

Commentary

Trait–environment relationships are timescale dependent

Plant traits, which are the observable characteristics of plants, play a crucial role in governing how plants adapt to, and interact with, their surrounding environment. Back in the early 1970s, Mooney (1972) summarized how plants maintain carbon balance by adjusting physiological and biochemical traits in diverse environments. The early work by Mooney laid the foundation for modern trait-based ecology, where researchers use quantitative approaches to analyze and model trait–environment relationships across various spatial and temporal scales (Reich, 2014; Wright *et al.*, 2017). Over the past 50 years, legions of researchers have explored trait–environment relationships, from within species to among communities, toward the prediction of vegetation dynamics under a changing climate. The universality of trait–environment relationships across plant communities and spatial scales has been extensively studied by linking plant traits to environment normals (Kempainen *et al.*, 2021). Yet, the stability of trait–environment relationships over time, a critical dimension for future ecological projections, has never been explored systematically. In an article published in this issue of *New Phytologist*, Famiglietti *et al.* (2024; 2423–2434) show that trait–environment relationships are timescale dependent. They develop multiple linear regression models, linking global *in situ* trait measurements with local climate variables summarized across different timescales (hereafter referred to as the climate integration time). The findings reveal that leaf traits are primarily influenced by recent climate fluctuations, whereas wood density is more accurately predicted by historical climate conditions. This study highlights the diverse ways in which plants integrate environmental information to optimize their function in various ecological contexts.

‘The discovery of optimal climate integration time for trait–environment relationships is critical for future ecological projections and trait-based modeling.’

The physiological mechanism for timescale dependent trait–environment relationships

Understanding the role of timescale in shaping trait–environment relationships is critical for gaining insights into how plants respond to environmental changes, encompassing both short-term changes

and long-term evolutionary adaptations. Leaves serve as metabolically active tissues in plants, with chloroplasts driving the essential process of photosynthesis. The high cellular activity in leaves enables rapid turnover, allowing plants to respond swiftly to environmental changes by adjusting their leaf physiological properties and morphological structures (Lin *et al.*, 2021). Wood growth is an accumulative process in the form of annual rings that form over years and decades. Wood density from tree rings is a trait that integrates the environmental conditions a tree has experienced in corresponding years over its lifetime. It is also considered a valuable proxy for paleoclimatic reconstruction. Therefore, leaf traits provide a snapshot of recent conditions, while wood density carries a legacy of past climate signals. The analysis conducted by Famiglietti *et al.* highlights divergent trait memory timescales, which are intuitively obvious yet previously unquantified for plant leaves and wood (Fig. 1a). Like other plant organs, roots also have a life history in which they pass from birth to death. In comparison, the lifespan of roots varies dramatically with root orders. Fine roots, responsible for resource acquisition, may last only a few weeks, while coarse roots that play a crucial role in anchoring and supporting the plant can persist for years, or even the entire lifespan. Therefore, when quantifying root trait–environment relationships, it is crucial to consider the diverse timescales associated with roots of different orders.

Leaf and wood traits differ not only in their timescale dependence, but also in the strength of their relationships with the environment. A recent study provided evidence supporting the results by Famiglietti *et al.* that wood density is more challenging to predict solely by environmental factors (Wieczynski *et al.*, 2019). The global distribution of plant traits is predominantly influenced by evolutionary history, which shapes the legacy of traits in lineages. Simultaneously, environmental filtering plays a crucial role by selecting traits that confer advantages in specific ecological contexts (Cui *et al.*, 2023). However, in current trait–environment modeling, the role of phylogenetic relationships remains unexplored. In summary, the challenge in predicting long-term memory traits may stem from the complexity of disentangling evolutionary influences from contemporary environmental effects.

Remaining confounding factors affecting trait–environment relationships

Predicting traits from the environment can be challenging due to the complexity and multifaceted nature of the interactions between organisms and their environments. In addition to trait-specific climate integration times, several other factors contribute to the difficulty of making accurate predictions. First of all, the mechanisms through which environmental changes drive trait variation fundamentally differ at different organizational levels

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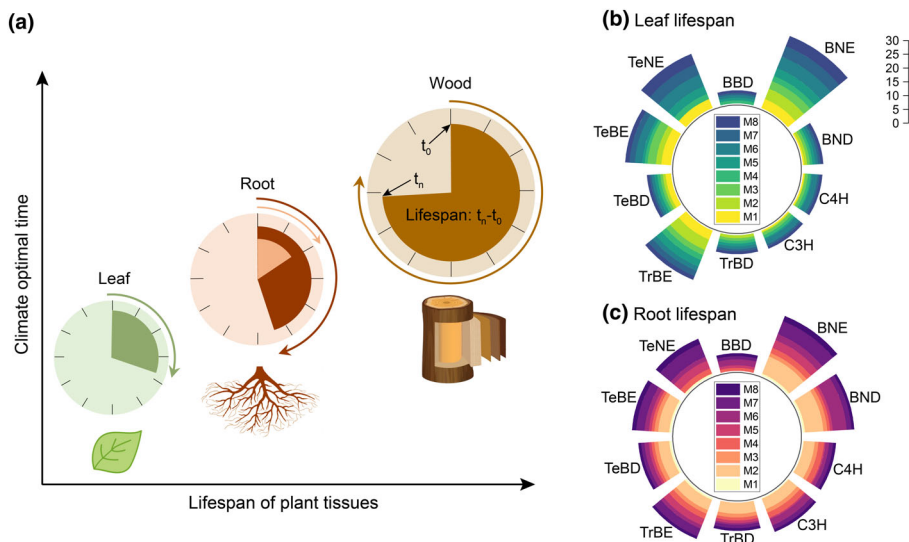


Fig. 1 Lifespan of different plant tissues and their representation in current vegetation demographic models. (a) Schematic of plant tissue lifespans and their interactions with the surrounding environment at different timescales. (b, c) Plant tissue lifespans of different plant functional types in eight vegetation demographic models. These models are color-coded and designated as M1 (CABLE-POP), M2 (JULES), M3 (LPJ-GUESS), M4 (LPJmL), M5 (ORCHIDEE), M6 (SEIB-DGVM), M7 (BiomeE), and M8 (CLM-FATES). Plant functional type classification: BND, boreal needle-leaved deciduous; BNE, boreal needle-leaved deciduous; BDD, boreal broadleaved deciduous; TeNE, temperate needle-leaved evergreen; TeBE, temperate broadleaved evergreen; TeBD, temperate broadleaved deciduous; TrBE, tropical broadleaved evergreen; TrBD, tropical broadleaved deciduous; C3H, C3 herb; C4H, C4 herb. Note that model parameters of models M1–M6 are obtained from Pugh *et al.* (2020).

(Anderegg, 2023). Trait–environment relationships are related to phenotypic plasticity within species, where a single species can express different traits in different environmental conditions. Trait–environment relationships across species likely result from interspecific differences in adaptation to environmental conditions. The community’s ability to adapt to changing environmental conditions relies on species turnover along environmental gradients and intraspecific trait plasticity. The complexity of community dynamics makes it challenging to identify clear and consistent trait–environment relationships. Consequently, community trait–environment relationships are typically less stable and weaker than among-species and within-species relationships. Second, some environmental factors may only influence traits above or below certain threshold levels. Failure to consider threshold effects may result in weak observed relationships when the impact of an environmental factor is nonlinear (Luo *et al.*, 1998; Poorter *et al.*, 2019). Finally, plants respond to a multitude of environmental factors simultaneously, and these factors can leave distinct legacy effects even on the same trait. Recognizing the challenges of considering the timescale dependence of different environmental factors and traits, the study by Famiglietti *et al.* proposes a uniform integration time of < 10 yr in developing trait–environment relationships.

Implications for trait-based modeling

In Earth system models (ESMs), plant traits are important parameters that contribute to the simulation of ecosystem structure and function. Leaf traits play a significant role in driving photosynthetic processes, while wood density is linked to individual mortality dynamics. There are two generations of vegetation models within the ESMs: big leaf models and vegetation demographic models. Big leaf models generally simplify the representation of vegetation at each grid cell as a single leaf that is characterized by a fixed set of plant functional traits (Cui *et al.*, 2019). Vegetation demographic models simulate plant

recruitment, growth, mortality, and competition processes for individual plant or size-based cohort, and the corresponding vegetation structure and distribution emerge from plant functional traits and their interactions with abiotic environmental conditions (Fisher *et al.*, 2018). Recently, plant trait diversity and trait environmental plasticity have been shown to be critical for predicting ecosystem resilience under climate change (Sakschewski *et al.*, 2016). Therefore, integrating the trait–environment relationship into vegetation demographic models provides an opportunity for more realistic and accurate simulations of the feedback between vegetation and climate. Yet, one challenge of recent efforts is the stability of such relationships over time. The trait-specific optimal climate integration times identified by Famiglietti *et al.* are salient to modeling efforts. The discovery of optimal climate integration time for trait–environment relationships is critical for future ecological projections and trait-based modeling.

The findings by Famiglietti *et al.* prompt us to revisit the expression of plant tissue lifespans in ESMs, which serves as a crucial basis for incorporating timescales into the construction of trait–environment relationships. Leaf and fine root lifespans are typically governed by phenological longevity parameters in models. However, most of the models do not explicitly incorporate root structure and function. Instead, they often focus on leaf phenology and implicitly assume the same timing between above- and belowground activity (Warren *et al.*, 2015). The development of models with demographic processes provides a good opportunity to characterize leaf and root phenology. Based on plant tissue lifespans from eight vegetation demographic models, the simulated leaf lifespan was relatively comparable among models, while there is a 10-fold difference in fine root lifespan (Fig. 1b,c). Large inter-model difference in parameterizing root phenology is attributed to an incomplete understanding of the physical processes that initiate root birth and death. In comparison, the longevity or persistence of a plant’s woody parts is connected to the turnover of vegetation biomass due to mortality processes. Pugh *et al.* (2020) documented

woody turnover times among six of the above models, with durations varying from 15.1 to 49.9 yr. The variations in turnover time among models primarily arise from their diverse mortality processes. These processes encompass factors such as vitality, disturbance, background mortality, heat stress, and other bioclimatic limits. Efforts to resolve uncertainty in plant tissue lifespans, and thus their impacts on establishing trait–environment relationships, will need to address both the representation of belowground processes and plant mortality that drives vegetation demography in current models.

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