himalayan treelines respond to recent climate change? An evaluation of sensitivity indicators. – *Earth Syst. Dyn.* 6: 245–265.
- Schwab, N. et al. 2016. Treeline responsiveness to climate warming: insights from a krummholz treeline in Rolwaling Himal, Nepal. – In: Singh, R. B. et al. (eds), *Climate change, glacier response and vegetation dynamics in the Himalaya: contributions toward*

- future Earth initiatives. Springer International Publishing, pp. 307–345.
- Sigdel, S. R. et al. 2020. Tree-to-tree interactions slow down Himalayan treeline shifts as inferred from tree spatial patterns. – *J. Biogeogr.* 47: 1816–1826.
- Silva, L. C. R. and Anand, M. 2011. Mechanisms of Araucaria (Atlantic) forest expansion into southern Brazilian grasslands. – *Ecosystems* 14: 1354–1371.
- Strayer, D. L. et al. 2003. A classification of ecological boundaries. – *Bioscience* 53: 723–729.
- Tomback, D. F. et al. 2016. Whitebark pine facilitation at treeline: potential interactions for disruption by an invasive pathogen. – *Ecol. Evol.* 6: 5144–5157.
- Tranquillini, W. 1979. Physiological ecology of the Alpine timberline: tree existence at high altitudes with special reference to the European Alps. – Springer.
- Travers-Smith, H. Z. and Lantz, T. 2020. Leading-edge disequilibrium in alder and spruce populations across the forest–tundra ecotone. – *Ecosphere* 11: e03118.
- Treml, V. and Chuman, T. 2015. Ecotonal dynamics of the altitudinal forest limit are affected by terrain and vegetation structure variables: an example from the Sudetes Mountains in central Europe. – *Arctic Antarct. Alp. Res.* 47: 133–146.
- Treml, V. and Veblen, T. T. 2017. Does tree growth sensitivity to warming trends vary according to treeline form? – *J. Biogeogr.* 44: 1469–1480.
- Treml, V. et al. 2019. Differences in growth between shrubs and trees: how does the stature of woody plants influence their ability to thrive in cold regions? – *Agric. For. Meteorol.* 271: 54–63.
- Vitali, A. et al. 2017. Deconstructing human-shaped treelines: microsite topography and distance to seed source control *Pinus nigra* colonization of treeless areas in the Italian Apennines. – *For. Ecol. Manage.* 406: 37–45.
- Vitali, A. et al. 2019. Pine recolonization dynamics in Mediterranean human-disturbed treeline ecotones. – *For. Ecol. Manage.* 435: 28–37.
- von Humboldt, A. and Bonpland, A. 1807. Ideen zu einer Geographie der Pflanzen nebst einem Naturgemälde der Tropenländer. – F. G. Cotta/F. Schoell.
- Wang, Y. et al. 2016. Impact of plot shape and size on the evaluation of treeline dynamics in the Tibetan Plateau. – *Trees* 30: 1045–1056.
- Wardle, P. 1965. A comparison of alpine timber lines in New Zealand and North America. – *N. Z. J. Bot.* 3: 113–135.
- Wardle, P. 1985. New Zealand timberlines. 1. Growth and survival of native and introduced tree species in the Craigieburn Range, Canterbury. – *N. Z. J. Bot.* 23: 219–234.
- Wardle, P. 2008. New Zealand forest to alpine transitions in global context. – *Arctic Antarct. Alp. Res.* 40: 240–249.
- Wardle, P. et al. 2001. Comparison of the flora and vegetation of the southern Andes and New Zealand. – *N. Z. J. Bot.* 39: 69–108.
- Wiegand, T. and Moloney, K. A. 2013. Handbook of spatial point pattern analysis in ecology. – CRC Press.
- Wiegand, T. et al. 2003. Using pattern-oriented modeling for revealing hidden information: a key for reconciling ecological theory and application. – *Oikos* 100: 209–222.
- Wiegand, T. et al. 2006. Abrupt population changes in treeline ecotones along smooth gradients. – *J. Ecol.* 94: 880–892.
- Wilson, J. B. and Agnew, A. D. Q. 1992. Positive-feedback switches in plant communities. – *Adv. Ecol. Res.* 23: 263–336.
- Zeng, Y. and Malanson, G. P. 2006. Endogenous fractal dynamics at alpine treeline ecotones. – *Geogr. Anal.* 38: 271–287.
- Zeng, Y. et al. 2007. Geomorphological limits to self-organization of alpine forest-tundra ecotone vegetation. – *Geomorphology* 91: 378–392.

Box A. Examples

A1 Gradual treelines

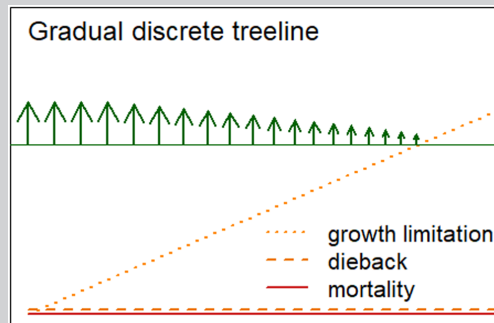


Figure A1a. Hypothesized first-level controls on gradual single-species treelines. Growth limitation (dotted orange line) is the strongest limitation at such treelines.

Controlling processes: growth only (null-model of treeline form). Growth declines with elevation, but must also increasingly decrease with tree height (i.e. with coupling to the atmosphere) with elevation. Alternatively, in the case of multi-species treelines, a gradual height decline may also be due to species turnover, from tree-forming species to small trees and shrubs. Thus, possibly in addition to decreased growth, inter-specific interactions and species-specific establishment chances play a role in forming such patterns.

Examples:

We are not aware of the existence of pure cases of single-species gradual treelines in nature, as some level of deformation is always observed in the smallest trees. It appears that very small tree individuals at treeline, which may be several decades years old and only 50-cm tall (Camarero and Gutierrez 1999), will always experience some level of damage during their long exposure to the alpine climate. Even if they are not strictly krummholz, such small trees are very likely to lose their main meristems and to experience stem bending at one or several occasions during their lifetime, making them grow as multi-stemmed, bushy and/or twisted individuals. However, the level of deformation varies, and if light, treelines may be considered as gradual discrete without krummholz.

Multi-species gradual treelines are more common and are known from very wet mild-temperate to tropical mountains, like the west coast of the southern Alps of New Zealand (Wardle 1965) and the eastern cordillera of the Andes in southern Ecuador (Bader et al. 2007a).

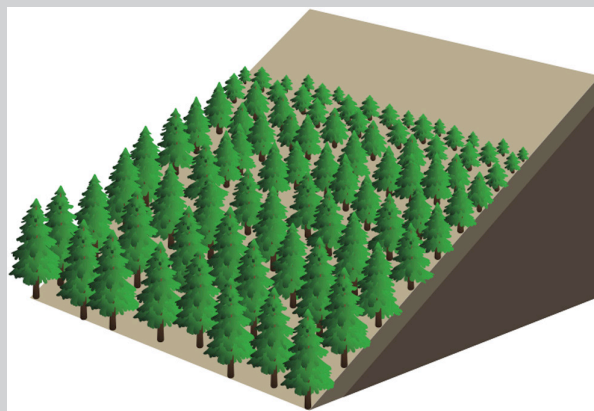


Figure A1b. Schematic example of a gradual discrete treeline.



Figure A1c. Gradual discrete multi-species treelines in the temperate zone (left) and the tropics (right): mixed broadleaf-Podocarp forest grading into tussock grassland, Kelly's Saddle, west slope of the southern Alps, New Zealand (photo: M. Y. Bader) and mixed evergreen cloud forest, Podocarpus National Park, Ecuador (photo: M. Y. Bader).

A2 Krummholz treelines

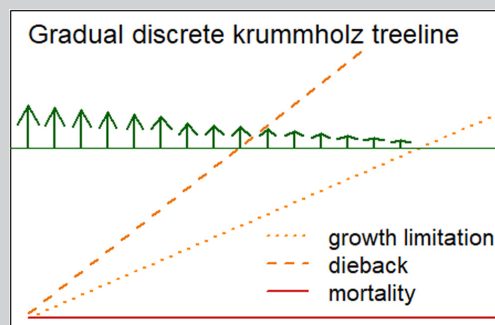


Figure A2a. Hypothesized first-level controls on gradual discrete krummholz treelines. Dieback (orange dashed line) is the strongest limitation, while growth limitation (dotted orange line) also plays an important role at such treelines.

Controlling processes: this type of treeline is considered by some authors as being typical for a natural treeline (Ellenberg 1966, Tranquillini 1979), growth and biomass maintenance of tree species being increasingly limited by a combination of low growth temperatures and other stress factors like wind and frost, but tree cover being closed, i.e. mortality not limiting tree occurrence, up to the tree-species line.

As explained above for gradual treelines, the level of deformation in gradual treelines can be quite variable, ranging from none (in theory) to very strong deformation leading to krummholz. In multi-species treelines, the turn-over from trees to shrubs may be accompanied by an additional environmental stunting of both trees and shrubs, in which case a gradual multi-species krummholz treeline would emerge. This is the case e.g. on very wet and windy ridges in southern Ecuador (Bader et al. 2007a).

Examples:

Examples of single-species gradual discrete krummholz treelines include natural treelines formed by *Erica trimera* on the Bale mountains of Ethiopia (Miehe and Miehe 1994), and a *Fuscospora cliffortioides* (previously known as *Nothofagus solandri* var. *cliffortioides*, Heenan and Smitten 2013) treeline described for a wind-exposed, shallow-soil or snow accumulating position in the southern Alps of New Zealand (Wardle 1965, Norton and Schönenberger 1984), and some sections of *Nothofagus pumilio* treelines in southern South America (Holtmeier 2009). In both cases, nearby treelines tend to be abrupt, which sometimes appears to be a sign of disturbance, e.g. by fire in the Bale Mountains. In these mountains, natural treelines are actually something in between a discrete and a diffuse form, with shrubby *Erica* being about 1.6 m tall at the discrete transition from closed scrub to alpine dwarf shrubs, while above that single dome-shaped *Erica* shrubs occur that decrease gradually to about 0.5 m in height (Miehe and Miehe 1994).

The case study from New Zealand is particularly interesting, because the dominant treeline form of *F. cliffortioides* as well as other Nothofagaceae in New Zealand and in southern South America is abrupt and discrete, tall forest giving way to alpine tussock grassland (Cuevas 2000, Wardle 2008, Case and Hale 2015). The difference between the gradual and the abrupt Nothofagaceae treelines indicates that different processes shape these treelines. While establishment is more limited than growth at the abrupt treelines, gradual Nothofagaceae treelines tend to occur in situations where trees are damaged by wind or excess snow cover, causing the strong deformation and the gradual decline in tree height so unusual for this part of the world (Wardle 1965).

A3 Diffuse treelines

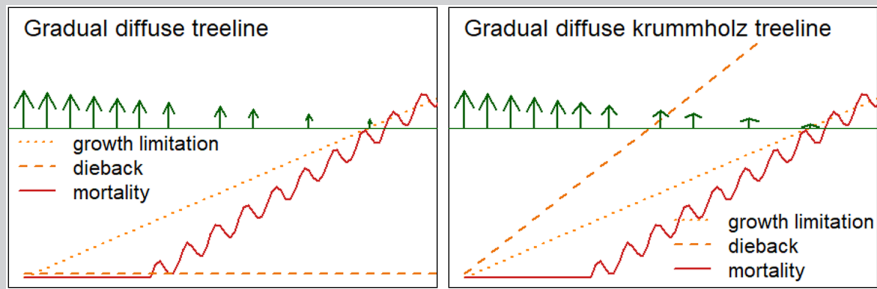


Figure A3a. Hypothesized first-level controls on gradual diffuse treelines without (left) and with (right) krummholz formation. Mortality (red line), including establishment failure outside of safe sites, controls the spacing of trees, while growth limitation (dotted orange line) controls the size of existing trees in the case without krummholz (left), while additionally dieback controls the size of trees in the case with krummholz (right).

Diffuse treelines without krummholz

Controlling processes: growth is limiting (gradual size decline is implied for diffuse treelines if an abrupt size decline is not explicitly mentioned) and survival (especially during establishment) is restricted to increasingly few microsites. This interpretation is especially likely in heterogeneous terrain. Alternatively, even on a hypothetical homogenous slope a diffuse pattern can arise if the treeline is actively advancing and the spread-out trees are thus young outposts, or if it has had one or more advance episodes in the past, implying temporal heterogeneity combined with spatial stochasticity in establishment chances.

Examples:

In dry areas, like the example of Sajama in Bolivia (Fig. A3d), the forest is already open also at lower elevations. Such treelines are considered diffuse only if the spacing becomes more open towards higher elevation in the ecotone.

Gradual discrete treelines are found in many mountains, though an absolute absence of dieback is rare, and this appears to be a natural pattern, although in some cases it may be the result of land use opening up the forest at formerly discrete treelines (Tranquillini 1979). For example, among typically discrete *Nothofagus* treelines in southern South America, some diffuse ecotones composed of the same species can also be found. For this, people and their livestock have been held responsible (Ellenberg 1966).

Diffuse treelines with krummholz

Controlling processes: dieback limits tree stature, likely in combination with reduced growth, and survival is restricted to increasingly few microsites (spatial heterogeneity) or controlled by spatial stochasticity combined with temporal heterogeneity (see above).

Examples:

Diffuse krummholz treelines are a rather common treeline form, as single trees above the closed forest are prone to wind damage and to winter desiccation (Tranquillini 1979).

As discussed above (A2), some relatively undisturbed Ethiopian *Erica* treelines form a combination of discrete and diffuse krummholz treeline, the forest being closed down to a tree size of about 1.6 m, followed by a zone of dispersed *Erica* shrubs/krummholz.

In situations where existing krummholz is the main source of sheltered sites it is likely that krummholz islands emerge (A7).

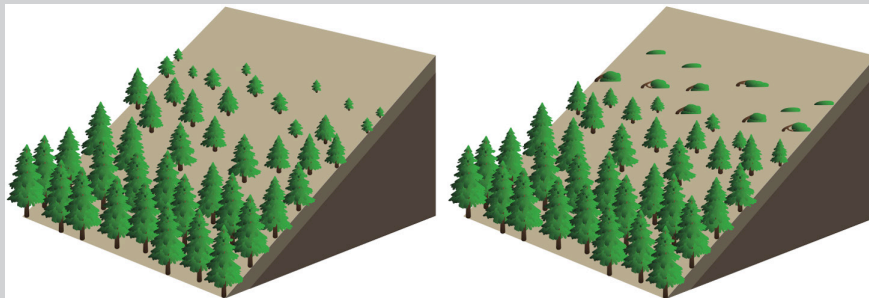


Figure A3b. Schematic example of a gradual diffuse treeline without (left) and with krummholz (right).



Figure A3c. Gradual diffuse treeline: Natural treeline in the Alps composed of *Larix decidua*, Stavel Crastu, Bosco/Gurin, Switzerland (photo: Matthias Jochner).



Figure A3d. Gradual diffuse krummholz treeline composed of *Polylepis tarapacana*, Sajama, Bolivia (photo: M. Y. Bader).



Figure A3e. Gradual diffuse krummholz treeline composed of *Pinus uncinata*, Ordesa, Pyrenees, Spain (photo: M. Y. Bader).

A4 Abrupt treelines

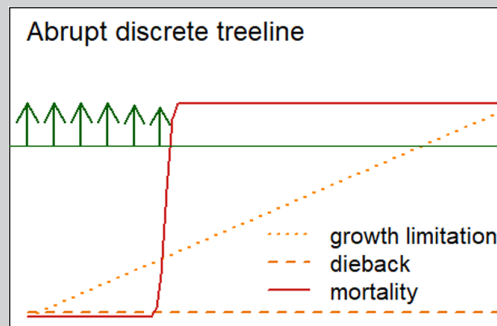


Figure A4a. Hypothesized first-level controls on abrupt discrete treelines. Mortality (red line) controls these treelines, the strong change in the gradient caused by the change in microclimatic conditions between forest and alpine zone, leading to a positive feedback switch (Wilson and Agnew 1992).

Controlling processes: survival outside existing forest is limited at an elevation where growth is not yet much limited. This may be due to low establishment in the harsh alpine conditions, especially for shade-dependent tree species, or to disturbance, e.g. recurrent burning of the alpine vegetation. At multi-species abrupt treelines, it is more likely that their origin and maintenance are anthropogenic, because with multiple species present it is unlikely that none would be able to establish in the alpine zone.

Examples:

The Nothofagaceae (southern beech) treelines in New Zealand and southern South America are the most well-known abrupt treelines, and the only ones for which an anthropogenic origin of this pattern is unlikely. No fossil tree wood charcoal has ever been discovered above treeline in New Zealand (McGlone 2004) and fire is unlikely to cause the regular landscape-scale pattern observed for most New Zealand treelines. It is instead suggested as an explanation for the unusually irregular treelines in the Tararua and Ruahine Ranges (Wardle 1965). How the regular and abrupt treelines in New Zealand came to be, is a puzzling question still awaiting an answer. However, their maintenance can be explained by the shade-dependence and frost-intolerance of the tree seedlings (Wardle 1965, 1985, Harsch et al. 2012), causing a positive feedback between tree establishment and microclimate that maintains the abrupt boundary (Wilson and Agnew 1992). A similar reasoning applies to *Nothofagus* treelines in South America (Cuevas 2000).

Abrupt discrete treelines are also found in *Fagus sylvatica* (European beech) in southern Europe, but here it appears to be mostly a result of historic land use in this long-inhabited region, combined with the difficulty of this species to re-establish outside shade. The anthropogenic nature of the abrupt *F. sylvatica* treelines is indicated by the existence of more gradual and diffuse *F. sylvatica* treelines in the Apennines, located at higher elevations than the abrupt treelines of this species (Bonanomi et al. 2018).

Abrupt treelines can also be composed of quite open forests, as found on e.g. Tenerife (Canary Islands) and the volcanos of central Mexico (Wardle 1965, Lauer 1978), with treelines of *Pinus canariensis* and *Pinus hartwegii*, respectively. As these forests are quite open also at lower elevations, these treelines, apart from being abrupt in terms of tree stature change, are not diffuse but discrete (Leuschner 1996). However, at least for *P. hartwegii* some sections of the treeline may also be more diffuse (Lauer 1978, Astudillo-Sánchez et al. 2019). In both regions, the treeline has been strongly affected by land use and fire, which may prevent tree establishment (Lauer 1978), so that the abrupt discrete shape is maintained.

Many multi-species tropical cloud-forest treelines are also very abrupt, which is probably due to fire in the alpine tussock grasslands, possibly combined with the difficulty of many tree species to establish outside forest cover (Bader et al. 2007b, Llambí et al. 2013, Rehm and Feeley 2015). Although tall shrub species are usually present that can tolerate the high radiation in the alpine zone and that could start a succession towards forest, this process is rather slow and, at many treelines, additionally hindered by frequent burning (Bader et al. 2007a, Ramírez et al. 2009, Llambí et al. 2013, Bueno and Llambí 2015). At many abrupt cloud-forest treelines, a fringe of such shrubs (e.g. *Diplostephium* spp., *Hesperomeles* spp., *Miconia* spp.) lines the abrupt treeline forest border (Bader et al. 2007a, Ramírez et al. 2009).

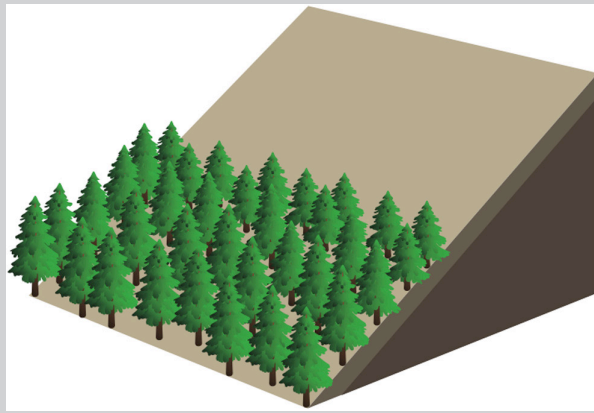


Figure A4b. Schematic example of an abrupt discrete treeline.



Figure A4c. Abrupt discrete single-species treeline composed of *Lophozonia menziesii* (Nothofagaceae), southern Alps, New Zealand (photo: M. Y. Bader).



Figure A4d. Abrupt discrete treeline of mixed cloud forest bordering tussock-grass paramo in the Guandera reserve of northern Ecuador. Although not currently used for livestock grazing, this paramo is regularly burned. A recent fire is clearly indicated by the charred stems of the *Espeletia* stem rosettes in the foreground, and burnt young growth of the small tree *Gaiadendron punctatum* showing dark orange in the background (photo: M. Y. Bader).



Figure A4e. Close-up of an abrupt discrete treeline of mixed cloud forest bordering tussock-grass paramo in the Guandera reserve of northern Ecuador. Note the fringe of tall shrub species like the bluish *Diplostegium* and *Blechnum* tree ferns (photo: M. Y. Bader).

A5 Abrupt diffuse treelines

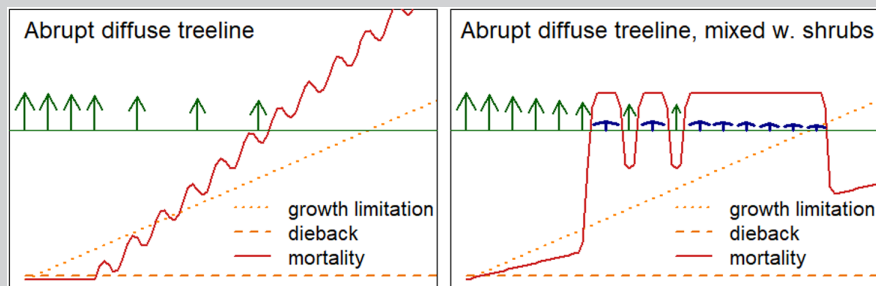


Figure A5a. Hypothesized first-level controls on a diffuse treeline on a slope with spatial or temporal heterogeneity in mortality (left) or in a matrix of shrubs or other non-invasible vegetation (right). Mortality (red line) controls the positioning of trees, either due to heterogeneity or due to competition from the shrubs. Growth limitation and dieback (orange lines) do not directly determine this pattern, although growth does determine the competitive strength of trees versus shrubs, in particular after disturbances.

Controlling processes: survival is restricted to increasingly few microsites and becomes impossible where growth is not yet much limited. In the case of a dense shrub cover between the trees, competition is a likely cause of establishment limitation (Liang et al. 2016, Schwab et al. 2016).

Examples:

Two examples: ‘Several *Juniper* species occurring from fairly dense stands to very open woodlands and finally to single isolated individuals’ on south-facing slopes in the eastern Himalayas (Schickhoff 2005), or treeline in Bhutan (Miehe et al. 2015), where trees also spread out (Fig. A5c). In both cases the trees grow in a matrix of tall *Rhododendron* shrubs, which probably prevents small trees from persisting. This likely leads to the pattern that only well-grown trees are found, but fewer and fewer of these with increasing elevation, as the competition balance shifts from trees to shrubs. Coupling to the atmosphere, which is related to plant height, should not differ between small trees and tall shrubs of the same height. Advantages of shrubs may lie in a more homogenous canopy, raising the boundary layer and presenting strong competition to establishing trees, and/or in their thinner stems, requiring a shorter growing season (Tremel et al. 2019). However, the conceptual difference between the treeline and the (tall) shrubline has not been fully explored so far.

Examples of abrupt diffuse treelines without a competing shrub belt include sections of *P. hartwegii* treelines in Mexico (see also above under A4). In this system, tree establishment indeed appears to be restricted to certain microsite types (causing a diffuse pattern, Astudillo-Sánchez et al. 2019), while the abruptness, i.e. the absence of small trees, may be related to mortality due to fire (Lauer 1978, Robles-Gutiérrez et al. 2016).

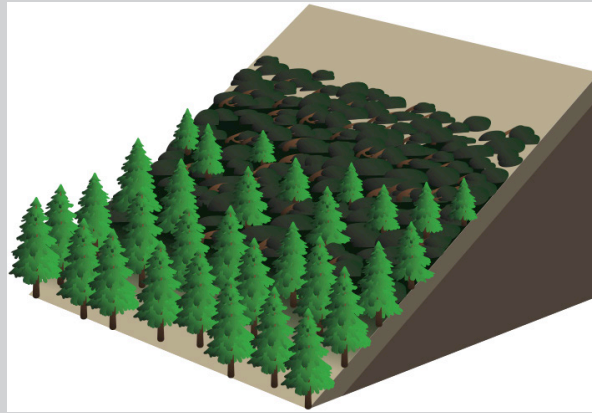


Figure A5b. Schematic example of an abrupt diffuse treeline in a shrub matrix, which is mostly gradual discrete itself.



Figure A5c. Natural treeline in Bhutan composed of *Abies densa* trees in *Rhododendron lanatum* thickets with *Sorbus* shrubs (photo: Georg Miehe).

A6 Tree-island treelines

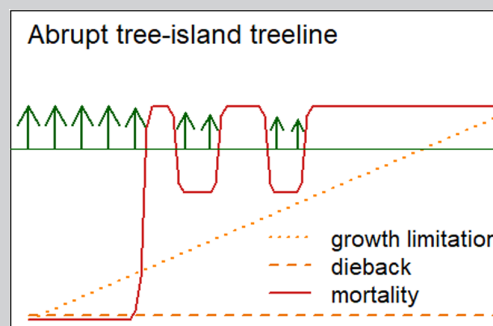


Figure A6a. Hypothesized first-level controls on abrupt tree-island treelines. Mortality (red line) controls the positioning of trees and depends on the presence of trees, leading to a positive feedback switch (Wilson and Agnew 1992). Growth limitation and dieback (orange lines) are not important for this pattern.

Controlling processes: survival depends on existing trees and becomes impossible away from these. In abrupt tree-island treelines, islands form at elevations where growth is not yet much limited and dieback does not play a large role. In gradual tree-island treelines, islands are additionally increasingly limited in size by growth limitation and/or dieback (then grading into krummholz-island treelines). One

possible feedback mechanism is reproduction through layering, allowing tree establishment where establishment from seed is not possible (Holtmeier 2009), or, similarly, growth into multi-stemmed trees from previously prostrate individuals (Devi et al. 2008). Feedback mechanisms involving establishment from seed include reduced seedling mortality near existing trees due to shading, sheltering or snow redistribution (Germino and Smith 1999, McIntire et al. 2016). Where tree performance is controlled by positive feedback, it is partially decoupled from external drivers and, for example, growth responses of trees to macroclimatic variation may be reduced (Elliott 2011).

Examples:

Examples of treelines with islands composed of tall trees are located in the Teton and Medicine Bay Mountains (Wyoming, USA) and in the Altai Mountains of Russia. In these sites, tree islands characterize the upper parts of the montane forest, thus creating a very long ecotone according to our definition. In the Tetons, trees continue to form islands towards the top of the ecotone and do get smaller and show signs of damage. Although we did not observe real krummholz, this may be because the slopes did not exceed the ecotone. In the Snowy Range (Medicine Bow Mountains), such forest islands (in that case ribbon-shaped) grade into krummholz islands, thus making that a gradual krummholz-island treeline (Germino and Smith 1999). Treelines with tree islands that are in fact multi-stemmed trees can be found, for example, in the Polar Urals, but also here krummholz formation occurs (Devi et al. 2008). Purely abrupt tree-island treelines may thus not exist in these mountains except where disturbances have removed the krummholz-island belt (perhaps in Fig. A6d).

In some cases, multi-species tropical treelines can have distinct forest tongues and islands that tend to be dominated by small tree and tall shrub species characteristic of the treeline (Fig. A6e). They can border the paramo vegetation quite abruptly or via a wider border ecotone. These tongues and islands can result from the presence of local topographic features (e.g. boulders, small depressions) but could also be promoted by a nucleation process resulting from initial facilitation of woody plant establishment by alpine shrubs (Ramírez et al. 2009, Llambí et al. 2013). Such varied treelines are hard to typify but can be described in terms of intermediate and mixed forms.

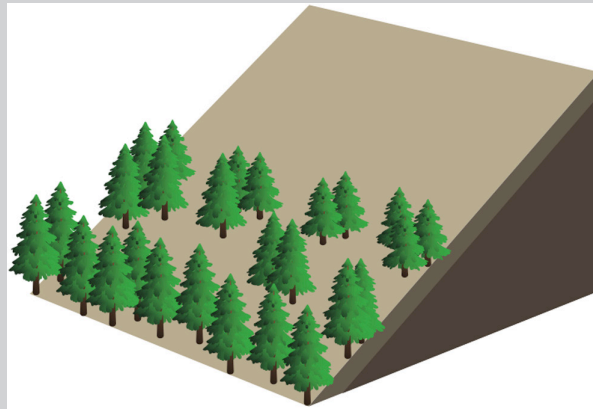


Figure A6b. Schematic example of an abrupt tree-island treeline.



Figure A6c. Tree islands in a treeline ecotone composed of *Abies lasiocarpa*, *Picea engelmannii* and *Pinus albicaulis*, Tetons, USA (photo: M. Y. Bader).



Figure A6d. Abrupt diffuse treeline ecotone with tree-islands, composed of *Abies lasiocarpa* and *Picea engelmannii*, Medicine Bow Mountains, USA (photo: L. M. Resler).



Figure A6e. Treeline ecotone bordering the paramo of Iguaque, Colombia. In this case the ecotone is quite wide and has a gradual decrease in plant size from trees to small shrubs among tussock-grass paramo, with a mixture of diffuse, discrete and island sections, plus strong topography-related patterns (photo: M. Y. Bader).

A7 *Krummholz-island treelines*

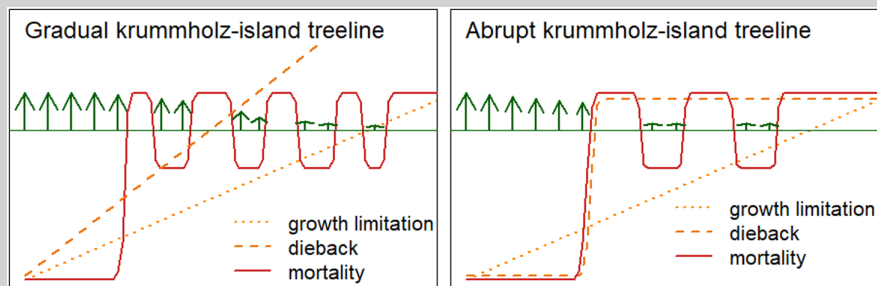


Figure A7a. Hypothesized first-level controls on gradual (left) and abrupt (right) krummholz-island treelines. Mortality (red line) controls the positioning of trees and depends on the presence of trees, leading to a positive feedback switch (Wilson and Agnew 1992). Dieback (dashed orange line) is the strongest control on size and shape of existing tree-species islands and either increases gradually (left) or abruptly as a result of leaving the shelter of the forest (right), implying another positive feedback mechanism.

Controlling processes: dieback limits tree stature more strongly than growth and tree survival depends on existing trees or krummholz, creating a positive feedback.

Examples:

This type of treeline is very common in North-American mountains (Marr 1977, Pereg and Payette 1998, Butler et al. 2009b, Holtmeier 2009). Positive feedback, with stimulation of tree growth inside or on the lee of islands combined with suppression on the sides and windward side of the island due to wind and snow redistribution, maintains and shapes such islands (Malanson 1997, Alftine and Malanson 2004). Island shapes can range from rounded patches to stripes or fingers, and islands have also been observed to 'walk' across the tundra, growing on the lee side and shrinking on the windward side (Marr 1977). Often, these islands are composed of two to three species, with the hardiest species establishing first (e.g. *Pinus albicaulis*), followed by species requiring more shelter (e.g. *Abies lasiocarpa* or *Picea engelmannii*).

Because the processes leading to krummholz formation are most pronounced at a height just above the average snow depth, while further from the ground these stresses decrease again, trees tend to get trapped as krummholz below this height. If able to escape the stressful layer, they may grow into tall trees. As a result, the height transition from trees to krummholz can be quite abrupt, with few or no intermediately-sized individuals.

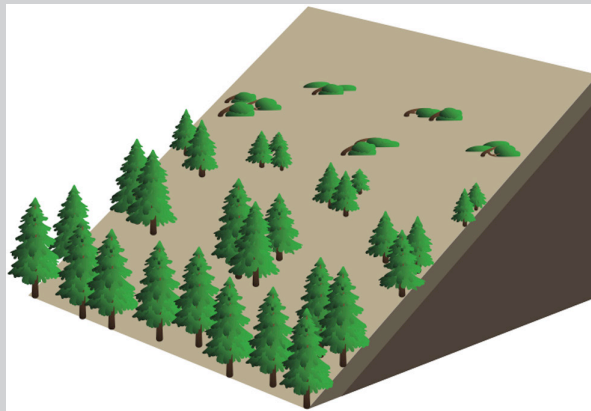


Figure A7b. Schematic example of a gradual krummholz-island treeline.



Figure A7c. Krummholz islands composed of *Abies lasiocarpa* and *Pinus albicaulis*, Lee Ridge, Glacier NP, USA (photo: M. Y. Bader).