Commentary

The third dimension of root economics space

Soil carbon (C) constitutes the largest pool of organic C on the planet (Jackson *et al.*, 2017), and predictive estimates of carbon dioxide emissions are highly sensitive to soil responses to warming (Jenkinson *et al.*, 1991). Warming can shift decomposition rates, while increased nitrogen availability can rebalance the constraints of other belowground resources, such as phosphorus for plants and active C for microbes (Bardgett *et al.*, 2014). However, how these shifting conditions influence root morphology, root exudation (sugary liquid C excreted by fine roots), and soil chemistry remains something of a black box compared to more easily observed aboveground responses.

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To understand how plants acquire and conserve resources under changing conditions, we traditionally look to root traits to describe contrasting pathways of root conservation and nutrient acquisition in the 'root economics space'. The 'root economics space' model presents belowground adaptations of root morphology along 2-axes: a 'Collaboration axis' (nutrient foraging) and a 'Conservation axis' (root construction and longevity). This framework may be inadequate as it is a simplification based on global means across a range of environments (Bergmann *et al.*, 2020). Indeed, under the microscope, roots often look unchanged even when their chemical behaviours change radically, implying root exudation is far more plastic and responsive than morphological traits. In an article recently published in *New Phytologist*, Muratore *et al.* (2026, https://doi.org/10.1111/nph.71398) seek to disentangle the potential interactions between root exudation and root morphological traits under environmental manipulation.

The authors investigate a suite of root traits for two co-occurring temperate forest species (*Quercus rubra* (red oak; ectomycorrhizal) and *Acer rubrum* (red maple; arbuscular mycorrhizal)). Taking advantage of a 16-yr-long factorial plot experiment at Harvard Forest LTER (USA), the authors examined root morphological traits, root chemistry, and root exudation rates across species in response to a range of experimental treatments including soil warming, N addition, controls, and combined treatments. The oak and maple species represent divergent nutrient-gathering styles and mycorrhizal associations, with the oak, a nutrient-conservative species, relying on ectomycorrhizal associations for nutrient acquisition and the maple, a nutrient-inquisitive species, with root traits that allow more exploration of the soil for direct nutrient uptake. Through this analysis, the authors investigated how long-term environmental manipulation altered three overlapping vectors (root morphology, internal root chemistry, and root exudation) and sought to determine whether these vectors acted independently.

Across both species, 16 yr of soil warming and fertilisation did not significantly alter macro-morphological root traits, which were instead best predicted by species identity (Muratore *et al.*). Traits such as specific root length, average root diameter, and branching traits remained fairly stable regardless of environmental treatment. These traits determine root shape and are indicators of root structural investment. Were these traits to be observed in isolation, root responses to environmental shifts might appear completely static. Conversely, specific root exudation rates (SER; exudation by fine roots per gram of tissue) were highly responsive to experimental treatments. N addition increased root exudation rates in both oaks and maples, while warming decreased root exudation in oaks. This study indicates that forest species vary the amount of root exudate as an immediate physiological response to changes in soil temperature and N availability (Robert *et al.*, 2025; Muratore *et al.*). Thus, the plasticity of exudation rates compared to the rigidity of root morphology in response to manipulation demonstrates an efficient metabolic shortcut that these temperate species can use to navigate sudden disruptions to the rhizosphere.

'Root economics space' consists of a two-axis conceptual model explaining nutrient acquisition and morphology pathways (Weigelt *et al.*, 2021). Under the currently accepted paradigm of 'root economics space', the first axis (the Collaboration axis; PC1 in Muratore *et al.*) charts a plant's reliance on mycorrhizal fungal partners in nutrient acquisition – aligning here with specific root length and diameter. The second axis (the Conservation axis; PC2 in Muratore *et al.*) defines root longevity against the fast and cheap capture of resources – aligning here with root tissue density, branching intensity, and root N concentrations. In this study, maple's acquisitive roots vs oak's conservative roots map onto this two-axis framework, corresponding with previous observations of root morphological traits mapping uniquely by species (e.g. Chen *et al.*, 2021). As rhizosphere C inputs from fine roots can shift without the need for changes in root morphology, they are more

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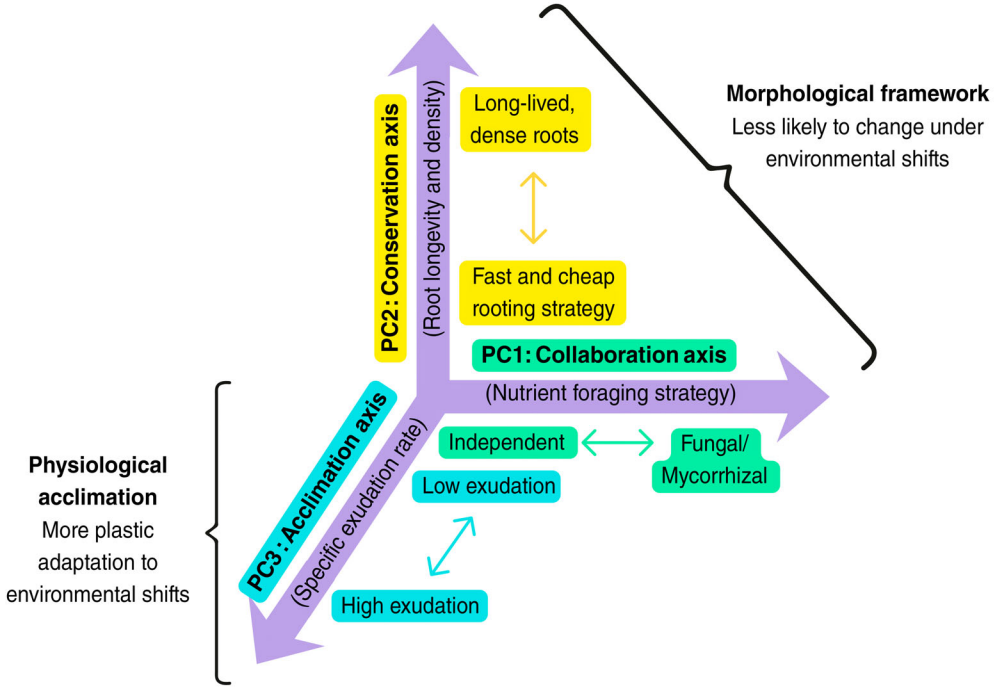

Fig. 1 A conceptual diagram of 'root economics space', detailing the previously defined Collaboration axis (PC1), the Conservation axis (PC2), and the proposed third Acclimation axis (PC3). For each axis, we describe the associated root traits and behaviours associated with different positions along each axis. This figure is an adaptation of the conceptual model described by Muratore *et al*. (2026).

closely associated with traits that can be harder to observe under a scanner: root tissue density, root N concentration, and the intensity of root branching (Muratore *et al.*). Indeed, in a PCA reconstruction of the root economics space, SER mapped strongly onto a third axis (the Acclimation axis; PC3), which also captures variation in root conservation traits. Through this observation, the authors challenge the typical model of the 'root economics space'.

The third 'Acclimation axis' represents root responses to acclimation gradients, or the plasticity of root construction and C efflux to changes in the belowground microenvironment, providing further nuance to species-specific root behaviours. In this study, it is posited that this third dimension may be used to explain regulation of root exudation into the rhizosphere under warming and changes in nutrient availability (see also Sun *et al.*, 2021; Yang *et al.*, 2025). When evaluated interactively, the combined warming and N treatments triggered an increase in SER for both oaks and maples, though this was achieved through contrasting root behaviours. In the more opportunistic red maple roots, increased SER covaried with a decrease in root tissue density and an increase in branching intensity. Conversely, in red oak, increased SER covaried with an increase in root density. This may represent a demonstration of oaks requiring a sturdier structural investment to support their ectomycorrhizal network and thus to manage stress induced by climate warming (see also Chen *et al.*, 2016). Here, the 'Acclimation axis' demonstrates a helpful descriptor for root plasticity in the face of environmental change, with trade-offs along the axis potentially explained by species and fungal partnerships (Fig. 1).

The potential of the third dimension of the root economic space to explain regulation in root exudation, thus rhizosphere C fluxes, has globally relevant implications. The next critical challenge will involve scaling these findings from a two-species factorial experiment to entire forest ecosystems for predictive climate and earth systems modelling (McCormack *et al.*, 2017). Globally, SER varies across woody vs nonwoody species types, increases significantly towards lower latitudes, interacts with mycorrhizal symbioses, and is moderated to a large degree by phosphorus availability – a nutrient that was not explicitly monitored by this study (Wen *et al.*, 2022; Han *et al.*, 2026). While SER reflects plasticity along the newly identified acclimation axis, macroscale predictions of soil C storage can be incorrectly obscured or amplified by concurrent adjustments in whole-stand fine root biomass (Muratore *et al.*). If a warming-stressed forest curtails individual root exudation in a trade-off with root biomass and root surface area for nutrient acquisition, the net C input to the soil may remain static or even increase (Heinzle *et al.*, 2023; Chari *et al.*, 2024). Therefore, a key challenge for earth systems modellers will be to decouple metabolic root responses from the physical volume of root biomass to prevent large miscalculations in soil priming or decomposition feedback loops.

The 'root economics space' model is widely accepted and represents global averages across a range of environments (Bergmann *et al.*, 2020). The additional acclimation axis identified in this study is limited to comparing two co-occurring temperate forest species, the ectomycorrhizal red oak comprising 52% of the stand basal area, and red maple comprising *c.* 22%. Future research could extend to how species fall along the third dimension of root economic space across multiple ecosystems. For example, a study on long-term warming in the Arctic tundra found that the root economic space is nuanced compared to the typical model, noting a need for more focus on traits of ericoid mycorrhizal and other fungal associations that do not dominate in forest stands (Hewitt *et al.*, 2024). As high-latitude soils store *c.* 50% of global soil carbon (Tamocai *et al.*, 2009), northerly

ecosystems will be critical to include in global estimates of soil carbon feedbacks.

This new study challenges the rhizosphere community to rethink how we quantify, sample, and understand the covariation of root traits. If genetically fixed, species-specific differences determine the structural dimensions of root economics space, it is the reactive regulation of SER and root tissue construction along the acclimation axis that charts root responses to environmental stressors. This research therefore implies a methodological call to quantify traits that cannot be observed under flatbed scanners, including quantifying root exudation relative to active root tip counts, branching orders, and fungal colonisation lengths. To scale up the predictive capacity of this newly identified third dimension, we must consider trade-offs between root biomass and SER, community composition, mycorrhizal symbioses, and the interactions between a changing climate and nutrient availability. In doing so, it will become possible to predict whether future forests will store C in structural tissues or burn it off as microbial fuel.

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