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Mountain Treelines: a Roadmap for Research Orientation

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Abstract

For over 100 years, mountain treelines have been the subject of varied research endeavors and remain a strong area of investigation. The purpose of this paper is to examine aspects of the epistemology of mountain treeline research—that is, to investigate how knowledge on treelines has been acquired and the changes in knowledge acquisition over time, through a review of fundamental questions and approaches. The questions treeline researchers have raised and continue to raise have undoubtedly directed the current state of knowledge. A continuing, fundamental emphasis has centered on seeking the general cause of mountain treelines, thus seeking an answer to the question, “What causes treeline?” with a primary emphasis on searching for ecophysiological mechanisms of low-temperature limitation for tree growth and regeneration. However, treeline research today also includes a rich literature that seeks local, landscape-scale causes of treelines and reasons why treelines vary so widely in three-dimensional patterns from one location to the next, and this approach and some of its consequences are elaborated here. In recent years, both lines of research have been motivated greatly by global climate change. Given the current state of knowledge, we propose that future research directions focused on a spatial approach should specifically address cross-scale hypotheses using statistics and simulations designed for nested hierarchies; these analyses will benefit from geographic extension of treeline research.

Introduction

Mountain treeline ecotones represent the spatial transition from forested to treeless mountain landscapes and are, therefore, considered among the most prominent features of mountain environments. Mountain treeline ecotones also represent the upper physiological limits of tree species and a lower boundary (though not a physiological limit) for alpine herbaceous species. The importance of this boundary for nutrient fluxes and biodiversity, the variety and complexity of spatial patterns found at treeline, and the intriguing and still enigmatic life-form limit it represents, has given rise to numerous and diverse research endeavors from a broad disciplinary base for over 100 years. An important motivation for many recent studies of treeline is ongoing global climate change due to their hypothesized use as an indicator of climate change and to potential loss of biodiversity and ecosystem function as tundra is replaced by woody species. The usefulness of treeline dynamics as indicators of climate change (or of general

ecological processes and relations) will depend on how they are approached and thus what we believe we know about this topic.

Our purpose here is not to review what is known, or thought to be known, about the geography, ecology, and plant physiology of mountain treeline ecotones; Holtmeier (2009) has already covered this ground from a worldwide perspective. Instead, our aim is to examine the nature of knowledge, through a review of *the paths* treeline researchers have followed to reach the current state of knowledge about alpine treeline ecotones, and also how the goals for knowledge acquisition differ. For simplicity, we refer to these as studies of mountain “treeline,” and distinguish a conceptual line versus ecotone only where necessary.

APPROACHES

From the variety of research conducted at mountain treelines worldwide, two major research approaches emerge: searches for

global-scale and landscape-scale causes, wherein the latter are within and modify the limits of the former (Troll, 1973; Wardle, 1974, 1993; Holtmeier, 2009). Körner (2003) identified these as fundamental/global and modulative/regional, and we also see these approaches as inquiry at different spatial scales within a geographic hierarchy but with the modulation being more local than regional. Studies exploring the broad causes of treeline attempt to answer the fundamental question, “What causes treelines?” Such studies attempt to understand the factors that cause treelines to exist on a global level, and we refer to it here as the global approach. Furthermore, these studies focus primarily on limitations to tree growth from an ecophysiological perspective because ecophysiology is replicated globally, but ecophysiological questions are also examined locally. Studies examining the fine-scale (or local) causes of treelines attempt to answer the question, “How and why do treelines differ across locations?” This approach focuses on landscape patterns, especially the effects of topography and treeline history (such as climatic changes, human impact, and wildfire), because these factors differ within regions, and we refer to it as the landscape approach. It is not a coincidence that these two approaches have different foci in terms of treeline studies, with the former most concerned with the upper elevational limit of ‘trees,’ i.e., full upright stems (or at least 2 m; e.g., Wieser and Tausz, 2007), and less with tree seedlings, while the latter is most concerned with the three-dimensional gradient or pattern across the ecotone with seedlings at the fore (e.g., Johnson et al., 2004).

Global treeline research is currently dominated by the search for mechanisms of low-temperature limitations on tree growth (e.g., Körner, 1998a). Here the discussion centers on the role of carbon acquisition versus use (i.e. source versus sink limitation) at low temperatures (particularly root zone temperature) and/or limitations related to the utilization of carbon within trees. In spite of abundant sampling in recent years (Li et al., 2002; Hoch and Körner, 2003; Piper et al., 2006; Bansal and Germino, 2008; Shi et al., 2008), there is generally no evidence for a poor carbon status in treeline trees in the long term, although it may influence local pattern (Cairns and Malanson, 1997; Cairns, 2005). Therefore, the attention is now turned to mechanisms of direct growth limitations, with an emphasis on understanding how a mean growing season temperature can best correlate with treeline positions worldwide (Körner and Paulsen, 2004), in spite of this mean being composed of widely differing temperature regimes (Hoch and Körner, 2009).

Investigations following the landscape approach have typically studied treelines from the perspective of spatial pattern and process (Walsh et al., 1997). Landscape change, linkages among biotic and physical elements of the environment, and human/environment interactions are often studied (Holtmeier, 1974; Broll et al., 2007; Holtmeier, 2009). Landscape studies may also look at specific ecophysiological causes of treeline patterns, e.g., studies that address establishment limitations rather than growth in adult trees (e.g., Germino et al., 2002; Piper et al., 2006; Johnson and Smith, 2007; Bader et al., 2007a; Bansal and Germino, 2008; Smith et al., 2009). Such studies often find that landscape position and facilitation by neighbors are very important.

Though a divergence in knowledge ‘camps’ currently exists, present-day research has evolved from a similar line of inquiry—one that originated and continues in the consideration of global-scale causes of treelines. A search for broad-scale causes of treelines evolved from the work of great observationists. After Leonardo da Vinci (1452–1519) had noticed the altitudinal belts and their specific organisms on Monte Rosa (Italian Alps), Conrad Gesner (1516–1565) from Zurich mentioned in his

“*descriptio montis fracti*” (1555) that the altitudinal position of the vegetation belts is related to the decrease of temperature and length of growing season with altitude (Holtmeier, 1965). It is likely that Alexander von Humboldt (von Humboldt and Bonpland, 1805) was among the first researchers to mention the existence of alpine treelines in a manner that connected observation with causality. His foundational work in physical geography and meteorology was the first to document isotherms and their relationship with elevation and plant geography of mountain slopes (Marek, 1910; Troll, 1962). Additional work included the early identification of heat (Däniker, 1923) and tree physiology (e.g., Michaelis, 1934; Steiner, 1935; Schmidt, 1936; Pisek and Cartellieri, 1939), and more recent summaries combine the two (Tranquillini, 1979; Wieser and Tausz, 2007). Holtmeier (2009) provides a more complete treatment of more recent research.

Here, we devote most of our analysis to the fundamental questions and themes in the landscape approach. We conclude by outlining needs for future research on mountain treelines conducted with a spatial perspective. In this paper, our emphasis on the landscape perspective in no way discredits the excellent contributions to understanding treelines offered by the global approach, and reflects, rather, the collective training and expertise of the authors.

LANDSCAPE FOUNDATIONS

The landscape approach, our main focus, is first and foremost a part of landscape ecology. Much of the early impetus for work in the Alps was from the perspective of landscape level management problems (Holtmeier, 2009), the root of European landscape ecology. Much of the pattern-process paradigm in landscape ecology derived from island biogeography, and so it blossomed in the 1970s and boomed in the 1980s (Turner, 1989). This latter history is mirrored in the increasing interest in three-dimensional pattern in treeline studies (e.g., Humphries et al., 2008; see Fig. 1). However, landscape ecology has been affected by ideas formed in mountain environments, perhaps beginning in the mid-20th century with Troll’s (1971) emphasis on ‘geo-ecology.’

The landscape approach, second, includes hierarchy theory in ecology, which developed in the 1980s (e.g., Allen and Starr, 1982) and has been applied to treeline research since the early 1990s. The core idea here is that processes and patterns develop at multiple spatial and temporal scales. Together they are comprised of interactions of processes at finer scales, while constrained by patterns at coarser scales (O’Neill et al., 1989). For example, the establishment of a forest patch in the treeline ecotone would depend on fine-scale processes such as seedling establishment but is also constrained by coarse-scale patterns such as mountain topography (slope aspect, exposure to wind). Also, the general temperature control on treelines can be seen as ‘merely’ a coarser scale constraint on the focal three-dimensional pattern dynamics driven by population level processes (e.g., Brown et al., 1994; Walsh et al., 1997).

Third, complexity science has, explicitly or implicitly, become part of many landscape-scale treeline studies. Complexity science is a body of concepts that examines how higher order pattern or structure in systems is produced by few, simple, but nonlinear interactions at a lower level, and thus includes hierarchy (e.g., Sole and Bascompte, 2006). The higher order patterns could not be predicted from the properties of the lower order units, but instead the ‘emergence’ of structure must be determined by observing the evolution of the system. Thus, a standard reductionist approach is overturned. Such systems can be said to be self-organized in that



FIGURE 1. Hedges, illustrating positive spatial association, and individual seedlings, illustrating association with microrelief, extend into tundra above the contiguous forest in the treeline ecotone at Lee Ridge, Glacier National Park, Montana, U.S.A. Photo: G. P. Malanson.

the higher order structure can be reduced to fewer, but still endogenous, nonlinear dimensions or drivers. Complexity science was developed and distinctly promoted by physicists (Gell-Mann, 1994; Bak, 1996), but quickly spread to other disciplines. Malanson (1999) discussed its applicability to treeline studies, and the work by Rietkerk et al. (2002) in spatial ecology influenced later advances by Zeng and Malanson (2006) and Bader et al. (2008). Advances in all three domains developed simultaneously and were clearly being used together by landscape ecologists. The work of O'Neill (O'Neill et al., 1982, 1986, 1989, 1992, *inter alia*) alone illustrates this synergy, and work in landscape ecology (e.g., Li, 2002) led to the initiation of a new journal, *Ecological Complexity*, in 2004.

One can see why linkages among these three areas (landscape ecology, hierarchy theory, and complexity) have been identified and are relevant to treeline research. They link spatial heterogeneity and feedbacks (Troll, 1971), scale dependence in a geographic hierarchy (Pattee, ed., 1973), and self-organization (Haken, 1975). The relations between processes and patterns, in this case between advances or retreats of treelines on mountain slopes and the spatial structure of patches and edges (Fig. 1), can be seen to have characteristics in common with other spatial phenomena at higher orders (e.g., fractal patterns or power-law distributions). Ecologists have found such higher order phenomena may explain important characteristics such as metabolic capacity (West et al., 1999) for which evolutionary processes may be revealed. For biogeography (e.g., Deng et al., 2006), including ecotones (Milne et al., 1996), the existence of these higher order patterns may indicate constraints on the variability and explanations possible (i.e., self-organization; Zeng and Malanson, 2006). We might hope that these linkages would provide predictive power for the response of treelines to climate change, but prediction may be limited. While self-organization, and thus fractal patterns, hold under strong exogenous forcing from either climate change or underlying geomorphic patterns (Zeng, 2010), the constraint that patterns will remain fractal does not provide the kind of prediction that ecologists or landscape managers desire.

Nevertheless, from these three perspectives we have learned to look at treelines at multiple scales, seeing organisms within patches within landscapes in three dimensions, and how the

coarser levels constrain the finer scale dynamics that create and reproduce them (e.g., Malanson et al., 2007). We further see the importance of dynamics as a conceptual framework, with both straightforward and higher order patterns of change as objects of study and both endogenous feedbacks and exogenous drivers as hypothetical processes.

These epistemological foundations were enabled, if not driven, by methodological developments. Common to landscape ecology in general, the landscape approach in treeline studies was advanced by remote sensing—airial photography at first (e.g., Troll, 1939), followed by satellite-based imagery (e.g., Baker and Weisberg, 1995; Allen and Walsh, 1996; Walsh et al., 2003) and geographic information systems (GIS) analysis (e.g., Brown, 1994; Hörsch, 2003). Quantification of pattern was an essential contributor to the concepts, and these technologies greatly increased the available data on spatial pattern and simplified its analysis. Computer power itself enabled the development of hierarchy theory and complexity science in general (Pagels, 1988). For example, cellular automata, or cellular models with stochasticity added to neighborhood effects, were core tools in the development of the complexity approach at ecotones in general (e.g., Loehle et al., 1996; Li, 2002) and treelines in particular (Alftine and Malanson, 2004; Malanson and Zeng, 2004; Zeng and Malanson, 2006; Wiegand et al., 2006; Zeng et al., 2007; Bader et al., 2008).

Understanding Landscape-Scale Relations

In landscape-scale treeline studies, an understanding of the treeline phenomenon and its local causes is obtained by focusing on *variations* of treeline spatial and temporal patterns (e.g., Blüthgen, 1942; Griggs, 1946; Holtmeier, 1965; Smith et al., 2003; Broll et al., 2007; Malanson et al., 2009; Butler et al., 2009a; see Holtmeier, 2009, for further references). Like broad-scale approaches to treeline, treeline dynamics under global climate change scenarios have been a major theme of current research from a landscape perspective. However, for landscape-scale treeline scientists (who acknowledge that heat deficiency is the ultimate limit on tree growth at high elevation), the problem is

that treeline ecotones present complex patterns in three dimensions that are beyond the explanatory power of temperature alone. The ribbons, hedges, and other patchy patterns (see Holtmeier, 1982, and Fig. 1), while constrained by temperature limits, require explanation. The landscape approach to treeline is motivated by interest in these three-dimensional patterns, and processes are seen as nested at multiple scales even within the landscape-scale domain (e.g., Elliott and Kipfmüller, 2010).

LOCAL DRIVERS

The primary fine-scale modulators of treeline patterns may be those that affect heat deficiency, but fine-scale modulators have effects on water, nutrients, and disturbance. Temperature deficiency is not only a broad-scale cause of treelines, but can also be a landscape-scale modulator of treeline pattern. At a landscape scale it is affected by local modulators such as topography, and it can also affect other landscape-scale modulators, such as distribution, depth, and duration of the winter snowpack. Factors that directly reduce temperatures at local scale are wind, cold air drainage, snow cover in summer, and shade. Temperature affects snow cover directly, in terms of determining the mix of rain vs. snow and the rate of melting and, indirectly, by determining snow density and thus snow removal and redeposition by wind.

Landscape-scale modulators not *directly* related to heat are quite diverse, but the one most important in ecophysiology is water (e.g., Brodersen et al., 2006). Treeline areas vary in the soil moisture available for plant growth at landscape scales, and much depends on the removal and redeposition of snow by wind. Some areas are scoured of snow and so experience drought conditions much beyond what the regional precipitation pattern would indicate, whereas other areas have multiples of the regional precipitation due to snow collection and eventual melt (e.g., Walsh et al., 1994; Hiemstra et al., 2002, 2006; Geddes et al., 2005; Holtmeier, 2005). Other effects of excessive snow cover, which may impede or even prevent successful seedling establishment, include shortened growing season, physical damage through creeping and settling snow, and snow fungi, which may affect seedlings and saplings of evergreen conifers (e.g., Cunningham et al., 2006).

Geomorphology is also a landscape-scale modulator of treeline patterns and dynamics, exerting its influence through more direct causes like snow, soil, and disturbance (e.g., Kullman, 1997; Walsh et al., 2003; Holtmeier and Broll, 2005; Butler et al., 2007; Zeng et al., 2007; Humphries et al., 2008; Butler et al., 2009a, 2009b; Bekker and Malanson, 2009; Munier et al., 2010). Local topography may provide shelter from the wind, as on the lee sides of small ridges, solifluction terraces, rocky outcrops and other convex sites (e.g., Resler et al., 2005, in the Rocky Mountains; Holtmeier et al., 2003; Anschlag et al., 2008, in Finland; see Fig. 1). Depressions may be covered too long with snow, however, and waterlogging can be an additional adverse factor in such poorly drained places. On wind-exposed convex topography with little or no winter snowpack, wind actions (physiologically, mechanically) may cause serious damage to seedlings and saplings (Cairns and Malanson, 1998). Temperatures—their pattern as well as limits—also affect local geomorphic processes such as solifluction and frost heaving that may affect seedling establishment (Butler et al., 2004, 2009b).

Further local causes of treeline not directly related to heat are due to biotic factors such as pathogens, insects, mycorrhizae, birds, and mammals. Pathogen outbreaks can cause regional mortality of trees that could ultimately influence spatial pattern at

alpine treeline. *Cronartium ribicola*, the introduced pathogen that causes blister rust in five-needled white pines, has caused widespread mortality in whitebark pine (*Pinus albicaulis*), a foundation and keystone species of northern Rocky Mountain subalpine and treeline ecosystems (Resler and Tomback, 2008), which has potentially serious and cascading consequences (Tomback and Resler, 2007). Mass outbreaks of the autumnal moth (*Epirrita autumnata*) have repeatedly destroyed vast areas of mountain birch (*Betula pubescens* ssp. *czerepanovii*) forests up to the treeline in Finland, which has been followed by severe soil erosion on sandy substrates that now impedes the re-establishment of this species (Holtmeier, 2002; Holtmeier et al., 2003; Broll et al., 2007). Mycorrhizae, which increase nutrient availability, may be important to successful seedling establishment, tree growth, and afforestation at and above the treeline (Hasselquist et al., 2005; Germino et al., 2006). Birds affect trees in the treeline ecotone by consuming seeds and buds, and dispersing and caching seeds (e.g., the nutcrackers [*Nucifraga caryocatactes* and subspecies in Eurasia, *Nucifraga columbiana* in North America]; Holtmeier, 1966, 2002; Tomback, 1977; Mattes, 1978, 1982, 1985). The impacts of burrowing animals can be positive because they expose the mineral soil and thus create open patches that may facilitate the establishment of seedlings (e.g., Butler et al., 2009b; Butler and Butler, 2009); conversely they can destroy seedlings and saplings by girdling and by pushing seedlings out of the ground (Holtmeier, 1987, 2002). At the other end of the size scale, grizzly bears tear swaths of tundra with similar mixed effects (Butler 1992, 1995). Also, the activities of wild-living ungulates are detrimental to treelines (Holtmeier, 2002, 2009; Cairns and Moen, 2004; Cairns et al., 2007). These phenomena are spatially variable and their relations with temperature are not well known.

Additionally, competition with alpine herbaceous species can limit or facilitate seedling establishment. Seedlings are facilitated by a moderate amount of herb cover and limited by too little or too much (Germino et al., 2002). These relations can affect pattern development (Malanson and Butler, 1994). Moreover, allelopathic effects of the associated vegetation (e.g., some lichen species or dwarf shrubs), may impair germination, mycorrhiza development and seedling development (Holtmeier, 2009, further references therein).

SPATIAL DYNAMICS

Change through time is integral to explaining three-dimensional treeline patterns in a spatial hierarchy (Armand, 1992; Wiegand et al., 2006). The feedbacks of growing tree populations on their neighborhood become increasingly important as the size of individuals and patches increases (e.g., Holtmeier, 1999, 2005, 2009), but fade as these patches merge into contiguous forest because of reduced edge (Zeng and Malanson, 2006). These feedbacks imply a strong effect of existing patterns on dynamics and indicate self-organization, and more generally, an important role for landscape history.

Patterns and Feedbacks

Treelines frequently exhibit very discrete patterns, consisting, for instance, of abrupt forest edges or distinct dwarf tree or krummholz patches (e.g., Walsh et al., 1992; Humphries et al., 2008). The variety of three-dimensional patterns observed are unlikely to emerge on environmental gradients of temperature due to lapse rates unless positive feedback processes amplify initial environmental differences (i.e., a positive feedback switch *sensu* Wilson and Agnew, 1992) or growth responses are nonlinear

(Batllori et al., 2009). The most notable driver in the pattern-process feedback is wind (e.g., Marr, 1977; Akhalkatsi et al., 2006; Holtmeier and Broll, 2010); shade and protection from sky exposure is probably next (e.g., Örländer, 1993; Germino and Smith, 2000; Germino et al., 2002; Smith et al., 2003; Slot et al., 2005); followed by nutrient enrichment (Holtmeier and Broll, 1992; Seastedt and Adams, 2001; Shiels and Sanford, 2001; Liptzin and Seastedt, 2009) and albedo. The negative feedback (shading and cooler soils) identified by Körner (1998a, 1998b) acts in the opposite direction. However, tree seedlings at treeline are often found preferentially beneath tree canopies (e.g., Griggs, 1946; Ball et al., 1991; Germino and Smith, 1999; Resler and Fonstad, 2009), indicating that the positive feedback through shelter and protection from radiative stress is more important for treeline spatial dynamics than the negative feedback of lower soil temperatures.

Several treeline studies have investigated the role of landscape position, including effects of neighboring plants, on demographic processes (e.g., Daly and Shankman, 1985; Bekker, 2005; Resler et al., 2005; Maher and Germino, 2006; Batllori et al., 2009, 2010; Hughes et al., 2009). However, few of these studies have included indices or direct measurements of ecophysiological parameters like photosynthetic capacity (Germino and Smith, 1999; Maher et al., 2005) or pigmentation (Akhalkatsi et al., 2006), thus indicating the mechanisms by which spatial associations have probably arisen (e.g., protection from cold-induced photoinhibition). Combinations of such detailed mechanistic knowledge could strongly improve predictions of response to climate change. Another interesting issue is the effect of landscape position on the growth and general performance of adult trees, bringing local detail to the general ecophysiological principles that may (or may not) be applicable at treelines globally (Li and Yang, 2004; Wilmking et al., 2004).

Given the difficulty of capturing feedbacks in space and time with field data, several authors have used simulations to try to understand the effects of feedbacks between spatial patterns and dynamics (e.g., Malanson, 1997; Malanson et al., 2001; Alftine and Malanson, 2004; Malanson and Zeng, 2004; Wiegand et al., 2006; Bader et al., 2008; Elliott, 2009; Diaz-Varela et al., 2010). These computer simulations predict that alpine treelines exhibit unusual dynamics. Zeng and Malanson (2006) found that a model that included both positive and negative feedback could generate many observed patterns (notably fractals, cf. Allen and Walsh, 1996) in a single long-term realization driven only by the endogenous feedback. Zeng et al. (2007) further found that such self-organization maintained higher order pattern relations even when exogenous geomorphic patterns might be expected to alter it (at least within realistic ranges). Bader et al. (2008) found that positive feedbacks could lead to abrupt transitions that decouple rates of advance from climate change (Fig. 2). These modeling efforts are best taken as hypothesis generators, rather than tests, and indicate the likely important feedbacks.

Historical Legacy

While self-organization may be maintained in principle, the evolution of pattern is also contingent on exogenous forces. The position and structures of present treelines often are the result of historical legacy rather than of the present climate (e.g., Holtmeier, 1974, 2009; Holtmeier and Broll, 2007). Extreme natural events such as severe storms, drought, extremely snow-rich or poor winters, natural and human-induced forest fires, mass outbreaks of leaf-eating insects, debris flows, snow avalanches, rock avalanches, and volcanic eruptions have long-lasting effects on current treeline ecotones (e.g. Butler and Walsh, 1994; Daniels

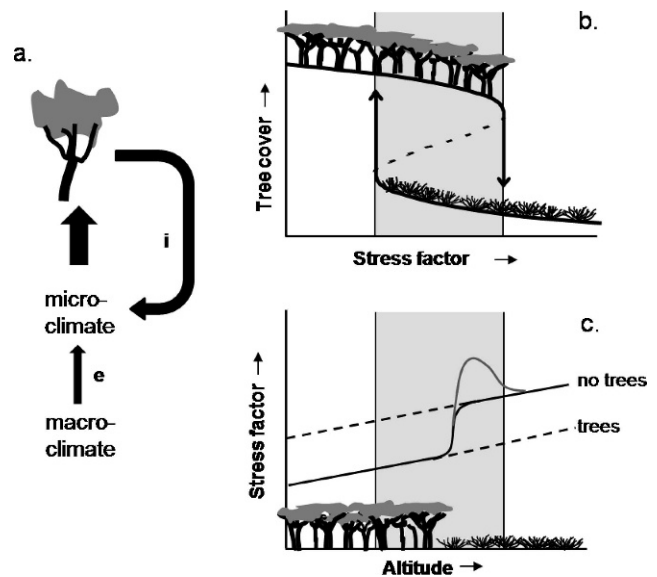


FIGURE 2. Emergence of abrupt treeline transitions in time and space. (a) Tree growth is determined by the microclimate, which is determined by the external macroclimate [e] and modifications caused by the vegetation itself [i]. Depending on the strength of i relative to e, the vegetation will be more (large e) or less (large i) coupled to the external climate and hence more or less sensitive to climatic changes. (b) Hysteresis fold demonstrating the alternative stable states of forest and alpine vegetation existing under the same external environmental conditions (gray area; at treelines the stress factor can be e.g., freezing temperatures, wind, or high solar radiation). Abrupt ('catastrophic') transitions from forest to alpine vegetation or vice versa can occur at threshold conditions or due to disturbances. (c) Changes in microclimatic conditions as a result of vegetation cover. Some stress factors can be aggravated just outside tree stands (gray graph) due to redirection of wind and snow. Adapted from Bader (2007).

and Veblen, 2003; Stueve et al., 2009; Colombaroli et al., 2010). For example, the destruction of the soil organic layer by severe fires can result in an almost complete loss of nutrient supply, reduced water-holding capacity of the soils, and consequent increased surface runoff and soil erosion (e.g., Holtmeier, 2009; Holtmeier and Broll, 2005; Holtmeier et al., 2003; Broll et al., 2007). Thus, the legacy of specific patterns in specific situations becomes a dominant local control. At a broader temporal scale, many regions of the Rocky Mountains possess 'relict treelines' formed by long-lived pines (*Pinus aristata*, *P. albicaulis*, *P. flexilis*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce (*Picea engelmannii*), which became established at higher elevations under a warmer-than-present climate many centuries or even millennia ago (e.g., Ives, 1973; Ives and Hansen-Bristow, 1983; Holtmeier, 1985, 1999, 2009). During the subsequent less favorable climatic conditions, subalpine fir and Engelmann spruce were able to reproduce by layering (i.e., formation of adventitious roots) in krummholz form. Some of these trees now produce viable seeds and facilitate seedling establishment by providing shelter from strong winds.

Apart from natural landscape processes and feedbacks, human land use has in many regions exerted a strong influence on treeline patterns. In the European Alps and many other Eurasian high mountains, which were already settled in prehistoric time, treeline has been lowered through pastoral use, mining, and burning the high-elevation forest. The present upper limit of the forest has become an ecological boundary that is as distinct as was the original climatic forest limit, at least in the Alps, Pyrenees, and

Andes (Holtmeier, 1965, 1974; Camarero and Gutierrez, 2002; Di Pasquale et al., 2008). A treeline depression by 150 to 300 m below the uppermost postglacial level of the climatic treeline can be taken for an average value (Holtmeier, 1974, 1986; Burga, 1988; Tinner et al., 1996; Carcaillet et al., 1998; Burga and Perret, 2001; Kaltenrieder et al., 2005). In tropical mountains the history of human settlement and its impact on treeline habitats is less clear. Humans are thought to have spread through South America before the beginning of the Holocene (e.g., Jackson et al., 2007), and the earliest evidence of fires at current treeline altitudes stem from this time, although clear signals of regional agriculture only appear in the second half of the Holocene (Di Pasquale et al., 2008). Paleocological records of past treeline altitudes are heterogeneous, but it is tempting to assume that humans have used tropical alpine habitats from very early times and at least locally have slowed or prevented a rise in treeline altitude from late Pleistocene levels (Horn, 1993; Di Pasquale et al., 2008). In some regions, however, recent destruction of tropical mountain forests by human land use is evident and has depressed treeline altitude considerably or in some cases has combined with deforestation from below to remove the forest belt altogether (e.g., Miede and Miede, 2000).

Underexplored Areas and Directions for Future Research

As noted, a motivation for much ongoing treeline research is anticipated global climate change. The key question resulting from this motivation is, “Will a warmer world result in globally comparable responses of treelines?” Given the hypothesized general causal control, we would expect a comparable upward movement of alpine treeline ecotones worldwide—comparable in the sense that the rise in elevation of controlling isotherms, though variable, would produce rises in treelines. However, given the landscape-scale controls, an increase in temperature will change the broad constraint, but the response in any one area will vary through the interaction of the fine- and broad-scale controls. Such a varied response is indeed observed when comparing treelines worldwide (Harsch et al., 2009). A good example is the observed dieback of treeline stands due to drought conditions accompanying temperature increases in the Sierra Nevada (Lloyd and Graumlich, 1997; cf. Johnson et al., 2004; Brodersen et al., 2006; Johnson and Smith, 2007; Millar et al., 2007). Differential responses, such as the limited advance of treeline in hedges on some areas with only densification but no advance in others in Glacier National Park, U.S.A., indicates that local-scale controls are more important than global temperature control here, at least in the short term (Butler et al., 1994; Klasner and Fagre, 2002; Alftine et al., 2003; Bekker, 2005). So although topography will change the spatial expression of the rise in elevation of any isotherm, the nonlinear relations created by positive feedbacks, in the context of existing spatial patterns and their legacies, will further complicate the dynamics (e.g., Bader and Ruijten, 2008; and Bader et al., 2008; Kharuk et al., 2010).

One productive area for new research would be in differentiating the responses to current climate change from those of past human impact; both climate and land use are major aspects of global change (Vitousek, 1994). Where treelines have been lowered by human activities such as grazing and burning, their response to release from these impacts may have similarities with responses to climatic warming. Differentiating the two responses could be informative in terms of understanding the relative importance of processes and how they relate to ecological theory as well as providing a sound basis for monitoring and mitigating climate

change impacts. To pursue this line of research will require analyses that compare geographic areas with different impacts. A starting point exists in current research, primarily in those locations with long records of human occupation, such as the European Alps (e.g., Didier, 2001; Heiri et al., 2006; Dullinger et al., 2003) and in the Andes (e.g., Young, 1993; Sarmiento, 2000; Sarmiento and Frolich, 2002; Young and León, 2007, and references therein), but treelines in Asia and Africa also are part of unique cultural landscapes. Because treeline forms are historically contingent, extensive sampling will be needed to gain enough statistical power to make sense of these interactions. While some such expansions could be within continents (e.g., Bader et al., 2007b [plus an island]; Weiss, 2009), expansion across continents to understudied areas, such as the southern hemisphere and remote tropical areas, especially in Africa and Asia, is potentially most fruitful (cf. Ohsawa, 1990; Schmidt-Vogt, 1990; Miede and Miede, 1994; Rundel et al., 1994; Schickhoff, 1995, 2005; Winkler, 1997; Wardle et al., 2001; Diaz et al., 2003; Hofstede et al., 2003; Baker and Moseley, 2007). Moreover, investigation of the treelines on oceanic islands, where the altitudinal treeline position is usually several hundred meters lower than the continental high-elevation treeline at the same latitude, needs to be intensified (e.g., Azores, Canary Islands, Hawaii, etc.; cf. Henning, 1974; Leuschner and Schulte, 1991; Leuschner, 1996; Bader et al., 2007b). Not least, the upper treeline in New Guinea would be a valuable site for field research because it is the largest tropical island with a treeline located above 3000 m and human-induced fires play an important role for treeline physiognomy and dynamics (Paijmans and Löffler, 1972).

Given the three major conceptual domains that help define and inform the landscape-scale approach to treeline research (landscape ecology, hierarchy theory, and complexity science), addressing this geographical and historical variation will require a research program that reaches across scales. Though a multitude of studies exist that address either, there is a scarcity of research aimed at bridging the gap between general and local patterns and causes of treeline (but see Harsch et al., 2009; Harsch and Bader, 2011). To build such a bridge, methodologies can be shared between the two approaches and specifically multiscale analyses can be adopted.

In more general terms, we propose that more formal hierarchical statistical methods (e.g., using Bayesian and/or multilevel statistics) be applied to link the two approaches that we have discerned (e.g., Beever et al., 2006; Clark and Gelfand, 2006; Qian and Shen, 2007). Multilevel regression could link approaches because of their nested, geographically hierarchical relationship. Multilevel analyses will be most informative where the levels of the hierarchy cross functionally important differences in underlying and constraining variables. Some work on treeline illustrates this approach but more variables are needed (e.g., Harsch et al., 2009; but contrast Gellrich et al., 2007).

Research likely to emerge includes reformulations of existing treeline models that incorporate higher spatial and temporal resolution data sets. Increasing the level of detail and geographic specificity within the present understanding of alpine treeline ecology is warranted because, generally speaking, global-scale controls on treelines are well understood, (that is, temperature is an important control on treelines worldwide, e.g., Körner and Paulsen, 2004). In contrast, landscape-scale treeline analyses vary greatly in their foci and level of detail, which often makes them challenging to compare directly and to synthesize across large geographic areas. Particularly desirable treeline analyses include those that (1) use theoretically and methodologically consistent analytical approaches to better define geographic variability in

treeline pattern-process relationships; (2) explicitly assess the role that local climatic conditions (e.g., the timing of events like first snowfalls, spring thaw dates, and late and early frosts) play in tree establishment and survival; and (3) combine sites with different histories of land use. Such analyses are needed to provide a basis for assessing localized ecotonal responses to geographically variable climate changes expected to occur in coming decades.

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