COMMENTARY

Limits to upward movement of subalpine forests in a warming climate

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Rapid changes to the earth's climate are well underway, already influencing biological systems across the globe. Among the key impacts are potential shifts in the geographic range of many species or ecosystems, often predicted to move either poleward or upward in response to warmer conditions (1, 2). In mountain biomes, as upper elevations become more climatically hospitable to tree establishment, upward shifts in tree cover could cause alpine ecosystems (nonforest vegetation above treeline) to become both reduced in extent and increasingly isolated into smaller "sky islands." However, currently we know relatively little about the actual nature of such shifts in treeline, or to what extent a warming climate alone will generate them. In PNAS, Macias-Fauria and Johnson (3) make an important step in quantifying the relative influence of temperature regime and geomorphic factors in determining current and future treeline across a large Rocky Mountain landscape. The authors' data suggest that upward treeline shifts in a warming climate may be heavily constrained by geologic factors that influence the availability of growing substrates at high elevations, leading to much less, or at least much slower, tree colonization into alpine areas than predicted by climate alone.

Macias-Fauria and Johnson (3) show that large extents of the alpine zone can be dominated by extremely steep slopes, cliffs, avalanche chutes, and exposed bedrock: that is, places where trees rarely can grow (Fig. 1). Prior efforts to model treeline shifts have focused primarily on the envelope of temperature and moisture conditions in relation to the physiological requirements of subalpine trees, with little consideration given to the underlying geomorphic template (topography, soils) upon which trees must ultimately grow. Although warming temperatures have been linked to tree expansion into alpine areas with relatively gentle topography and suitable soils (4, 5), such sites can be relatively limited in many high-mountain landscapes. As such, movement of woody vegetation into some alpine areas may occur over millennial rather than decadal time scales (i.e., periods relevant to the weathering and erosion of mountain surfaces rather than the reproduction of trees). This intuitive concept has been recognized by many researchers (6, 7), but there have been few studies quantifying the degree to which factors other than climate might drive spatial variability in treeline migration over large landscapes. The quantitative niche-modeling approach applied by Macias-Fauria and Johnson (3), incorporating both geomorphology and climate, moves us toward more realistic and sophisticated predictions of potential shifts in mountain treelines.

More broadly, such efforts fit into a larger context of understanding the diverse set of factors that influence biogeographic shifts under a changing climate, many of which are not directly related to the climatic "envelope" in which species grow. Other subfields of ecology have long recognized these other factors, perhaps most notably in the conservation biology realm. For example, the ability of threatened plant and animal species to migrate latitudinally in response to changing conditions may be limited by the low connectivity of many human-modified landscapes (8), prompting a long-running and spirited debate as to whether we should engage in assisted relocation efforts (9, 10). Fundamental to this debate is an awareness that not only climate, but also the landscape template, will affect species' movements.

Like most responses to changing climate, treeline dynamics emerge from a series of complex and interacting drivers, each of which may have its own response to a changing environmental context. In addition to the critical factors of climate and geomorphology (3), altered disturbance regimes and

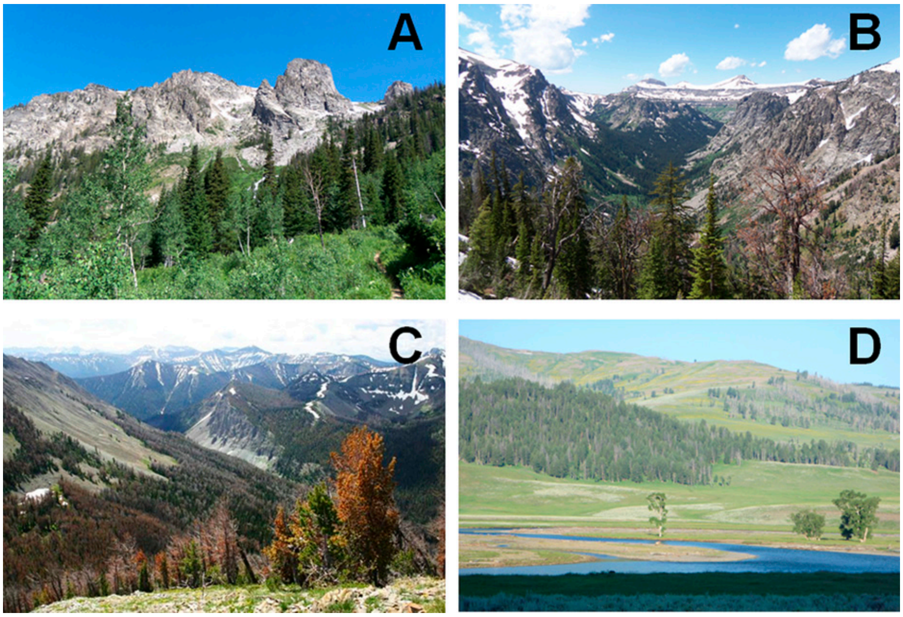

Fig. 1. Mountain treelines may move upward in a warming climate, but such shifts will likely be constrained in many alpine landscapes because of significant areas of unsuitable growing substrates (3), such as cliffs, bedrock, and recently deglaciated slopes (*A* and *B*). Treeline dynamics are further complicated by altered disturbance regimes in a changing climate: for example, bark beetles recently have gained increased access to areas formerly too cold for them and have killed off large swaths of "naïve" subalpine tree hosts (*C*). Such altered disturbance regimes affect dynamics of both upper and lower treelines (*D*). Photo credits: T. Butusov (*A* and *B*), M. Simard (*C*), D. C. Donato (*D*).

Author contributions: D.C.D. wrote the paper.

The author declares no conflict of interest.

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competitive relationships among organisms will play key roles (11, 12). For example, in many subalpine forests of western North America, any subtle climate-induced shifts in tree establishment are currently being dwarfed by profound changes in forest cover because of outbreaks of tree-killing bark beetles (13). Historically restricted from high elevations by cold winter temperatures, mountain pine beetles (*Dendroctonus ponderosae*) are now expanding into the highest-elevation forests dominated by whitebark pine (*Pinus albicaulis*), a foundation species (14) in subalpine ecosystems. Having experienced only intermittent exposure to bark beetles in the past, the whitebark pine is a "naïve host": that is, one with few coevolved defenses relative to the beetles' principal host tree species (13). At the same time, an introduced pathogen, the white pine blister rust, is also heavily impacting whitebark pine. Consequently, vast swaths of subalpine forests, much of them several hundred years old, are currently experiencing rapid mortality and a reduction in treeline forest cover rather than upslope expansion (Fig. 1). We are just beginning to understand how such changes may ultimately play out in terms of potential range shifts of host trees versus their predators, altered competitive relations among tree species, and interactions with other disturbances, such as wildfires. These questions pertain to both upper and lower treelines in mountainous landscapes (15) (Fig. 1), as well as other types of ecological boundaries. This type of nonlinear system behavior, in which ecosystems do not simply shift geographically according to direct climatic effects on tree establishment, remains a crucial research direction in the ecology of environmental change.

The analysis presented by Macias-Fauria and Johnson (3) represents an important step in teasing apart these various influences on mountain treelines in a changing climate. Their specific results are useful in elucidating the role of one key factor, alpine geomorphology; but more broadly speaking, the approach they use is instructive in its quantitative, landscape-scale consideration of multiple factors that determine ecological change, many of which are not directly related to climate itself, and have not been adequately studied in the global change literature. Ultimately, such approaches should prove useful in improving our forecasting of ecosystem behavior under changing environmental conditions.

1 IPCC (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (Cambridge Univ Press, Cambridge, UK).

2 Parmesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421(6918):37–42.

3 Macias-Fauria M, Johnson EA (2013) Warming-induced upslope advance of subalpine forest is severely limited by geomorphic processes. *Proc Natl Acad Sci USA* 110:8117–8122.

4 Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecol Lett* 12(10):1040–1049.

5 Körner C, Paulsen J (2004) A world-wide study of high altitude treeline temperatures. *J Biogeogr* 31(5):713–732.

6 Leonelli G, Pelfini M, di Cella UM, Garavaglia V (2011) Climate warming and the recent treeline shift in the European Alps: The role of geomorphological factors in high-altitude sites. *AMBIO* 40(3):264–273.

7 Butler DR, Malanson GP, Walsh SJ, Fagre DB (2007) Influences of geomorphology and geology on alpine treeline in the American West—More important than climatic influences? *Physical Geography* 28(5):434–450.

8 Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: A review of 22 years of recommendations. *Biol Conserv* 142:14–32.

9 Hoegh-Guldberg O, et al. (2008) Ecology. Assisted colonization and rapid climate change. *Science* 321(5887):345–346.

10 Ricciardi A, Simberloff D (2009) Assisted colonization is not a viable conservation strategy. *Trends Ecol Evol* 24(5):248–253.

11 Turner MG (2010) Disturbance and landscape dynamics in a changing world. *Ecology* 91(10):2833–2849.

12 Liancourt P, et al. (2013) Plant response to climate change varies with topography, interactions with neighbors, and ecotype. *Ecology* 94(2):444–453.

13 Raffa KF, Powell EN, Townsend PA (2012) Temperature-driven range expansion of an irruptive insect heightened by weakly coevolved plant defenses. *Proc Natl Acad Sci USA* 110(6):2193–2198.

14 Ellison AM, et al. (2010) Loss of foundation species: Consequences for the structure and dynamics of forested ecosystems. *Front Ecol Environ* 3(9):479–486.

15 Donato DC, Harvey BJ, Romme WH, Simard M, Turner MG (2013) Bark beetle effects on fuel profiles across a range of stand structures in Douglas-fir forests of Greater Yellowstone. *Ecol Appl* 23(1):3–20.