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CORRESPONDENCE

Inclusions and exclusions in treeline definitions

Abstract

Körner and Hoch's (2023) definition of "treeline" to include only forest edges that are arctic or alpine, globally distributed and thermally limited is reconsidered for the alpine, with attention to the alpine treeline ecotone. They characterize the alpine treeline and the ecotone as a single phenomenon at a single fundamental niche limit, with all other montane forest edges at realized niche limits. The framework restricts treeline and the treeline ecotone to narrow but interesting ecophysiological questions but leaves other fundamentally limited edges, those in disequilibrium with a changed temperature regime, and the extensive zone of krummholz and tree-species seedlings now often referred to as the treeline ecotone, without terminology. Recognizing other fundamental niche limited edges as treelines, if not alpine, and defining "alpine treeline" as a zone or line within the broader "alpine treeline ecotone", are proposed to promote synergies in research in these related systems.

Körner and Hoch (2023) (hereafter, K&H) have provided a definition of "treeline" that can sharpen research questions by tightly circumscribing this biogeographic phenomenon. However, questions remain about the terminology of what they have excluded, and their fusion of "treeline ecotone" with "treeline" is problematic. Here, I will focus on alpine or elevational treelines, which were the larger part of K&H's perspective. Whether the use of "treeline" or the "alpine treeline ecotone" for drought-limited forest edges or the transition zone of krummholz and tree seedlings has retarded progress in ecology is a subjective position, and the dialogue among researchers in different systems may have had the opposite effect. I offer a modification of K&H's position in the spirit of this dialogue.

K&H frame treeline in four ways:

First, 'tree' is the limited subject:

> We assume a 'tree' to represent an upright woody plant of a minimum height that exposes its canopy to the full strength of atmospheric conditions (aerodynamic coupling to prevailing air temperature, commonly at heights of >2 m).

Second, 'line' is actually a zone, the treeline ecotone:

> A 'line', in this case, represents a more or less gradual transition.... confined to a vertical thermal range of <0.2 K of air temperature.

Third, treeline is global in cause and effect and exclusive to arctic and alpine environments:

> A global phenomenon; A global driver; Global mechanisms (headers of their Figure 2).
>
> And
>
> ...conditions specific to high elevation or high latitude.

Fourth, the thermal limit is the fundamental niche limit, and other alpine and arctic forest edges are at realized niche limits:

> The thermal fundamental niche edge thus defines where a tree could grow from a thermo- physiological point of view, and attributes all other factors to the realized niche.

This framing eliminates any question of the cause of treeline: it is the thermal limit, a seasonal mean isotherm near 6° with a range of 0.2 K (a thermal limit is perhaps preordained by the choice of 'tree' as a form coupled to air temperature). The remaining questions are on the specifics of temperatures and mechanisms, which, for example, could address how the steep gradient in aerodynamic coupling from a closed canopy forest across the alpine treeline is altered by feedbacks to leaf and soil temperatures; these feedbacks will have consequences for the identification of treelines, given that the range of 0.2 K would span c. 30 meters of elevation or c. 90 m of a 20° slope, using the normal lapse rate.

The link of "treeline" to a single fundamental niche dimension is unnecessary and misconstrues the conceptual framework (cf. Holt, 2009; Hutchinson, 1957). Hutchinson's (1957) fundamental niche is an n-dimensional hypervolume determined by ecophysiological or resource tolerances and requirements of species in environmental space, not geographical space, with the realized niche constrained within it by biotic factors. Where either has been placed in geographical space, an explicit conceptual framework is necessary to include disturbance and dispersal limits, but both the fundamental and realized niches are still multidimensional (e.g. Holt, 2009). The

thermal treeline is not the only montane forest edge at its fundamental niche limit. K&H acknowledge that other ecophysiologically limited elevational forest edges exist:

> Exceptions are severe drought or water logging, and the absence of soil,

but they still relegate them to realized niche limits. Recognizing that these limits are fundamental should improve the interpretation of the elevational limits of forest, especially with climate change.

Recognizing fundamental versus realized niche limits of forest edges is still useful for revising definitions. The exclusion from "treeline" of forest edges caused by disturbances, such as K&H's example of fire on Mount Kilimanjaro, is patent. Other realized niche limits, such as those caused by grazing in the Alps, would require discrimination, but their rationale for exclusion is sound. Such forest edges have a distinct, extensive literature (e.g. Matlack, 1994). The fundamental niche limits of chronic drought (an episodic drought would be a disturbance) in alpine environments are more intriguing because they will change with the climate along with the position of the thermal limit. In some mountains of the western US, it appears that the limiting factor has already switched from thermal to drought as treelines have moved upslope following the Little Ice Age, with episodic wetter periods (e.g. Alftine et al., 2003; Fajardo & McIntire, 2012; Figure 1). It would be difficult to characterize drought-limited edges as precisely as the 6° and 0.2 K temperature and range for alpine treelines because soil moisture varies more at finer scale (and is more difficult to measure) than temperature (e.g. Müller et al., 2016), and as K&H noted, they are less likely to be 'lines'. K&H are correct when they note that the selection of which drought edges have sufficient elevation to be alpine treelines is subjective, so their exclusion has a rationale. However, their description as alpine treelines may have accelerated research because it has allowed consideration of the interactions of tolerances and requirements across spatial and temporal scales (Malanson et al., 2019). Also, mountain soils thin with increasing elevation or are abruptly absent on many mountain slopes, interact with water limitation and are often in disequilibrium with climate (Butler et al., 2007; Holtmeier, 2009), so fundamental niche-limited edaphic forest edges are common. Acknowledging their commonalities as treelines with thermally limited ones would maintain the potential synergies of studying them as multidimensional as well as multiscale systems.

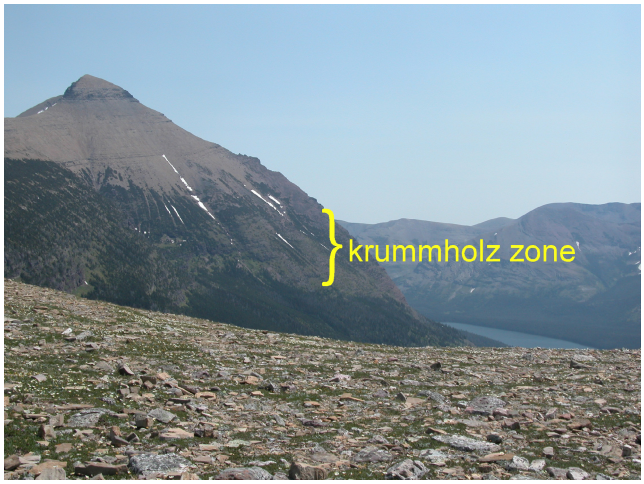

FIGURE 1 Treeline ecotones can extend hundreds of meters of elevation higher than local forest edges. Here, krummholz extends 300 m of elevation above a treeline on a 33° slope on Rising Wolf, Glacier National Park, USA. With a seasonal mean temperature of >10° and mean seasonal precipitation of c. 275 mm (PRISM Climate Group, Data Explorer, https://prism.oregonstate.edu, data accessed 6 June 2023), this treeline has become drought-limited.

Lastly, K&H elided "alpine treeline" and "alpine treeline ecotone," and clarification is needed. A zone that can include krummholz and tree seedlings is often present, and K&H noted:

> Can expand far above treeline, setting the stage for potential future treeline advance.

Körner (2012) illustrated this as a zone between the timberline and the upper tree species limit. It is the focus of much of the research that has used the term "alpine treeline ecotone" in clear contradiction to the suggested bounds of K&H (e.g. Holtmeier, 2009; Martínez et al., 2011), and the unification of "alpine treeline ecotone" with "alpine treeline" leaves this important landscape element undefined. This loss is important with respect to ongoing climate change research for four reasons:

- The extent of this zone can be much greater than the 0.2 K range of the alpine treeline (Figure 1).
- Given that difference, the feedback to the climate system through changes in albedo, roughness and evapotranspiration with the expansion of krummholz and shrubs (e.g. Formica et al., 2014; Millar et al., 2004) will be greater than with change in tree height at the treeline.
- Diversity will decrease if alpine vegetation is replaced by the few tree and/or shrub species that are present.
- Regeneration, not the development of trees, is the predominant process determining treeline dynamics (e.g. Elliott, 2011), and the dynamics include the interaction of biotic and abiotic limits, legacy effects, and feedbacks at multiple scales (e.g. Bader et al., 2008).

The restriction of "treeline" and "treeline ecotone" to the narrow thermal limit of mountain forests leaves this important landscape element undefined.

Given that the K&H definitions of "alpine treeline" and "alpine treeline ecotone" make them redundant, I propose that "alpine treeline" be used as they have suggested, that is for the band spanning 0.2 K, but that "alpine treeline ecotone" be applied to the zone from the alpine timberline to the tree-species limit, which is always in alpine vegetation. This phrasing includes "alpine treeline" within the "alpine treeline ecotone," which is simple enough, maintains Körner's (2012) definition of the latter, and centres research on the 0.2 K zone while discarding the idea of a line, per se, which has always been problematic due to scale dependence. The "alpine treeline ecotone" should include instances of disequilibrium if the 6° isotherm

moves upslope faster than tree cover can. By using 'treeline' as an adjective, ecotones in climatic disequilibrium are always within the context of the thermal "alpine treeline". Going forward, the reverse conflation, for example, using "treeline ecotone, hereafter treeline …" as a shortcut, should stop.

Recognition of the differences *and* common ground of all treelines limited by fundamental resources or tolerances in niche space and their usually more extensive and important ecotones promotes inclusion and consideration of the multidimensional and multiscale nature of these landscapes. This framework can, thus, increase the synergy among multifold diverse researchers (e.g. see Chen et al., 2022) across mountain systems.

KEYWORDS

alpine, climate change, drought, ecotone, forest edge, fundamental niche, realized niche, temperature

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George P. Malanson

The University of Iowa, Iowa City, Iowa, USA

Correspondence
George P. Malanson, The University of Iowa, Iowa City, IA 52242, USA.
Email: george-malanson@uiowa.edu

ORCID

George P. Malanson https://orcid.org/0000-0001-9527-0086

REFERENCES

Alftine, K. J., Malanson, G. P., & Fagre, D. B. (2003). Feedback-driven response to multi-decadal climatic variability at an alpine forest-tundra ecotone. *Physical Geography*, *24*, 520–535.

Bader, M. Y., Rietkerk, M., & Bregt, A. K. (2008). A simple spatial model exploring positive feedbacks at tropical alpine treelines. *Arctic, Antarctic, and Alpine Research*, *40*, 269–278.

Butler, D. R., Malanson, G. P., Walsh, S. J., & Fagre, D. B. (2007). Influences of geomorphology and geology on alpine treeline in the American West—More important than climatic influences? *Physical Geography*, *28*, 434–450.

Chen, W., Ding, H., Li, J., Chen, K., & Wang, H. (2022). Alpine treelines as ecological indicators of global climate change: Who has studied? What has been studied? *Ecological Informatics*, *70*, 101691.

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 Ecology and Biogeography*, *20*, 46–57.

Fajardo, A., & McIntire, E. J. (2012). Reversal of multicentury tree growth improvements and loss of synchrony at mountain tree lines point to changes in key drivers. *Journal of Ecology*, *100*, 782–794.

Formica, A., Farrer, E. C., Ashton, I. W., & Suding, K. N. (2014). Shrub expansion over the past 62 years in Rocky Mountain alpine tundra: Possible causes and consequences. *Arctic, Antarctic, and Alpine Research*, *46*, 616–631.

Holt, R. D. (2009). Bringing the Hutchinsonian niche into the 21st century: Ecological and evolutionary perspectives. *Proceedings of the National Academy of Sciences*, *106*(S2), 19659–19665.

Holtmeier, F.-K. (2009). *Mountain timberlines*. Springer.

Hutchinson, G. E. (1957). Concluding remarks. *Cold Spring Harbor Symposium in Quantitative Biology*, *22*, 415–427.

Körner, C. (2012). *Alpine treelines*. Springer.

Körner, C., & Hoch, G. (2023). Not every high-latitude or high-elevation forest edge is a treeline. *Journal of Biogeography*, *50*, 838–845.

Malanson, G. P., Resler, L. M., Butler, D. R., & Fagre, D. B. (2019). Mountain plant communities: uncertain sentinels? *Progress in Physical Geography*, *43*, 521–543.

Martínez, I., Wiegand, T., Camarero, J. J., Batllori, E., & Gutiérrez, E. (2011). Disentangling the formation of contrasting tree-line physiognomies combining model selection and Bayesian parameterization for simulation models. *American Naturalist*, *177*, E136–E152.

Matlack, G. R. (1994). Vegetation dynamics of the forest edge—Trends in space and successional time. *Journal of Ecology*, *82*, 113–123.

Millar, C. I., Westfall, R. D., Delany, D. L., King, J. C., & Graumlich, L. J. (2004). Response of subalpine conifers in the Sierra Nevada, California, USA, to 20th-century warming and decadal climate variability. *Arctic, Antarctic, and Alpine Research*, *36*, 181–200.

Müller, M., Schwab, N., Schickhoff, U., Böhner, J., & Scholten, T. (2016). Soil temperature and soil moisture patterns in a Himalayan alpine treeline ecotone. *Arctic, Antarctic, and Alpine Research*, *48*, 501–521.

BIOSKETCH

George P. Malanson has pursued research on mountain vegetation since 1983 with a focus on treelines since 1990 but with major excursions into fire ecology, riparian systems and land use science. He has used theory-based simulations to inform fieldwork-based analyses, with most of the latter centred on the Rocky Mountains.