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Commentary

Ecological theory matters when linking plant functional traits and ecosystem carbon cycles

Erqian Cui*

Research Center for Global Change and Ecological Forecasting, Zhejiang Tiantong Forest Ecosystem National Observation and Research Station, School of Ecological and Environmental Sciences, Institute of Eco-Chongming, East China Normal University, Shanghai 200241, China

*Corresponding author. E-mail: eqcui@des.ecnu.edu.cn, online publication July 17, 2025

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This article is a commentary on Shao Junjiong, Zhou Xuhui, Zhou Lingyan, *et al.* (2025) Plant biomass-leaf area allometry and ambient plant traits predict biomass responses to global warming. *J Plant Ecol* 18: rtaf029. https://doi.org/10.1093/jpe/rtaf029

Plant functional traits are powerful tools to understand ecological processes at multiple scales, from individual performance to ecosystem functioning (Lavorel and Garnier 2002; Reich 2012; Violle *et al.* 2007). During the prevalence of trait-based ecology, numerous studies have reported strong linkages between plant traits and ecosystem processes, e.g. leaf economic traits driving ecosystem productivity (He *et al.* 2023), litter quality traits regulating decomposition rate (Wu *et al.* 2025), hydraulic traits influencing drought-induced mortality (Choat *et al.* 2018) and plant height correlating with carbon sequestration (Quan *et al.* 2024). However, a recent study based on 41 plant traits and 42 ecosystem properties in grassland ecosystems states that plant functional traits are poor predictors of ecosystem functioning (van der Plas *et al.* 2020). Another study revisiting the above synthesis argues that when mechanistic linkages between plant traits and ecosystem properties are carefully considered, plant traits should have stronger predictive power (Hagan *et al.* 2023). Therefore, it still remains controversial whether plant functional traits are useful for understanding and predicting ecological functions.

Shao *et al.* (2025) demonstrate a linkage between plant biomass–leaf area allometry and whole-plant biomass, grounded in metabolic scaling theory and functional equilibrium theory. Their analysis reveals that a universal allometric relationship explains 58% of the variance in plant biomass responses to warming across all studied species. More remarkably, the incorporation of ambient plant traits significantly improves predictive performance, increasing the explained variance from 58% to 81%. This study highlights the necessity of incorporating plant traits for better predicting the ecosystem carbon cycle in a changing world. Building upon these findings, this commentary synthesizes major advances and challenges in trait-based prediction of the ecosystem carbon cycle.

TRACING THE KEY TRAITS THAT DETERMINE ECOSYSTEM CARBON CYCLE

The findings of Shao *et al.* (2025) partially align with the emerging consensus that the rational trait selection is critical not only for predicting but, more fundamentally, for understanding ecosystem functions (Hagan *et al.* 2023; Liu *et al.* 2021). In the case of carbon cycling, all ecosystem types share several fundamental processes, including photosynthetic carbon assimilation, allocation to plant organs and leaf area development, carbon transfer among ecosystem pools

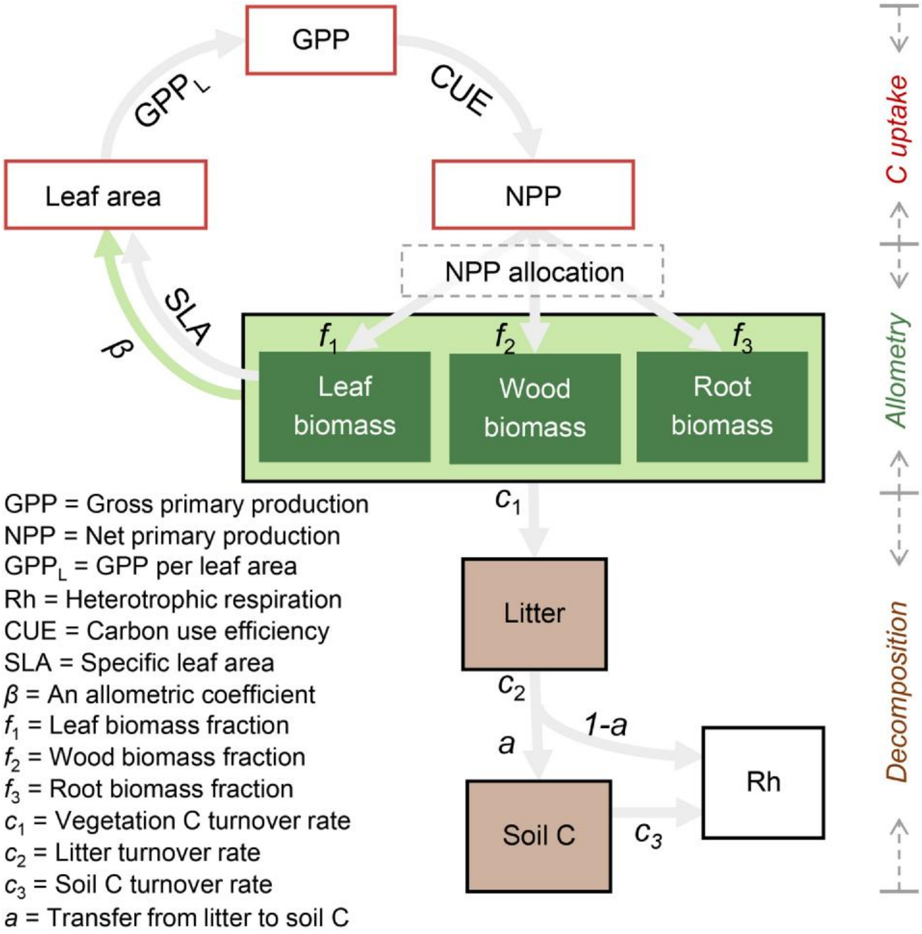

Figure 1: The conceptual framework tracing the influence of plant functional traits on ecosystem carbon cycle. Note that f_1–f_3 represent the biomass fraction of leaf, wood and root. c_1 is the aggregated vegetation carbon turnover rate over leaf, wood and root.

and organic matter decomposition (Luo *et al.* 2015). They are connected in a feedback loop by incorporating a set of functional traits (Cui *et al.* 2019). Therefore, we can construct a universal traceability framework to identify the traceable plant traits that determine the ecosystem carbon cycle (Fig. 1). For example, changes in plant biomass can be directly transmitted to leaf area and the allometric coefficient of the plant biomass–leaf area relationship. The allometric coefficient can be further mathematically decomposed into specific leaf area (SLA) and leaf biomass fraction (f_1). These properties together constrain the response of plant biomass to environmental changes. The global synthesis by Shao *et al.* (2025) confirms the strong predictive potential of allometric relationships and related traits (SLA and f_1) for plant biomass responses to warming. Their findings support the effectiveness of the traceability framework in tracking predictable traits.

TRAIT-BASED CARBON CYCLE MODELLING

The observed effects of plant traits on ecosystem functioning raise another important challenge of how to quantify functional composition and diversity of a given community (Ricotta and Moretti 2011). The mass ratio hypothesis holds that ecosystem functions are mainly determined by the functional traits of dominant species in the community. Therefore, Garnier *et al.* (2004) proposed summarizing the functional composition of single traits by using community-weighted mean trait value. The niche complementarity hypothesis suggests the combination of functionally different species drives ecosystem functions through niche partitioning, biotic feedbacks or facilitation. Thus, Villéger *et al.* (2008) proposed a number of indices (e.g. functional richness, functional evenness and functional divergence) to quantify

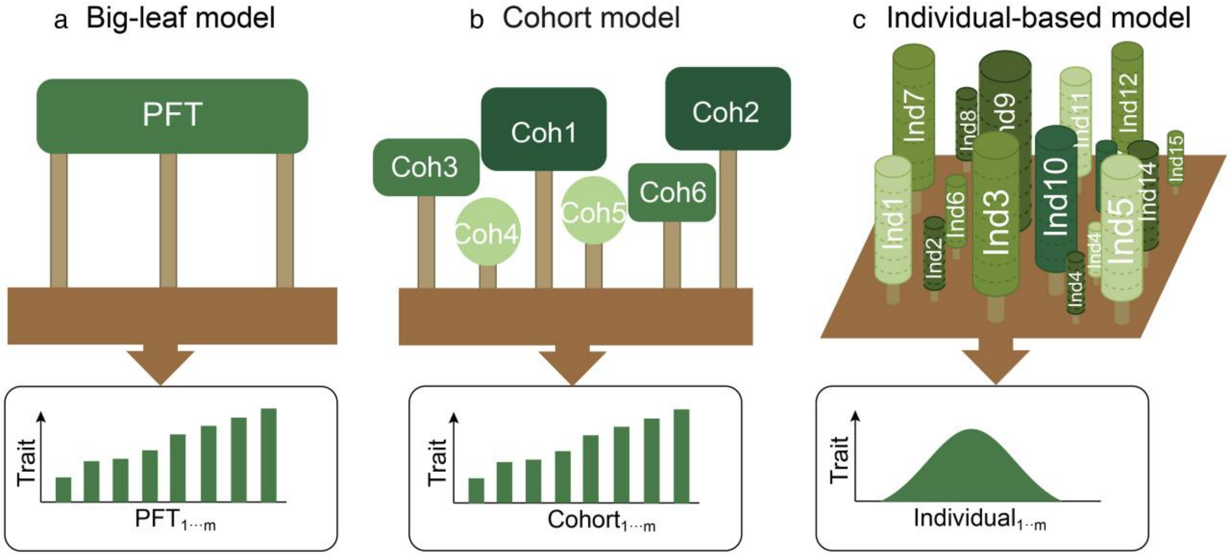

Figure 2: Parameterization of key plant functional traits in different dynamic global vegetation models. (a) In big-leaf models, the basic simulation unit is the plant functional type with a fixed set of functional traits. (b) In cohort models, each plant functional type is further divided into multiple cohorts with different disturbance histories. (c) Individual-based models simulate the establishment, growth, competition and mortality of individual trees and grasses with flexible trait combinations.

functional diversity of a community. Recent advances have shown that functional diversity plays a crucial role in shaping carbon pools and fluxes in ecosystems (Bongers *et al.* 2021; Díaz and Cabido 2001; Sobral *et al.* 2023). It is important to incorporate these two trait dimensions into a unified framework as they describe two complementary aspects of the relationship between plant traits and the carbon cycle.

Plant functional traits are increasingly being used to develop dynamic global vegetation models to improve the representation of vegetation patterns and associated biogeochemical cycles. Based on the way plants aggregate, there are currently three important modelling families (Fig. 2; Fisher *et al.* 2018). Big-leaf models (e.g. CLM and CABLE) typically simplify complex communities into a single leaf that is characterized by a fixed set of plant functional traits. Cohort-based models (e.g. CLM-FATES and LPJ-GUESS) aggregate plant individuals into cohorts represented by several functional types and size classes. Finally, individual-based models (e.g. SEIB and LPJmL-FIT) allow each individual in space to have a unique combination of trait values, and the resource competition scheme among individuals is explicitly simulated. The first two modelling families approximately follow the mass ratio hypothesis and are widely used in Earth system models. Individual-based models implement ideas derived from coexistence theory and community assembly theory and incorporate functional diversity in the representation of vegetation dynamics (Scheiter *et al.* 2013). However, the implementation of the individual-based model requires the introduction of a vast amount of observational data and stochastic processes, posing huge challenges to its application on a global scale. In comparison, the cohort model is an ideal model that strikes a balance between structural simplification and mechanistic integrity. Therefore, the integration of functional diversity into the cohort models is a critical step towards improving the prediction of carbon cycle changes driven by biodiversity.

PLANT TRAIT–ECOSYSTEM FUNCTION LINKAGES ARE CONTEXT DEPENDENT

When linking plant traits and ecosystem function, it is essential to recognize that plant functional traits are dynamic predictors of ecosystem function. As Shao *et al.* (2025) found in their global synthesis, the warming-induced changes in allometric coefficients are occasionally contrary to the expectations of metabolic scaling theory or functional equilibrium theory. A plausible explanation lies in the foundational assumption of most ecological theories that plants are optimally adapted to their native habitats. However, plants' adaptive responses generally fail to keep pace with the rapid pace of climate change. For example, in a matter of months to a few years, physiological traits associated with photosynthetic rate strongly drive biomass production, whereas decadal-scale ecosystem dynamics become increasingly governed by bottom-up resource limitation (Reich *et al.* 2018). Based on the world's largest biodiversity experiment in subtropical China, Bongers *et al.* (2021) demonstrated that as stand age increased, the explanatory power of functional diversity for productivity gradually exceeded that of community-weighted mean trait values. These findings suggest that the best trait predictors of ecosystem functions may differ substantially between short-term and long-term timescales.

Additionally, while existing research predominantly emphasizes the central role of biotic mechanisms in driving ecosystem function, growing empirical evidence reveals that environmental factors mediate the predictive power of functional traits (Huxley *et al.* 2023). Extensive empirical evidence indicates that mass ratio effects predominantly govern ecosystem productivity in high-resource/low-stress environments, whereas niche complementarity effects gain prominence under resource-limited/high-stress conditions (da Costa *et al.* 2025; Wang *et al.* 2013). Furthermore, conventional trait–function relationships may break down under extreme climate events, limiting the effectiveness of trait-based predictive models. These findings highlight the need to investigate temporal variability in trait-based predictions for a better understanding of ecosystem responses to climate change.

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