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Commentary

As a permafrost ecosystem warms, plant community traits become more acquisitive

Permafrost is thawing, as a result of both increasing temperatures and snow depth. Temperatures in permafrost are increasing at 0.3–1°C per decade, possibly accelerating as global warming progresses (Smith *et al*., 2022), leading to estimated losses of over 40% of permafrost area even if warming is stabilized at 2°C (Chadburn *et al*., 2017). This rapid warming might not only lead to large losses of carbon (C) and nitrogen (N) previously locked up in frozen soil layers but will also inevitably influence plant communities growing in the increasingly deeper layer of seasonally thawed soil above the permafrost. How plant community traits respond to the release of nutrients from warming permafrost could have important implications for carbon and nutrient cycling in these ecosystems. Plant communities are adapted to the harsh climate in permafrost areas, with roots growing in the thawed but still cold soil layers above the permafrost. But what happens when soils above permafrost warm? How do plant communities and their traits respond? Are plant trait responses coordinated above- and belowground? These are some key questions that are tackled in an recently published article by Wei *et al.* (2023; 1802–1816), published in this issue of *New Phytologist*.

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Plant traits and their values are important for understanding community responses to global change. For example, in resource-limited or harsh conditions, plant communities have been found to either have more acquisitive traits that promote the acquisition of resources (e.g. finer roots and higher nitrogen content), or conservative traits, such as thicker roots and lower nitrogen content (Laughlin *et al*., 2021). Indeed, multiple studies have been conducted along elevational gradients to understand the relationship between plant traits and temperature (e.g. Weemstra *et al*., 2021; Spitzer *et al*., 2023). These studies have shown that although some species have clear elevational trait value responses, at the community level there are idiosyncratic relationships with elevation, probably due to the spatial heterogeneity and nonlinear nutrient dynamics along natural gradients. Wei *et al.*'s study directly tests the effects of warming on permafrost-affected soils, which resulted in increased net soil N mineralization and nitrate concentrations. This shifted plant community traits to more acquisitive values both above- and belowground, for example, higher specific root length, higher root N concentration, higher specific leaf area, and photosynthetic N use efficiency. Previous studies have found strong links between experimental warming and increased N content in plant tissues (Jónsdóttir *et al*., 2023). However, this study from Wei *et al.* shows a strong coordinated shift towards acquisitive strategies in both above- and belowground tissues in the plant communities under experimental warming, although tissue density had opposing responses above- and belowground. This study therefore provides an important mechanistic link between the warming of permafrost soils and plant community trait responses.

Plant trait research has progressed rapidly over the past decades, but with a much stronger focus on aboveground traits. Recently, there is a much better understanding of trait variation belowground, that is, 'the root trait space', as well as aboveground, that is, 'the leaf economic spectrum'; however, whether there is trait coordination between leaf and root tissue is currently being debated (Carmona *et al*., 2021; Weigelt *et al*., 2021, 2023). Wei *et al.* go beyond the discussion about trait coordination with an exciting approach to investigating trait networks based on previous work by Messier *et al.* (2017). Specifically, they examine whether they could identify hub traits (i.e. traits that are correlated to several other traits), which may be important for plant response to environmental change factors, such as increased soil temperature or available nutrients. This is because a change in hub traits could likely cause cascading effects on other traits in response to environmental change (Kleyer *et al*., 2019; Rao *et al*., 2023). First, they measured 26 plant functional traits (i.e. phenological, morphological, chemical, and photosynthetic traits). They found that the hub trait under ambient conditions was specific root area, which is not surprising as permafrost ecosystems are characterized by a generally large proportion of belowground relative to aboveground biomass. Interestingly, under warming they found that trait centrality (i.e. the hub trait) shifted from specific root area to leaf area, but that there were very minor shifts in the connectivity of trait networks. This suggests that the plant communities shifted towards larger leaf area as a means of adapting to light competition aboveground under more favourable belowground conditions, but that there were no obvious cascading effects on other plant traits.

Another key aspect of plant community trait response to warming is their intraspecific trait variability. Wei *et al.* found that in their species-poor site, intraspecific trait variation contributed substantially to the total variation in community-weighted trait means, and their associated trait responses to warming. This is consistent with recent studies at other species-poor sites for leaf and

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root traits (Jónsdóttir *et al.*, 2023; Spitzer *et al.*, 2023). High intraspecific variation in plant communities enables a rapid response to environmental change or newly available resources without a change in species composition. This suggests that trait plasticity plays an important role in these ecosystems as a means of adaptation to environmental change. It further strengthens the evidence for the importance of intraspecific trait variability in species-poor ecosystems relative to species turnover in response to environmental change. However, Wei *et al.* measured traits on the four most dominant species in their system, all of which are sedges. Graminoids generally tend to be more responsive to environmental change compared with slower growing, more conservative shrubs (Veen (Ciska) *et al.*, 2015), and it thus remains unclear whether similar patterns are observed in more functionally diverse communities that include shrubs common in permafrost ecosystems. Indeed, many permafrost areas show strong changes in species composition in response to warming, with particular increases in shrub abundance and productivity, at least in relatively drier, upland areas (Heijmans *et al.*, 2022).

The study by Wei *et al.* paves the way for many new questions related to plant community trait responses in warming permafrost ecosystems. First, how long do permafrost ecosystems need to be warmed before effects are seen, and how long will these effects last? Wei *et al.* conducted a 7-year warming experiment and found increased net soil N mineralization and higher soil nitrate concentration. What would be the effects of much longer term warming on soil nutrient availability and what implications would this have for plant communities and their traits? How would more species-diverse plant communities with graminoids and shrubs respond? A second exciting line of inquiry is how plant–microbe interactions are influenced by warming permafrost. For example, the extent to which plant trait shifts drive microbial community development over time or influence fungal : bacterial ratios in soil needs further investigation. These interactions could have implications for soil carbon storage and may be important for mitigating C loss in warming permafrost. At the same time, trait shifts to plant tissue with higher nutrient content could influence the activity of decomposers and speed up nutrient cycling rates in the warmer permafrost. There is therefore a need for decomposition experiments in thawed permafrost. Third, will community composition and species diversity shift, or, if community composition stays similar, will trait values still shift further in response to longer term warming? Many questions remain about the longer term effects, but Wei *et al.* have provided key insights into understanding plant community responses to warming in permafrost ecosystems.

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