

Commentary

Catching up with the trees: empirical advancements to improve herbaceous representation in models

Ecosystems dominated by herbaceous vegetation (i.e. nonwoody species) represent *c.* 40% of the terrestrial land surface on Earth (White *et al.*, 2000), facilitate large quantities of carbon sequestration (reviewed by Bai & Cotrufo, 2022), and provide much of the food production for humans (O'Mara, 2012). Many of these ecosystems are currently in danger of being lost due to global change drivers, shrub encroachment, and calls for afforestation (Bond *et al.*, 2019). Yet, our predictive understanding of these systems is limited, which can be seen from high levels of uncertainty in modeled future carbon (C) storage of these systems (e.g. fig. 3 in McGuire *et al.*, 2018). This is in part due to a limited understanding of the first principles driving the growth and demographic processes of herbaceous species. In this issue of *New Phytologist*, Curasi *et al.* (2023; pp. 562–575) provide an important understanding for a dominant tussock-forming sedge, *Eriophorum vaginatum*, within Arctic tundra ecosystems. The authors integrated measurements from over 2300 individual tussocks, across a range of environmental characteristics, and time since disturbance into a population and mass balance model. This enabled them to provide specific estimates of how long it takes for these tussock individuals to reach maximal size, which is on the order of decades (40–50 yr in their population model), and the specific physical, structural, and demographic mechanisms driving these patterns. These findings are not only relevant for Arctic tundra but also for a variety of ecosystems where tussock-forming species (e.g. bunchgrasses) are dominant contributors to ecosystem function (Fig. 1a–d). For example, the long-lived nature of *E. vaginatum* is found in other herbaceous ecosystems, such as *Nassella* spp. tussocks estimated to live more than 100 yr in Californian (USA) grasslands (Hamilton *et al.*, 2002), and estimates of tussock longevity of *Sesleria albicans* exceeding 110 yr in European grasslands (Janišová & Gömöry, 2007). Historically, predictive scientific disciplines such as ecological modeling have largely focused on tree-dominated ecosystems, yet the insights gained by Curasi *et al.*, highlight the need to recognize the long-lived and dynamic

nature of tussock-forming species to promote our predictive capacity for these important herbaceous ecosystems.

Their study found that the volume of E. vaginatum tussocks are best described as a cylinder, which provides an important alternative to the current model representation of herbaceous growth.

Process-based models are tools that can be used to translate mechanistic understanding of physical and biotic processes to predictions of future states of ecosystems under novel conditions. This has importance for the future of ecosystem services (e.g. C sequestration) and even the entire Earth system. There exists a suite of different models that are designed to represent various types of vegetation (i.e. plant functional types) and allow for competition for light, water, and nutrients (e.g. ED2, FATES, LPJ-GUESS, and TEM-DVM, among many others; see review by Fisher *et al.*, 2018). Many of these models are linked to land surface models that simulate biogeochemical cycles such as C inputs and losses and ultimately can scale up to simulate the entire Earth system. These models enable us to make predictions about how vegetation types will change in the future and what the system-wide impacts of these changes will be. Yet, the predictive capacity of most process-based models for herbaceous ecosystems lags substantially behind that of forested ecosystems. One consequence of this lag is that we do not currently understand the full ramifications of losing herbaceous ecosystems, which is critical for evaluating the long-term effects of replacing these systems with forests (*sensu* Bastin *et al.*, 2019).

Many current vegetation models represent herbaceous plant functional types as either a uniform continuous layer at ground level (the 'green blanket' or 'green slime' schematic), or as small trees. In the former representation, competition for light among herbaceous vegetation does not occur. In the latter representation, the diameter of individual stems is used along with allometric parameters to calculate leaf and canopy area, which is subsequently used to influence photosynthetic C uptake and plant growth. Although this formulation works relatively well to represent growth and competition among trees, it does not capture the biological characteristics of many herbaceous species, including tussock-forming species. For example, as Curasi *et al.*, showed, growth of tussock-forming individuals is determined by production, maintenance, and mortality of new stems or tillers, as well as the individual performance of tillers throughout the growing season. These components are in turn driven by a variety of ecological processes, including competition for water and nutrients below-ground, and competition for light above-ground. Even models that

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Fig. 1 (a–d) Pictures of dominant tussock-forming graminoids, (a) *Eriophorum vaginatum* in North American Arctic tundra (photo credit: A. Rocha), (b) *Paspalum quadrifarium* in South American Pampas grassland (photo credit: L. Yahdjian), (c) *Megathyrsus maximus* (formerly *Panicum maximum*) in a South African savanna grassland, and (d) *Schizachyrium scoparium* in a North American tallgrass prairie. (e) A model of tussock-forming grasses based on basal and canopy diameters, heights, and volumetric vegetation density estimated for all tussock-forming individuals in a 4.5 m × 4.5 m plot in a savanna grassland in Kruger National Park, South Africa. The colored cones represent tussocks, with green representing *M. maximus*, gold representing *Urochloa mosambicensis*, and blue representing *Bothriochloa radicans*. The transparency of cones signifies the volumetric vegetation density estimated for each tussock. For scale, the yellow cylinder in the top right corner is 1 m tall. The plot was created using the RGL package (Murdoch & Adler, 2023) in R (R Core Team, 2022).

include more sophisticated representation of tussock plant functional types (e.g. TEM-DVM; Euskirchen *et al.*, 2009; aDGVM, Scheiter & Higgins, 2009) still do not represent competition for light among herbaceous groups of species. This is not due to a lack of desire to better represent herbaceous plant functional types in these models, nor is it for lack of studies focused on the biology of these herbaceous species. Rather, it is largely because the empirical understanding of ecological processes defining growth, competition, and spread of herbaceous species is not in a form readily incorporated into these models. For example, abundant empirical evidence suggests that eutrophication in herbaceous ecosystems results in biodiversity declines and increased dominance by weedy, fast-growing species. However, the mechanisms behind these responses are unclear; some research suggests

nutrient addition causes fast-growing species to outcompete other species for light early in the growing season (DeMalach & Kadmon, 2017), while other research suggests that colimitation by multiple resources is alleviated under eutrophication, which releases plants with high-resource-use strategies to dominate the ecosystem (Harpole *et al.*, 2017). Furthermore, these studies do not link their findings to measured rates of nutrient uptake or to growth rates, which makes incorporating these findings into process-based models challenging.

Tussock-forming species are critical components of many ecosystems, including the Alaskan Arctic tundra, South American Cerrado, North American tallgrass prairie, and African savannas (Fig. 1a–d). Investigations like those here (Curasi *et al.*) should be conducted in other herbaceous ecosystems to facilitate better

representation of these systems into process-based models. Their study found that the volume of *E. vaginatum* tussocks is best described as a cylinder, which provides an important alternative to the current model representation of herbaceous growth. Using this cylinder or inverted cone allometric approach would allow models to simulate new tillers being produced and 'packed' into a tussock (see the useful hexagonal packing schematic in Curasi *et al.*), which could then be converted to changes in tussock size, canopy extent, and total leaf area. This is an important alternative to the current determination of herbaceous canopies within many models, which take stem diameter and use allometric equations to scale up to canopy and total leaf area (Lawrence *et al.*, 2018). Due to links with total leaf area within canopies, understanding these allometric relationships becomes important for a variety of model functions such as C assimilation and albedo.

In many herbaceous ecosystems, multiple different tussock-forming species compete with one another for light, nutrients, and water. For example, my team and I measured three different bunchgrasses within a 4.5 m by 4.5 m area within an African savanna describing basal area, canopy area, proportional coverage, tiller number, and vegetative height. The overlapping canopies and variation in height structure revealed by these measurements point to the potential for strong light competition among these different species. In Fig. 1(e), I converted these measurements to a 3D model to show how dynamic vegetation models might represent competition among these different species. In the savanna ecosystem where these measurements were taken, the outcome of competition among different tussock-forming species is nontrivial, as they provide varying degrees of ecosystem stabilization under ecological perturbations such as herbivory (Koerner *et al.*, 2014), drought (Wilcox *et al.*, 2020a), and fire (Bond & Archibald, 2003).

An additional piece of information that would assist the ready incorporation into vegetation models is the allometric relationships between tussock volume and total leaf area to drive modeled canopy photosynthesis. This information could then be combined with information about photosynthetic parameters (e.g. V_{cmax} & J_{max} ; Schedlbauer *et al.*, 2018) to improve the representation of tussock plant functional traits in models (Wullschlegel *et al.*, 2014), thus decreasing the uncertainty surrounding responses of herbaceous ecosystems to climate change scenarios.

Overall, I contend that more studies like Curasi *et al.*, be conducted in a variety of herbaceous ecosystem types and that herbaceous demographic data be linked with abiotic mechanisms such as water availability, nutrient availability, and canopy light interception. A key to enhance predictive capacity of herbaceous ecosystems is to ensure the empirical data collected are ready to be used within predictive tools, such as process-based models. As such, collaborations between modelers and empiricists are crucial (Wilcox *et al.*, 2020b; Kyker-Snowman *et al.*, 2022). Additionally, efforts should not be limited to tussock-forming herbaceous species; similar studies could expand to address rhizomatous graminoids and forbs, annual species, mat-forming species, and even mosses. Until we improve the predictive capacity for these types of species and ecosystems, we will be severely limited with respect to how to move forward with solutions to the climate change crisis.

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