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Elevation alters ecosystem properties across temperate treelines globally

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Temperature is a primary driver of the distribution of biodiversity as well as of ecosystem boundaries[1,2]. Declining temperature with increasing elevation in montane systems has long been recognized as a major factor shaping plant community biodiversity, metabolic processes, and ecosystem dynamics[3,4]. Elevational gradients, as thermoclines, also enable prediction of long-term ecological responses to climate warming[5–7]. One of the most striking manifestations of increasing elevation is the abrupt transitions from forest to treeless alpine tundra[8]. However, whether there are globally consistent above- and belowground responses to these transitions remains an open question[4]. To disentangle the direct and indirect effects of temperature on ecosystem properties, here we evaluate replicate treeline ecotones in seven temperate regions of the world. We find that declining temperatures with increasing elevation did not affect tree leaf nutrient concentrations, but did reduce ground-layer community-weighted plant nitrogen, leading to the strong stoichiometric convergence of ground-layer plant community nitrogen to phosphorus ratios across all regions. Further, elevation-driven changes in plant nutrients were associated with changes in soil organic matter content and quality (carbon to nitrogen ratios) and microbial properties. Combined, our identification of direct and indirect temperature controls over plant communities and soil properties in seven contrasting regions suggests that future warming may disrupt the functional properties of montane ecosystems, particularly where plant community reorganization outpaces treeline advance.

Montane ecosystems are undergoing and will continue to undergo rapid changes as global temperatures rise. These ecosystems are critical for maintaining global patterns of biodiversity and ecosystem functioning, but we know little about whether disparate montane regions around the world will change in similar and predictable ways. Globally, mountain ecosystems differ in geological age, relative land area, historical disturbances, climatic regimes, topographic complexity, and species composition. However, the most universally consistent and biologically influential effect of increasing elevation is an adiabatic decline in temperature[9]. Declining temperature has an overarching influence over vegetation responses along elevational gradients[4,9], including one of the most visually striking effects of decreasing temperatures: the formation of treelines[9]. The most plausible explanation for treeline formation, the growth limitation hypothesis, posits that declining carbon sink strength at treelines, rather than declining carbon supplied from photosynthesis, results from the direct effect of low temperatures on metabolic processes essential for wood production[8,10]. As a result of low temperatures, trees—regardless of taxon—form treeline ecotones within a narrow and globally consistent isotherm with mean growing season temperatures of 6.7–7 °C wherever growing seasons are at least three months long[10]. Because of this global thermocline, the position and dynamics of ecosystem properties near treelines have the potential to act as a powerful signal of the cascading effects of climate change[4].

In addition to reduction of tree growth and loss of trees, other ecological properties are driven by elevation-associated temperature declines. For instance, leaf nutrient concentrations can decline[11,12], stay consistent, or even increase with increasing elevation[9]. This suggests that processes associated with nutrient availability, communities of soil microbes that regulate plant nutrient supply, and plant nutrient demands could all indirectly contribute to ecosystem properties as second-order drivers after the effects of treeline position and plant community properties are considered[13,14].

In this study we asked how elevation-mediated temperature directly and indirectly affects the nutrient status of plant communities, whether there are coupled responses of above- and belowground properties with temperature, and whether patterns and processes are consistent across biotic community transitions in seven disparate montane regions globally. We measured ecosystem properties across multiple treeline ecotones to permit the regional standardization of growing season temperatures because treelines occur at similar air temperature thresholds (Supplementary Methods). For each of five (or, in one case, four) replicate transects in each region, we sampled at six elevations: 150 and 50 m below the treeline, just below and just above the treeline, and 50 and 150 m above the treeline; elevational ranges represented approximately 2 °C isoclines[10] (Supplementary Methods). The regions differed in geological age (1–400 Myr), climate (Supplementary Table 1), and floristic composition (Supplementary Table 2), yet all treelines exhibited characteristic responses to declining temperatures, including a decline in tree height and stand basal area, an increase in stem density (Extended Data Fig. 1a–c and Supplementary Table 3), and the formation of distinct treeline ecotones (Extended Data Fig. 2). Our regionally replicated approach enabled us to test (1) if the concentrations of potentially growth limiting nitrogen (N) and phosphorus (P), and their ratio, in the foliage of trees and ground-layer plants, and in roots, consistently covary with decreasing temperature among regions, despite differences in biotic communities and regionally specific factors[4]; and (2) whether these patterns in plant nutrient concentrations are tightly coupled to soil nutrient availability and/or microbial community structure.

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