Received: 6 March 2024 | Revised: 28 March 2024 | Accepted: 2 April 2024

DOI: 10.1111/gcb.17288

Global Change Biology WILEY

PERSPECTIVE

Introducing the concepts of range-pinning and Allee effects to explain reduced temperature sensitivity of global treeline dynamics

Ulf Büntgen[1,2,3] | Audrey Palosse[1] | Jiri Dolezal[4,5] | Andrew Liebhold[6,7]

[1]Department of Geography, University of Cambridge, Cambridge, UK
[2]Global Change Research Institute (CzechGlobe), Czech Academy of Sciences, Brno, Czech Republic
[3]Department of Geography, Faculty of Science, Masaryk University, Brno, Czech Republic
[4]Institute of Botany, Czech Academy of Sciences, Pruhonice, Czech Republic
[5]Department of Botany, Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic
[6]US Forest Service Northern Research Station, Morgantown, West Virginia, USA
[7]Faculty of Forestry and Wood Sciences, Czech University of Life Sciences Prague, Prague, Czech Republic

Correspondence
Ulf Büntgen, Department of Geography, University of Cambridge, Cambridge CB2 3EN, UK.
Email: ulf.buentgen@geog.cam.ac.uk

KEYWORDS
biogeography, climate sensitivity, density dependence, global warming, plant growth, population ecology, treeline

Treeline studies are often motivated by the general assumption that cold distribution limits of the lifeform tree represent a universal biogeographic margin that is particularly sensitive to recent global warming. But the existing body of scientific literature is less consistent and raises more questions than it provides answers. Not only is the rate of treeline advancement in response to rising temperatures poorly understood, but interactions between biotic and abiotic drivers of treeline dynamics, as well as ecological mechanisms behind surprisingly stable treeline positions also remain unclear.

Here, we argue that natural treeline ecotones in undisturbed alpine and arctic settings are less sensitive to the ongoing anthropogenic warming trend than commonly assumed. To foster our hypothesis, we first recognize that the conceptual distinction between actual (realized) and potential (theoretical) treeline positions requires an additional differentiation of actual treelines into those that are undisturbed natural versus those that are created artificially (i). We also suggest that the growth sensitivity of individual treeline trees to climate should not be confused with the climate dependency of recruitment rates and age structures of entire treeline populations (ii). We then introduce the concept of range-pinning, an emergent property resulting from the interactions of dispersal with the Allee effect (i.e. a positive relationship between population density and individual fitness), which also may constrain species ranges from expanding at the edge of suitable habitats. (iii). Finally, we advocate that future treeline studies should consider state-of-the-art eco-physiological and biochemical insights from perennial plants, search out empirical evidence for Allee effects in treeline populations that may help explain their highly static nature in many undisturbed ecotones around the world, and use these findings to advance biogeographic and ecological knowledge across a wide range of spatiotemporal scales (iv).

(i) Alpine and arctic treelines are commonly understood as the zone where excessively cold growing season temperatures limit the upright growth of trees (Körner, 2021). However, it is important to distinguish between actual (i.e. realized) and potential (i.e. theoretical) treeline positions (Figure 1a). While realized treelines refer to all elevational and latitudinal ecotones that can be found around the world, potential treelines describe the hypothetical upper or poleward niche edge of upright tree growth that closely follows a highly variable isotherm (Körner & Hoch, 2023). Potential and realized treeline positions are therefore almost never in equilibrium, and their

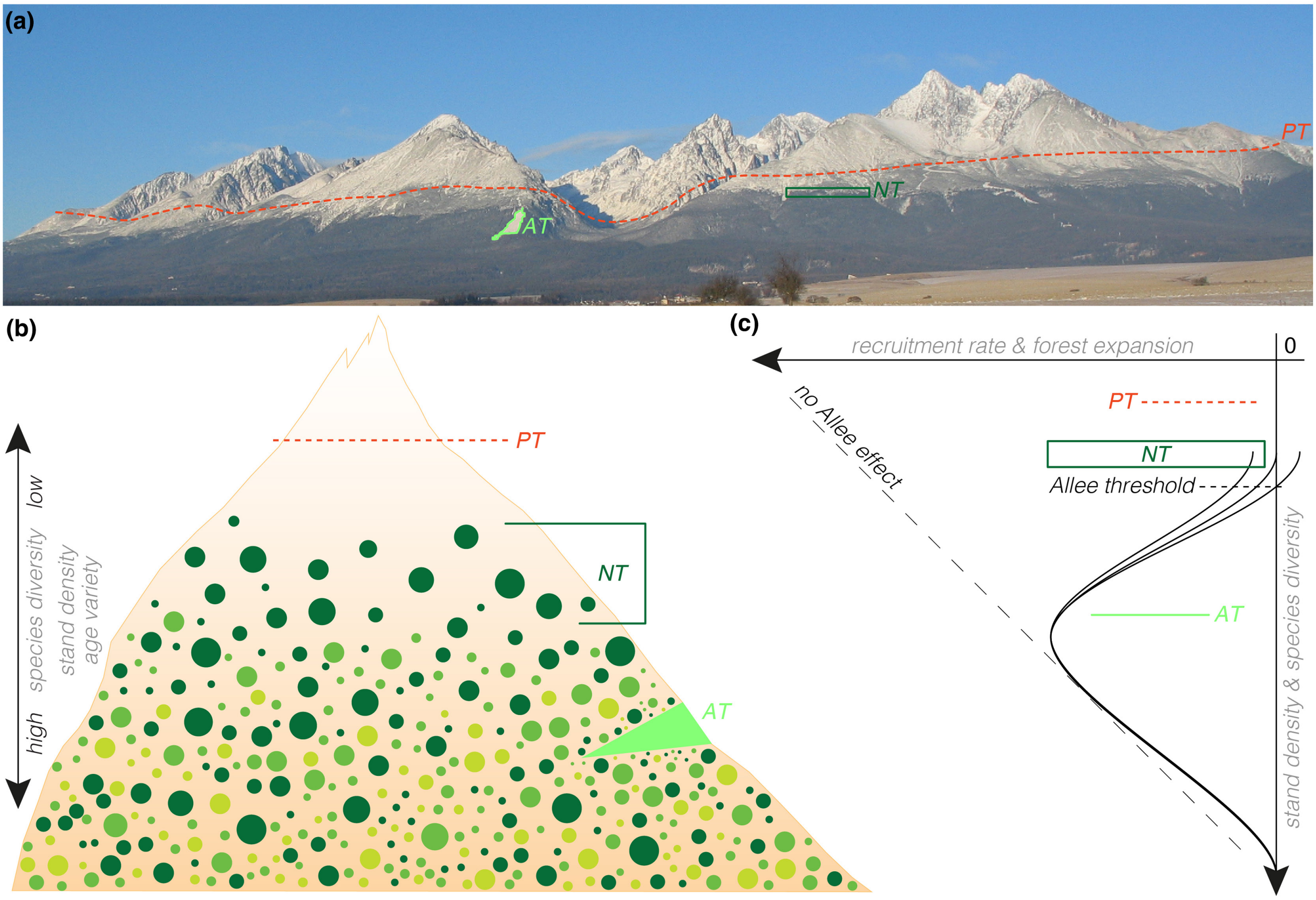

FIGURE 1 Rethinking treeline dynamics. (a) South facing slope of the High Tatra Mountains in Slovakia, where the undisturbed, natural treeline ecotone is around 1550 m asl (green box; NT), the potential treeline isotherm would be substantially higher (PT; orange dashed line), and ski slopes resulted in lower artificial treelines (AT). (b) Schematic example of range-pinning at the upper treeline, where species diversity, stand density and age variety are low. The spatial shape of treeline ecotones is of considerable importance to range pinning, because portions of the range margin with greatest exposure to unoccupied regions are most prone to emigration loss and subsequent extinction. (c) Conceptual overview of how critical Allee thresholds can explain reduced temperature sensitivity of treeline ecotones.

current offset under rapid global warming can reach several hundreds of meters in elevation (Büntgen et al., 2022), with the realized treeline lagging the potential one. Though helpful, this simple distinction between realized and potential treelines is not sufficient and should further separate realized treelines into undisturbed natural and suppressed artificial ecotones (Figure 1a). Since undisturbed natural and suppressed artificial treelines are usually characterized by different levels of species diversity, stand density and age structure, they are likely to exhibit slower and faster responses to recent warming, respectively.

(ii) Despite strong evidence for a potential global treeline isotherm that reaches highest elevations near the equator and approaches sea-level at high latitudes (Körner & Hoch, 2023), the mechanistic determinants of alpine and arctic distribution limits of upright tree growth remain puzzling. Although the interplay of biotic and abiotic factors and processes that may contribute to natural treeline positions around the world have been studied intensively, the various growth- and stress-related hypotheses focus on ring formation in trees under relatively cold conditions. The definition of growing seasons is, however, still challenging (Körner et al., 2023), and consideration of temperature effects on the xylogenesis of individual trees cannot explain the putative climate dependency of entire treeline populations. In fact, we suggest that ephemeral climate extremes rather than long-term trends ultimately shape vegetation composition through constraints on the germination and establishment of seedlings and saplings. Since many treeline ecotones are dominated by old specimens and a general lack of recruitment, uneven aged distributions in treeline populations imply a limited temperature sensitivity, and thus reduced capacity for range expansion under global warming.

(iii) Range-pinning is an additional factor that may help to explain why treelines are less sensitive to global warming than commonly assumed (see Figure 1 for a conceptual overview). The phenomenon of range-pinning emerges from the interaction of Allee effects with dispersal in populations at the margin of a species range to constrain them from occupying suitable habitats (Keitt et al., 2001). At the edge of a species' range, emigration tends to be greater than immigration. When excessive emigration drains population below a critical Allee threshold, they will decline to extinction even where environmental conditions may otherwise support stable and even expanding populations. First described almost 100 years ago by the American ecologist Allee (1931), the homonymous Allee effect refers to the phenomenon of decreased per capita fitness with decreasing population size, that is, positive density dependence (Kramer et al., 2009; Stephens et al., 1999). Allee effects exist in many populations and can arise from different mechanisms (Courchamp et al., 2008). Possible mechanisms leading to Allee effects in treeline populations can include pollen limitation, seed and seedling predation and even in-breeding. Range-pinning is generally understood to only arise in the presence of a strong Allee effect (Figure 1b,c), in which population growth dips below unity at low densities driving populations toward extinction. Although range-pinning has never been considered in treeline research, it seems obvious that reduced reproductive success of a small number of old treeline trees, as well as reduced survival rates of seedlings and saplings above the treeline hamper forest expansion, even under favorable environmental conditions. Range-pinning thus can maintain a highly static range boundary even under variable environmental conditions. Undisturbed, realized treeline positions far below the potential treeline isotherm may therefore be biogeographic manifestations of range-pinning (Figure 1b,c), rather than the result of disturbance factors, such as drought, fire or grazing.

(iv) Even two centuries after von Humboldt's pioneering treeline studies (von Humboldt & Bonpland, 1805), and considerable work thereafter (e.g. Troll, 1973), there is still scope for fundamental discoveries at the cold range limit of upright tree growth. The globally synchronized occurrence of so-called Blue Rings during exceptionally cold summers after large volcanic eruptions, for instance, can provide unique time-for-space surrogates in support of the still debated hypothesis of a thermal-induced lack of lignin biosynthesis in the secondary cell walls of woody shrubs and herbs that grow above the elevational or latitudinal treeline (Büntgen, 2023; Büntgen et al., 2023; Crivellaro et al., 2022). Answers for the absence of trees above the treeline cannot be found in trees below the treeline but instead require assessments of plants growing under colder conditions. In other words, investigations of trees below and within treeline ecotones cannot tell us why they do not recruit and survive above the treeline. Moreover, offsets between realized and potential treeline positions not only affect in situ observations, but most likely also inflate the amplitude and compresses the variance of tree ring-based temperature reconstructions (Büntgen et al., 2022). Hence, we advocate for interdisciplinary investigations at the crossroads of biogeography, dendrochronology, population ecology, plant physiology and wood anatomy that combine empirical evidence with conceptual knowledge. We also expect future treeline research to critically review existing paradigms, expand focus from trees to smaller perennial plants, and consider mechanistic insights from the cell level to understand patterns and behaviours at the global scale.

AUTHOR CONTRIBUTIONS

Ulf Büntgen: Conceptualization; writing – original draft; writing – review and editing. **Audrey Palosse:** Conceptualization; writing – original draft. **Jiri Dolezal:** Writing – original draft. **Andrew Liebhold:** Conceptualization; writing – original draft.

ACKNOWLEDGEMENTS

UB was supported by the Czech Science Foundation (# 23-08049S; Hydro8), the ERC Advanced Grant (# 882727; Monostar), and the ERC Synergy Grant (# 101118880; Synergy-Plague). JD was supported by the Czech Science Foundation (# 24-11954S), and MSMT inter-excellence (# LUAUS24258).

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

No data have been used in this study.

ORCID

Ulf Büntgen https://orcid.org/0000-0002-3821-0818

Jiri Dolezal https://orcid.org/0000-0002-5829-4051

REFERENCES

Allee, W. C. (1931). *Animal aggregations*. University of Chicago Press.

Büntgen, U. (2023). Experimental evidence for a thermal limitation of plant cell wall lignification at the alpine treeline. *Alpine Botany*, *133*, 179–182.

Büntgen, U., Piermattei, A., Crivellaro, A., Reinig, F., Krusic, P. J., Trnka, M., Torbenson, M., & Esper, J. (2022). Common era treeline fluctuations and their implications for climate reconstructions. *Global and Planetary Change*, *219*, 103979.

Büntgen, U., Piermattei, A., Dolezal, J., Dupree, P., & Crivellaro, A. (2023). Reply to: Biogeographic implications of plant stature and microclimate in cold regions. *Communications Biology*, *6*, 662.

Courchamp, F., Berec, L., & Gascoigne, J. (2008). *Allee effects in ecology and conservation*. Oxford Academic.

Crivellaro, A., Piermattei, A., Dolezal, J., Dupree, P., & Büntgen, U. (2022). Biogeographic implication of temperature-induced plant cell wall lignification. *Communications Biology*, *5*, 767.

Keitt, T. H., Lewis, M. A., & Holt, R. D. (2001). Allee effects, invasion pinning, and species' borders. *American Naturalist*, *157*, 203–216.

Körner, C. (2021). The cold range limit of trees. *Trends in Ecology & Evolution*, *36*, 979–989.

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

Körner, C., Möhl, P., & Hiltbrunner, E. (2023). Four ways to define the growing season. *Ecology Letters*, *26*, 1277–1292.

Kramer, A. M., Dennis, B., Liebhold, A. M., & Drake, J. M. (2009). The evidence for Allee effects. *Population Ecology*, *51*, 341–354.
Stephens, P. A., Sutherland, W. J., & Freckleton, R. P. (1999). What is the Allee effect? *Oikos*, *87*, 185–190.
Troll, C. (1973). The upper timberlines in different climatic zones. *Arctic and Alpine Research*, *5*, 3–18.
von Humboldt, A., & Bonpland, A. (1805). *Essai sur la géographie des Plantes*. Chez Levrault, Schoell et Compagnie, Libraires.

How to cite this article: Büntgen, U., Palosse, A., Dolezal, J., & Liebhold, A. (2024). Introducing the concepts of range-pinning and Allee effects to explain reduced temperature sensitivity of global treeline dynamics. *Global Change Biology*, *30*, e17288. https://doi.org/10.1111/gcb.17288