INVITED REVIEW

Accounting for herbaceous communities in process-based models will advance our understanding of "grassy" ecosystems

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Abstract

Grassland and other herbaceous communities cover significant portions of Earth's terrestrial surface and provide many critical services, such as carbon sequestration, wildlife habitat, and food production. Forecasts of global change impacts on these

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services will require predictive tools, such as process-based dynamic vegetation models. Yet, model representation of herbaceous communities and ecosystems lags substantially behind that of tree communities and forests. The limited representation of herbaceous communities within models arises from two important knowledge gaps: first, our empirical understanding of the principles governing herbaceous vegetation dynamics is either incomplete or does not provide mechanistic information necessary to drive herbaceous community processes with models; second, current model structure and parameterization of grass and other herbaceous plant functional types limits the ability of models to predict outcomes of competition and growth for herbaceous vegetation. In this review, we provide direction for addressing these gaps by: (1) presenting a brief history of how vegetation dynamics have been developed and incorporated into earth system models, (2) reporting on a model simulation activity to evaluate current model capability to represent herbaceous vegetation dynamics and ecosystem function, and (3) detailing several ecological properties and phenomena that should be a focus for both empiricists and modelers to improve representation of herbaceous vegetation in models. Together, empiricists and modelers can improve representation of herbaceous ecosystem processes within models. In so doing, we will greatly enhance our ability to forecast future states of the earth system, which is of high importance given the rapid rate of environmental change on our planet.

KEYWORDS
biogeochemistry, ecology, ecophysiology, plant competition, plant growth, process-based models, vegetation demographic models

1 | INTRODUCTION

Herbaceous and grass-dominated ecosystems are critical components of Earth's land surface (Faber-Langendoen et al., 2016), occupying a large proportion of Earth's ice-free terrestrial surface (Dixon et al., 2014; White et al., 2000) and providing many important ecosystem services such as carbon sequestration, livestock grazing, and wildlife habitat (Bai & Cotrufo, 2022; Gibson, 2009). Examples of these "grassy" ecosystems are grasslands, shrublands, tundra, open tree savannas, and woodlands. Human impacts, such as land use change, suppression or ignition of fire, and climate change, are changing herbaceous ecosystems rapidly (e.g., Bowd et al., 2018; Dieleman, 2016; Harrison, 2020; Komatsu et al., 2019; Myers-Smith & Hik, 2018). Such changes not only alter local and regional ecosystem functioning provided by these ecosystems (Smith et al., 2009), but they may also feed back to the climate system to impact ecosystem processes and services beyond their geographical boundaries (Cook et al., 2009; Zhou et al., 2019). To capture this broad range of ecosystem changes and their impacts on human and climate systems, it is necessary to develop and improve models that provide detailed representations of herbaceous ecosystem processes. With these models, it is also possible to evaluate mechanisms underlying ecological patterns at scales that are difficult to measure empirically (e.g., Luo & Reynolds, 1999; Walker et al., 2015), and to make predictions

for novel environmental conditions without the need for spatial extrapolation (Evans et al., 2013). This is particularly important as global change and human demand for natural resources are pushing many herbaceous ecosystems beyond historical boundaries (Alexander et al., 2015; Easterling et al., 2000; IPBES, 2019; IPCC, 2021; Wang et al., 2022).

Herbaceous plant communities can be significantly transformed by climate change, including shifts in dominance from one herbaceous species to another (Collins et al., 2020) or replacement by other plant functional types (e.g., shrubs; Collins et al., 2021; D'Odorico et al., 2012). Herbaceous plant community dynamics have been shown empirically to depend on the type, magnitude, and duration of global change drivers (Komatsu et al., 2019). In some cases, punctuated variability in environmental conditions (e.g., extreme climatic events, pulse events sensu Lake, 2000) may drive temporary shifts in plant community composition (Figure 1a); alternatively, monotonic shifts in the environment (e.g., increased average rainfall, press events) are more likely to result in altered coexistence dynamics (Van Dyke et al., 2022) and directional change in plant community composition (Figure 1b; Smith et al., 2015). These community changes may have additive or multiplicative consequences for ecosystem function (Smith et al., 2009; Suding et al., 2008). Experimental and observational studies have shown effects of herbaceous community change on soil biogeochemical cycling (Hobbie, 1996; Kardol et al., 2010; Sundqvist, 2011; Williams & Vries, 2020; Xu et al., 2015),
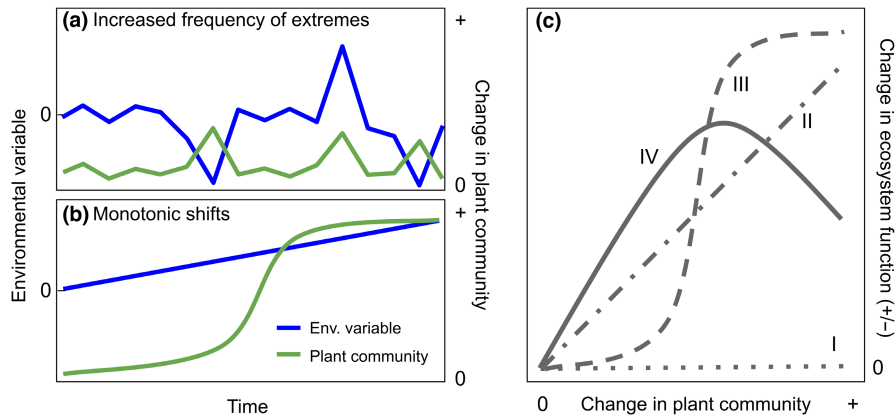
FIGURE 1 Conceptualized changes in environmental variables and plant community composition under two different components of global change: (a) increased frequency of extreme events, and (b) monotonic changes in the environment. (c) Hypothesized and observed relationships between changes in plant communities and their effects on ecosystem function responses to environmental factors. Different scenarios are based on hypotheses and findings from the literature: I no change in function despite change in community—Wilcox, Koerner, et al., 2020; Wilcox, Komatsu, et al., 2020; II linear change in function with altered community—Wilcox et al. (2016), III threshold change in function—Briske et al. (2006), Smith et al. (2009); IV unimodal or oscillating change in function—Langley and Hungate (2014). Changes in plant communities and ecosystem function will likely vary widely depending on site-level characteristics, the type of existing vegetation present, and the ecosystem functions being assessed.

net primary productivity (Shi et al., 2018; Wilcox et al., 2016), carbon sequestration (Petrie et al., 2015), abundance and diversity of other trophic levels (Hartley & Jones, 2003; Scharfy et al., 2010; Stevens et al., 2018), and changes in surface albedo and evapotranspiration (Chapin et al., 2005; Scott & Sudmeyer, 1993; Tang et al., 2020). Given that shifts in plant community composition and structure can have a range of effects on ecosystem function (Figure 1c; Langley & Hungate, 2014; Polley et al., 2014; Shaw et al., 2022), improved forecasting capability is needed to represent ecosystem functioning more effectively as plant community composition changes in response to global environmental change. Additionally, we posit that better representation of herbaceous community dynamics will improve our ability to use first principles to model distributions of herbaceous vegetation, which is currently limited (Griffith et al., 2015; Still et al., 2019).

Here, we address the above challenges and provide a way forward for both model development and empirical research for improving herbaceous representation in land surface and earth system models (LSMs and ESMs, respectively). More specifically, we: (1) Provide a brief history of how herbaceous vegetation dynamics have been represented in process-based models, which offers the necessary background for the discussion of current knowledge gaps and future improvements. (2) Report on a model simulation exercise where we compared modeled plant community change and aboveground net primary productivity (ANPP) to observations from a long-term water addition experiment in a US tallgrass prairie. This was done to assess current model capabilities to simulate herbaceous community dynamics and resulting effects on ecosystem function. (3) Identify herbaceous properties and ecological processes important for accurately simulating herbaceous vegetation dynamics. In so doing, we hope to provide general approaches for modelers and empiricists to work together toward a better understanding and more predictive

model representation of herbaceous plant community and ecosystem dynamics.

2 | REPRESENTATION OF HERBACEOUS PLANT COMMUNITY DYNAMICS IN MODELS: A BRIEF HISTORY

There has been a rich history of using process-based models to simulate and predict vegetation dynamics and their effects on ecosystem functioning. Dynamic global vegetation models (hereafter DGVMs) are gridded, process-based ecosystem models that represent the biophysics, biogeochemistry, and biogeography of global vegetation and soil, with different models having substantial variation in capabilities, completeness, and approaches.

Because of their computational expense, and to be able to map vegetation with satellite observations, these models simplify vegetation diversity into a few major types to capture the dominant contributors to surface–atmosphere exchange and the carbon storage in biomass and soil carbon. Vegetation types are typically categorized into a limited selection of "plant functional types" (PFTs), on the order of 5–20 classes, distinguished variously by growth form (grass, shrub, tree), allometric relations, photosynthetic pathway (C_3, C_4), phenology (deciduous/evergreen, rain green, annual/perennial), leaf type (broadleaf, needleleaf), and climate range (e.g., arctic, temperate, tropical; reviews by Argles et al., 2022; Fisher et al., 2018; Prentice et al., 2007). Each PFT's physiology and structure is characterized by unique sets of values for large parameter sets that allow different PFTs to independently respond to environmental drivers and compete for light and soil resources in different ways from one another. DGVMs do not simulate individual plants, but there is a range of model complexity in representation of plant cover, including

"big leaf" models where the entire canopy is represented as a single leaf, mosaicked plant cover to roughly capture coexistence of PFTs in the same grid cell, multi-layer canopies of single PFTs, and most recently communities of vertically stratified mixed PFTs to allow relative cover of PFTs or mixed community structure to shift in response to environmental drivers.

When linked to ESMs, which couple land, ocean, and an atmospheric general circulation model (GCM), DGVMs can simulate feedbacks between the land surface and climate and serve as a component in the full carbon cycle. Such coupling can allow investigation of such questions as long-term vegetation–climate feedbacks under climate change, the impacts of episodic climate extremes on vegetation dynamics, as well as how vegetation change alters ecosystem functions, such as carbon and water cycling (e.g., Sitch et al., 2008).

Representation of size-structured competition in mixed communities for above- and belowground resources has only recently been introduced in a few DGVMs (see review by Fisher et al., 2018). We refer to earlier DGVMs that lack size-structured communities as "first-generation DGVMs", to differentiate them from the newer mixed community models, often referred to as "demographic DGVMs" or "vegetation demographic models" (VDMs) that represent individuals or cohorts of plants within PFTs. Gap models—a type of VDM—are not global in scale but were used to investigate individual forest dynamics by explicit representation of different sized individual plants able to compete for light and other resources (Bugmann, 2001; Mladenoff, 2004), driving canopy growth and shifts in species composition and community structure. Gap models are computationally expensive and must be parameterized to represent species-level interactions and community dynamics at a specific site (Botkin et al., 1972; Pacala et al., 1996; Shugart et al., 1992, 2018). Theoretical constructs have been developed to bridge the first-generation DGVMs and gap models, such as the ecosystem demography (ED) model (Moorcroft et al., 2001) and the perfect plasticity approximation model (Strigul et al., 2008). They group similar individuals into cohorts to simulate succession dynamics, but with different schemes for modeling crown organization and height-structured light competition. These theories have been applied singly or together within land models (e.g., Geophysical Fluid Dynamics Laboratory [GFDL] Land Model 4.0. (Martínez Cano et al., 2020; Weng et al., 2015; Zhao et al., 2018), functionally assembled terrestrial ecosystem simulator (FATES; Fisher et al., 2015; Koven et al., 2020), and robust ecosystem demography (RED, Argles et al., 2020). By incorporating these theories that allow for finer scale groupings than simple PFTs while keeping model complexity low, land models can offer a more computationally efficient approach for representing size-based competition and compositional succession that are intermediate between the first-generation DGVMs and gap models.

Model development on community dynamics has primarily been for forests, while herbaceous ecosystems have received less attention (Detto et al., 2022; Pacala et al., 1993; Shugart et al., 1992; Wilcox, Koerner, et al., 2020). However, there has been relatively recent progress in representing herbaceous ecosystems within DGVMs. First, Euskirchen et al. (2014) improved phenology of four arctic PFTs (heath tundra, tussock tundra, wet sedge tundra, and shrub tundra) using TEM-DVM (Euskirchen et al., 2009), which had substantial ramifications for projections of C fluxes in the arctic. Second, Scheiter and Higgins (2009) describe the adaptive dynamic global vegetation model (aDGVM) which uses an individual-based framework to improve representation of tree–grass dynamics in fire adapted savannas. This model supports two general PFTs, one for trees and one for grasses. Within the tree PFT, individual trees are simulated where C allocation and phenology of each tree vary with environmental conditions. Within the grass PFT, two "super-individuals" are simulated to represent grass between and under tree canopies. Scheiter et al. (2013) added trait filtering to the model to create aDGVM2, allowing for distributions of functional traits to be assigned among individuals. Third, Boone et al. (2018) used components from CENTURY (Parton et al., 1993) and SAVANNA (Coughenour, 1992) models to create G-Range. G-Range incorporates two herbaceous vegetation types and implements a schematic for herbivory. These important forays into improving representation of herbaceous components within models can be built upon (Fitz & Trimble, 2006; Oleson et al., 2004) as we find ways to relieve constraints in computational ability and advance our understanding of the ecophysiological, morphological, and demographic mechanisms driving herbaceous plant communities.

Many models only representing two to three natural herbaceous PFTs (e.g., C_3, C_4, and sometimes C_3 arctic grasses, Table 1), which limits the ability of these models to predict herbaceous community shifts. For comparison, there are 11 woody PFTs in the Community Land Model 5.0 (Lawrence et al., 2019). If groups of herbaceous vegetation types respond differently to biotic and abiotic drivers, then overly coarse PFTs for herbaceous vegetation may be part of the reason for difficulties in modeling distributions of C_3 versus C_4 vegetation (Fox et al., 2018; Still et al., 2019) or forest–grassland boundaries (Poulter et al., 2011). For example, two different and globally abundant C_4 grass lineages, Andropogoneae and Chloridoideae, have substantially different climatic envelopes and fire return intervals where they exist, and the Chloridoideae distribution overlaps with many C_3 lineages (Lehmann et al., 2019). It follows that a single C_4 PFT may limit the ability of the model to accurately predict where the boundaries of C_4 plants exist (Griffith et al., 2020). How many and the types of herbaceous PFTs to add is an open question that needs further research. We approach this subject more fully in Section 4.

These model weaknesses in representation of herbaceous plant form, function, and diversity are apparent in current DGVMs' inability to reproduce globally observed herbaceous community changes that are having strong effects on ecosystem function. For example, most vegetation models do not differentiate annual grasses from typical C_3 or C_4 grass PFTs. Yet, invasive annual grasses have expanded across large portions of the United States due to their annual life cycle and impacts on fire regimes (McArthur et al., 1990; Smith et al., 2022). This expansion has caused declines of other herbaceous functional types leading to loss of forage for grazing animals, a critical function of many herbaceous systems (Bartolome

TABLE 1 Descriptions of models used in the simulation exercise.

Model type	Model name	Herbaceous PFT (base)	PFT parameter complexity[a]	Key processes	Plant competition	Best use in herbaceous systems
Ecosystem model	TECO[b]	None	None	Photosynthesis, plant growth, C cycling, water budget, N cycling	NA	C dynamics at single sites
First-generation DGVM	sDGVM[c]	C3, C4 grasses	**	Photosynthesis, plant growth, C cycling, water budget, plant demographic processes, PFT competition for resources	Water (no competitive exclusion, or PFT gains)	Site-scale to global-scale C dynamics
Vegetation demographic Model	BiomeE[d]	C3, C4 grasses	*	Photosynthesis, plant growth, C cycling, water budget, N cycle, energy budget, plant demographic processes, PFT competition for resources	Light, water, N	Predicting community composition (presence/absence) and (age/size, abundance) structure and competitive strategy at site scale
Vegetation demographic Model	LPJ-GUESS[e]	C3, C4 grasses	***	Photosynthesis, plant growth, C cycling, water budget, plant mortality, plant demographic processes, PFT competition for resources	Light and water	Site scale to global scale C dynamics pays attention to community dynamics-species range shifts

[a]Complexity of parameterization specifically of plant functional groups or cohorts ranging from low (*), moderate (**), and high (***) number of parameters.

[b] Weng and Luo (2008).

[c] Woodward et al. (1995).

[d] Weng et al. (2022).

[e] Smith et al. (2013).

et al., 2013), altered net primary productivity and carbon cycling (Koteen et al., 2011; Ogle et al., 2003), and heightened sensitivity to environmental drivers (Munson et al., 2013). These consequences likely stem from characteristics of annual grasses such as high growth rates and rapid nutrient uptake (Leffler et al., 2013), early phenological cycles (Ogle et al., 2003), shallow rooting depth and water use (Koteen et al., 2011), and low root density (Hulbert, 1955). In sum, we posit that current limitations in model representation of herbaceous communities may preclude our ability to forecast the full effects of both monotonic environmental shifts and increased frequency of extremes on ecosystem function in grassy ecosystems (Figure 1).

3 | COMPARING MODEL SIMULATIONS TO OBSERVATIONS OF HERBACEOUS COMMUNITY DYNAMICS AND ECOSYSTEM FUNCTION

To demonstrate current capabilities in modeling herbaceous ecosystems, we selected four different process-based models that vary in their representation of community change from no community representation to VDMs (Table 1). These models were used to simulate a long-term irrigation experiment at a US tallgrass prairie (Konza Prairie Biological Station) following a standardized simulation protocol (Appendix S1). Specifically, we were interested in how model output under a monotonic increase in water availability matched up to experimental findings of (1) herbaceous plant community change and (2) ANPP before and after the plant community change.

When the irrigation experiment began in 1991, a single C_4 perennial rhizomatous grass species, *Andropogon gerardii*, comprised ca. 60% of the plant canopy coverage. *Andropogon gerardii* largely retained dominance in both the control (mean annual precipitation: 847 mm) and water addition (mean annual precipitation + water addition: 1108 mm) plots over the first 10 years of the experiment (Collins et al., 2012). The persistence of *A. gerardii* during this time was likely due to inertia exerted by the clonal nature of the species, such that replacement by more mesic species only occurred after slow infiltration into the rooting and tillering zone of the grassland. While *A. gerardii* was the dominant species at the site, the effect of water addition on ecosystem function (ANPP) was relatively consistent, increasing ANPP by an average of 49% compared with control plots (Knapp et al., 2012). Around 10 years into the experiment, cover of *Panicum virgatum* (another C_4 perennial rhizomatous grass) increased substantially in the irrigated plots, becoming the new dominant species for the following 10 years of the experiment (Wilcox et al., 2016). This species shift was accompanied by a more than doubling of the effect of water addition on ANPP in the irrigated plots, from a 49% to 140% increase in ANPP caused by irrigation (Knapp et al., 2012; Wilcox et al., 2016). Further details about experimental implementation, measurements, and additional findings can be found in Collins et al. (2012).

To simulate the Konza irrigation experiment, we used meteorological forcing data, environmental information (e.g., soil texture), and functional traits for *A. gerardii* and *P. virgatum* (collated from author measurements [Table S1] and TRY; Kattge et al., 2020) to calibrate and operate four models (Table 1) from 1991 to 2012. The goal was to evaluate the models' ability to simulate the community shift and accompanying changes in ANPP (see Appendix S1 for additional details about simulation protocol). For these simulations, two PFTs were parameterized based on empirical information about functional traits for *A. gerardii* and *P. virgatum* (Table S1) and models were tuned to match observations from non-irrigated plots (i.e., controls). This led to slightly different starting PFT abundances among models when irrigated simulations began (Figure 2a).

To aid interpretation of results from model simulations, we assessed model performance with regards to both the change in composition (represented by responses of two PFTs designed to represent *A. gerardii* and *P. virgatum*) and ANPP. Comparable observations from the irrigated plots were available for both metrics.

3.1 | PFT dynamics

We evaluated whether the models were able to simulate both the direction and magnitude of plant compositional shifts observed in the short term (years 1–10) or long term (years 11–20). The criteria for whether models were able to simulate plant compositional dynamics were as follows: *Direction*—did the model estimate dominance by the correct species found in observations (years 1–10: *A. gerardii*, years 11–20 *P. virgatum*)? *Magnitude*—did the model represent the magnitude of PFT change relative to starting conditions?—this would result in coexistence by both species. The three models with capacity to simulate composition shifts (i.e., SDGVM, BiomeE, LPJ-GUESS) matched observed trends in at least one of these areas, yet no models matched observed trends in all categories (Figure 2a,b).

BiomeE was able to match observed trends in the short term but struggled to capture the long-term community dynamics. The model matched observations for the first 10 years of the experiment (i.e., greater abundance of *A. gerardii* than *P. virgatum*), but potentially for the wrong reasons. Whereas the model simulated dominance of *A. gerardii* PFT in the short term, it was not due to slow rates of displacement of *A. gerardii*, but because parameters of the *P. virgatum* PFT were not sufficient to ever allow for displacement of the initial dominant species, *A. gerardii*. Instead, the empirical explanation for the slow turnover of plant community was likely because *P. virgatum* spreads relatively slowly via clonal growth when plant competitors are present (Hartnett, 1993), which leads to lagged responses of species abundances during monotonic shifts in environmental conditions (Collins et al., 2012).

SDGVM was able to capture both the direction and magnitude of PFT change in the long term but failed to do so in the short term. This is again likely due to a mismatch between the time frames of changes in plant abundance in models versus observations. SDGVM represented the *P. virgatum* PFT as competitively
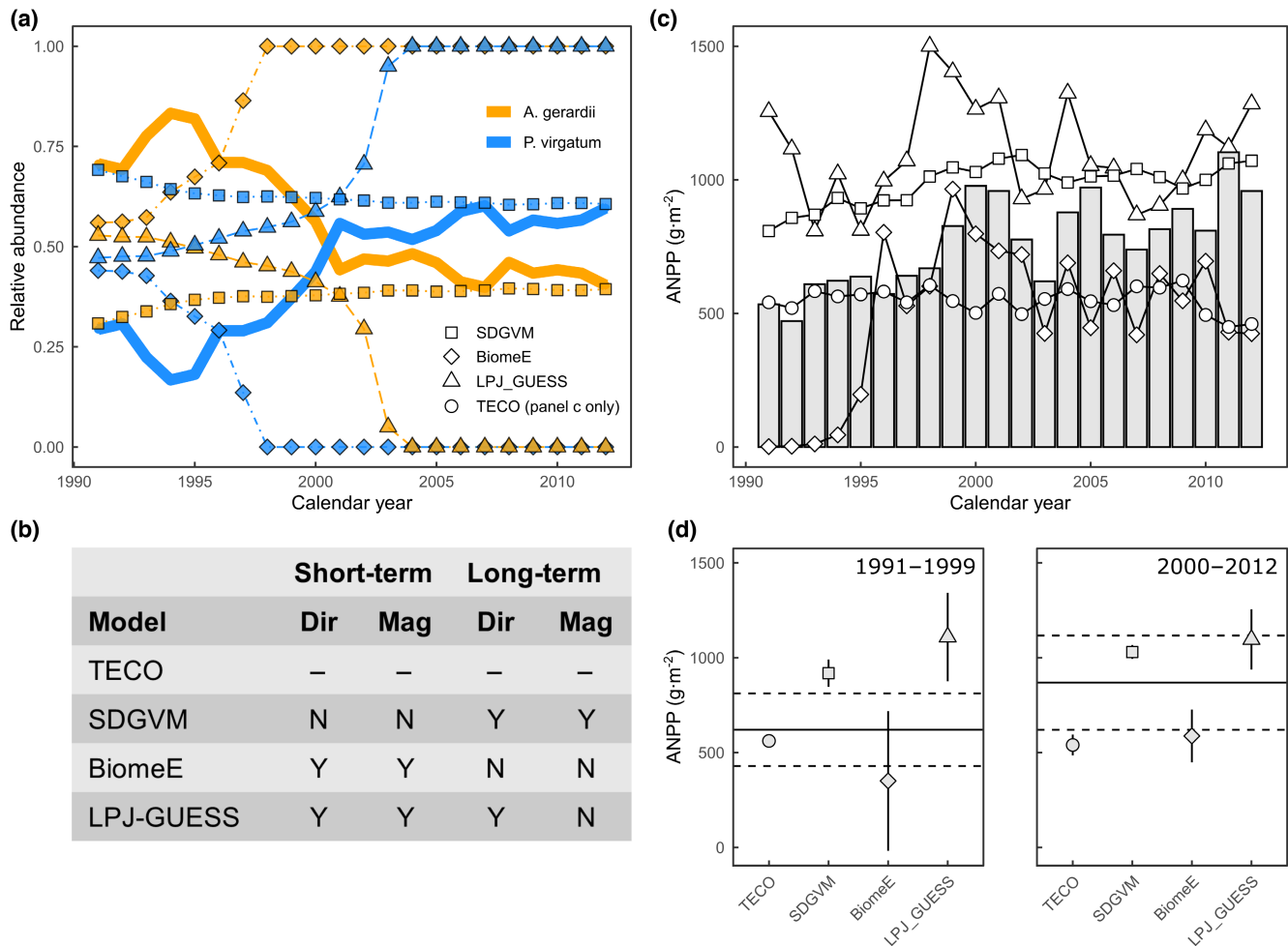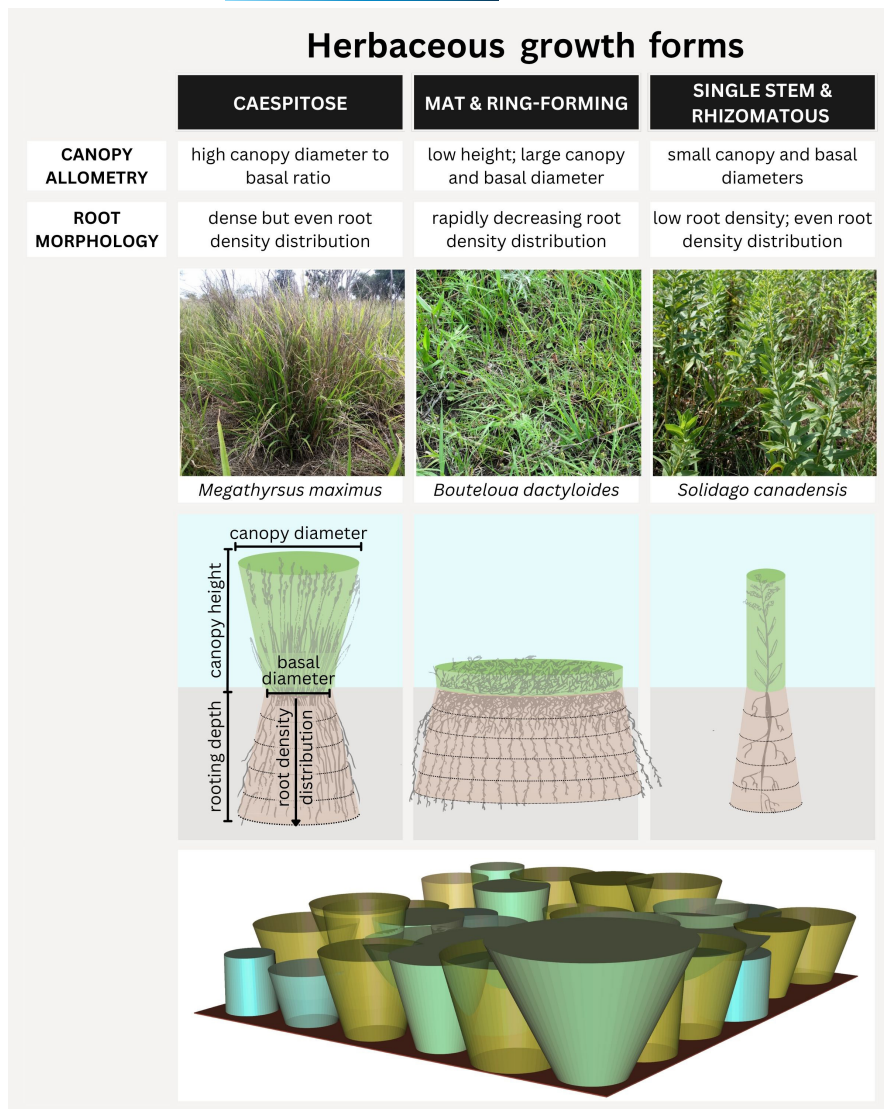
FIGURE 2 Quantitative assessment comparing observations from irrigated plots within a long-term irrigation experiment in tallgrass prairie to model simulations from a variety of process-based models. (a) Observed relative abundance of two C4 grass species (thick lines) is compared with model PFTs (symbols and lines) designed to represent these two species. (b) Authors' interpretation of the ability of each model to capture the directionality (dir) and magnitude (mag) of community shifts in the short term (1991–1999) and long term (2000–2012). Only models that simulate PFTs are included in (a) and (b). (c) Aboveground net primary productivity (ANPP) observations (grey bars) and model simulations (symbols, see panel c for legend of symbol shapes) over the course of the irrigation experiment. (d) Average simulated ANPP over the short term (1991–1999) and long term (2000–2012) of irrigated grassland. Horizontal lines represent the mean (solid) and 1 SD intervals (dashed) of the observed ANPP during each time period. Error bars on symbols represent 1 SD of the simulations through time.

superior to the *A. gerardii* PFT under irrigated conditions and was even able to represent coexistence in the long term. However, in the model this change happened within the first year of irrigation while observation suggests that plant competition between these two species should take much longer. This occurrence may present difficulties when trying to represent pulses of water availability (i.e., wet years) since models would predict full plant community change in a single year.

LPJ-GUESS was able to represent all but the magnitude of long-term community change. However, this was only after a modification was made to the model. Initially, relatively wet conditions throughout the growing season and higher growth potential of *P. virgatum* facilitated competitive exclusion even under non-irrigated conditions. LPJ-GUESS was then modified to allow for greater percolation rates overall and when the shallow soil layer (0–50 cm) was at field capacity. This created drier conditions overall without

irrigation and provided *A. gerardii* an advantage due to its greater root density in shallow soil layers (Table S1). Then under irrigation, deeper soil layers became chronically wetter, which allowed for *P. virgatum* growth to increase and reduce the abundance of the *A. gerardii* PFT, eventually excluding it from the community. Calibration of LPJ-GUESS points to the importance of properly representing water physics and rooting densities with depth when representing herbaceous systems.

Aboveground net primary productivity dynamics—Interestingly, only the model agnostic to community change (TECO) matched short-term ANPP simulations to observed values, yet predictably the model was unable to simulate the increased ANPP trend observed in years 11–20 (Figure 3c,d). Similarly, BiomeE under-projected ANPP in the long term, likely due to dominance of the *A. gerardii* PFT from years 11 to –20 in its simulations (Figure 3a). Conversely, because SDGVM and LPJ-GUESS successfully simulated the shift to

Herbaceous growth forms

	CAESPITOSE	MAT & RING-FORMING	SINGLE STEM & RHIZOMATOUS
CANOPY ALLOMETRY	high canopy diameter to basal ratio	low height; large canopy and basal diameter	small canopy and basal diameters
ROOT MORPHOLOGY	dense but even root density distribution	rapidly decreasing root density distribution	low root density; even root density distribution
	Megathyrsus maximus	*Bouteloua dactyloides*	*Solidago canadensis*

FIGURE 3 Top: Allometric descriptions of three potential shapes for herbaceous PFTs to be incorporated in vegetation models. The artist depictions of the shapes in the bottom row are inspired from illustrations of US prairie plant species by Weaver (1954). Bottom: 3-D model created from measurements from a 4.5×4.5 m plot in a South African savanna describing the following measurements of three different bunchgrass species: basal and canopy diameters, vegetation height, and volumetric bunch density (transparency). The yellow cylinder on the right is 1 m tall for scale. The 3D model is adapted from Wilcox (2023).

dominance by *P. virgatum* in years 11–20, they were better at capturing long-term ANPP dynamics (Figure 3c,d). Yet, both SDGVM and LPJ-GUESS over-projected ANPP during year 1–10 because the simulated PFT shift occurred within 1–2 years, which failed to capture the inertia of the current PFT.

This simulation exercise teaches us two major things with respect to modeling herbaceous community changes and ecosystem responses under global change scenarios. First, the exercise highlights the importance of capturing herbaceous plant community change to accurately represent temporal trends of ecosystem function (sensu Knapp et al., 2012), especially in systems that have dynamic plant communities. Second, to capture both increased variability and monotonic global change (Figure 1), we must both improve our empirical understanding of the mechanisms driving plant community shifts and incorporate this understanding into representations of herbaceous vegetation in models. It is not surprising that the models were unable to simulate all aspects of the community and ANPP patterns shown here, since we still do not fully understand the mechanisms responsible for these empirical patterns. Enhancing this understanding should be a primary goal

for empiricists and modelers alike to better represent herbaceous ecological processes in models.

4 | DIRECTIONS FORWARD: THE INTEGRATION OF EMPIRICAL UNDERSTANDING AND MODEL REPRESENTATION FOR KEY HERBACEOUS COMMUNITY PROCESSES

Based on our review of the model development history and the simulation exercise above, we suggest that current model representations of herbaceous communities and their dynamics, and the effects of community change on ecosystem function are still relatively limited. While several excellent texts have described many of the potential drivers of processes that structure herbaceous communities (Keddy & Laughlin, 2021; Mittelbach & McGill, 2019; Morin, 2009; Tilman, 2020), many of these drivers are either not used by models or are not in forms readily usable by process-based models. For example, we know from empirical studies that nitrogen addition

in many herbaceous ecosystems reduces the abundance of native perennial species and species that form relationships with nitrogen fixing symbionts (Suding et al., 2005). A proposed mechanism for this phenomenon is that nitrogen addition often causes taller, fast-growing (i.e. "weedy") species to increase in abundance, which reduces light penetration and causes reduction or elimination of shorter statured or slower growing species (Dickson et al., 2014). To represent the tradeoff between light and nutrient competition, we need to better understand nitrogen-fixation rates for native perennial vegetation (Taylor et al., 2020) as well as specific morphological, ecophysiological, and phenological information (Table 2) about how and why these tall fast-growing species perform well under nitrogen addition (i.e., lower root:shoot ratios, higher photosynthetic rates, earlier phenology). On the modeling side, we need to further develop model structure to allow for nitrogen fixation at different rates or at least allow for nitrogen uptake rates that implicitly represent these processes without necessarily linking to root production and distribution. Additionally, finer PFT groupings for herbaceous vegetation would be necessary to represent these types of community shifts. Although challenging, we content that improving herbaceous representation of processes such as these will enhance the predictive capacity for a large component of the Earth's terrestrial surface under future global change scenarios.

In the remainder of this review, we suggest numerous ways forward for improving model treatment of grassy ecosystems. However, it is important to note that the complexity, structure, and parameterization needed within models will vary substantially across projects. Ultimately, the improvements and level of detail required will depend on the specific objectives of particular modeling endeavors. Individual researchers or research teams can use data to parameterize models to address specific questions, but the underlying model structure is needed to enable this parameterization. For example, in our simulation above, representation of the slow (10 years) replacement of the rhizomatous C_4 perennial grass *A. gerardii* by the other C_4 perennial grass *P. virgatum* was likely limited by the seed-based reproduction scheme in vegetation models. So, although incorporating multiple C_4 perennial rhizomatous PFTs may not be feasible or advisable for researchers focused on, for example, global estimates of carbon sequestration under altered water availability, if the functionality of slow spreading clonal species is readily available in VDMs, this functionality can be leveraged for more site-level research questions.

In Table 2, we provide a summary of some key empirical needs for better representation of the diverse herbaceous plant functions and competitive strategies within models. Then below, we work through several aspects of herbaceous growth and competition where additional research would enhance predictive capacity of herbaceous dynamics within models. These include structural growth of herbaceous plants, uptake and competition for water and nutrients, vegetation dispersal and spatial dynamics, and fire and grazing regimes. In each section, we outline how current models represent these processes, current gaps in model representation, current empirical understanding of these processes, and finally, directions forward for both empiricists and modelers.

4.1 | Structural growth and reproduction of herbaceous plants

In vegetation models, herbaceous plants may form part of a closed understory or canopy, or open and undifferentiated canopy. For plant growth, most models use allometric relationships between stem diameter, leaf mass, and canopy area to convert leaf carbon to total leaf area and individual canopy area to the community canopy cover. These derived variables are then important drivers of various other model processes.

From empirical work, we know that many herbaceous plants have dense canopies and competition for light can drive numerous ecological processes (Dickson et al., 2014; Eskelinen et al., 2022). In addition, herbaceous plants exhibit multiple distinct growth forms, which affect their response to environmental conditions and their potential representation in models. Forb and grass species grow either as a single stem or as clones forming bunches, tufts (i.e., caespitose), or as rhizomatous spreaders forming mats of stems (Figure 3, Luong et al., 2021). These different growth forms may result in substantially differential effects of fire (Zomer & Ramsay, 2021), herbivory (Díaz et al., 2007), and drought (Luo et al., 2018). Further research into the generality of these effects within and across herbaceous growth forms will be important for determining how many and which PFTs to represent in model simulations.

A major challenge in representing herbaceous vegetation is that allometric equations between stem diameter and plant canopy or total leaf area often do not apply for forb and grass species (Johnson et al., 1988). Recently, work has been undertaken to relate basal crown area of caespitose bunchgrasses to canopy area, with relative success (X. Gao unpublished data). This is different from trees in that crown area of bunchgrasses is composed of many individual stems, which are packed into the crown in particular ways (Curasi et al., 2023). Using this allometric relationship to scale to canopy area and ultimately total leaf area also means that the model would use crown area as a proxy for stem diameter, and this introduces new challenges such as incorporating relationships of crown area with water and nutrient flow. As such, additional allometric relationships such as crown area to total stem area could be particularly useful to optimize both the canopy formation and hydraulic components of modeling grasses (Table 2).

Allometric relationships have previously been developed for herbaceous ecosystems, and these techniques could be leveraged to aid in better representation of different herbaceous growth forms. For example, Muldavin et al. (2008) used volume measurements linked with aboveground biomass to create robust allometric relationships, and then used multiple time points per growing season to estimate ANPP. An important consideration with these types of relationships for inclusion into models is how they relate to canopy cover and total leaf area since this will impact how these different groups influence and respond to light. The need for multi-layer canopies has been shown for forests (Bonan et al., 2021), yet we contend based on empirical evidence showing strong light competition among individual species (Eskelinen et al., 2022), that multi-layer

TABLE 2 Empirical needs for better incorporation of community shifts into process-based models.

Empirical needs	Model function	Need[a] (*, **, ***)	Ease[b] (*, **, ***)	Process relevance[c]
Allometry parameters—hand measurements, fixed point photos, aerial photography	Used within the plant growth module to determine leaf mass, stem mass, leaf area, and crown area relationships. Important for light interception and competition. Reproduction investment is also important for demographic processes	**	*	sg, vd
Leaf growth/turnover/senescence—hand measurements or phenology cameras	Used to benchmark and calibrate plant growth and LAI relationships. Important for numerous processes including resource and light limitation. Also can be used in conjunction with soil and meteorological time series to build relationships of phenology with soil moisture, temperature, and day length	**	**	sg, b
A/Ci curves, stomatal slope and minimum—photosynthesis system instrument	Max rates of carboxylation (V_{cmax}) and electron transport (J_{max}), stomatal conductance (g_0, g_1) are key parameters in photosynthetic and stomatal processes, particularly important for plant responses to water limitation	***	*	w
Soil moisture—near continuous and at multiple depths using instruments with data loggers	Can be used to drive water uptake in model. Also may be used in data assimilation or calibration/benchmarking of water physics processes	***	***	w, b
Rooting profile—isotopes and/or root cores by depth	Controls water uptake at different soil depths and decomposition rates.	**	Isotopes* Cores**	w, n
Leaf water potential—measured using pressure chamber at times of high and low water availability	Determines water stress of plants and can be used in conjunction with soil moisture to assess plant tolerance to water limitation. Can be used to calibrate other parameters within the model	**	**	w, b
Hydraulic leaf and stem traits—leaf pressure chamber or vapor pressure osmometer	Turgor loss point (ψ_{TLP}), osmotic potential at full turgor (ψ_{osm}), leaf capacitance (C_{leaf}), and leaf water potential at 50% of stem conductivity (P_{50}) are parameters used within hydraulic schematics to determine photosynthetic rates within models	**	**	w
Leaf dry matter content—leaf collection and basic laboratory measurements	Could be incorporated into hydraulics models as a proxy for other hydraulic parameters. Could be linked with tradeoffs in growth rate	*	***	w, n
Leaching losses—lysimeter	Parameter that regulates water and nutrient balance. Especially important for models that use stoichiometric balance to drive nutrient movement (e.g., Rastetter et al., 2022)	**	*	w, n
Stoichiometry of roots, shoots, and litter—average and variation of C:N:P	Determines nutrient limitation and uptake within models. Can be used to inform parameters associated with nutrient cycling	***	***	n
Root turnover	Direct parameters important for carbon and nutrient cycling	***	**	n
Mycorrhizal status	Will directly alter nutrient and water uptake rates regardless of root abundance and root traits	**	**	n
Soil N availability—soil resin bags/strips or incubations	Used to calibrate N cycle parameters	**	Resin*** incub.*	n, b
N fixation presence and rates—isotopes or ARAs	Parameter that controls additional source of nitrogen inputs	**	Isotopes* ARAs*	n

TABLE 2 (Continued)

Empirical needs	Model function	Need[a] (*, **, ***)	Ease[b] (*, **, ***)	Process relevance[c]
Success rates and energy costs of different types of reproduction—measurements of seed and ramet characteristics	Used to determine the rate of increase in PFTs. Also, this would be important in future developments of dispersal limitations for PFT spatial spread.	**	**	vd, sg
Carbon mass/storage in the rhizome—pool of carbon and turnover rate measured using non-structural carbohydrate assays	Benchmark non-structural carbohydrate storage for different plant functional groups	**	*	d, w
C and N allocation to defense compounds	Not yet implemented parameters that reduce mortality or leaf and stem loss due to herbivory	**	*	d
Soil pH	Informs parameters regulating soil carbon decomposition	*	***	b

[a]Need column indicates general importance of the data type for improving representation of herbaceous processes within models. * indicates lesser need, ** moderate need, *** greatest need.

[b]Ease column indicates the difficulty of collecting the suggested measurements with * indicating difficult, time consuming, and/or expensive measurements, ** moderately difficult, time consuming, or expensive measurements, and *** indicating easy, quick, and/or inexpensive measurements.

[c]Column describes the most relevant model processes that the measurements may inform. The entries in this column match up with sections below: sg = Structural growth of herbaceous plants, w = water uptake and competition, n = nutrient cycling and competition, vd = vegetation dispersal and spatial dynamics, d = fire and grazing regimes for herbaceous systems, b = benchmarking. Note that benchmarking is not a section below, but it is relevant for checking model simulations related to all the above ecological processes.

canopies are also important for herbaceous layers. To this end, we showcase a 3-D model visualizing empirical measurements of basal and canopy diameters, vegetative height, and volumetric density for three bunchgrass species within a $4.5 \times 4.5\,m$ plot in a South African savanna (Figure 3 bottom).

Reproduction strategy is another important consideration when modeling herbaceous ecosystems. Most models represent reproduction via seed, which ignores some key processes that can drive herbaceous community dynamics. For example, rhizomatous species, such as those in our simulations above (Ott & Hartnett, 2015), which limits the rate of spread in a single year. Contrasted with annual reproduction strategies, clonal growth by rhizomatous species results in slower rates of displacement of one species or functional group by another. The lack of this reproduction strategy within most vegetation models may be why our simulated community dynamics above (Figure 2) were far more rapid than observations. Also, less allocation to seed production and more to belowground carbon stores may be driving observations of herbaceous systems being able to persist during stressful conditions and to recover quickly after perturbations (Stuart-Haëntjens et al., 2018).

Belowground rooting morphology varies across species and herbaceous functional groups (Gibbens & Lenz, 2001; Weaver, 1958). Many grasses have fibrous roots occupying much of the top 30 cm of the soil profile (Jackson et al., 1996), while many forb species have branching roots that are less abundant in surface soil layers but extend deeper into the soil column (Sun et al., 1997). This has been shown to be a coexistence mechanism where grasses utilize shallow water sources during wet periods and forbs utilize deeper water sources during dry periods (Nippert & Knapp, 2007a; Ward et al., 2013). These dynamics similarly apply to interactions between woody and herbaceous plant groups (February et al., 2013; Scholes & Archer, 1997). There are also important differences in rooting morphology within functional groups. For example, rhizomatous grasses tend to have a coarse-grained foraging approach with a low density of larger roots, while caespitose grasses have been shown to have a high density of fine roots and can concentrate nutrients in the soils beneath their canopy (Derner & Briske, 1999; Weaver, 1954). This may also link to increased microbial biomass and activity under bunchgrasses (Vinton & Burke, 1995), which has implications for carbon respiration rates.

In accordance with previous calls for using morphological and structural characteristics to differentiate plant functional types within vegetation models (Wullschleger et al., 2014), we suggest starting by differentiating among caespitose/tussock-forming, mat-forming, and single-stem herbaceous vegetation groups. From there, these groups could be further differentiated where appropriate based on the research questions and region of inquiry. Additional splitting criteria could be by height (e.g., tall vs. short grasses—these are distinctly different plant groups in many grasslands), photosynthetic pathway (C_3, C_4, CAM), and reproductive strategy (e.g., annual, perennial).

Although we maintain that better representation of herbaceous PFTs is important for improving models, we also recognize the need for parsimony in assigning PFTs (Fisher & Koven, 2020). After all, representing every plant species on Earth is not computationally feasible. As such, a priority for future research is assessing how functionally similar or different various groupings of species are to one another so decisions can be made as to how many PFTs are needed to parsimoniously represent herbaceous ecosystems. Interesting research is currently underway focused on using plant lineages (Anderegg et al., 2022; Griffith et al., 2020; Lehmann et al., 2019), eco-evolutionary competition tradeoff strategies (Harrison et al., 2021), and gradients of functional traits (Butler et al., 2017) to explore the best ways to represent PFTs within models. Continued work on this frontier should provide insight into how finely we should split herbaceous vegetation groups within models. Yet regardless of the answer to this question, we still must provide understanding of the first principles that drive plant community dynamics to properly simulate vegetation responses to global change.

4.2 | Water uptake and competition for water

Models represent water dynamics and competition for water by simulating both biotic and physical processes. Water enters a system via rainfall and horizontal flow, and water exits the system via plant uptake and subsequent evapotranspiration as well as evaporation from the soil, overland flow, and leaching losses. Plant water stress is determined by a plant's ability to take up soil water and their rate of loss, which is controlled by water availability combined with stomatal conductance and associated parameters. Ultimately, plant growth is facilitated or hindered by water availability and cellular turgor pressure (Boyer & Potter, 1973; Hilty et al., 2021).

Water transport to various soil layers, overland runoff, and leaching losses are simulated within models using water physics components that incorporate information about soil texture (sometimes represented implicitly via field capacity and wilting point), soil moisture from previous time steps, and rates of precipitation inputs. Water uptake by plants is often resolved separately by soil layer and is a function of the amount of water in the soil layer and the quantity of roots in that soil layer. Total root production is a function of the amount of photosynthesis plants conduct, their maintenance costs, and their allocation strategies. Then, root proportion/density among different soil layers is determined using a parameter within an asymptotic relationship between cumulative root fraction and soil depth (Jackson et al., 1996), which can vary across PFTs in most DGVMs and VDMs (Lawrence et al., 2019). Recent efforts have focused on enhancing representation of hydrodynamics in process-based models (Christoffersen et al., 2016; Eller et al., 2020; Liu et al., 2021). These schematics typically use water potential gradients across the soil, plant organs, and the atmosphere along with hydraulic conductivity and vegetation parameters associated with

plant ability to tolerate water stress (e.g., leaf osmotic potential at 50% conductivity (P_{50}; Li et al., 2021).

Empirical evidence has shown that herbaceous plants utilize three primary strategies to contend with water limitation—drought tolerance, avoidance, and escape (Levitt, 1980; Ludlow, 1989; Ocheltree et al., 2020; Noy-Meir, 1973). Drought tolerance is the continued performance of plants despite water stress. Plants use multiple structural mechanisms to accomplish this, including having thick cell walls to regulate turgor pressure and avoid hydraulic failure (Marshall & Dumbroff, 1999; Ocheltree et al., 2016), regulating osmotic potential (Zhou & Yu, 2010), and stomatal control (McDowell et al., 2008). Often, plant traits such as P_{50} and leaf dry matter content (LDMC) are linked with drought resistance of grasses as well as phenology (Ocheltree et al., 2020). Fortunately, these strategies and parameters are becoming better represented within hydraulics schematics in models (Christoffersen et al., 2016; Eller et al., 2020). This means that empirical information directly describing herbaceous hydrodynamics, such as turgor loss point, leaf capacitance, and P_{50} can be easily incorporated into current versions of plant hydraulic schematics (Table 2). Incorporation of traits such as LDMC into models is more difficult because LDMC is only indirectly related to hydraulic characteristics and processes, being the ratio of the dry leaf mass to fully hydrated leaf mass. Yet LDMC integrates across a few important plant characteristics, such as the rigidity of cell walls, which influences turgor loss point. As such, incorporating LDMC into model hydraulic schematics could be an area for further inquiry.

Drought avoidance is when plants can access sources of water that allow for growth under drier conditions. A prime example of this drought response mechanism is when deeply rooted species persist under dry conditions while surrounding shallow fibrous-rooted grasses decline, which has been shown in a wide variety of ecosystems (Aroca et al., 2012; Báez et al., 2013; Nippert & Knapp, 2007b). Empirical findings have shown that water uptake from various locations in the soil is an important coexistence mechanism between deeply rooted (e.g., shrubs, forbs) and shallowly rooted plants (e.g., grasses; Ward et al., 2013). Nippert and Knapp (2007a) showed evidence that shrubs use deeper soil moisture only during times of water stress, which may necessitate modification of the simple schematic of water uptake in models that simulates water uptake as a function of soil moisture and root density by soil layer. However, additional empirical understanding should be gained about the generality of this depth switching phenomenon and moisture thresholds of when this occurs.

Drought escape is when plant growth occurs during times of greater water availability despite overall drier conditions, as with desert annuals (Venable, 2007). This process helps explains a long-standing conundrum associated with the historic drought in the United States during the 1920s (i.e., dustbowl; Schubert et al., 2004) where cool season grasses increased in abundance after the drought due to early-season growth strategies (Knapp et al., 2020). This community change was likely a combination of direct impacts on cool season species since most of the water availability was during the primary growth period of these species, and competitive release by

warm season species that were strongly water limited during their growth periods. Another example of drought escape is seed dormancy until environmental conditions support plant growth, which is often rapid (Chesson, 2000).

To move forward in modeling water dynamics for herbaceous systems (Hickler et al., 2006), we propose that hydraulic information be gathered (much of it already exists in the literature) for many species spanning different herbaceous growth forms, photosynthetic pathways, and reproductive strategies. The hydraulic infrastructure is rapidly being developed within many models (Chitra-Tarak et al., 2021; Powell et al., 2013), but this has primarily been for trees. Understanding how rooting distributions (density by depth), hydraulic conductance, stomatal conductance, and other hydraulic traits (Table 2) vary both within and across plant forms would greatly aid in developing reasonable and representative groupings for herbaceous species. Additionally, to improve the representation of drought escape, we suggest that ecophysiological information, such as stomatal conductance, could be linked with soil moisture, leaf growth, and turnover at relatively high frequency, especially during the early growing season when many cool season species complete their growth cycles (Table 2). To better represent annual species flushes in arid landscapes, thresholds for germination related to rainfall (e.g., Chávez et al., 2019), soil moisture, and temperature could be incorporated into plant growth components of models. Also, empirical information describing the respiration/maintenance costs during reproduction of annual plants could help models better represent rapid senescence events of annual-dominated ecosystems.

Improving representation of water dynamics in herbaceous ecosystems should be a high priority due to increasing frequency of precipitation extremes, such as the recent extreme droughts in the southwestern United States, large portions of Europe, and Kenya, and deluges occurring in the western United States. Additionally, climate model projections suggest that the current frequency of precipitation extremes will increase by ca. 30% by 2100 under medium emissions pathways (Thackeray et al., 2022) so predicting ecosystem function during and after these events will be critical for assessing future states of the earth system.

4.3 | Nutrient cycling and competition for nutrients

Incorporation of both nutrient supply and demand is key to representing nutrient constraints on ecosystem processes (Walker et al., 2015) and to allow for more flexible/dynamic ecosystem responses to nutrient availability. There are multiple ways in which different models represent nutrient dynamics. One approach is to use mass balance equations and stoichiometric information related to various soil and biotic pools to estimate nutrient pools and fluxes, such as the multiple element limitation model (Rastetter et al., 2022). The Plant Allocation and Reactive Transport Extensible Hypotheses (PARTEH; Knox et al., 2023) can model allocation of nutrients across different plant organs, building on plant nutrient demand, soil nutrient supply, storage, acquisition, and tissue

stoichiometry (ideal and minimal) for carbon, nitrogen, and phosphorus. In PARTEH, these within-plant nutrient dynamics interact with a soil biogeochemical module for nutrient acquisition to model nutrient uptake competition between plants and microbes (Zaehle et al., 2014). Yet these processes are often resolved on a coarse scale which precludes heterogeneity in nutrient availability within the unit (e.g., grid cell) where competition occurs. In CLM 5.0, there are multiple key parameters that control the uptake of nutrients, including a set of parameters controlling the energetic costs associated with mycorrhizal and non-mycorrhizal nutrient uptake (Brzostek et al., 2014), the fractional productivity of N-fixing plants, and the fine root mass per unit leaf mass (Lawrence et al., 2019). The interactive effects of nutrients (e.g., nitrogen) and other soil parameters are not represented in many models (e.g., N effects on soil pH, interactions among N, P, K, and micronutrients; Du et al., 2020).

Increasing nutrient availability generally increases primary productivity in many terrestrial ecosystems (Elser et al., 2007; Fay et al., 2015; Gruner et al., 2008), but typically reduces or eradicates certain species and groups of species (Avolio et al., 2014; Hillebrand et al., 2018; Komatsu et al., 2019; Yang et al., 2011). These effects have been demonstrated with both experimental nutrient additions (Harpole et al., 2016; Ladouceur et al., 2022; Seabloom et al., 2021) and anthropogenic N deposition (Bobbink et al., 2010; Simkin et al., 2016; Stevens et al., 2004, 2015). Multiple competitive dynamics among plant species may be at play in driving these responses to altered nutrient availability (Cleland & Harpole, 2010). Debate remains regarding the relative strength of the underlying mechanisms of competition with nutrient additions between the shifting of limiting factors to aboveground competition for light (DeMalach et al., 2017; Hautier et al., 2009, but see Eskelinen et al., 2022; Harpole et al., 2017) compared to reduced niche dimensionality belowground (Harpole & Tilman, 2007; Harpole et al., 2016). Furthermore, altered stoichiometric balance and plasticity of plants with increased nutrient availability can drive species and community responses (Tilman, 1981; Yu et al., 2011, 2015). For example, Yu et al. (2015) showed that plants with less plastic nutrient contents in their tissues tended to be more dominant in natural grasslands, but species with greater plasticity became dominant in nutrient-enriched grasslands. Although these findings show important patterns of nitrogen controls on herbaceous plant communities, the first principles driving these responses are still largely unknown.

Beyond direct competition, other biotic interactions can affect plant community responses to altered nutrient availability, including mutualisms with mycorrhizae and N-fixing bacteria (Tognetti et al., 2021). We know that associations with mycorrhizae are critical for many species' ability to take up nutrients (Van Der Heijden et al., 2008) and water (Smith & Read, 2008), and can drive coexistence in herbaceous communities (Stanescu & Maherali, 2017). Additionally, mycorrhizal colonization rates vary substantially among species (Wen et al., 2019) and functional groups (Unger et al., 2016). Plants that associate with N-fixing bacteria may be positively impacted by P additions (Hungria & Vargas, 2000), but negatively

impacted by N additions (Tognetti et al., 2021). These responses likely vary across species that range in N-fixing traits from facultative to obligate mutualists (Taylor et al., 2020). Other impacts on plant groups that associate with N-fixing bacteria include N-fixation limitation by drought (Serraj et al., 1999), although this effect may be alleviated by increased atmospheric CO_2 (Parvin et al., 2019). Fire has also been found to have positive effects on plants associated with N-fixing bacteria (Kerns & Day, 2018).

There are numerous avenues for advancement of nutrient competition and dynamics in vegetation models. One particularly important component for many herbaceous ecosystems is to increase our understanding of the drivers of N fixer abundance in the community. Sensitivity analyses show that fertilization effects within models are highly responsive to the proportion of N fixers within the community (Fisher et al., 2019), making this a high priority for research. Second, modeling work has shown that competition among PFTs based on root surface area creates a tradeoff between above- and belowground competition for light and nutrients (Weng et al., 2017, 2019), which should be explored further empirically. Third, associations with mycorrhizae and the variation in such associations could be better described for different PFTs—as such, information about mechanisms driving mycorrhizal association to increase or decrease, and implementation of these mechanisms within the nutrient cycle representations within models, would assist in providing better representations of eutrophication effects on ecosystems. Lastly, gathering information about aboveground–belowground tradeoffs among different herbaceous groups, and their ability to alter their allocations above- versus belowground, would allow for better parameterization of herbaceous PFTs in their acquisition of nutrients.

4.4 | Vegetation dispersal and spatial dynamics

As discussed in depth above, most vegetation models represent reproduction via seed. These models typically do this by allocating a set proportion of excess carbon (assimilated during the growing season) to seed (e.g., Moorcroft et al., 2001). These seeds enter the system and drive germination rates the following season. Representation of spatial patterns (e.g., across grid cells) of seed dispersal is largely not accounted for within vegetation models. Two modeling studies have focused on this issue. First, Blanco et al. (2014) created a version of aDGVM (2D-aDGVM) that allowed for plant dispersal and found that environmental heterogeneity and dispersal of trees (dispersal of herbaceous vegetation was not represented in the model) were important for simulating tree–grass coexistence. Another study used a spatially explicit individual-based dynamic global vegetation model (SEIB-DGVM; Sato & Ise, 2012) to show how dispersal dynamics, again for trees, alter temporal vegetation trajectories, especially when resident vegetation abundance is decreased (Sato & Ise, 2012).

Spatial dynamics, such as dispersal within a metapopulation, have been shown to allow for species to exist as "sink" populations within communities despite being less competitive in the local environment (Hanski, 1982; Leibold et al., 2004; Shmida & Wilson, 1985).

Reproductive strategies of different species and functional groups are particularly important when considering how plants will respond to stressful conditions. For example, species with strategies that allow for further dispersal (e.g., wind dispersed small seeded species) and fast growth rates, may allow for faster expansion into disturbed areas (Monty et al., 2013). Additionally, germination rates of some species have particular conditions that lead to substantial increases in primary production. For example, an extreme drought occurred in a US shortgrass prairie in 2012. Prior to the drought, an annual cool season grass (*Vulpia octoflora*) was a relatively rare species in the community. However, the year after the drought, it became the dominant vegetation in unburned areas, and stayed dominant for many years after the drought (Dufek et al., 2018).

Investigating the relative importance within models of long-distance propagule dispersal on herbaceous community dynamics would be useful to assess whether seed dispersal across grid cells is an important driver that should be included, given its complexity to simulate (Nabel, 2015). Shorter distance dispersal representation within models would benefit from collection of information pertaining to herbaceous dispersal distance, germination rate, and conditions for germination within and among plant functional types. Additional information on how reproduction clonally versus by seed differ, other than by dispersal distance, would aid in developing clonal reproduction schemes for certain plant functional types within models.

An open question related to representation of spatial dynamics within models is whether local-scale community dynamics propagate to larger spatial scales. If on the one hand, local dynamics are "averaged out" at larger spatial scales, it becomes less critical to represent local processes when research goals exist at the regional or global scale. Alternatively, if community dynamics are consistent across spatial scales, these effects will scale up and will be important to represent within most modeling objectives. Empirically, asynchrony among local plant communities has been shown to stabilize ecosystem functioning at larger scales (Wang & Loreau, 2016; Wilcox et al., 2017), yet global change drivers and disturbance can reduce this asynchrony effect (Hautier et al., 2020). Additional global change studies that bridge spatial scales will be important to answer this question.

4.5 | Fire and grazing regimes for herbaceous systems

The SPITFIRE (Spread and InTensity of FIRE; Thonicke et al., 2010) model has been incorporated into several vegetation models, including LPJ-DGVM (Thonicke et al., 2010), ORCHIDEE (Yu et al., 2015), and FATES. The model represents two major components, the probability of ignition and the rate of fire spread. The probability of ignition is based on the amount and moisture content of the vegetation, which is obtained from the vegetation model. There is also differentiation between natural and anthropomorphic sources of ignition. Human-caused ignition rates are a unimodal function of

human population density; this function describes an initial increase in ignition rate with population due to accidental ignitions, and then a decline at larger population sizes due to human effects such as land fragmentation. Rate of fire spread is a function of numerous variables including wind speed, the dryness of dead vegetation, and the surface to volume ratio of vegetation (Thonicke et al., 2010). A resistance factor can be assigned to PFTs, which is inversely related to the likelihood of mortality during fire. Often, herbaceous PFTs are assigned a high value for this parameter to represent observed herbaceous regrowth after fire. Many models do not yet account for management burns (Thonicke et al., 2010), which typically do not follow the population size-burn frequency relationships set up for anthropogenic fire (Allen & Palmer, 2011; Hulbert, 1986).

Herbivory is not represented in most process-based vegetation models. One model that has represented grazing is the G-Range model (Boone et al., 2018). In this model, there are two herbaceous plant functional types, perennial and annual. A given total amount (determined for each grid cell) of aboveground plant biomass is removed, and is divided among PFTs such that herbaceous vegetation loss is relatively high compared with shrub and woody PFTs. Loss of plant C and N is proportional to the amount of biomass removed via grazing. Nitrogen is returned as feces and urine, and the proportion of nitrogen removed is a function of soil texture. One consideration missing from this representation of grazing effects is representation of herbaceous PFTs that differ in their susceptibility and response to grazing.

Disturbance has long been identified as a key driver of numerous ecological processes in a wide variety of landscapes (Newman, 2019; Turner, 2010), and has been found to have particularly strong effects in herbaceous ecosystems (Belsky, 1992). For example, frequent fire in tallgrass prairie has been shown to cause dominance by highly productive C_4 rhizomatous grasses (Collins & Calabrese, 2012), while grazing in the same system reduces these same grass species and negates the positive fire effect (Collins, 1998). Interactions with herbivores (i.e., apparent competition) and/or pathogens (Gruner et al., 2008; Hillebrand et al., 2007) are other important determinants of herbaceous community structure. Disturbance effects also interact with water availability. For example, in a South African savanna, herbivory resistance of a dominant bunchgrass, *Bothriochloa radicans*, due to high concentrations of terpenoids within leaves, provided structure necessary to support many other species despite herbivore pressure (Koerner et al., 2014). However, energetic costs associated with this herbivore resistance caused the species to experience mass mortality during drought (Wilcox, Komatsu, et al., 2020), effectively altering the future responses of the entire ecosystem to both precipitation and herbivore pressure.

Disturbance is a critical component of maintaining mixed assemblages of herbaceous and woody plant species, such as savannas (Lehmann et al., 2014; Staver & Bond, 2014). In more arid savannas, tree–grass coexistence is maintained by the ability of grasses to rapidly take up soil water, especially at the seedling stage (Belovitch et al., 2023). This effectively limits the ability of trees to proliferate

and outcompete grasses for light (Holdo & Nippert, 2023). In more mesic savannas, coexistence is maintained by disturbance, where fire and herbivory keep tree canopies from closing and excluding grasses through light competition (Sankaran et al., 2004; Staver et al., 2009). We also know that these types of disturbance may interact such that fire effects may be different in the presence of herbivory, and vice versa. For example, herbivores that eat herbaceous vegetation (i.e., grazers) reduce fuel loads through consumption, which ultimately reduces fire intensity and can cause tree encroachment if grazing intensity is too high (Ward, 2005). Conversely, the occurrence of fire often increases herbivore pressure due to short-term increases in nutrients after fire (Ojima et al., 1994) that are incorporated into plant tissues, thereby increasing forage quality. These effects may also vary depending on the plant growth form or PFT under consideration (Gao & Schwilk, 2018, 2022).

Some primary characteristics of plant species found to promote existence and spread under fire include annual life strategies (Midgley, 1996; Monty et al., 2013), dense or deep crown tissue (Wigley et al., 2020), location of reproductive buds and meristematic tissue (Clarke et al., 2013; Medwecka-Kornaś & Kornaś, 1985), and allocation of resources to rhizomes and other belowground storage organs (Clarke et al., 2013). Similar plant traits have been found to link to grazing resistance, but additional traits related to herbivore selectivity have been found to be important, including lignin content (Semmartin & Ghersa, 2006), and the presence of defensive compounds in plant tissue (Briske, 1996; Kaul & Vats, 1998; Maestre et al., 2022). Disturbance-related traits may map neatly onto some of the plant groups outlined above (Figure 3; Hempson et al., 2015), and this may be a productive direction for future research.

To improve the representation of disturbances such as herbivory and fire into herbaceous components of models, information about herbivory and fire-related traits should be assessed within and among different plant growth forms and other splitting categories (e.g., annual vs. perennial, C_3 vs. C_4). When the goal is to represent susceptibility and responses to herbivory, it is likely that additional splitting of PFTs will be necessary due to variation of grazing tolerance and avoidance linked with different evolutionary histories and environmental characteristics (Adler et al., 2004). Lastly, better representation of anthropogenic fire ignition events will be important for areas where fire is used as a management tool. As one of the primary drivers of herbaceous vegetation in many ecosystems worldwide, improvements of the occurrence and effects of disturbance should be high priority for development in models if the goal is to represent ecological processes associated with herbaceous vegetation.

5 | CONCLUSIONS

The literature review and simulation exercises presented above highlight the current capacities and limitations of ecological knowledge for incorporating herbaceous plant communities and ecosystems into process-based models. Importantly, the need for improvement

lies in both the empirical and modeling sides. Co-design and implementation of ecological studies with both empiricists and modelers is the ideal path forward for improving herbaceous dynamics within ecosystem models (Lu et al., 2011, 2021). We suggest this process should be iterative, beginning with conversations between modelers and empiricists about the goals of modeling activities and the ecological components and processes of interest (Kyker-Snowman et al., 2022). These conversations may be driven by observed patterns of ecological phenomena or other prior empirical understanding. Then, initial model simulations should be used to identify parameters or modeled processes and their ecological analogs where uncertainty exists. Empirical studies can then be designed to address these uncertainties and provide information necessary for improving model parameters and processes. Finally, using these improved models, empirical findings may be expanded to greater temporal and spatial scales, which is important for informing land management and policy decisions (Cuddington et al., 2013), as well as providing paths forward for future scientific inquiry. We contend that each iteration of this cycle will lead not only to developments in process-based models, but also to substantial improvements in our mechanistic understanding of ecological processes. Observation networks such as FLUXNET (Swenson & Lawrence, 2014) and AmeriFlux (Kucharik et al., 2006; Novick et al., 2018) have been instrumental in benchmarking and improving predictive capacity of many process-based models. We suggest that other experimental or observational networks, of which there are currently many within herbaceous ecosystem types (e.g., NutNet, DroughtNet, HerbVar, NEON data streams, BromeCast), be leveraged to improve herbaceous representation within models. The franchise nature of many of these networks could be leveraged to allow a variety of researchers to opt-in and collect standardized measurements that could then be incorporated into models (Table 2). All these efforts are important to improve our predictive capacity for herbaceous ecosystems, which will in turn reduce uncertainty of predictions of future states of the entire earth system. Ultimately, our goal should be to increase our ability to make robust predictions of future states of Earth's ecosystems, which will be vital for guiding policy and management over the coming decades.

AUTHOR CONTRIBUTIONS

Kevin R. Wilcox and Anping Chen co-led the writing of this manuscript. Guopeng Liang, Ben Poulter, Katherine Renwick, Anthony Walker, and Ensheng Weng ran model simulations. All authors contributed to intellectual creation of ideas presented here as part of a working group led by Kimberly J. Komatsu, Meghan L. Avolio, and Kevin R. Wilcox. All authors contributed to writing and editing of the manuscript.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All data used in model parameterization and to drive simulations are available in Appendix S1 as a part of this article or online at http://lter.konza.ksu.edu/data. Empirical data from the irrigation experiment is available from the EDI Data Portal at https://doi.org/10.6073/pasta/3037d44d496df3d12fbe9668c7d618a6. Within this project, the csv files used were WAT012.csv and WAT013.csv to obtain species cover and ANPP, respectively.

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REFERENCES

Adler, P. B., Milchunas, D. G., Lauenroth, W. K., Sala, O. E., & Burke, I. C. (2004). Functional traits of graminoids in semi-arid steppes: A test of grazing histories: Functional traits and grazing history. *Journal of Applied Ecology*, *41*(4), 653–663. https://doi.org/10.1111/j.0021-8901.2004.00934.x

Alexander, P., Rounsevell, M. D. A., Dislich, C., Dodson, J. R., Engström, K., & Moran, D. (2015). Drivers for global agricultural land use change: The nexus of diet, population, yield and bioenergy. *Global Environmental Change*, *35*, 138–147. https://doi.org/10.1016/j.gloenvcha.2015.08.011

Allen, M. S., & Palmer, M. W. (2011). Fire history of a prairie/forest boundary: More than 250 years of frequent fire in a North

American tallgrass prairie. *Journal of Vegetation Science*, *22*(3), 436–444. https://doi.org/10.1111/j.1654-1103.2011.01278.x

Anderegg, L. D. L., Griffith, D. M., Cavender-Bares, J., Riley, W. J., Berry, J. A., Dawson, T. E., & Still, C. J. (2022). Representing plant diversity in land models: An evolutionary approach to make "Functional Types" more functional. *Global Change Biology*, *28*(8), 2541–2554. https://doi.org/10.1111/gcb.16040

Argles, A. P. K., Moore, J. R., & Cox, P. M. (2022). Dynamic global vegetation models: Searching for the balance between demographic process representation and computational tractability. *PLOS Climate*, *1*(9), e0000068. https://doi.org/10.1371/journal.pclm.0000068

Argles, A. P. K., Moore, J. R., Huntingford, C., Wiltshire, A. J., Harper, A. B., Jones, C. D., & Cox, P. M. (2020). Robust ecosystem demography (RED version 1.0): A parsimonious approach to modelling vegetation dynamics in earth system models. *Geoscientific Model Development*, *13*(9), 4067–4089. https://doi.org/10.5194/gmd-13-4067-2020

Aroca, R., Porcel, R., & Ruiz-Lozano, J. M. (2012). Regulation of root water uptake under abiotic stress conditions. *Journal of Experimental Botany*, *63*(1), 43–57. https://doi.org/10.1093/jxb/err266

Avolio, M. L., Koerner, S. E., La Pierre, K. J., Wilcox, K. R., Wilson, G. W. T., Smith, M. D., & Collins, S. L. (2014). Changes in plant community composition, not diversity, during a decade of nitrogen and phosphorus additions drive above-ground productivity in a tallgrass prairie. *Journal of Ecology*, *102*(6), 1649–1660. https://doi.org/10.1111/1365-2745.12312

Báez, S., Collins, S. L., Pockman, W. T., Johnson, J. E., & Small, E. E. (2013). Effects of experimental rainfall manipulations on Chihuahuan Desert grassland and shrubland plant communities. *Oecologia*, *172*(4), 1117–1127. https://doi.org/10.1007/s00442-012-2552-0

Bai, Y., & Cotrufo, M. F. (2022). Grassland soil carbon sequestration: Current understanding, challenges, and solutions. *Science*, *377*(6606), 603–608.

Bartolome, J. W., Klukkert, S. E., & Barry, W. J. (2013). Opal Phytoliths as evidence for displacement of native Californian grassland. *Madrono*, *60*(4), 342–347. https://doi.org/10.3120/0024-9637-60.4.342

Belovitch, M. W., NeSmith, J. E., Nippert, J. B., & Holdo, R. M. (2023). African savanna grasses outperform trees across the full spectrum of soil moisture availability. *New Phytologist*, *239*(1), 66–74. https://doi.org/10.1111/nph.18909

Belsky, A. J. (1992). Effects of grazing, competition, disturbance and fire on species composition and diversity in grassland communities. *Journal of Vegetation Science*, *3*(2), 187–200. https://doi.org/10.2307/3235679

Blanco, C. C., Scheiter, S., Sosinski, E., Fidelis, A., Anand, M., & Pillar, V. D. (2014). Feedbacks between vegetation and disturbance processes promote long-term persistence of forest–grassland mosaics in South Brazil. *Ecological Modelling*, *291*, 224–232. https://doi.org/10.1016/j.ecolmodel.2014.07.024

Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., Bustamante, M., Cinderby, S., Davidson, E., Dentener, F., Emmett, B., Erisman, J.-W., Fenn, M., Gilliam, F., Nordin, A., Pardo, L., & De Vries, W. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications*, *20*(1), 30–59. https://doi.org/10.1890/08-1140.1

Bonan, G. B., Patton, E. G., Finnigan, J. J., Baldocchi, D. D., & Harman, I. N. (2021). Moving beyond the incorrect but useful paradigm: Reevaluating big-leaf and multilayer plant canopies to model biosphere-atmosphere fluxes—A review. *Agricultural and Forest Meteorology*, *306*, 108435. https://doi.org/10.1016/j.agrformet.2021.108435

Boone, R. B., Conant, R. T., Sircely, J., Thornton, P. K., & Herrero, M. (2018). Climate change impacts on selected global rangeland ecosystem services. *Global Change Biology*, *24*(3), 1382–1393. https://doi.org/10.1111/gcb.13995

Botkin, D. B., Janak, J. F., & Wallis, J. R. (1972). Some ecological consequences of a computer model of forest growth. *Journal of Ecology*, *60*(3), 849–872. https://doi.org/10.2307/2258570

Bowd, E. J., Lindenmayer, D. B., Banks, S. C., & Blair, D. P. (2018). Logging and fire regimes alter plant communities. *Ecological Applications*, *28*(3), 826–841. https://doi.org/10.1002/eap.1693

Boyer, J. S., & Potter, J. R. (1973). Chloroplast response to low leaf water potentials: I. Role of turgor 1. *Plant Physiology*, *51*(6), 989–992. https://doi.org/10.1104/pp.51.6.989

Briske, D. D. (1996). Strategies of plant survival in grazed systems: A functional interpretation. In *The ecology and management of grazing systems* (pp. 37–66). CABI Publishing.

Briske, D. D., Fuhlendorf, S. D., & Smeins, F. E. (2006). A unified framework for assessment and application of ecological thresholds. *Rangeland Ecology & Management*, *59*(3), 225–236. https://doi.org/10.2111/05-115R.1

Brzostek, E. R., Fisher, J. B., & Phillips, R. P. (2014). Modeling the carbon cost of plant nitrogen acquisition: Mycorrhizal trade-offs and multipath resistance uptake improve predictions of retranslocation. *Journal of Geophysical Research: Biogeosciences*, *119*(8), 1684–1697. https://doi.org/10.1002/2014JG002660

Bugmann, H. (2001). A review of forest gap models. *Climatic Change*, *51*(3), 259–305. https://doi.org/10.1023/A:1012525626267

Butler, E. E., Datta, A., Flores-Moreno, H., Chen, M., Wythers, K. R., Fazayeli, F., Banerjee, A., Atkin, O. K., Kattge, J., Amiaud, B., Blonder, B., Boenisch, G., Bond-Lamberty, B., Brown, K. A., Byun, C., Campetella, G., Cerabolini, B. E. L., Cornelissen, J. H. C., Craine, J. M., … Reich, P. B. (2017). Mapping local and global variability in plant trait distributions. *Proceedings of the National Academy of Sciences of the United States of America*, *114*(51), E10937–E10946. https://doi.org/10.1073/pnas.1708984114

Chapin, F. S., Sturm, M., Serreze, M. C., McFadden, J. P., Key, J. R., Lloyd, A. H., McGuire, A. D., Rupp, T. S., Lynch, A. H., Schimel, J. P., Beringer, J., Chapman, W. L., Epstein, H. E., Euskirchen, E. S., Hinzman, L. D., Jia, G., Ping, C.-L., Tape, K. D., Thompson, C. D. C., … Welker, J. M. (2005). Role of land-surface changes in arctic summer warming. *Science*, *310*(5748), 657–660. https://doi.org/10.1126/science.1117368

Chávez, R. O., Moreira-Muñoz, A., Galleguillos, M., Olea, M., Aguayo, J., Latín, A., Aguilera-Betti, I., Muñoz, A. A., & Manríquez, H. (2019). GIMMS NDVI time series reveal the extent, duration, and intensity of "blooming desert" events in the hyper-arid Atacama Desert, northern Chile. *International Journal of Applied Earth Observation and Geoinformation*, *76*, 193–203. https://doi.org/10.1016/j.jag.2018.11.013

Chesson, P. (2000). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366.

Chitra-Tarak, R., Xu, C., Aguilar, S., Anderson-Teixeira, K. J., Chambers, J., Detto, M., Faybishenko, B., Fisher, R. A., Knox, R. G., Koven, C. D., Kueppers, L. M., Kunert, N., Kupers, S. J., McDowell, N. G., Newman, B. D., Paton, S. R., Pérez, R., Ruiz, L., Sack, L., … McMahon, S. M. (2021). Hydraulically-vulnerable trees survive on deep-water access during droughts in a tropical forest. *New Phytologist*, *231*(5), 1798–1813. https://doi.org/10.1111/nph.17464

Christoffersen, B. O., Gloor, M., Fauset, S., Fyllas, N. M., Galbraith, D. R., Baker, T. R., Kruijt, B., Rowland, L., Fisher, R. A., Binks, O. J., Sevanto, S., Xu, C., Jansen, S., Choat, B., Mencuccini, M., McDowell, N. G., & Meir, P. (2016). Linking hydraulic traits to tropical forest function in a size-structured and trait-driven model (TFS v.1-hydro). *Geoscientific Model Development*, *9*(11), 4227–4255. https://doi.org/10.5194/gmd-9-4227-2016

Clarke, P. J., Lawes, M. J., Midgley, J. J., Lamont, B. B., Ojeda, F., Burrows, G. E., Enright, N. J., & Knox, K. J. E. (2013). Resprouting as a key functional trait: How buds, protection and resources drive persistence after fire. *New Phytologist*, *197*(1), 19–35. https://doi.org/10.1111/nph.12001

Cleland, E. E., & Harpole, W. S. (2010). Nitrogen enrichment and plant communities. *Annals of the New York Academy of Sciences*, *1195*(1), 46–61. https://doi.org/10.1111/j.1749-6632.2010.05458.x

Collins, S. L. (1998). Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science*, *280*(5364), 745–747. https://doi.org/10.1126/science.280.5364.745

Collins, S. L., & Calabrese, L. B. (2012). Effects of fire, grazing and topographic variation on vegetation structure in tallgrass prairie. *Journal of Vegetation Science*, 23(3), 563–575. https://doi.org/10.1111/j.1654-1103.2011.01369.x

Collins, S. L., Chung, Y. A., Baur, L. E., Hallmark, A., Ohlert, T. J., & Rudgers, J. A. (2020). Press–pulse interactions and long-term community dynamics in a Chihuahuan Desert grassland. *Journal of Vegetation Science*, 31(5), 722–732. https://doi.org/10.1111/jvs.12881

Collins, S. L., Koerner, S. E., Plaut, J. A., Okie, J. G., Brese, D., Calabrese, L. B., Carvajal, A., Evansen, R. J., & Nonaka, E. (2012). Stability of tallgrass prairie during a 19-year increase in growing season precipitation: Long-term irrigation in native tallgrass prairie. *Functional Ecology*, 26(6), 1450–1459. https://doi.org/10.1111/j.1365-2435.2012.01995.x

Collins, S. L., Nippert, J. B., Blair, J. M., Briggs, J. M., Blackmore, P., & Ratajczak, Z. (2021). Fire frequency, state change and hysteresis in tallgrass prairie. *Ecology Letters*, 24(4), 636–647. https://doi.org/10.1111/ele.13676

Cook, B. I., Miller, R. L., & Seager, R. (2009). Amplification of the North American "Dust Bowl" drought through human-induced land degradation. *Proceedings of the National Academy of Sciences of the United States of America*, 106(13), 4997–5001. https://doi.org/10.1073/pnas.0810200106

Coughenour, M. B. (1992). Spatial modeling and landscape characterization of an African pastoral ecosystem: A prototype model and its potential use for monitoring drought. In D. H. McKenzie, D. E. Hyatt, & V. J. McDonald (Eds.), *Ecological indicators* (pp. 787–810). Springer US. https://doi.org/10.1007/978-1-4615-4659-7_45

Cuddington, K., Fortin, M.-J., Gerber, L. R., Hastings, A., Liebhold, A., O'Connor, M., & Ray, C. (2013). Process-based models are required to manage ecological systems in a changing world. *Ecosphere*, 4(2), art20. https://doi.org/10.1890/ES12-00178.1

Curasi, S. R., Fetcher, N., Wright, K. S., Weldon, D. P., & Rocha, A. V. (2023). Insights into the tussock growth form with model–data fusion. *New Phytologist*, 239(2), 562–577. https://doi.org/10.1111/nph.18751

DeMalach, N., Zaady, E., & Kadmon, R. (2017). Light asymmetry explains the effect of nutrient enrichment on grassland diversity. *Ecology Letters*, 20(1), 60–69. https://doi.org/10.1111/ele.12706

Derner, J. D., & Briske, D. D. (1999). Intraclonal regulation in a perennial caespitose grass: A field evaluation of above- and below-ground resource availability. *Journal of Ecology*, 87(5), 737–747. https://doi.org/10.1046/j.1365-2745.1999.00387.x

Detto, M., Levine, J. M., & Pacala, S. W. (2022). Maintenance of high diversity in mechanistic forest dynamics models of competition for light. *Ecological Monographs*, 92(2), e1500. https://doi.org/10.1002/ecm.1500

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., Skarpe, C., Rusch, G., Sternberg, M., Noy-Meir, I., Landsberg, J., Zhang, W., Clark, H., & Campbell, B. D. (2007). Plant trait responses to grazing—A global synthesis. *Global Change Biology*, 13(2), 313–341. https://doi.org/10.1111/j.1365-2486.2006.01288.x

Dickson, T. L., Mittelbach, G. G., Reynolds, H. L., & Gross, K. L. (2014). Height and clonality traits determine plant community responses to fertilization. *Ecology*, 95(9), 2443–2452. https://doi.org/10.1890/13-1875.1

Dieleman, C. M. (2016). *Ecosystem level effects of climate change on northern peatlands*. PhD Thesis, The University of Western Ontario, Canada.

Dixon, A. P., Faber-Langendoen, D., Josse, C., Morrison, J., & Loucks, C. J. (2014). Distribution mapping of world grassland types. *Journal of Biogeography*, 41(11), 2003–2019. https://doi.org/10.1111/jbi.12381

D'Odorico, P., Okin, G. S., & Bestelmeyer, B. T. (2012). A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. *Ecohydrology*, 5(5), 520–530. https://doi.org/10.1002/eco.259

Du, E., Terrer, C., Pellegrini, A. F. A., Ahlström, A., van Lissa, C. J., Zhao, X., Xia, N., Wu, X., & Jackson, R. B. (2020). Global patterns of terrestrial nitrogen and phosphorus limitation. *Nature Geoscience*, 13(3), 221–226. https://doi.org/10.1038/s41561-019-0530-4

Dufek, N. A., Augustine, D. J., Blumenthal, D. M., Kray, J. A., & Derner, J. D. (2018). Dormant-season fire inhibits Sixweeks fescue and enhances forage production in shortgrass steppe. *Fire Ecology*, 14(1), 33–49. https://doi.org/10.4996/fireecology.140132048

Easterling, D. R., Meehl, G. A., Parmesan, C., Changnon, S. A., Karl, T. R., & Mearns, L. O. (2000). Climate extremes: Observations, modeling, and impacts. *Science, New Series*, 289(5487), 2068–2074.

Eller, C. B., Rowland, L., Mencuccini, M., Rosas, T., Williams, K., Harper, A., Medlyn, B. E., Wagner, Y., Klein, T., Teodoro, G. S., Oliveira, R. S., Matos, I. S., Rosado, B. H. P., Fuchs, K., Wohlfahrt, G., Montagnani, L., Meir, P., Sitch, S., & Cox, P. M. (2020). Stomatal optimization based on xylem hydraulics (SOX) improves land surface model simulation of vegetation responses to climate. *New Phytologist*, 226(6), 1622–1637. https://doi.org/10.1111/nph.16419

Elser, J. J., Bracken, M. E. S., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., Ngai, J. T., Seabloom, E. W., Shurin, J. B., & Smith, J. E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, 10(12), 1135–1142. https://doi.org/10.1111/j.1461-0248.2007.01113.x

Eskelinen, A., Harpole, W. S., Jessen, M.-T., Virtanen, R., & Hautier, Y. (2022). Light competition drives herbivore and nutrient effects on plant diversity. *Nature*, 611(7935), 301–305. https://doi.org/10.1038/s41586-022-05383-9

Euskirchen, E. S., Carman, T. B., & McGuire, A. D. (2014). Changes in the structure and function of northern Alaskan ecosystems when considering variable leaf-out times across groupings of species in a dynamic vegetation model. *Global Change Biology*, 20(3), 963–978. https://doi.org/10.1111/gcb.12392

Euskirchen, E. S., McGuire, A. D., Chapin, F. S., III, Yi, S., & Thompson, C. C. (2009). Changes in vegetation in northern Alaska under scenarios of climate change, 2003–2100: Implications for climate feedbacks. *Ecological Applications*, 19(4), 1022–1043. https://doi.org/10.1890/08-0806.1

Evans, M. R., Bithell, M., Cornell, S. J., Dall, S. R. X., Díaz, S., Emmott, S., Ernande, B., Grimm, V., Hodgson, D. J., Lewis, S. L., Mace, G. M., Morecroft, M., Moustakas, A., Murphy, E., Newbold, T., Norris, K. J., Petchey, O., Smith, M., Travis, J. M. J., & Benton, T. G. (2013). Predictive systems ecology. *Proceedings of the Royal Society B: Biological Sciences*, 280(1771), 20131452. https://doi.org/10.1098/rspb.2013.1452

Faber-Langendoen, D., Keeler-Wolf, T., Meidinger, D. V., Josse, C., Weakley, A. S., Tart, D., Navarro, G., Hoagland, B. W., Ponomarenko, S., & Fults, G. (2016). *Classification and description of world formation types*. United States Department of Agriculture, Forest Service.

Fay, P. A., Prober, S. M., Harpole, W. S., Knops, J. M. H., Bakker, J. D., Borer, E. T., Lind, E. M., MacDougall, A. S., Seabloom, E. W., Wragg, P. D., Adler, P. B., Blumenthal, D. M., Buckley, Y. M., Chu, C., Cleland, E. E., Collins, S. L., Davies, K. F., Du, G., Feng, X., … Yang, L. H. (2015). Grassland productivity limited by multiple nutrients. *Nature Plants*, 1(7), Article 7. https://doi.org/10.1038/nplants.2015.80

February, E. C., Higgins, S. I., Bond, W. J., & Swemmer, L. (2013). Influence of competition and rainfall manipulation on the growth responses of savanna trees and grasses. *Ecology*, 94(5), 1155–1164. https://doi.org/10.1890/12-0540.1

Fisher, R. A., & Koven, C. D. (2020). Perspectives on the future of land surface models and the challenges of representing complex terrestrial systems. *Journal of Advances in Modeling Earth Systems*, 12(4), e2018MS001453. https://doi.org/10.1029/2018MS001453

Fisher, R. A., Koven, C. D., Anderegg, W. R. L., Christoffersen, B. O., Dietze, M. C., Farrior, C. E., Holm, J. A., Hurtt, G. C., Knox, R. G., Lawrence, P. J., Lichstein, J. W., Longo, M., Matheny, A. M., Medvigy, D., Muller-Landau, H. C., Powell, T. L., Serbin, S. P., Sato, H., Shuman, J. K., … Moorcroft, P. R. (2018). Vegetation demographics in earth system models: A review of progress and priorities. *Global Change Biology*, 24(1), 35–54. https://doi.org/10.1111/gcb.13910

Fisher, R. A., Muszala, S., Verteinstein, M., Lawrence, P., Xu, C., McDowell, N. G., Knox, R. G., Koven, C., Holm, J., Rogers, B. M., Spessa, A., Lawrence, D., & Bonan, G. (2015). Taking off the training wheels: The properties of a dynamic vegetation model without climate envelopes, CLM4.5(ED). *Geoscientific Model Development*, 8(11), 3593–3619. https://doi.org/10.5194/gmd-8-3593-2015

Fisher, R. A., Wieder, W. R., Sanderson, B. M., Koven, C. D., Oleson, K. W., Xu, C., Fisher, J. B., Shi, M., Walker, A. P., & Lawrence, D. M. (2019). Parametric controls on vegetation responses to biogeochemical forcing in the CLM5. *Journal of Advances in Modeling Earth Systems*, 11(9), 2879–2895. https://doi.org/10.1029/2019MS001609

Fitz, H. C., & Trimble, B. (2006). *Documentation of the everglades landscape model: ELM v25*. SFWMD.

Fox, D. L., Pau, S., Taylor, L., Strömberg, C. A. E., Osborne, C. P., Bradshaw, C., Conn, S., Beerling, D. J., & Still, C. J. (2018). Climatic controls on C4 grassland distributions during the Neogene: A model-data comparison. *Frontiers in Ecology and Evolution*, 6, 1–19. https://doi.org/10.3389/fevo.2018.00147. https://www.frontiersin.org/articles/

Gao, X., & Schwilk, D. W. (2018). Grass canopy architecture influences temperature exposure at soil surface. *Fire*, 1(3), Article 3. https://doi.org/10.3390/fire1030035

Gao, X., & Schwilk, D. W. (2022). Burn hot or tolerate trees: Flammability decreases with shade tolerance in grasses. *Oikos*, 2022(4), e08930. https://doi.org/10.1111/oik.08930

Gibbens, R. P., & Lenz, J. M. (2001). Root systems of some Chihuahuan desert plants. *Journal of Arid Environments*, 49(2), 221–263. https://doi.org/10.1006/jare.2000.0784

Gibson, D. J. (2009). *Grasses and grassland ecology*. Oxford University Press.

Griffith, D. M., Anderson, T. M., Osborne, C. P., Strömberg, C. A. E., Forrestel, E. J., & Still, C. J. (2015). Biogeographically distinct controls on C3 and C4 grass distributions: Merging community and physiological ecology. *Global Ecology and Biogeography*, 24(3), 304–313. https://doi.org/10.1111/geb.12265

Griffith, D. M., Osborne, C. P., Edwards, E. J., Bachle, S., Beerling, D. J., Bond, W. J., Gallaher, T. J., Helliker, B. R., Lehmann, C. E. R., Leatherman, L., Nippert, J. B., Pau, S., Qiu, F., Riley, W. J., Smith, M. D., Strömberg, C. A. E., Taylor, L., Ungerer, M., & Still, C. J. (2020). Lineage-based functional types: Characterising functional diversity to enhance the representation of ecological behaviour in land surface models. *New Phytologist*, 228(1), 15–23. https://doi.org/10.1111/nph.16773

Gruner, D. S., Smith, J. E., Seabloom, E. W., Sandin, S. A., Ngai, J. T., Hillebrand, H., Harpole, W. S., Elser, J. J., Cleland, E. E., Bracken, M. E. S., Borer, E. T., & Bolker, B. M. (2008). A cross-system synthesis of consumer and nutrient resource control on producer biomass. *Ecology Letters*, 11(7), 740–755. https://doi.org/10.1111/j.1461-0248.2008.01192.x

Hanski, I. (1982). Dynamics of regional distribution: The core and satellite species hypothesis. *Oikos*, 38(2), 210–221. https://doi.org/10.2307/3544021

Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., Chase, J., Fay, P. A., Hautier, Y., Hillebrand, H., MacDougall, A. S., Seabloom, E. W., Bakker, J. D., Cadotte, M. W., Chaneton, E. J., Chu, C., Hagenah, N., Kirkman, K., La Pierre, K. J., ... Stevens, C. J. (2017). Out of the shadows: Multiple nutrient limitations drive relationships among biomass, light and plant diversity. *Functional Ecology*, 31(9), 1839–1846. https://doi.org/10.1111/1365-2435.12967

Harpole, W. S., Sullivan, L. L., Lind, E. M., Firn, J., Adler, P. B., Borer, E. T., Chase, J., Fay, P. A., Hautier, Y., Hillebrand, H., MacDougall, A. S., Seabloom, E. W., Williams, R., Bakker, J. D., Cadotte, M. W., Chaneton, E. J., Chu, C., Cleland, E. E., D'Antonio, C., ... Wragg, P. D. (2016). Addition of multiple limiting resources reduces grassland diversity. *Nature*, 537(7618), Article 7618. https://doi.org/10.1038/nature19324

Harpole, W. S., & Tilman, D. (2007). Grassland species loss resulting from reduced niche dimension. *Nature*, 446(7137), Article 7137. https://doi.org/10.1038/nature05684

Harrison, S. (2020). Plant community diversity will decline more than increase under climatic warming. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 375(1794), 20190106. https://doi.org/10.1098/rstb.2019.0106

Harrison, S. P., Cramer, W., Franklin, O., Prentice, I. C., Wang, H., Brännström, Å., de Boer, H., Dieckmann, U., Joshi, J., Keenan, T. F., Lavergne, A., Manzoni, S., Mengoli, G., Morfopoulos, C., Peñuelas, J., Pietsch, S., Rebel, K. T., Ryu, Y., Smith, N. G., ... Wright, I. J. (2021). Eco-evolutionary optimality as a means to improve vegetation and land-surface models. *New Phytologist*, 231(6), 2125–2141. https://doi.org/10.1111/nph.17558

Hartley, S. E., & Jones, T. H. (2003). Plant diversity and insect herbivores: Effects of environmental change in contrasting model systems. *Oikos*, 101(1), 6–17. https://doi.org/10.1034/j.1600-0706.2003.12566.x

Hartnett, D. C. (1993). Regulation of clonal growth and dynamics of *Panicum virgatum* (Poaceae) in tallgrass prairie: Effects of neighbor removal and nutrient addition. *American Journal of Botany*, 80(10), 1114–1120. https://doi.org/10.2307/2445538

Hautier, Y., Niklaus, P. A., & Hector, A. (2009). Competition for light causes plant biodiversity loss after eutrophication. *Science*, 324(5927), 636–638. https://doi.org/10.1126/science.1169640

Hautier, Y., Zhang, P., Loreau, M., Wilcox, K. R., Seabloom, E. W., Borer, E. T., Byrnes, J. E. K., Koerner, S. E., Komatsu, K. J., Lefcheck, J. S., Hector, A., Adler, P. B., Alberti, J., Arnillas, C. A., Bakker, J. D., Brudvig, L. A., Bugalho, M. N., Cadotte, M., Caldeira, M. C., ... Wang, S. (2020). General destabilizing effects of eutrophication on grassland productivity at multiple spatial scales. *Nature Communications*, 11(1), Article 1. https://doi.org/10.1038/s41467-020-19252-4

Hempson, G. P., Archibald, S., Bond, W. J., Ellis, R. P., Grant, C. C., Kruger, F. J., Kruger, L. M., Moxley, C., Owen-Smith, N., Peel, M. J. S., Smit, I. P. J., & Vickers, K. J. (2015). Ecology of grazing lawns in Africa. *Biological Reviews*, 90(3), 979–994. https://doi.org/10.1111/brv.12145

Hickler, T., Prentice, I. C., Smith, B., Sykes, M. T., & Zaehle, S. (2006). Implementing plant hydraulic architecture within the LPJ dynamic global vegetation model. *Global Ecology and Biogeography*, 15(6), 567–577. https://doi.org/10.1111/j.1466-8238.2006.00254.x

Hillebrand, H., Blasius, B., Borer, E. T., Chase, J. M., Downing, J. A., Eriksson, B. K., Filstrup, C. T., Harpole, W. S., Hodapp, D., Larsen, S., Lewandowska, A. M., Seabloom, E. W., Van de Waal, D. B., & Ryabov, A. B. (2018). Biodiversity change is uncoupled from species richness trends: Consequences for conservation and monitoring. *Journal of Applied Ecology*, 55(1), 169–184. https://doi.org/10.1111/1365-2664.12959

Hillebrand, H., Gruner, D. S., Borer, E. T., Bracken, M. E. S., Cleland, E. E., Elser, J. J., Harpole, W. S., Ngai, J. T., Seabloom, E. W., Shurin, J. B., & Smith, J. E. (2007). Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. *Proceedings of the National Academy of Sciences of the United States of America*, 104(26), 10904–10909. https://doi.org/10.1073/pnas.0701918104

Hilty, J., Muller, B., Pantin, F., & Leuzinger, S. (2021). Plant growth: The what, the how, and the why. *New Phytologist*, 232(1), 25–41. https://doi.org/10.1111/nph.17610

Hobbie, S. E. (1996). Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs*, 66(4), 503–522. https://doi.org/10.2307/2963492

Holdo, R. M., & Nippert, J. B. (2023). Linking resource- and disturbance-based models to explain tree–grass coexistence in savannas. *New Phytologist*, 237(6), 1966–1979. https://doi.org/10.1111/nph.18648

Hulbert, L. C. (1955). Ecological studies of Bromus tectorum and other annual Bromegrasses. *Ecological Monographs*, 25(2), 181–213. https://doi.org/10.2307/1943550

Hulbert, L. C. (1986). Fire effects on tallgrass prairie. In G. K. Clambey & R. H. Pemble (Eds.). Proceedings of the Ninth north American Prairie Conference, Fargo, North Dakota, 138-142.

Hungria, M., & Vargas, M. A. T. (2000). Environmental factors affecting N_2 fixation in grain legumes in the tropics, with an emphasis on Brazil. *Field Crops Research*, 65(2), 151–164. https://doi.org/10.1016/S0378-4290(99)00084-2

IPBES. (2019). *Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* [E. S. Brondízio, J. Settele, S. Díaz, & H. T. Ngo (Eds.), pp. 1–1082]. IPBES Secretariat.

IPCC. (2021). Climate change 2021: The physical science basis. In V. Masson-Delmotte, P. Zhai, A. Pirani, S. L. Connors, C. Péan, S. Berger, N. Caud, Y. Chen, L. Goldfarb, M. I. Gomis, M. Huang, K. Leitzell, E. Lonnoy, J. B. R. Matthews, T. K. Maycock, T. Waterfield, O. Yelekçi, R. Yu, & B. Zhou (Eds.), *Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, in press. https://doi.org/10.1017/9781009157896

Jackson, R. B., Canadell, J., Ehleringer, J. R., Mooney, H. A., Sala, O. E., & Schulze, E. D. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia*, 108(3), 389–411. https://doi.org/10.1007/BF00333714

Johnson, P. S., Johnson, C. L., & West, N. E. (1988). Estimation of phytomass for ungrazed crested wheatgrass plants using allometric equations. *Journal of Range Management*, 41(5), 421. https://doi.org/10.2307/3899582

Kardol, P., Cregger, M. A., Campany, C. E., & Classen, A. T. (2010). Soil ecosystem functioning under climate change: Plant species and community effects. *Ecology*, 91(3), 767–781. https://doi.org/10.1890/09-0135.1

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G. D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert, C. H., Alcántara, J. M., Alcázar, C. C., Aleixo, I., Ali, H., ... Wirth, C. (2020). TRY plant trait database—Enhanced coverage and open access. *Global Change Biology*, 26(1), 119–188. https://doi.org/10.1111/gcb.14904

Kaul, V. K., & Vats, S. K. (1998). Essential oil composition of *Bothriochloa pertusa* and phyletic relationship in aromatic grasses. *Biochemical Systematics and Ecology*, 26(3), 347–356. https://doi.org/10.1016/S0305-1978(97)00103-8

Keddy, P. A., & Laughlin, D. C. (2021). *A framework for community ecology: Species pools, filters and traits*. Cambridge University Press.

Kerns, B. K., & Day, M. A. (2018). Prescribed fire regimes subtly alter ponderosa pine forest plant community structure. *Ecosphere*, 9(12), e02529. https://doi.org/10.1002/ecs2.2529

Knapp, A. K., Briggs, J. M., & Smith, M. D. (2012). Community stability does not preclude ecosystem sensitivity to chronic resource alteration. *Functional Ecology*, 26(6), 1231–1233.

Knapp, A. K., Chen, A., Griffin-Nolan, R. J., Baur, L. E., Carroll, C. J. W., Gray, J. E., Hoffman, A. M., Li, X., Post, A. K., Slette, I. J., Collins, S. L., Luo, Y., & Smith, M. D. (2020). Resolving the dust bowl paradox of grassland responses to extreme drought. *Proceedings of the National Academy of Sciences of the United States of America*, 117(36), 22249–22255. https://doi.org/10.1073/pnas.1922030117

Knox, R. G., Koven, C., Riley, W. J., Bisht, G., Chambers, J. Q., Christoffersen, B. O., Holm, J., Fisher, R., Kueppers, L. M., Medvigy, D., Shuman, J. K., Walker, A., Wei, L., & Xu, C. (2018). A framework for testing plant allocation and reactive transport hypotheses. 2018, B13I-2241.

Koerner, S. E., Burkepile, D. E., Fynn, R. W. S., Burns, C. E., Eby, S., Govender, N., Hagenah, N., Matchett, K. J., Thompson, D. I., Wilcox, K. R., Collins, S. L., Kirkman, K. P., Knapp, A. K., & Smith, M. D. (2014). Plant community response to loss of large herbivores differs between North American and South African savanna grasslands. *Ecology*, 95(4), 808–816. https://doi.org/10.1890/13-1828.1

Komatsu, K. J., Avolio, M. L., Lemoine, N. P., Isbell, F., Grman, E., Houseman, G. R., Koerner, S. E., Johnson, D. S., Wilcox, K. R., Alatalo, J. M., Anderson, J. P., Aerts, R., Baer, S. G., Baldwin, A. H.,

Bates, J., Beierkuhnlein, C., Belote, R. T., Blair, J., Bloor, J. M. G., ... Zhang, Y. (2019). Global change effects on plant communities are magnified by time and the number of global change factors imposed. *Proceedings of the National Academy of Sciences of the United States of America*, 116(36), 17867–17873. https://doi.org/10.1073/pnas.1819027116

Koteen, L. E., Baldocchi, D. D., & Harte, J. (2011). Invasion of non-native grasses causes a drop in soil carbon storage in California grasslands. *Environmental Research Letters*, 6(4), 44001. https://doi.org/10.1088/1748-9326/6/4/044001

Koven, C. D., Knox, R. G., Fisher, R. A., Chambers, J. Q., Christoffersen, B. O., Davies, S. J., Detto, M., Dietze, M. C., Faybishenko, B., Holm, J., Huang, M., Kovenock, M., Kueppers, L. M., Lemieux, G., Massoud, E., McDowell, N. G., Muller-Landau, H. C., Needham, J. F., Norby, R. J., ... Xu, C. (2020). Benchmarking and parameter sensitivity of physiological and vegetation dynamics using the functionally assembled terrestrial ecosystem simulator (FATES) at Barro Colorado Island, Panama. *Biogeosciences*, 17(11), 3017–3044. https://doi.org/10.5194/bg-17-3017-2020

Kucharik, C. J., Barford, C. C., Maayar, M. E., Wofsy, S. C., Monson, R. K., & Baldocchi, D. D. (2006). A multiyear evaluation of a dynamic global vegetation model at three AmeriFlux forest sites: Vegetation structure, phenology, soil temperature, and CO_2 and H_2O vapor exchange. *Ecological Modelling*, 196(1), 1–31. https://doi.org/10.1016/j.ecolmodel.2005.11.031

Kyker-Snowman, E., Lombardozzi, D. L., Bonan, G. B., Cheng, S. J., Dukes, J. S., Frey, S. D., Jacobs, E. M., McNellis, R., Rady, J. M., Smith, N. G., Thomas, R. Q., Wieder, W. R., & Grandy, A. S. (2022). Increasing the spatial and temporal impact of ecological research: A roadmap for integrating a novel terrestrial process into an Earth system model. *Global Change Biology*, 28(2), 665–684. https://doi.org/10.1111/gcb.15894

Ladouceur, E., Blowes, S. A., Chase, J. M., Clark, A. T., Garbowski, M., Alberti, J., Arnillas, C. A., Bakker, J. D., Barrio, I. C., Bharath, S., Borer, E. T., Brudvig, L. A., Cadotte, M. W., Chen, Q., Collins, S. L., Dickman, C. R., Donohue, I., Du, G., Ebeling, A., ... Harpole, W. S. (2022). Linking changes in species composition and biomass in a globally distributed grassland experiment. *Ecology Letters*, 25(12), 2699–2712. https://doi.org/10.1111/ele.14126

Lake, P. S. (2000). Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society*, 19(4), 573–592. https://doi.org/10.2307/1468118

Langley, J. A., & Hungate, B. A. (2014). Plant community feedbacks and long-term ecosystem responses to multi-factored global change. *AoB Plants*, 6, plu035. https://doi.org/10.1093/aobpla/plu035

Lawrence, D. M., Fisher, R. A., Koven, C. D., Oleson, K. W., Swenson, S. C., Bonan, G., Collier, N., Ghimire, B., van Kampenhout, L., Kennedy, D., Kluzek, E., Lawrence, P. J., Li, F., Li, H., Lombardozzi, D., Riley, W. J., Sacks, W. J., Shi, M., Vertenstein, M., ... Zeng, X. (2019). The community land model version 5: Description of new features, benchmarking, and impact of forcing uncertainty. *Journal of Advances in Modeling Earth Systems*, 11(12), 4245–4287. https://doi.org/10.1029/2018MS001583

Leffler, A. J., James, J. J., & Monaco, T. A. (2013). Temperature and functional traits influence differences in nitrogen uptake capacity between native and invasive grasses. *Oecologia*, 171(1), 51–60. https://doi.org/10.1007/s00442-012-2399-4

Lehmann, C. E. R., Anderson, T. M., Sankaran, M., Higgins, S. I., Archibald, S., Hoffmann, W. A., Hanan, N. P., Williams, R. J., Fensham, R. J., Felfili, J., Hutley, L. B., Ratnam, J., San Jose, J., Montes, R., Franklin, D., Russell-Smith, J., Ryan, C. M., Durigan, G., Hiernaux, P., ... Bond, W. J. (2014). Savanna vegetation-fire-climate relationships differ among continents. *Science*, 343(6170), 548–552. https://doi.org/10.1126/science.1247355

Lehmann, C. E. R., Griffith, D. M., Simpson, K. J., Anderson, T. M., Archibald, S., Beerling, D. J., Bond, W. J., Denton, E., Edwards, E. J., Forrestel, E. J., Fox, D. L., Georges, D., Hoffmann, W. A.,

Kluyver, T., Mucina, L., Pau, S., Ratnam, J., Salamin, N., Santini, B., ... Osborne, C. P. (2019). Functional diversification enabled grassy biomes to fill global climate space. *bioRxiv*, 583625. https://doi.org/10.1101/583625

Leibold, M. A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J. M., Hoopes, M. F., Holt, R. D., Shurin, J. B., Law, R., Tilman, D., Loreau, M., & Gonzalez, A. (2004). The metacommunity concept: A framework for multi-scale community ecology: The meta-community concept. *Ecology Letters*, 7(7), 601–613. https://doi.org/10.1111/j.1461-0248.2004.00608.x

Levitt, J. (1980). *Responses of plants to environmental stresses. Volume II. Water, radiation, salt, and other stresses*. Academic Press.

Li, L., Yang, Z.-L., Matheny, A. M., Zheng, H., Swenson, S. C., Lawrence, D. M., Barlage, M., Yan, B., McDowell, N. G., & Leung, L. R. (2021). Representation of plant hydraulics in the Noah-MP land surface model: Model development and multiscale evaluation. *Journal of Advances in Modeling Earth Systems*, 13(4), e2020MS002214. https://doi.org/10.1029/2020MS002214

Liu, Y., Holtzman, N. M., & Konings, A. G. (2021). Global ecosystem-scale plant hydraulic traits retrieved using model–data fusion. *Hydrology and Earth System Sciences*, 25(5), 2399–2417. https://doi.org/10.5194/hess-25-2399-2021

Lu, D., Pierce, E., Kao, S.-C., Zhang, G., Restrepo, J., Womble, D., Li, L., & Rempe, D. (2021). An AI-enabled MODEX framework for improving predictability of subsurface water storage across local and continental scales (AI4ESP-1082). Artificial Intelligence for Earth System Predictability (AI4ESP) Collaboration (United States). https://doi.org/10.2172/1769675

Ludlow, M. M. (1989). *Strategies of response to water stress* (pp. 269–281). Water Shortage.

Luo, W., Xu, C., Ma, W., Yue, X., Liang, X., Zuo, X., Knapp, A. K., Smith, M. D., Sardans, J., Dijkstra, F. A., Peñuelas, J., Bai, Y., Wang, Z., Yu, Q., & Han, X. (2018). Effects of extreme drought on plant nutrient uptake and resorption in rhizomatous vs bunchgrass-dominated grasslands. *Oecologia*, 188(2), 633–643. https://doi.org/10.1007/s00442-018-4232-1

Luo, Y., Melillo, J., Niu, S., Beier, C., Clark, J. S., Classen, A. T., Davidson, E., Dukes, J. S., Evans, R. D., Field, C. B., Czimczik, C. I., Keller, M., Kimball, B. A., Kueppers, L. M., Norby, R. J., Pelini, S. L., Pendall, E., Rastetter, E., Six, J., ... Torn, M. S. (2011). Coordinated approaches to quantify long-term ecosystem dynamics in response to global change: Long-term global change experiments. *Global Change Biology*, 17(2), 843–854. https://doi.org/10.1111/j.1365-2486.2010.02265.x

Luo, Y., & Reynolds, J. F. (1999). Validity of extrapolating field CO_2 experiments to predict carbon sequestration in natural ecosystems. *Ecology*, 80(5), 1568–1583. https://doi.org/10.1890/0012-9658(1999)080[1568:VOEFCE]2.0.CO;2

Luong, J. C., Holl, K. D., & Loik, M. E. (2021). Leaf traits and phylogeny explain plant survival and community dynamics in response to extreme drought in a restored coastal grassland. *Journal of Applied Ecology*, 58(8), 1670–1680. https://doi.org/10.1111/1365-2664.13909

Maestre, F. T., Bagousse-Pinguet, Y. L., Delgado-Baquerizo, M., Eldridge, D. J., Saiz, H., Berdugo, M., Gozalo, B., Ochoa, V., Guirado, E., García-Gómez, M., Valencia, E., Gaitán, J. J., Asensio, S., Mendoza, B. J., Plaza, C., Díaz-Martínez, P., Rey, A., Hu, H.-W., He, J.-Z., ... Gross, N. (2022). Grazing and ecosystem service delivery in global drylands. *Science*, 378(6622), 915–920.

Marshall, J. G., & Dumbroff, E. B. (1999). Turgor regulation via cell wall adjustment in white Spruce1. *Plant Physiology*, 119(1), 313–320. https://doi.org/10.1104/pp.119.1.313

Martínez Cano, I., Shevliakova, E., Malyshev, S., Wright, S. J., Detto, M., Pacala, S. W., & Muller-Landau, H. C. (2020). Allometric constraints and competition enable the simulation of size structure and carbon fluxes in a dynamic vegetation model of tropical forests (LM3PPA-TV). *Global Change Biology*, 26(8), 4478–4494. https://doi.org/10.1111/gcb.15188

McArthur, E., Durant, R., Evan, M., Smith, S. D., & Tueller, P. T. (1990). Proceedings-symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5–7; Las Vegas, NV. Gen. Technical Report. INT-GTR-276 (p. 351). U.S. Department of Agriculture, Forest Service, Intermountain Research Station. https://doi.org/10.2737/INT-GTR-276

McDowell, N., Pockman, W. T., Allen, C. D., Breshears, D. D., Cobb, N., Kolb, T., Plaut, J., Sperry, J., West, A., Williams, D. G., & Yepez, E. A. (2008). Mechanisms of plant survival and mortality during drought: Why do some plants survive while others succumb to drought? *New Phytologist*, 178(4), 719–739. https://doi.org/10.1111/j.1469-8137.2008.02436.x

Medwecka-Kornaś, A., & Kornaś, J. (1985). Fire-resistant sedges (Cyperaceae) in Zambia1 Herrn Prof. Dr. H. Meusel zum 75. Geburtstag gewidmet. *Flora*, 176(1), 61–71. https://doi.org/10.1016/S0367-2530(17)30103-2

Midgley, J. J. (1996). Why the World's vegetation is not totally dominated by resprouting plants; because resprouters are shorter than re-seeders. *Ecography*, 19(1), 92–95.

Mittelbach, G. G., & McGill, B. J. (2019). *Community ecology*. Oxford University Press.

Mladenoff, D. J. (2004). LANDIS and forest landscape models. *Ecological Modelling*, 180(1), 7–19. https://doi.org/10.1016/j.ecolmodel.2004.03.016

Monty, A., Brown, C. S., & Johnston, D. B. (2013). Fire promotes downy brome (*Bromus tectorum* L.) seed dispersal. *Biological Invasions*, 15(5), 1113–1123. https://doi.org/10.1007/s10530-012-0355-1

Moorcroft, P. R., Hurtt, G. C., & Pacala, S. W. (2001). A method for scaling vegetation dynamics: The ecosystem demography model (ed). *Ecological Monographs*, 71(4), 557–586. https://doi.org/10.1890/0012-9615(2001)071[0557:AMFSVD]2.0.CO;2

Morin, P. J. (2009). *Community ecology*. John Wiley & Sons.

Muldavin, E. H., Moore, D. I., Collins, S. L., Wetherill, K. R., & Lightfoot, D. C. (2008). Aboveground net primary production dynamics in a northern Chihuahuan Desert ecosystem. *Oecologia*, 155(1), 123–132. https://doi.org/10.1007/s00442-007-0880-2

Munson, S. M., Muldavin, E. H., Belnap, J., Peters, D. P. C., Anderson, J. P., Reiser, M. H., Gallo, K., Melgoza-Castillo, A., Herrick, J. E., & Christiansen, T. A. (2013). Regional signatures of plant response to drought and elevated temperature across a desert ecosystem. *Ecology*, 94(9), 2030–2041. https://doi.org/10.1890/12-1586.1

Myers-Smith, I. H., & Hik, D. S. (2018). Climate warming as a driver of tundra shrubline advance. *Journal of Ecology*, 106(2), 547–560. https://doi.org/10.1111/1365-2745.12817

Nabel, J. E. M. S. (2015). Upscaling with the dynamic two-layer classification concept (D2C): TreeMig-2L, an efficient implementation of the forest-landscape model TreeMig. *Geoscientific Model Development*, 8(11), 3563–3577. https://doi.org/10.5194/gmd-8-3563-2015

Newman, E. A. (2019). Disturbance ecology in the Anthropocene. *Frontiers in Ecology and Evolution*, 7, 1–6. https://doi.org/10.3389/fevo.2019.00147

Nippert, J. B., & Knapp, A. K. (2007a). Linking water uptake with rooting patterns in grassland species. *Oecologia*, 153(2), 261–272. https://doi.org/10.1007/s00442-007-0745-8

Nippert, J. B., & Knapp, A. K. (2007b). Soil water partitioning contributes to species coexistence in tallgrass prairie. *Oikos*, 116(6), 1017–1029. https://doi.org/10.1111/j.0030-1299.2007.15630.x

Novick, K. A., Biederman, J. A., Desai, A. R., Litvak, M. E., Moore, D. J. P., Scott, R. L., & Torn, M. S. (2018). The AmeriFlux network: A coalition of the willing. *Agricultural and Forest Meteorology*, 249, 444–456. https://doi.org/10.1016/j.agrformet.2017.10.009

Noy-Meir, I. (1973). Desert ecosystems: Environment and producers. *Annual Review of Ecology and Systematics*, 4(1), 25–51. https://doi.org/10.1146/annurev.es.04.110173.000325

Ocheltree, T. W., Mueller, K. M., Chesus, K., LeCain, D. R., Kray, J. A., & Blumenthal, D. M. (2020). Identification of suites of traits that

explains drought resistance and phenological patterns of plants in a semi-arid grassland community. *Oecologia*, 192(1), 55–66. https://doi.org/10.1007/s00442-019-04567-x

Ocheltree, T. W., Nippert, J. B., & Prasad, P. V. V. (2016). A safety vs efficiency trade-off identified in the hydraulic pathway of grass leaves is decoupled from photosynthesis, stomatal conductance and precipitation. *New Phytologist*, 210(1), 97–107. https://doi.org/10.1111/nph.13781

Ogle, S. M., Reiners, W. A., & Gerow, K. G. (2003). Impacts of exotic annual brome grasses (Bromus spp.) on ecosystem properties of northern mixed grass prairie. *The American Midland Naturalist*, 149(1), 46–58. https://doi.org/10.1674/0003-0031(2003)149[0046:IOEABG]2.0.CO;2

Ojima, D. S., Schimel, D. S., Parton, W. J., & Owensby, C. E. (1994). Long- and short-term effects of fire on nitrogen cycling in tallgrass prairie. *Biogeochemistry*, 24(2), 67–84. https://doi.org/10.1007/BF02390180

Oleson, K., Dai, Y., Bonan, B., Bosilovichm, M., Dickinson, R., Dirmeyer, P., Hoffman, F., Houser, P., Levis, S., Niu, G. Y., & Thornton, P. (2004). Technical description of the community land model (CLM).

Ott, J. P., & Hartnett, D. C. (2015). Bud bank dynamics and clonal growth strategy in the rhizomatous grass, *Pascopyrum smithii*. *Plant Ecology*, 216(3), 395–405. https://doi.org/10.1007/s11258-014-0444-6

Pacala, S. W., Canham, C. D., Saponara, J., Silander, J. A., Jr., Kobe, R. K., & Ribbens, E. (1996). Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecological Monographs*, 66(1), 1–43. https://doi.org/10.2307/2963479

Pacala, S. W., Canham, C. D., & Silander, J. A., Jr. (1993). Forest models defined by field measurements: I. The design of a northeastern forest simulator. *Canadian Journal of Forest Research*, 23(10), 1980–1988. https://doi.org/10.1139/x93-249

Parton, W., Scurlock, J., Ojima, D., Gilmanov, T., Scholes, R. J., Schimel, D. S., Kirchner, T., Menaut, J.-C., Seastedt, T., Garcia Moya, E., Kamnalrut, A., & Kinyamario, J. (1993). Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles*, 7(4), 785–809.

Parvin, S., Uddin, S., Fitzgerald, G. J., Tausz-Posch, S., Armstrong, R., & Tausz, M. (2019). Free air CO_2 enrichment (FACE) improves water use efficiency and moderates drought effect on N_2 fixation of *Pisum sativum* L. *Plant and Soil*, 436(1), 587–606. https://doi.org/10.1007/s11104-019-03949-7

Petrie, M. D., Collins, S. L., Swann, A. M., Ford, P. L., & Litvak, M. E. (2015). Grassland to shrubland state transitions enhance carbon sequestration in the northern Chihuahuan Desert. *Global Change Biology*, 21(3), 1226–1235. https://doi.org/10.1111/gcb.12743

Polley, H. W., Derner, J. D., Jackson, R. B., Wilsey, B. J., & Fay, P. A. (2014). Impacts of climate change drivers on C_4 grassland productivity: Scaling driver effects through the plant community. *Journal of Experimental Botany*, 65(13), 3415–3424. https://doi.org/10.1093/jxb/eru009

Poulter, B., Ciais, P., Hodson, E., Lischke, H., Maignan, F., Plummer, S., & Zimmermann, N. E. (2011). Plant functional type mapping for earth system models. *Geoscientific Model Development*, 4(4), 993–1010. https://doi.org/10.5194/gmd-4-993-2011

Powell, T. L., Galbraith, D. R., Christoffersen, B. O., Harper, A., Imbuzeiro, H. M. A., Rowland, L., Almeida, S., Brando, P. M., Costa, A. C. L., Costa, M. H., Levine, N. M., Malhi, Y., Saleska, S. R., Sotta, E., Williams, M., Meir, P., & Moorcroft, P. R. (2013). Confronting model predictions of carbon fluxes with measurements of Amazon forests subjected to experimental drought. *New Phytologist*, 200(2), 350–365. https://doi.org/10.1111/nph.12390

Prentice, I. C., Bondeau, A., Cramer, W., Harrison, S. P., Hickler, T., Lucht, W., Sitch, S., Smith, B., & Sykes, M. T. (2007). Dynamic global vegetation modeling: Quantifying terrestrial ecosystem responses to large-scale environmental change. In J. G. Canadell, D. E. Pataki, & L. F. Pitelka (Eds.), *Terrestrial ecosystems in a changing world* (pp. 175–192). Springer. https://doi.org/10.1007/978-3-540-32730-1_15

Rastetter, E. B., Kwiatkowski, B. L., Kicklighter, D. W., Barker Plotkin, A., Genet, H., Nippert, J. B., O'Keefe, K., Perakis, S. S., Porder, S., Roley, S. S., Ruess, R. W., Thompson, J. R., Wieder, W. R., Wilcox, K., & Yanai, R. D. (2022). N and P constrain C in ecosystems under climate change: Role of nutrient redistribution, accumulation, and stoichiometry. *Ecological Applications*, 32(8), 1–29. https://doi.org/10.1002/eap.2684

Sankaran, M., Ratnam, J., & Hanan, N. P. (2004). Tree–grass coexistence in savannas revisited—Insights from an examination of assumptions and mechanisms invoked in existing models. *Ecology Letters*, 7(6), 480–490. https://doi.org/10.1111/j.1461-0248.2004.00596.x

Sato, H., & Ise, T. (2012). Effect of plant dynamic processes on African vegetation responses to climate change: Analysis using the spatially explicit individual-based dynamic global vegetation model (SEIB-DGVM). *Journal of Geophysical Research Biogeosciences*, 117(G3), 1–18. https://doi.org/10.1029/2012JG002056

Scharfy, D., Güsewell, S., Gessner, M. O., & Venterink, H. O. (2010). Invasion of *Solidago gigantea* in contrasting experimental plant communities: Effects on soil microbes, nutrients and plant-soil feedbacks: Invasion of *Solidago gigantea* in contrasting experimental plant communities. *Journal of Ecology*, 98(6), 1379–1388. https://doi.org/10.1111/j.1365-2745.2010.01722.x

Scheiter, S., & Higgins, S. I. (2009). Impacts of climate change on the vegetation of Africa: An adaptive dynamic vegetation modelling approach. *Global Change Biology*, 15(9), 2224–2246. https://doi.org/10.1111/j.1365-2486.2008.01838.x

Scheiter, S., Langan, L., & Higgins, S. I. (2013). Next-generation dynamic global vegetation models: Learning from community ecology. *New Phytologist*, 198(3), 957–969. https://doi.org/10.1111/nph.12210

Scholes, R. J., & Archer, S. R. (1997). Tree-grass interactions in savannas. *Annual Review of Ecology and Systematics*, 28(1), 517–544. https://doi.org/10.1146/annurev.ecolsys.28.1.517

Schubert, S. D., Suarez, M. J., Pegion, P. J., Koster, R. D., & Bacmeister, J. T. (2004). On the Cause of the 1930s Dust Bowl. *Science*, 303(5665), 1855–1859. https://doi.org/10.1126/science.1095048

Scott, P. R., & Sudmeyer, R. A. (1993). Evapotranspiration from agricultural plant communities in the high rainfall zone of the southwest of Western Australia. *Journal of Hydrology*, 146, 301–319. https://doi.org/10.1016/0022-1694(93)90281-D

Seabloom, E. W., Adler, P. B., Alberti, J., Biederman, L., Buckley, Y. M., Cadotte, M. W., Collins, S. L., Dee, L., Fay, P. A., Firn, J., Hagenah, N., Harpole, W. S., Hautier, Y., Hector, A., Hobbie, S. E., Isbell, F., Knops, J. M. H., Komatsu, K. J., Laungani, R., … Borer, E. T. (2021). Increasing effects of chronic nutrient enrichment on plant diversity loss and ecosystem productivity over time. *Ecology*, 102(2), e03218. https://doi.org/10.1002/ecy.3218

Semmartin, M., & Ghersa, C. M. (2006). Intraspecific changes in plant morphology, associated with grazing, and effects on litter quality, carbon and nutrient dynamics during decomposition. *Austral Ecology*, 31(1), 99–105. https://doi.org/10.1111/j.1442-9993.2006.01556.x

Serraj, R., Sinclair, T. R., & Purcell, L. C. (1999). Symbiotic N_2 fixation response to drought. *Journal of Experimental Botany*, 50(331), 143–155. https://doi.org/10.1093/jxb/50.331.143

Shaw, E. A., White, C. T., Silver, W. L., Suding, K. N., & Hallett, L. M. (2022). Intra-annual precipitation effects on annual grassland productivity and phenology are moderated by community responses. *Journal of Ecology*, 110(1), 162–172. https://doi.org/10.1111/1365-2745.13792

Shi, Z., Lin, Y., Wilcox, K. R., Souza, L., Jiang, L., Jiang, J., Jung, C. G., Xu, X., Yuan, M., Guo, X., Wu, L., Zhou, J., & Luo, Y. (2018). Successional change in species composition alters climate sensitivity of grassland productivity. *Global Change Biology*, 24(10), 4993–5003. https://doi.org/10.1111/gcb.14333

Shmida, A., & Wilson, M. V. (1985). Biological determinants of species diversity. *Journal of Biogeography*, 12(1), 1–20. https://doi.org/10.2307/2845026

Shugart, H. H., Smith, T. M., & Post, W. M. (1992). The potential for application of individual-based simulation models for assessing the effects of global change. *Annual Review of Ecology and Systematics*, 23(1), 15–38. https://doi.org/10.1146/annurev.es.23.110192.000311

Shugart, H. H., Wang, B., Fischer, R., Ma, J., Fang, J., Yan, X., Huth, A., & Armstrong, A. H. (2018). Gap models and their individual-based relatives in the assessment of the consequences of global change. *Environmental Research Letters*, 13(3), 33001. https://doi.org/10.1088/1748-9326/aaaacc

Simkin, S. M., Allen, E. B., Bowman, W. D., Clark, C. M., Belnap, J., Brooks, M. L., Cade, B. S., Collins, S. L., Geiser, L. H., Gilliam, F. S., Jovan, S. E., Pardo, L. H., Schulz, B. K., Stevens, C. J., Suding, K. N., Throop, H. L., & Waller, D. M. (2016). Conditional vulnerability of plant diversity to atmospheric nitrogen deposition across the United States. *Proceedings of the National Academy of Sciences of the United States of America*, 113(15), 4086–4091. https://doi.org/10.1073/pnas.1515241113

Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., Betts, R., Ciais, P., Cox, P., Friedlingstein, P., Jones, C. D., Prentice, I. C., & Woodward, F. I. (2008). Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five dynamic global vegetation models (DGVMs): Uncertainty in land carbon cycle feedbacks. *Global Change Biology*, 14(9), 2015–2039. https://doi.org/10.1111/j.1365-2486.2008.01626.x

Smith, B., Wårlind, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., & Zaehle, S. (2013). Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model [preprint]. *Biogeochemistry: Modelling, Terrestrial*, 11, 2027–2054. https://doi.org/10.5194/bgd-10-18613-2013

Smith, J. T., Allred, B. W., Boyd, C. S., Davies, K. W., Jones, M. O., Kleinhesselink, A. R., Maestas, J. D., Morford, S. L., & Naugle, D. E. (2022). The elevational ascent and spread of exotic annual grass dominance in the Great Basin, USA. *Diversity and Distributions*, 28(1), 83–96. https://doi.org/10.1111/ddi.13440

Smith, M. D., Knapp, A. K., & Collins, S. L. (2009). A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology*, 90(12), 3279–3289. https://doi.org/10.1890/08-1815.1

Smith, M. D., La Pierre, K. J., Collins, S. L., Knapp, A. K., Gross, K. L., Barrett, J. E., Frey, S. D., Gough, L., Miller, R. J., Morris, J. T., Rustad, L. E., & Yarie, J. (2015). Global environmental change and the nature of aboveground net primary productivity responses: Insights from long-term experiments. *Oecologia*, 177(4), 935–947. https://doi.org/10.1007/s00442-015-3230-9

Smith, S. E., & Read, D. (2008). The symbionts forming arbuscular mycorrhizas. *Mycorrhizal Symbiosis*, 13–41. https://doi.org/10.1016/b978-012370526-6.50003-9

Stanescu, S., & Maherali, H. (2017). Arbuscular mycorrhizal fungi alter the competitive hierarchy among old-field plant species. *Oecologia*, 183(2), 479–491. https://doi.org/10.1007/s00442-016-3771-6

Staver, A. C., & Bond, W. J. (2014). Is there a 'browse trap'? Dynamics of herbivore impacts on trees and grasses in an African savanna. *Journal of Ecology*, 102(3), 595–602. https://doi.org/10.1111/1365-2745.12230

Staver, A. C., Bond, W. J., Stock, W. D., van Rensburg, S. J., & Waldram, M. S. (2009). Browsing and fire interact to suppress tree density in an African savanna. *Ecological Applications*, 19(7), 1909–1919. https://doi.org/10.1890/08-1907.1

Stevens, C. J., David, T. I., & Storkey, J. (2018). Atmospheric nitrogen deposition in terrestrial ecosystems: Its impact on plant communities and consequences across trophic levels. *Functional Ecology*, 32(7), 1757–1769. https://doi.org/10.1111/1365-2435.13063

Stevens, C. J., Dise, N. B., Mountford, J. O., & Gowing, D. J. (2004). Impact of nitrogen deposition on the species richness of grasslands. *Science*, 303(5665), 1876–1879. https://doi.org/10.1126/science.1094678

Stevens, C. J., Lind, E. M., Hautier, Y., Harpole, W. S., Borer, E. T., Hobbie, S., Seabloom, E. W., Ladwig, L., Bakker, J. D., Chu, C., Collins, S., Davies, K. F., Firn, J., Hillebrand, H., Pierre, K. J. L., MacDougall, A., Melbourne, B., McCulley, R. L., Morgan, J., ... Wragg, P. D. (2015). Anthropogenic nitrogen deposition predicts local grassland primary production worldwide. *Ecology*, 96(6), 1459–1465. https://doi.org/10.1890/14-1902.1

Still, C. J., Cotton, J. M., & Griffith, D. M. (2019). Assessing earth system model predictions of C_4 grass cover in North America: From the glacial era to the end of this century. *Global Ecology and Biogeography*, 28(2), 145–157. https://doi.org/10.1111/geb.12830

Strigul, N., Pristinski, D., Purves, D., Dushoff, J., & Pacala, S. (2008). Scaling from trees to forests: Tractable macroscopic equations for forest dynamics. *Ecological Monographs*, 78(4), 523–545. https://doi.org/10.1890/08-0082.1

Stuart-Haëntjens, E., De Boeck, H. J., Lemoine, N. P., Mänd, P., Kröel-Dulay, G., Schmidt, I. K., Jentsch, A., Stampfli, A., Anderegg, W. R. L., Bahn, M., Kreyling, J., Wohlgemuth, T., Lloret, F., Classen, A. T., Gough, C. M., & Smith, M. D. (2018). Mean annual precipitation predicts primary production resistance and resilience to extreme drought. *Science of the Total Environment*, 636, 360–366. https://doi.org/10.1016/j.scitotenv.2018.04.290

Suding, K. N., Collins, S. L., Gough, L., Clark, C., Cleland, E. E., Gross, K. L., Milchunas, D. G., & Pennings, S. (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, 102(12), 4387–4392. https://doi.org/10.1073/pnas.0408648102

Suding, K. N., Lavorel, S., Chapin, F. S., Cornelissen, J. H. C., Díaz, S., Garnier, E., Goldberg, D., Hooper, D. U., Jackson, S. T., & Navas, M.-L. (2008). Scaling environmental change through the community-level: A trait-based response-and-effect framework for plants. *Global Change Biology*, 14(5), 1125–1140. https://doi.org/10.1111/j.1365-2486.2008.01557.x

Sun, G., Coffin, D. P., & Lauenroth, W. K. (1997). Comparison of root distributions of species in north American grasslands using GIS. *Journal of Vegetation Science*, 8(4), 587–596. https://doi.org/10.2307/3237211

Sundqvist, M. (2011). *Nitrogen and phosphorus dynamics across an elevational gradient in a Swedish subarctic tundra*. Department of Forest Ecology and Management, Swedish University of Agricultural Sciences.

Swenson, S. C., & Lawrence, D. M. (2014). Assessing a dry surface layer-based soil resistance parameterization for the Community Land Model using GRACE and FLUXNET-MTE data. *Journal of Geophysical Research: Atmospheres*, 119(17), 10,299–10,312. https://doi.org/10.1002/2014JD022314

Tang, X., Cui, Y., Li, N., Fu, Y., Liu, X., Run, Y., Li, M., Zhao, G., & Dong, J. (2020). Human activities enhance radiation forcing through surface albedo associated with vegetation in Beijing. *Remote Sensing*, 12(5), Article 5. https://doi.org/10.3390/rs12050837

Taylor, B. N., Simms, E. L., & Komatsu, K. J. (2020). More than a functional group: Diversity within the legume–rhizobia mutualism and its relationship with ecosystem function. *Diversity*, 12(2), Article 2. https://doi.org/10.3390/d12020050

Thackeray, C. W., Hall, A., Norris, J., & Chen, D. (2022). Constraining the increased frequency of global precipitation extremes under warming. *Nature Climate Change*, 12(5), Article 5. https://doi.org/10.1038/s41558-022-01329-1

Thonicke, K., Spessa, A., Prentice, I. C., Harrison, S. P., Dong, L., & Carmona-Moreno, C. (2010). The influence of vegetation, fire spread and fire behaviour on biomass burning and trace gas emissions: Results from a process-based model. *Biogeosciences*, 7(6), 1991–2011. https://doi.org/10.5194/bg-7-1991-2010

Tilman, D. (1981). Tests of resource competition theory using four species of Lake Michigan algae. *Ecology*, *62*(3), 802–815. https://doi.org/10.2307/1937747

Tilman, D. (2020). *Plant strategies and the dynamics and structure of plant communities (MPB-26), volume 26* (Vol. *102*). Princeton University Press.

Tognetti, P. M., Prober, S. M., Báez, S., Chaneton, E. J., Firn, J., Risch, A. C., Schuetz, M., Simonsen, A. K., Yahdjian, L., Borer, E. T., Seabloom, E. W., Arnillas, C. A., Bakker, J. D., Brown, C. S., Cadotte, M. W., Caldeira, M. C., Daleo, P., Dwyer, J. M., Fay, P. A., … Sankaran, M. (2021). Negative effects of nitrogen override positive effects of phosphorus on grassland legumes worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, *118*(28), e2023718118. https://doi.org/10.1073/pnas.2023718118

Turner, M. G. (2010). Disturbance and landscape dynamics in a changing world. *Ecology*, *91*(10), 2833–2849. https://doi.org/10.1890/10-0097.1

Unger, S., Friede, M., Hundacker, J., Volkmar, K., & Beyschlag, W. (2016). Allocation trade-off between root and mycorrhizal surface defines nitrogen and phosphorus relations in 13 grassland species. *Plant and Soil*, *407*(1), 279–292. https://doi.org/10.1007/s11104-016-2994-y

Van Der Heijden, M. G. A., Bardgett, R. D., & Van Straalen, N. M. (2008). The unseen majority: Soil microbes as drivers of plant diversity and productivity in terrestrial ecosystems. *Ecology Letters*, *11*(3), 296–310. https://doi.org/10.1111/j.1461-0248.2007.01139.x

Van Dyke, M. N., Levine, J. M., & Kraft, N. J. B. (2022). Small rainfall changes drive substantial changes in plant coexistence. *Nature*, *611*(7936), 507–511. https://doi.org/10.1038/s41586-022-05391-9

Venable, D. L. (2007). Bet hedging in a guild of desert annuals. *Ecology*, *88*(5), 1086–1090. https://doi.org/10.1890/06-1495

Vinton, M. A., & Burke, I. C. (1995). Interactions between individual plant species and soil nutrient status in shortgrass steppe. *Ecology*, *76*(4), 1116–1133. https://doi.org/10.2307/1940920

Walker, A. P., Zaehle, S., Medlyn, B. E., De Kauwe, M. G., Asao, S., Hickler, T., Parton, W., Ricciuto, D. M., Wang, Y.-P., Wårlind, D., & Norby, R. J. (2015). Predicting long-term carbon sequestration in response to CO_2 enrichment: How and why do current ecosystem models differ? *Global Biogeochemical Cycles*, *29*(4), 476–495. https://doi.org/10.1002/2014GB004995

Wang, S., & Loreau, M. (2016). Biodiversity and ecosystem stability across scales in metacommunities. *Ecology Letters*, *19*(5), 510–518. https://doi.org/10.1111/ele.12582

Wang, Y.-R., Hessen, D. O., Samset, B. H., & Stordal, F. (2022). Evaluating global and regional land warming trends in the past decades with both MODIS and ERA5-land land surface temperature data. *Remote Sensing of Environment*, *280*, 113181. https://doi.org/10.1016/j.rse.2022.113181

Ward, D. (2005). Do we understand the causes of bush encroachment in African savannas? *African Journal of Range & Forage Science*, *22*(2), 101–105. https://doi.org/10.2989/10220110509485867

Ward, D., Wiegand, K., & Getzin, S. (2013). Walter's two-layer hypothesis revisited: Back to the roots! *Oecologia*, *172*(3), 617–630. https://doi.org/10.1007/s00442-012-2538-y

Weaver, J. E. (1954). *North American prairie*. Johnson Publishing Company.

Weaver, J. E. (1958). Summary and interpretation of underground development in natural grassland communities. *Ecological Monographs*, *28*(1), 55–78. https://doi.org/10.2307/1942275

Wen, Z., Li, H., Shen, Q., Tang, X., Xiong, C., Li, H., Pang, J., Ryan, M. H., Lambers, H., & Shen, J. (2019). Tradeoffs among root morphology, exudation and mycorrhizal symbioses for phosphorus-acquisition strategies of 16 crop species. *New Phytologist*, *223*(2), 882–895. https://doi.org/10.1111/nph.15833

Weng, E., Aleinov, I., Singh, R., Puma, M. J., McDermid, S. S., Kiang, N. Y., Kelley, M., Wilcox, K., Dybzinski, R., Farrior, C. E., Pacala, S. W., & Cook, B. I. (2022). Modeling demographic-drivenvegetation dynamics and ecosystem biogeochemical cycling in NASA GISS's Earthsystem model (ModelE-BiomeE v.1.0). *Geoscientific Model Development*, *15*(22), 8153–8180. https://doi.org/10.5194/gmd-15-8153-2022

Weng, E., & Luo, Y. (2008). Soil hydrologicalproperties regulate grassland ecosystem responses to multifactor global change: A modeling analysis. *Journal of Geophysical Research: Biogeosciences*, *113*(G3). https://doi.org/10.1029/2007JG000539

Weng, E., Dybzinski, R., Farrior, C. E., & Pacala, S. W. (2019). Competition alters predicted forest carbon cycle responses to nitrogen availability and elevated CO_2: Simulations using an explicitly competitive, game-theoretic vegetation demographic model. *Biogeosciences*, *16*(23), 4577–4599. https://doi.org/10.5194/bg-16-4577-2019

Weng, E., Farrior, C. E., Dybzinski, R., & Pacala, S. W. (2017). Predicting vegetation type through physiological and environmental interactions with leaf traits: Evergreen and deciduous forests in an earth system modeling framework. *Global Change Biology*, *23*(6), 2482–2498. https://doi.org/10.1111/gcb.13542

Weng, E. S., Malyshev, S., Lichstein, J. W., Farrior, C. E., Dybzinski, R., Zhang, T., Shevliakova, E., & Pacala, S. W. (2015). Scaling from individual trees to forests in an earth system modeling framework using a mathematically tractable model of height-structured competition. *Biogeosciences*, *12*(9), 2655–2694. https://doi.org/10.5194/bg-12-2655-2015

White, R. P., Murray, S., Rohweder, M., Prince, S., & Thompson, K. (2000). *Grassland ecosystems*. World Resources Institute.

Wigley, B. J., Charles-Dominique, T., Hempson, G. P., Stevens, N., TeBeest, M., Archibald, S., Bond, W. J., Bunney, K., Coetsee, C., Donaldson, J., Fidelis, A., Gao, X., Gignoux, J., Lehmann, C., Massad, T. J., Midgley, J. J., Millan, M., Schwilk, D., Siebert, F., … Kruger, L. M. (2020). A handbook for the standardised sampling of plant functional traits in disturbance-prone ecosystems, with a focus on open ecosystems. *Australian Journal of Botany*, *68*(8), 473. https://doi.org/10.1071/BT20048

Wilcox, K. R. (2023). Catching up with the trees: Empirical advancements to improve herbaceous representation in models. *New Phytologist*, *239*(2), 452–455. https://doi.org/10.1111/nph.19013

Wilcox, K. R., Blair, J. M., Smith, M. D., & Knapp, A. K. (2016). Does ecosystem sensitivity to precipitation at the site-level conform to regional-scale predictions? *Ecology*, *97*(3), 561–568. https://doi.org/10.1890/15-1437.1

Wilcox, K. R., Koerner, S. E., Hoover, D. L., Borkenhagen, A. K., Burkepile, D. E., Collins, S. L., Hoffman, A. M., Kirkman, K. P., Knapp, A. K., Strydom, T., Thompson, D. I., & Smith, M. D. (2020). Rapid recovery of ecosystem function following extreme drought in a South African savanna grassland. *Ecology*, *101*(4), 1–9. https://doi.org/10.1002/ecy.2983

Wilcox, K. R., Komatsu, K. J., Avolio, M. L., & C2E Consortium. (2020). Improving collaborations between empiricists and modelers to advance grassland community dynamics in ecosystem models. *New Phytologist*, *228*(5), 1467–1471. https://doi.org/10.1111/nph.16900

Wilcox, K. R., Tredennick, A. T., Koerner, S. E., Grman, E., Hallett, L. M., Avolio, M. L., La Pierre, K. J., Houseman, G. R., Isbell, F., Johnson, D. S., Alatalo, J. M., Baldwin, A. H., Bork, E. W., Boughton, E. H., Bowman, W. D., Britton, A. J., Cahill, J. F., Collins, S. L., Du, G., … Zhang, Y. (2017). Asynchrony among local communities stabilises ecosystem function of metacommunities. *Ecology Letters*, *20*(12), 1534–1545. https://doi.org/10.1111/ele.12861

Williams, A., & Vries, F. T. (2020). Plant root exudation under drought: Implications for ecosystem functioning. *New Phytologist*, *225*(5), 1899–1905. https://doi.org/10.1111/nph.16223

Woodward, F. I., Smith, T. M., & Emanuel, W. R. (1995). A global land primary productivity and phytogeography model. *Global Biogeochemical Cycles*, *9*(4), 471–490. https://doi.org/10.1029/95GB02432

Wullschleger, S. D., Epstein, H. E., Box, E. O., Euskirchen, E. S., Goswami, S., Iversen, C. M., Kattge, J., Norby, R. J., van Bodegom, P. M., & Xu,

X. (2014). Plant functional types in Earth system models: Past experiences and future directions for application of dynamic vegetation models in high-latitude ecosystems. *Annals of Botany*, 114(1), 1–16. https://doi.org/10.1093/aob/mcu077

Xu, X., Shi, Z., Li, D., Zhou, X., Sherry, R. A., & Luo, Y. (2015). Plant community structure regulates responses of prairie soil respiration to decadal experimental warming. *Global Change Biology*, 21(10), 3846–3853. https://doi.org/10.1111/gcb.12940

Yang, H., Li, Y., Wu, M., Zhang, Z., Li, L., & Wan, S. (2011). Plant community responses to nitrogen addition and increased precipitation: The importance of water availability and species traits. *Global Change Biology*, 17(9), 2936–2944. https://doi.org/10.1111/j.1365-2486.2011.02423.x

Yu, Q., Elser, J. J., He, N., Wu, H., Chen, Q., Zhang, G., & Han, X. (2011). Stoichiometric homeostasis of vascular plants in the Inner Mongolia grassland. *Oecologia*, 166(1), 1–10. https://doi.org/10.1007/s00442-010-1902-z

Yu, Q., Wilcox, K., Pierre, K. L., Knapp, A. K., Han, X., & Smith, M. D. (2015). Stoichiometric homeostasis predicts plant species dominance, temporal stability, and responses to global change. *Ecology*, 96(9), 2328–2335. https://doi.org/10.1890/14-1897.1

Zaehle, S., Medlyn, B. E., De Kauwe, M. G., Walker, A. P., Dietze, M. C., Hickler, T., Luo, Y., Wang, Y.-P., El-Masri, B., Thornton, P., Jain, A., Wang, S., Warlind, D., Weng, E., Parton, W., Iversen, C. M., Gallet-Budynek, A., McCarthy, H., Finzi, A., … Norby, R. J. (2014). Evaluation of 11 terrestrial carbon–nitrogen cycle models against observations from two temperate free-air CO_2 enrichment studies. *New Phytologist*, 202(3), 803–822. https://doi.org/10.1111/nph.12697

Zhao, M., Golaz, J.-C., Held, I. M., Guo, H., Balaji, V., Benson, R., Chen, J.-H., Chen, X., Donner, L. J., Dunne, J. P., Dunne, K., Durachta, J., Fan, S.-M., Freidenreich, S. M., Garner, S. T., Ginoux, P., Harris, L. M., Horowitz, L. W., Krasting, J. P., … Xiang, B. (2018). The GFDL global atmosphere and land model AM4.0/LM4.0: 1 simulation characteristics with prescribed SSTs. *Journal of Advances in Modeling Earth Systems*, 10(3), 691–734. https://doi.org/10.1002/2017MS001208

Zhou, D., Hao, L., Kim, J. B., Liu, P., Pan, C., Liu, Y., & Sun, G. (2019). Potential impacts of climate change on vegetation dynamics and ecosystem function in a mountain watershed on the Qinghai-Tibet Plateau. *Climatic Change*, 156(1), 31–50. https://doi.org/10.1007/s10584-019-02524-4

Zhou, Q., & Yu, B. (2010). Changes in content of free, conjugated and bound polyamines and osmotic adjustment in adaptation of vetiver grass to water deficit. *Plant Physiology and Biochemistry*, 48(6), 417–425. https://doi.org/10.1016/j.plaphy.2010.03.003

Zomer, M. A., & Ramsay, P. M. (2021). Post-fire changes in plant growth form composition and diversity in Andean páramo grassland. *Applied Vegetation Science*, 24(1), e12554. https://doi.org/10.1111/avsc.12554

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.