

## Viewpoints

# Lineage-based functional types: characterising functional diversity to enhance the representation of ecological behaviour in Land Surface Models

## Summary

Process-based vegetation models attempt to represent the wide range of trait variation in biomes by grouping ecologically similar species into plant functional types (PFTs). This approach has been successful in representing many aspects of plant physiology and biophysics but struggles to capture biogeographic history and ecological dynamics that determine biome boundaries and plant distributions. Grass-dominated ecosystems are broadly distributed across all vegetated continents and harbour large functional diversity, yet most Land Surface Models (LSMs) summarise grasses into two generic PFTs based primarily on differences between temperate C<sub>3</sub> grasses and (sub)tropical C<sub>4</sub> grasses. Incorporation of species-level trait variation is an active area of research to enhance the ecological realism of PFTs, which form the basis for vegetation processes and dynamics in LSMs. Using reported measurements, we developed grass functional trait values (physiological, structural, biochemical, anatomical, phenological, and disturbance-related) of dominant lineages to improve LSM representations. Our method is fundamentally different from previous efforts, as it uses phylogenetic relatedness to create lineage-based functional types (LFTs), situated between species-level trait data and PFT-level abstractions, thus providing a realistic representation of functional diversity and opening the door to the development of new vegetation models.

## Introduction

Functional trait variation within biomes arises from evolutionary histories that vary biogeographically, leading to plant taxa with differing ecological behaviour and differences in ecosystem structure and function across continents (Lehmann *et al.*, 2014; Higgins *et al.*, 2016; Griffith *et al.*, 2019). Land Surface Models (LSMs), fundamental components of Earth System Models, typically apply abstracted plant functional types (PFTs; but see Pavlick *et al.*, 2013;

Scheiter *et al.*, 2013; Medlyn *et al.*, 2016) to represent physical, biological and chemical processes crucial for soil and climate-related decision making and policy. However, PFTs must generalise across species, and inevitably encapsulate a wide range of plant strategies and vegetation dynamics, a demand that contrasts with efforts to investigate nuanced and species specific ecological behaviour (Cramer *et al.*, 2001; Bonan, 2008; Sitch *et al.*, 2008; Kattge *et al.*, 2011). Furthermore, PFTs account for only a modest degree of variation in a wide array of functional traits, ranging from seed mass to leaf lifespan (LL), in the TRY database (Kattge *et al.*, 2011). For example, standard PFTs may not generally capture key drought responses in tree species (Anderegg, 2015), although models with a hydraulics module can be specifically applied for this purpose (e.g. *ecosys*; Grant *et al.*, 1995). Oversimplification of the physiognomic characteristics of PFTs can have major unintended consequences when simulating ecosystem function (Griffith *et al.*, 2017a), such as highly biodiverse savanna ecosystems (Searchinger *et al.*, 2015). However, studies that explicitly incorporate species-level trait variation into vegetation models (e.g. Grant *et al.*, 1995, 2019; Sakschewski *et al.*, 2016; Lu *et al.*, 2017; Mekonnen *et al.*, 2019) have demonstrated improvements in model performance. Selecting trait data from multivariate trait distributions for model parameterisation (Wang *et al.*, 2012; Pappas *et al.*, 2016) is very challenging for global modelling applications, particularly in hyperdiverse regions like the tropics, and may not be feasible for areas with biased or limited data. Until these data gaps are filled, a finer-grained representation of the functional diversity among species might be achieved by reorganising PFTs based on trade-offs and evolutionary relatedness.

Importantly, in seeking approaches to restructure PFTs, numerous observations over the last decade have shown that both plant traits and biome occupancy are commonly phylogenetically conserved, with closely related species having similar traits and niches (e.g. Cavender-Bares *et al.*, 2009, 2016; Crisp *et al.*, 2009; Liu *et al.*, 2012; Donoghue & Edwards, 2014; Coelho de Souza *et al.*, 2016). The existence of strong evolutionary constraints on plant functioning and distribution suggests that, as an alternative, vegetation types should be organised in a manner consistent with phylogeny. Eco-evolutionary models have increased our mechanistic understanding of ecological patterns in fields ranging from community ecology (e.g. Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009) to global biogeography (e.g. the Latitudinal Diversity Gradient; Visser *et al.*, 2014; Pontarp *et al.*, 2019). We advocate for explicit inclusion of evolutionary history and a consistent framework for integrating traits into global vegetation models. This approach brings a testable method for defining vegetation types, enables the functional traits of uncharacterised species to be inferred from relatives, and allows evolutionary history to be explicitly considered in studies of biome history. Here, we illustrate this approach for grasses and grass-dominated ecosystems, where

we use our framework to aggregate species into lineage-based functional types (LFTs) to capture the species-level trait diversity in a tractable manner for large-scale vegetation process models used in LSMs. Capturing the evolutionary history of woody plants is also critical to understanding variation in ecosystems function in savannas (Lehmann *et al.*, 2014; Osborne *et al.*, 2018), and in general we are advocating for the development of LFTs in other vegetation types and in other ecosystems. Grasses provide a tractable demonstration for the utility of LFTs; we also discuss the potential to significantly improve ecological and biogeographical representations of other plants in LSMs.

Grasses are one of the most ecologically successful plant types on Earth (Linder *et al.*, 2018) and provide great opportunity for increasing understanding of plant functional diversity. Ecosystems containing or dominated by grasses (i.e. temperate, tropical, and subtropical grasslands and savannas) account for a >40% of global land area and productivity, and are a staple for humanity's sustenance (Tilman *et al.*, 2002; Still *et al.*, 2003; Asner *et al.*, 2004; Gibson, 2009). The photosynthetic pathway composition ( $C_3$  or  $C_4$ ) of grass species is a fundamental aspect of grassland and savanna function, ecology and biogeography. Of the *c.* 11 000 grass species on Earth, some *c.* 4500 use the  $C_4$  photosynthetic pathway (Osborne *et al.*, 2014). Although they account for <2% of all vascular plant species (Kellogg, 2001),  $C_4$  grasses are estimated to account for 20–25% of terrestrial productivity (Still *et al.*, 2003), having risen to such prominence only in the last 8 Myr (Edwards *et al.*, 2010). Dominance by  $C_4$  vs  $C_3$  grasses has major influences on gross primary productivity and ecosystem structure and function (Still *et al.*, 2003) and strongly influences interannual variability of the global carbon cycle, due to a combination of ecological and climatic factors (Poulter *et al.*, 2014; Griffith *et al.*, 2015). Dynamic vegetation models largely fail to reproduce spatial patterns of grass cover – both past and present – and productivity at regional to continental scales, limiting ability to predict future plant community changes (Fox *et al.*, 2018; Still *et al.*, 2018). As a consequence, LSMs require significant improvement to adequately represent vegetation responses to increasing  $CO_2$  (De Kauwe *et al.*, 2016; Smith *et al.*, 2016). Many models also miss key transitions between biome states (e.g. Still *et al.*, 2018) that exist as a result of disturbance or biogeographic history (e.g. Staver *et al.*, 2011; Dexter *et al.*, 2018).

Most LSMs classify grasses into two PFTs based on differences between temperate  $C_3$  grasses and subtropical and tropical  $C_4$  grasses. However, grass ecological adaptations and physiological properties are highly diverse, ranging from cold-specialised to fire- and herbivore-dependent species. While grasses are often equated functionally, in reality they exhibit a high degree of variation in hydraulic, leaf economic and phenological traits (Taylor *et al.*, 2010; Liu *et al.*, 2012) that are likely to explain their broad geographic dominance in different regions (Edwards *et al.*, 2010; Visser *et al.*, 2014). These differences include economically important forest-forming grasses such as bamboos, although here we focus on globally dominant herbaceous lineages. Grasses exhibit strong phylogenetic diversity in leaf economics variation and associations with disturbance (Taylor *et al.*, 2010; Liu *et al.*, 2012; Simpson *et al.*, 2016). Disturbances such as fire and herbivory have

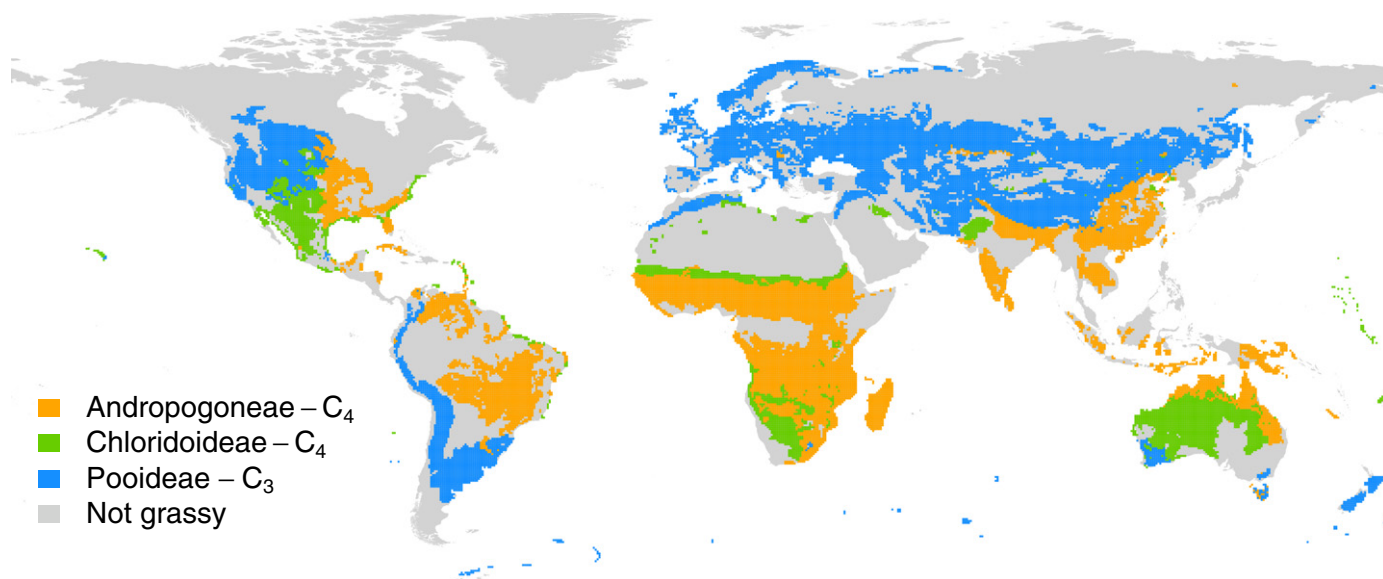
large impacts on ecosystem function and distributions, and PFT-based approaches are unlikely to capture these differences among lineages. At broad phylogenetic and spatial scales, niche and biome conservatism of major plant lineages is common (Crisp *et al.*, 2009; Becklin *et al.*, 2014; Cornwell *et al.*, 2014; Donoghue & Edwards, 2014) and we therefore argue that evolution and biogeography provide a framework for aggregating species (across ecosystems and strata) into LFTs that capture species-level trait diversity in a way that can be feasibly incorporated for use in global vegetation models and that will improve PFT-based modelling approaches. Focusing on grasses, we developed this approach by collecting grass traits from databases (e.g. Osborne *et al.*, 2011) and literature (e.g. Atkinson *et al.*, 2016; Supporting Information Methods S1), for five key categories (physiology, structure, biochemistry, phenology and disturbance). We summarise these species traits at the lineage level and relate these functional types to their observed global distributions.

## Methods for establishing lineage-based functional types (LFTs) for grasses

There are 26 monophyletic  $C_4$  lineages described in the Poaceae family, yet only two (the Andropogoneae and Chloridoideae) account for most of the areal abundance of  $C_4$  grasses globally (Fig. 1; Edwards & Still, 2008; Edwards *et al.*, 2010; Grass Phylogeny Working Group II, 2012; Lehmann *et al.*, 2019). Among  $C_3$  grasses, only the Pooideae are globally dominant today. The Pooideae occupy cooler climates than the  $C_4$  Andropogoneae and Chloridoideae, which dominate in warm and wetter and drier climates, respectively. Therefore, we focused on collecting species-level trait data from the literature and from databases for grass species from these three lineages. The term 'trait' is defined differently across research disciplines (Violle *et al.*, 2007). Our aims necessitated a collection of broad trait space beyond that typically used for the leaf economic spectrum to include morphological and physiological determinants of plant hydraulics, physicochemical controls of photosynthesis, allocation to reproduction and spectral reflectance. Many traits are highly correlated, reflecting plant functional strategies. Furthermore, a single trait can relate to multiple forms of plant fitness. Here, traits were assigned to groups (Table 1) based on their use in models and how they might be used in future applications (e.g. hyperspectral remote sensing of LFTs, or modelling of fire). We present median and variation in trait values among species for three major grass lineages (LFTs) as per Fig. 1, and compare these with commonly used values for  $C_3$  and  $C_4$  PFTs (Table 1).

## LFTs for grasses differ drastically in key functional traits

Our LFTs demonstrate both the importance of considering lineage to explain ecological patterning, and the need for modification of current LSM PFT approaches. For instance,  $C_4$  plants typically have lower RuBisCO activity ( $V_{\max}$ ) but higher electron transport capacity ( $J_{\max}$ ) than  $C_3$  plants, reflecting both the additional energetic cost of  $C_4$  physiology and the greater efficiency of



**Fig. 1** Distributions of the three globally dominant grass lineages in the herbaceous layer. These data come from Lehmann *et al.* (2019) and show where each lineage is more abundant compared with the other two lineages based on a 0.5-degree grid.

RuBisCO in higher  $\text{CO}_2$  environments (Collatz *et al.*, 1998). The Chloridoideae ( $\text{C}_4$ ) grasses have intermediate  $V_{\text{cmax}}$  and  $J_{\text{max}}$  compared with the Andropogoneae ( $\text{C}_4$ ) and the Pooideae ( $\text{C}_3$ ) (Table 1). Furthermore, the Pooideae have evolved to tolerate much colder conditions (reflected in Trange; Sandve & Fjellheim, 2010; Vigeland *et al.*, 2013; McKeown *et al.*, 2016), and our results suggested that  $\text{C}_4$  lineages may differ in their thermal tolerances (Watcharamongkol *et al.*, 2018). These differences suggested that macroecological synthesis studies with global implications (e.g. Walker *et al.*, 2014; Heskell *et al.*, 2016) should, at minimum, include more grass species in their datasets, ideally organised as LFTs.

Trade-offs among adaptations and tolerances in natural systems promote coexistence among plant species (Tilman, 1988; Tilman & Pacala, 1993; Kneitel & Chase, 2004). Specific leaf area (SLA) measures the cost of constructing a leaf, which represents a trade-off between acquisitive (high relative growth rate) and conservative (high LL) plant strategies (Westoby, 1998; Westoby *et al.*, 2002; Wright *et al.*, 2004). Model simulations of growth are highly dependent on the value of SLA used (Körner, 1991; Sitch *et al.*, 2003; Bonan, 2008). However, in most of these LSMs,  $\text{C}_3$  grass PFTs have higher or similar SLA values as  $\text{C}_4$  PFTs are likely to bias predictions. By contrast, we found that the  $\text{C}_4$  LFTs had higher SLA than the  $\text{C}_3$  LFT, but SLA did not differ between the two dominant  $\text{C}_4$  grass lineages (Atkinson *et al.*, 2016). SLA can be highly variable within lineages in grasses, probably due to the importance of herbivore pressure as a competing demand on leaf economics (Anderson *et al.*, 2011; Griffith *et al.*, 2017b) as well as intraspecific variation. As a result, SLA highlighted that some traits are harder to generalise than others using the LFT approach and suggested that a range of values may be more appropriate than a single value for constraining LFT parameters. The phylogenetic signal among grass lineages is stronger for stature (Taylor *et al.*, 2010; Liu *et al.*, 2012), with the Andropogoneae being considerably taller on average than the Chloridoideae. This difference

suggests that not all traits are oriented along a fast–slow axis at broad taxonomic scales across  $\text{C}_3$  and  $\text{C}_4$  grass lineages (Reich, 2014; Díaz *et al.*, 2016; Archibald *et al.*, 2019). Furthermore, the  $\text{C}_3$ - and eudicot-centric approach in the current leaf economics framework suggested that a higher SLA should also correlate with a higher specific leaf nitrogen content, yet the evolution of  $\text{C}_4$  photosynthesis allows for a significant reduction in RuBisCO content, and hence plant nitrogen requirements (Taylor *et al.*, 2010). Thus, grass lineages differ in numerous leaf traits; this has consequences that extend from palatability and flammability to hydrological differences.

Physiological and morphological leaf vascular traits underlie variation in SLA, constrain the hydrology of plants (e.g. Blonder *et al.*, 2014; Sack *et al.*, 2014) and are key traits related to the evolution of  $\text{C}_4$  photosynthesis (Sage, 2004; Ueno *et al.*, 2006). We describe next key hydraulic differences between the two dominant  $\text{C}_4$  lineages that correspond to the  $\text{C}_4$  biochemical subtypes (Ueno *et al.*, 2006; Liu & Osborne, 2015). The Chloridoideae have low conductance and high embolism resistance hydraulic traits (Table 1), and tend to inhabit drier sites (Fig. 1). Some Andropogoneae have been described as ‘water spenders’ (Williams *et al.*, 1998), and their hydraulic traits help to explain their affinity with higher rainfall habitats where they rapidly expend available soil water (Taub, 2000) and promote fire after curing. These hydraulic differences should have large effects in models, especially those that consider tree–grass coexistence (Higgins *et al.*, 2000) and explicit representation of plant hydraulics (Grant *et al.*, 1995; Mekonnen *et al.*, 2019).

Lineages also differ in biogeochemical traits that influence nutrient turnover rates and the reflectance and absorbance properties of vegetation. For example, Andropogoneae have higher C : N than Chloridoideae grasses, likely to be a result of growth rate differences and the frequent association of Andropogoneae grasses with fire. Similarly, a greater proportion of N in Chloridoideae leaves is allocated to RuBisCO, which is related to  $V_{\text{cmax}}$



**Table 1** Common plant functional type (PFT) parameters from Land Surface Models (LSMs), and median lineage-based functional type (LFT) parameters (interquartile range (IQR) in parentheses, where calculable) for three dominant grass lineages, taken from the literature and trait databases.

Category	Parameter	PFT			LFT†		
		C <sub>4</sub>	C <sub>3</sub>	Source	Andropogoneae	Chloridoideae	Pooideae
Physiological	$V_{\text{cmax}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	39	90	1, 2	38	45.6 (4.4)	63.6 (28)
	$J_{\text{max}}$ ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	400	100	3	180	108.1 (43)	128.8 (45)
	Rd ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ )	0.8	1.1	1, 2	<b>0.9a (0.2)</b>	<b>2a (1.4)</b>	<b>0.9a (0.7)</b>
	Phi ( $\mu\text{mol } \mu\text{mol}^{-1}$ )	0.06	0.085	4, 5	0.06	0.06	0.09
	Trange ( $^{\circ}\text{C}$ )	< 15.5	> 15.5	6	> 5‡	> -5‡	> -30 and < 5‡
Structural	SLA ( $\text{m}^2 \text{kg}^{-1}$ )	16	33	7	<b>33b (11)</b>	<b>29b (14)</b>	<b>25a (12)</b>
	LDMC ( $\text{g g}^{-1}$ )	—	—	—	—	—	—
	SRL ( $\text{m g}^{-1}$ )	—	—	—	—	—	—
	Culm height (cm)	—	—	—	<b>150c (150)</b>	<b>80b (50)</b>	<b>60a (60)</b>
	R : S ( $\text{g g}^{-1}$ )	2	2	7	<b>0.4b (0.07)</b>	<b>0.3a (0.07)</b>	<b>0.4b (0.1)</b>
Biogeochemical/spectral	C : N ( $\text{g g}^{-1}$ )	10	17	7	<b>66.1b (14.7)</b>	<b>39.9a (22.2)</b>	<b>55.7ab (10)</b>
	Nrubisco (proportion)	0.09	0.137	7	0.05 (0.01)	0.08 (0.03)	0.2
	Reflectance (300–2500 nm)	—	—	—	—	—	—
	e.g. rNIR (reflectance)	0.35	0.35	7	0.4	0.5	0.3
Anatomical/hydraulic	IVD ( $\mu\text{m}$ )	—	—	—	<b>85.7a (25.2)</b>	<b>136.8b (40)</b>	<b>242.1c (58)</b>
	Xylem dia. ( $\mu\text{m}$ )	—	—	7	<b>21.4b (12.2)</b>	<b>16.8a (10.7)</b>	<b>19.3a (6.7)</b>
	Kleaf	—	—	—	—	—	—
	Vein hierarchy (Primary vein secondary vein <sup>-1</sup> )	—	—	—	<b>0.11a (0.09)</b>	<b>0.29b (0.2)</b>	<b>0.58c (0.6)</b>
	Leaf width : Length	—	—	—	<b>0.04b (0.05)</b>	<b>0.03a (0.04)</b>	<b>0.03a (0.02)</b>
Life history	LL (months)	1.68	12	7	2 (0.4)	1.1	2 (1.8)
	1000-seed mass (g)	—	—	7	<b>1.4b (2.4)</b>	<b>0.2a (0.4)</b>	<b>1.4b (3.8)</b>
	Life history (% annual)	—	—	7	0.25	0.28	0.15
Disturbance	Curing rate (%)	80	20	8	80	50‡	20
	Bud bank	—	—	—	—	—	—
	Flammability ( $\text{g s}^{-1}$ )	—	—	—	—	—	—

Lineage assignments are based on Osborne *et al.* (2014). The table shows a subset of common parameters, with up to five parameters from each of six major categories. Blank values in the plant/lineage functional type (PFT/LFT) columns signify parameters that are not typically included in Land Surface Models (LSM) but are potentially important for describing the ecological behaviour of grasses. Bolded numbers with letters (i.e. a compact letter display; sharing a letter (a, b, c) indicates no difference) indicate significant differences with a Tukey's test from simple linear model fits when all three lineages had at least three data points. Sources are below.

1, Farquhar *et al.* (1980); 2, Collatz *et al.* (1992); 3, von Caemmerer (2000); 4, Ehleringer *et al.* (1997); 5, Collatz *et al.* (1998); 6, Sitch *et al.* (2003); 7, Oleson *et al.* (2010); 8, Scheiter *et al.* (2012). Curing rate is the percentage cured 30 d after the end of the growing season, as described in Scheiter *et al.* (2012). Abbreviations: C : N, carbon to nitrogen ratio; IVD, interveinal distance;  $J_{\text{max}}$ , light saturated rate of electron transport; Kleaf, leaf hydraulic conductance; LDMC, leaf dry matter content; LL, leaf lifespan; Phi, quantum efficiency; R : S, root to shoot ratio; Rd, dark respiration; SLA, specific leaf area; SRL, specific root length;  $V_{\text{cmax}}$ , maximum carboxylation rate.

†Published citations for LFT values can be found in Methods Supporting Information S1. Anatomical data came from T. J. Gallaher *et al.* (unpublished).

‡Estimated value.

(Ghannoum *et al.*, 2011). Finally, C<sub>3</sub> and C<sub>4</sub> grasses are distinguishable spectrally at the leaf, canopy and landscape level based on differences between the functional types in the chlorophyll *a/b* ratio, canopy structure and seasonality (Foody & Dash, 2007; Irisarri *et al.*, 2009; Siebke & Ball, 2009). C<sub>3</sub> and C<sub>4</sub> grasses are typically given many of the same optical properties in vegetation models, but we show here that Chloridoideae might have considerably higher near infrared (NIR) reflectance than other lineages, possibly producing interesting optical variation and affecting the surface energy balance and albedo (Ustin & Gamon, 2010) (Table 1). Foliar spectral traits are also correlated with morphological and chemical traits related to nutrient cycling and plant physiology (Dahlin *et al.*, 2013; Serbin *et al.*, 2014).

Grass lineages also show key differences in reproductive traits and the timing of related biological events (e.g. leaf-out times) that should be captured in models, especially those that include demographic predictions (Davis *et al.*, 2010). Chloridoideae grasses have seeds with lower mass than other lineages (Liu *et al.*,

2012; Bergmann *et al.*, 2017), and this may represent a life history trade-off with higher seed production and other 'fast' growth strategies (Adler *et al.*, 2014). Wind versus animal dispersal strategies might also affect diaspore size in a way not directly related to disturbance (e.g. Westoby, 1998; Bergmann *et al.*, 2017), whereas some reproductive traits may also indicate fire-related and disturbance-related adaptations. Phenological traits, such as flowering and leaf-out times and their cues (which can include disturbance factors), exhibit conservatism across many plant lineages (Davies *et al.*, 2013). Fire and herbivory are two globally important and contrasting disturbances for grass-dominated vegetation (Archibald & Hempson, 2016; Archibald *et al.*, 2019) and adaptations to both can be characterised by phenological and reproductive traits in addition to physiological and leaf traits. It is less clear how herbivory effects can be captured in such models, given that many herbivore-related traits vary greatly in grasses (Anderson *et al.*, 2011). Many fire-related traits show patterns of phylogenetic conservatism, with high flammability clustering into

particular lineages such as the Andropogoneae (Simpson *et al.*, 2016). Large-scale vegetation models that have simulated grass fires in Africa have attributed faster curing (becoming dry fuel) rates to  $C_4$  vegetation (Scheiter *et al.*, 2012), and this behaviour appears to be due largely to dominant Andropogoneae grasses.

We have identified large differences among LFTs, across six trait categories, that are not captured by the standard PFT approach. Many of these trait data have very low sample sizes (from 1 to 1365) and come from nonoverlapping species, highlighting the need for systematic data collection for grasses. Such a data collection effort would be an excellent opportunity to test for coordination among trait axes in a phylogenetic context, which has rarely been done in other systems, despite the likelihood that relatedness drives patterns of trait covariation (e.g. Griffith *et al.*, 2016; Salguero-Gómez *et al.*, 2016). Furthermore, intragroup (whether PFTs or LFTs) trait variation deserves to be properly estimated (only some traits in Table 1 have enough data to estimate variability) as convergence and adaptation produce meaningful trait variation that should be incorporated into models.

### Potential for LFTs in other vegetation types

Many current PFTs implicitly represent groupings of closely related lineages (e.g. pinaceous conifers, grasses). However, even in these cases, biogeographic distributions and the coarseness of the phylogenetic unit generate a lack of useful resolution. Currently, there are efforts to incorporate species-level trait data; methods such as those proposed by Cornwell *et al.* (2014) could be employed to cluster species into prominent lineage-based groupings representing unique trait combinations. Phylogenies are hierarchical by nature and allow the LFT approach to be scalable and adjustable to the research question being addressed. While many technical challenges still remain, the ability to remotely sense plant lineages adds the potential for rapidly developing LFTs from spectral data (e.g. Cavender-Bares *et al.*, 2016). LFTs would be valuable for a wide range of systems. For example, trees in Eurasian boreal forests suppress canopy fires through the structure of their canopies, whereas North American boreal trees enable greater intensity canopy fires (Rogers *et al.*, 2015). These distinctions led to major differences in  $CO_2$  emissions and function (Rogers *et al.*, 2015) that might be captured in an LFT framework. First, the boreal tree example is challenging because these communities are comprised of closely related species that are ecologically different, potentially requiring species-level parameterisation or being better represented by fire-based PFTs. Second, LFTs for savanna tree communities could better represent differing climatic responses that are driven by unique evolutionary and biogeographic histories (Lehmann *et al.*, 2014; Osborne *et al.*, 2018). Finally, tropical ecosystems such as the dipterocarp forests in Southeast Asia would be well suited to LFTs which might better represent carbon storage (Brearley *et al.*, 2016).

Potential challenges with a lineage-based functional approach include the fact that many plant traits do not show strong phylogenetic conservatism (Cadotte *et al.*, 2017), with several being labile. There are likely spatial and phylogenetic scales at which the LFT approach will be most appropriate, for example on a large scale

(regional to continental) lineage conservatism is common (Crisp *et al.*, 2009). By contrast, at the scale of local communities, we might expect character displacement and limiting similarity (processes that lead to reduced trait similarity of coexisting species) could obscure phylogenetic patterns and limit the utility of LFTs, as proposed here (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009; HilleRisLambers *et al.*, 2012). However, in grassy ecosystems, there is evidence that the patterns of spatial ecological sorting of lineages would be captured with LFTs also at landscape scales (e.g. within Serengeti National Park, Anderson *et al.*, 2011; Forrester *et al.*, 2017). Ultimately, we focus on extant lineages that are functionally important today, but their past interactions with other clades may have shaped the biomes they inhabit (Edwards *et al.*, 2010).

### Conclusions

We conclude that an LFT perspective captures important variation in functional diversity for grasses (Table 1). Our analysis of current knowledge of grass functional diversity (in terms of physiology, structure, biochemistry, phenology and disturbance), distributions and phylogeny indicates that to represent grass ecological behaviour, division of today's ecologically dominant grasses into at least two  $C_4$  and at least one  $C_3$  LFT could potentially improve the representation in LSMs. These proposed LFTs capture key evolutionary differences in physiological, structural, biogeochemical, anatomical, phenological and disturbance-related traits. We also highlight the need for systematic trait data collection for grasses, which we show are vastly underrepresented in trait databases, despite their ecological and economic importance. More broadly, we outline the LFT framework, which is highly flexible and has the potential for use in a wide range of applications. Here, we speak to incorporating LFTs as groupings in vegetation models, but we also suggest that trait-based models might capture important biogeographic variation (e.g. due to historical contingency) through the inclusion of phylogenetic conservatism. We advocate the use of phylogeny as a way to help guide and constrain the inclusion of burgeoning plant trait data, to expand the range of functional types considered by global vegetation models.



### Acknowledgements















This work was in part inspired by a workshop at the National Evolutionary Synthesis Center. DMG acknowledges support from NASA under the auspices of the Surface Biology and Geology (SBG) Study and from USGS through the National Innovation Center. CJS, SP, BRH, SB, MU, FQ, JBN were supported by National Science Foundation award 1342703, 1926431 and 1856587; CAES and TJG by NSF awards 1253713, 1342787 and 1120750. CERL was supported by an award from The Royal Society. WJR was supported as part of the RUBISCO Scientific Focus Area in the Regional and Global Climate Modeling Program of the US Department of Energy, Office of Science, Office of Biological and Environmental Research under contract DE-AC2-5CH11231.

## Author contributions

DMG, CJS and CPO planned and designed the work. All authors contributed data and writing to the manuscript.

## ORCID

Seton Bachle  <https://orcid.org/0000-0003-2970-862X>  
 David J. Beerling  <https://orcid.org/0000-0003-1869-4314>  
 William J. Bond  <https://orcid.org/0000-0002-3441-2084>  
 Timothy J. Gallaher  <https://orcid.org/0000-0002-5781-6874>  
 Daniel M. Griffith  <https://orcid.org/0000-0001-7463-4004>  
 Brent R. Helliker  <https://orcid.org/0000-0001-7621-2358>  
 Jesse B. Nippert  <https://orcid.org/0000-0002-7939-342X>  
 Colin P. Osborne  <https://orcid.org/0000-0002-7423-3718>  
 Stephanie Pau  <https://orcid.org/0000-0001-8135-9266>  
 William J. Riley  <https://orcid.org/0000-0002-4615-2304>  
 Melinda D. Smith  <https://orcid.org/0000-0003-4920-6985>  
 Christopher J. Still  <https://orcid.org/0000-0002-8295-4494>  
 Caroline A. E. Strömberg  <https://orcid.org/0000-0003-0612-0305>  
 Lyla Taylor  <https://orcid.org/0000-0002-3406-7452>

**Daniel M. Griffith<sup>1,2,3\*</sup>** , **Colin P. Osborne<sup>4</sup>** , **Erika J. Edwards<sup>5</sup>**, **Seton Bachle<sup>6</sup>** , **David J. Beerling<sup>4</sup>** , **William J. Bond<sup>7,8</sup>** , **Timothy J. Gallaher<sup>9,10</sup>** , **Brent R. Helliker<sup>11</sup>** , **Caroline E. R. Lehmann<sup>12</sup>**, **Lila Leatherman<sup>1</sup>**, **Jesse B. Nippert<sup>6</sup>** , **Stephanie Pau<sup>13</sup>** , **Fan Qiu<sup>6</sup>**, **William J. Riley<sup>14</sup>** , **Melinda D. Smith<sup>15</sup>** , **Caroline A. E. Strömberg<sup>9</sup>** , **Lyla Taylor<sup>4</sup>** , **Mark Ungerer<sup>6</sup>** and **Christopher J. Still<sup>1</sup>** 

<sup>1</sup>Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, USA;

<sup>2</sup>US Geological Survey Western Geographic Science Center, Moffett Field, CA 94035, USA;

<sup>3</sup>NASA Ames Research Center, Moffett Field, CA 94035, USA;

<sup>4</sup>Department of Animal and Plant Sciences, University of Sheffield, Sheffield, S10 2TN, UK;

<sup>5</sup>Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06520, USA;

<sup>6</sup>Division of Biology, Kansas State University, Manhattan, KS 66506, USA;

<sup>7</sup>South African Environmental Observation Network, National Research Foundation, Claremont, 7735, South Africa;

<sup>8</sup>Department of Biological Sciences, University of Cape Town, Rondebosch, 7701, South Africa;

<sup>9</sup>Department of Biology and the Burke Museum of Natural History and Culture, University of Washington, Seattle, WA 98195, USA;

<sup>10</sup>Bishop Museum, Honolulu, HI 96817, USA;

<sup>11</sup>Department of Biology, University of Pennsylvania, Philadelphia, PA 19401, USA;

<sup>12</sup>School of GeoSciences, University of Edinburgh, Edinburgh, EH8 9XP, UK;

<sup>13</sup>Department of Geography, Florida State University, Tallahassee, FL 32303, USA;

<sup>14</sup>Lawrence Berkeley National Laboratory, Berkeley, CA 94720, USA;

<sup>15</sup>Department of Biology, Colorado State University, Fort Collins, CO 80521, USA

(\*Author for correspondence: tel +1 9105450632; email griffith.dan@gmail.com)

## References

- Adler PB, Salguero-Gomez R, Compagnoni A, Hsu JS, Ray-Mukherjee J, Mbeau-Ache C, Franco M. 2014. Functional traits explain variation in plant life history strategies. *Proceedings of the National Academy of Sciences, USA* 111: 740–745.
- Anderegg WRL. 2015. Spatial and temporal variation in plant hydraulic traits and their relevance for climate change impacts on vegetation. *New Phytologist* 205: 1008–1014.
- Anderson TM, Shaw J, Olf H. 2011. Ecology's cruel dilemma, phylogenetic trait evolution and the assembly of Serengeti plant communities: trait evolution and plant community assembly. *Journal of Ecology* 99: 797–806.
- Archibald S, Hempson GP. 2016. Competing consumers: contrasting the patterns and impacts of fire and mammalian herbivory in Africa. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 371: 20150309.
- Archibald S, Hempson GP, Lehmann C. 2019. A unified framework for plant life-history strategies shaped by fire and herbivory. *New Phytologist* 224: 1490–1503.
- Asner GP, Elmore AJ, Olander LP, Martin RE, Harris AT. 2004. Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources* 29: 261–299.
- Atkinson RRL, Mockford EJ, Bennett C, Christin P-A, Spriggs EL, Freckleton RP, Thompson K, Rees M, Osborne CP. 2016. C<sub>4</sub> photosynthesis boosts growth by altering physiology, allocation and size. *Nature Plants* 2: 16038.
- Becklin KM, Medeiros JS, Sale KR, Ward JK. 2014. Evolutionary history underlies plant physiological responses to global change since the last glacial maximum. *Ecology Letters* 17: 691–699.
- Bergmann J, Ryo M, Prati D, Hempel S, Rillig MC. 2017. Root traits are more than analogues of leaf traits: the case for diaspore mass. *New Phytologist* 216: 1130–1139.
- Blonder B, Violle C, Bentley LP, Enquist BJ. 2014. Inclusion of vein traits improves predictive power for the leaf economic spectrum: a response to Sack *et al.* (2013). *Journal of Experimental Botany* 65: 5109–5114.
- Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320: 1444–1449.
- Brearely FQ, Banin LF, Saner P. 2016. The ecology of the Asian dipterocarps. *Plant Ecology & Diversity* 9: 429–436.
- Cadotte MW, Jonathan Davies T, Peres-Neto PR. 2017. Why phylogenies do not always predict ecological differences. *Ecological Monographs* 87: 535–551.
- von Caemmerer S. 2000. *Biochemical models of leaf photosynthesis*. Collingwood, Vic, Australia: CSIRO.
- Cavender-Bares J, Ackerly DD, Hobbie SE, Townsend PA. 2016. Evolutionary legacy effects on ecosystems: biogeographic origins, plant traits, and implications for management in the era of global change. *Annual Review of Ecology, Evolution, and Systematics* 47: 433–462.
- Cavender-Bares J, Kozak KH, Fine PVA, Kembel SW. 2009. The merging of community ecology and phylogenetic biology. *Ecology Letters* 12: 693–715.
- Coelho de Souza F, Dexter KG, Phillips OL, Brienens RJW, Chave J, Galbraith DR, Lopez Gonzalez G, Monteagudo Mendoza A, Pennington RT, Poorter L *et al.* 2016. Evolutionary heritage influences Amazon tree ecology. *Proceedings of the Royal Society B: Biological Sciences* 283: 20161587.
- Collatz GJ, Berry JA, Clark JS. 1998. Effects of climate and atmospheric CO<sub>2</sub> partial pressure on the global distribution of C<sub>4</sub> grasses: present, past, and future. *Oecologia* 114: 441–454.
- Collatz G, Ribas-Carbo M, Berry J. 1992. Coupled photosynthesis-stomatal conductance model for leaves of C<sub>4</sub> plants. *Australian Journal of Plant Physiology* 19: 519.



- Cornwell WK, Westoby M, Falster DS, FitzJohn RG, O'Meara BC, Pennell MW, McGlenn DJ, Eastman JM, Moles AT, Reich PB *et al.* 2014. Functional distinctiveness of major plant lineages. *Journal of Ecology* 102: 345–356.
- Cramer W, Bondeau A, Woodward FI, Prentice IC, Betts RA, Brovkin V, Cox PM, Fisher V, Foley JA, Friend AD *et al.* 2001. Global response of terrestrial ecosystem structure and function to CO<sub>2</sub> and climate change: results from six dynamic global vegetation models. *Global Change Biology* 7: 357–373.
- Crisp MD, Arroyo MTK, Cook LG, Gandolfo MA, Jordan GJ, McGlone MS, Weston PH, Westoby M, Wilf P, Linder HP. 2009. Phylogenetic biome conservatism on a global scale. *Nature* 458: 754–756.
- Dahlin KM, Asner GP, Field CB. 2013. Environmental and community controls on plant canopy chemistry in a Mediterranean-type ecosystem. *Proceedings of the National Academy of Sciences, USA* 110: 6895–6900.
- Davies TJ, Wolkovich EM, Kraft NJB, Salamin N, Allen JM, Ault TR, Betancourt JL, Bolmgren K, Cleland EE, Cook BI *et al.* 2013. Phylogenetic conservatism in plant phenology (S Bonser, Ed.). *Journal of Ecology* 101: 1520–1530.
- Davis CC, Willis CG, Primack RB, Miller-Rushing AJ. 2010. The importance of phylogeny to the study of phenological response to global climate change. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 365: 3201–3213.
- De Kauwe M, Keenan T, Medlyn B *et al.* 2016. Satellite based estimates underestimate the effect of CO<sub>2</sub> fertilization on net primary productivity. *Nature Climate Change* 6: 892–893.
- Dexter KG, Pennington RT, Oliveira-Filho AT, Bueno ML, Silva de Miranda PL, Neves DM. 2018. Inserting tropical dry forests into the discussion on biome transitions in the tropics. *Frontiers in Ecology and Evolution* 6: 104.
- Díaz S, Kattge J, Cornelissen JHC, Wright IJ, Lavorel S, Dray S, Reu B, Kleyer M, Wirth C, Colin Prentice I *et al.* 2016. The global spectrum of plant form and function. *Nature* 529: 167–171.
- Donoghue MJ, Edwards EJ. 2014. Biome shifts and niche evolution in plants. *Evolution, and Systematics* 45: 547–572.
- Edwards EJ, Osborne CP, Strömberg CAE, Smith SAC<sup>4</sup> Grasses Consortium. 2010. The origins of C<sub>4</sub> grasslands: integrating evolutionary and ecosystem science. *Science* 328: 587–591.
- Edwards EJ, Still CJ. 2008. Climate, phylogeny and the ecological distribution of C<sub>4</sub> grasses. *Ecology Letters* 11: 266–276.
- Ehleringer JR, Cerling TE, Helliker BR. 1997. C<sub>4</sub> photosynthesis, atmospheric CO<sub>2</sub>, and climate. *Oecologia* 112: 285–299.
- Farquhar GD, von Caemmerer S, Berry JA. 1980. A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* 149: 78–90.
- Foody GM, Dash J. 2007. Discriminating and mapping the C<sub>3</sub> and C<sub>4</sub> composition of grasslands in the northern Great Plains, USA. *Ecological Informatics* 2: 89–93.
- Forrestel EJ, Donoghue MJ, Edwards EJ, Jetz W, du Toit JCO, Smith MD. 2017. Different clades and traits yield similar grassland functional responses. *Proceedings of the National Academy of Sciences, USA* 114: 705–710.
- Fox DL, Pau S, Taylor L, Strömberg CA, Osborne CP, Bradshaw C, Conn S, Beerling DJ, Still CJ. 2018. Climatic controls on C<sub>4</sub> grassland distributions during the Neogene: a model-data comparison. *Frontiers in Ecology and Evolution* 6: 147.
- Ghannoum O, Evans JR, Caemmerer S. 2011. Nitrogen and water use efficiency of C<sub>4</sub> plants. In: Raghavendra AS, Sage RF, eds. *C<sub>4</sub> Photosynthesis and related CO<sub>2</sub> concentrating mechanisms*. Dordrecht, the Netherlands: Springer, 129–146.
- Gibson DJ. 2009. *Grasses and grassland ecology*. Oxford, UK: Oxford University Press.
- Grant RF, Garcia RL, Pinter JPJ, Hunsaker D, Wall GW, Kimball BA, LaMORTE RL. 1995. Interaction between atmospheric CO<sub>2</sub> concentration and water deficit on gas exchange and crop growth: testing of ecosys with data from the Free Air CO<sub>2</sub> Enrichment (FACE) experiment. *Global Change Biology* 1: 443–454.
- Grant RF, Mekonnen ZA, Riley WJ. 2019. Climate change impacts on permafrost thaw in an Arctic polygonal tundra depend on changes in vegetation and drainage. *JGR-Biogeosciences* 124: 1323–1341.
- Grass Phylogeny Working Group II. 2012. New grass phylogeny resolves deep evolutionary relationships and discovers C<sub>4</sub> origins. *New Phytologist* 193: 304–312.
- Griffith DM, Anderson TM, Hamilton EW. 2017b. Ungulate grazing drives higher ramet turnover in sodium-adapted Serengeti grasses. *Journal of Vegetation Science* 28: 815–823.
- Griffith DM, Anderson TM, Osborne CP, Strömberg CAE, Forrestel EJ, Still CJ. 2015. Biogeographically distinct controls on C<sub>3</sub> and C<sub>4</sub> grass distributions: merging community and physiological ecology: climate disequilibrium in C<sub>4</sub> grass distributions. *Global Ecology and Biogeography* 24: 304–313.
- Griffith DM, Lehmann CE, Strömberg CA, Parr CL, Pennington RT, Sankaran M, Ratnam J, Still CJ, Powell RL, Hanan NP *et al.* 2017a. Comment on “The extent of forest in dryland biomes”. *Science* 358: eaao1309.
- Griffith DM, Quigley KM, Anderson TM. 2016. Leaf thickness controls variation in leaf mass per area (LMA) among grazing-adapted grasses in Serengeti. *Oecologia* 181: 1035–1040.
- Griffith DM, Still CJ, Osborne CP. 2019. Editorial: Revisiting the biome concept with a functional lens. *Frontiers in Ecology and Evolution* 7: 144.
- Heskel MA, O'Sullivan OS, Reich PB, Tjoelker MG, Weerasinghe LK, Penillard A, Egerton JJG, Creek D, Bloomfield KJ, Xiang J *et al.* 2016. Convergence in the temperature response of leaf respiration across biomes and plant functional types. *Proceedings of the National Academy of Sciences, USA* 113: 3832–3837.
- Higgins SI, Bond WJ, Trollope WSW. 2000. Fire, resprouting and variability: a recipe for grass-tree coexistence in savanna. *Journal of Ecology* 88: 213–229.
- Higgins SI, Buitenwerf R, Moncrieff GR. 2016. Defining functional biomes and monitoring their change globally. *Global Change Biology* 22: 3583–3593.
- HilleRisLambers J, Adler PB, Harpole WS, Levine JM, Mayfield MM. 2012. Rethinking community assembly through the lens of coexistence theory. *Annual Review of Ecology, Evolution, and Systematics* 43: 227–248.
- Irisarri JGN, Oesterheld M, Verón SR, Paruelo JM. 2009. Grass species differentiation through canopy hyperspectral reflectance. *International Journal of Remote Sensing* 30: 5959–5975.
- Kattge J, Díaz S, Lavorel S, Prentice IC, Leadley P, Börsch G, Garnier E, Westoby M, Reich PB, Wright IJ *et al.* 2011. TRY – a global database of plant traits. *Global Change Biology* 17: 2905–2935.
- Kellogg EA. 2001. Evolutionary history of the grasses. *Plant Physiology* 125: 1198–1205.
- Kneitel JM, Chase JM. 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. *Ecology Letters* 7: 69–80.
- Körner C. 1991. Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. *Functional Ecology* 5: 162–173.
- Lehmann CER, Anderson TM, Sankaran M, Higgins SI, Archibald S, Hoffmann WA, Hanan NP, Williams RJ, Fensham RJ, Felfli J *et al.* 2014. Savanna vegetation-fire-climate relationships differ among continents. *Science* 343: 548–552.
- Lehmann CER, Griffith DM, Simpson KJ, Anderson TM, Archibald S, Beerling DJ, Bond WJ, Denton E, Edwards EJ, Forrestel EJ *et al.* 2019. Functional diversification enabled grassy biomes to fill global climate space. *bioRxiv*: doi: 10.1101/583625.
- Linder HP, Lehmann CER, Archibald S, Osborne CP, Richardson DM. 2018. Global grass (Poaceae) success underpinned by traits facilitating colonization, persistence and habitat transformation. *Biological Reviews* 93: 1125–1144.
- Liu H, Edwards EJ, Freckleton RP, Osborne CP. 2012. Phylogenetic niche conservatism in C<sub>4</sub> grasses. *Oecologia* 170: 835–845.
- Liu H, Osborne CP. 2015. Water relations traits of C<sub>4</sub> grasses depend on phylogenetic lineage, photosynthetic pathway, and habitat water availability. *Journal of Experimental Botany* 66: 761–773.
- Lu X, Wang Y-P, Wright IJ, Reich PB, Shi Z, Dai Y. 2017. Incorporation of plant traits in a land surface model helps explain the global biogeographical distribution of major forest functional types: plant traits explain biogeographical variation in forest types. *Global Ecology and Biogeography* 26: 304–317.
- McKeown M, Schubert M, Marcussen T, Fjellheim S, Preston JC. 2016. Evidence for an early origin of vernalization responsiveness in temperate Pooidae grasses. *Plant Physiology* 172: 416–426.
- Medlyn BE, De Kauwe MG, Duursma RA. 2016. New developments in the effort to model ecosystems under water stress. *New Phytologist* 212: 5–7.
- Mekonnen ZA, Riley WJ, Randerson JT, Grant RF, Rogers BM. 2019. Fire and climate warming will drive expansion of high-latitude deciduous forests. *Nature Plants* 5: 952–958.

- Oleson KW, Lawrence DM, Bonan GB, Flanner MG, Kluzek E, Lawrence PJ, Levis S, Swenson SC, Thornton PE, Dai A *et al.* 2010. *Technical description of version 4.0 of the Community Land Model (CLM)*. NCAR technical note NCAR/TN-478+ STR. Boulder, CO, USA: National Center for Atmospheric Research.
- Osborne CP, Charles-Dominique T, Stevens N, Bond WJ, Midgley G, Lehmann CER. 2018. Human impacts in African savannas are mediated by plant functional traits. *New Phytologist* 220: 10–24.
- Osborne CP, Salomaa A, Kluyver TA, Visser V, Kellogg EA, Morrone O, Vorontsova MS, Clayton WD, Simpson DA. 2014. A global database of  $C_4$  photosynthesis in grasses. *New Phytologist* 204: 441–446.
- Osborne CP, Visser V, Chapman S, Barker A, Freckleton RP, Salamin N. 2011. *GrassPortal – ecological and evolutionary data*. [WWW document] URL [www.grassportal.org](http://www.grassportal.org) [accessed 4 July 2017].
- Pappas C, Fatichi S, Burlando P. 2016. Modeling terrestrial carbon and water dynamics across climatic gradients: does plant trait diversity matter? *New Phytologist* 209: 137–151.
- Pavlick R, Drewry DT, Bohn K, Reu B, Kleidon A. 2013. The Jena Diversity-Dynamic Global Vegetation Model (JeDi-DGVM): a diverse approach to representing terrestrial biogeography and biogeochemistry based on plant functional trade-offs. *Biogeosciences* 10: 4137–4177.
- Pontarp M, Bunnefeld L, Cabral JS, Etienne RS, Fritz SA, Gillespie R, Graham CH, Hagen O, Hartig F, Huang S *et al.* 2019. The latitudinal diversity gradient: novel understanding through mechanistic eco-evolutionary models. *Trends in Ecology & Evolution* 34: 211–223.
- Poulter B, Frank D, Ciais P, Myrneni RB, Andela N, Bi J, Broquet G, Canadell JG, Chevallier F, Liu YY *et al.* 2014. Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature* 509: 600.
- Reich PB. 2014. The world-wide ‘fast-slow’ plant economics spectrum: a traits manifesto (H Cornelissen, Ed.). *Journal of Ecology* 102: 275–301.
- Rogers BM, Soja AJ, Goulden ML, Randerson JT. 2015. Influence of tree species on continental differences in boreal fires and climate feedbacks. *Nature Geoscience* 8: 228–234.
- Sack L, Scoffoni C, John GP, Poorter H, Mason CM, Mendez-Alonzo R, Donovan LA. 2014. Leaf mass per area is independent of vein length per area: avoiding pitfalls when modelling phenotypic integration (reply to Blonder *et al.* 2014). *Journal of Experimental Botany* 65: 5115–5123.
- Sage RF. 2004. The evolution of  $C_4$  photosynthesis. *New Phytologist* 161: 341–370.
- Sakschewski B, von Bloh W, Boit A, Poorter L, Peña-Claros M, Heinke J, Joshi J, Thonicke K. 2016. Resilience of amazon forests emerges from plant trait diversity. *Nature Climate Change* 6: 1032–1036.
- Salguero-Gómez R, Jones OR, Jongejans E, Blomberg SP, Hodgson DJ, Mbeau-Ache C, Zuidema PA, de Kroon H, Buckley YM. 2016. Fast–slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences, USA* 113: 230–235.
- Sandve SR, Fjellheim S. 2010. Did gene family expansions during the Eocene–Oligocene boundary climate cooling play a role in Pooideae adaptation to cool climates? *Molecular ecology* 19: 2075–2088.
- Scheiter S, Higgins SI, Osborne CP, Bradshaw C, Lunt D, Ripley BS, Taylor LL, Beerling DJ. 2012. Fire and fire-adapted vegetation promoted  $C_4$  expansion in the late Miocene. *New Phytologist* 195: 653–666.
- Scheiter S, Langan L, Higgins SI. 2013. Next-generation dynamic global vegetation models: learning from community ecology. *New Phytologist* 198: 957–969.
- Searchinger TD, Estes L, Thornton PK, Beringer T, Notenbaert A, Rubenstein D, Heimlich R, Licker R, Herrero M. 2015. High carbon and biodiversity costs from converting African wet savannas to cropland. *Nature Climate Change* 5: 481–486.
- Serbin SP, Singh A, McNeil BE, Kingdon CC, Townsend PA. 2014. Spectroscopic determination of leaf morphological and biochemical traits for northern temperate and boreal tree species. *Ecological Applications* 24: 1651–1669.
- Siebbe K, Ball MC. 2009. Non-destructive measurement of chlorophyll *b*: *a* ratios and identification of photosynthetic pathways in grasses by reflectance spectroscopy. *Functional Plant Biology* 36: 857.
- Simpson KJ, Ripley BS, Christin P-A, Belcher CM, Lehmann CER, Thomas GH, Osborne CP. 2016. Determinants of flammability in savanna grass species. *Journal of Ecology* 104: 138–148.
- Sitch S, Huntingford C, Gedney N, Levy PE, Lomas M, Piao SL, Betts R, Ciais P, Cox P, Friedlingstein P *et al.* 2008. Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five Dynamic Global Vegetation Models (DGVMs). *Global Change Biology* 14: 2015–2039.
- Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W, Sykes MT *et al.* 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* 9: 161–185.
- Smith KW, Reed S, Cleveland C *et al.* 2016. Large divergence of satellite and Earth system model estimates of global terrestrial  $CO_2$  fertilization. *Nature Climate Change* 6: 306–310.
- Staver AC, Archibald S, Levin SA. 2011. The global extent and determinants of savanna and forest as alternative biome states. *Science* 334: 230–232.
- Still CJ, Berry JA, Collatz GJ, DeFries RS. 2003. Global distribution of  $C_3$  and  $C_4$  vegetation: carbon cycle implications. *Global Biogeochemical Cycles* 17: 1006.
- Still CJ, Cotton JM, Griffith DM. 2018. 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* 24: 304–313.
- Taub DR. 2000. Climate and the US distribution of  $C_4$  grass subfamilies and decarboxylation variants of  $C_4$  photosynthesis. *American Journal of Botany* 87: 1211–1215.
- Taylor SH, Hulme SP, Rees M, Ripley BS, Ian Woodward F, Osborne CP. 2010. Ecophysiological traits in  $C_3$  and  $C_4$  grasses: a phylogenetically controlled screening experiment. *New Phytologist* 185: 780–791.
- Tilman D. 1988. *Plant strategies and the dynamics and structure of plant communities*. Princeton, NJ, USA: Princeton University Press.
- Tilman D, Cassman KG, Matson PA, Naylor R, Polasky S. 2002. Agricultural sustainability and intensive production practices. *Nature* 418: 671–677.
- Tilman D, Pacala S. 1993. The maintenance of species richness in plant communities. In: Ricklefs RE, Schuler D, eds. *Species diversity in ecological communities*. Chicago, IL, USA: University of Chicago Press, 13–25.
- Ueno O, Kawano Y, Wakayama M, Takeda T. 2006. Leaf vascular systems in  $C_3$  and  $C_4$  grasses: a two-dimensional analysis. *Annals of Botany* 97: 611–621.
- Ustin SL, Gamon JA. 2010. Remote sensing of plant functional types: Tansley review. *New Phytologist* 186: 795–816.
- Vigeland MD, Spannagl M, Asp T, Paina C, Rudi H, Rognli O-A, Fjellheim S, Sandve SR. 2013. Evidence for adaptive evolution of low-temperature stress response genes in a Pooideae grass ancestor. *New Phytologist* 199: 1060–1068.
- Violle C, Navas M-L, Vile D, Kazakou E, Fortunel C, Hummel I, Garnier E. 2007. Let the concept of trait be functional! *Oikos* 116: 882–892.
- Visser V, Clayton WD, Simpson DA, Freckleton RP, Osborne CP. 2014. Mechanisms driving an unusual latitudinal diversity gradient for grasses: insights from an unusual latitudinal diversity gradient. *Global Ecology and Biogeography* 23: 61–75.
- Walker AP, Beckerman AP, Gu L, Kattge J, Cernusak LA, Domingues TF, Scales JC, Wohlfahrt G, Wullschlegel SD, Woodward FI. 2014. The relationship of leaf photosynthetic traits –  $V_{max}$  and  $J_{max}$  – to leaf nitrogen, leaf phosphorus, and specific leaf area: a meta-analysis and modeling study. *Ecology and Evolution* 4: 3218–3235.
- Wang YP, Lu XJ, Wright IJ, Dai YJ, Rayner PJ, Reich PB. 2012. Correlations among leaf traits provide a significant constraint on the estimate of global gross primary production. *Geophysical Research Letters* 39: 19.
- Watcharamongkol T, Christin P-A, Osborne CP. 2018.  $C_4$  photosynthesis evolved in warm climates but promoted migration to cooler ones. *Ecology Letters* 21: 376–383.
- Webb CO, Ackerly DD, McPeck MA, Donoghue MJ. 2002. Phylogenies and community ecology. *Annual Review of Ecology and Systematics* 33: 475–505.
- Westoby M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil* 199: 213–227.
- Westoby M, Falster DS, Moles AT, Vesk PA, Wright IJ. 2002. Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* 33: 125–159.
- Williams KJ, Wilsey BJ, McNaughton SJ, Banyikwa FF. 1998. Temporally variable rainfall does not limit yields of Serengeti grasses. *Oikos* 81: 463.
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M *et al.* 2004. The worldwide leaf economics spectrum. *Nature* 428: 821–827.



## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Methods S1** Description of data and code for Table 1.

Please note: Wiley Blackwell are not responsible for the content or functionality of any Supporting Information supplied by the

authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.

**Key words:** C<sub>4</sub> photosynthesis, Earth system models, evolution, grass biogeography, land surface models, plant functional types, vegetation models.

Received, 23 December 2019; accepted, 28 April 2020.



## About *New Phytologist*

- *New Phytologist* is an electronic (online-only) journal owned by the New Phytologist Trust, a **not-for-profit organization** dedicated to the promotion of plant science, facilitating projects from symposia to free access for our Tansley reviews and Tansley insights.
- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged. We are committed to rapid processing, from online submission through to publication 'as ready' via *Early View* – our average time to decision is <26 days. There are **no page or colour charges** and a PDF version will be provided for each article.
- The journal is available online at Wiley Online Library. Visit **www.newphytologist.com** to search the articles and register for table of contents email alerts.
- If you have any questions, do get in touch with Central Office (np-centraloffice@lancaster.ac.uk) or, if it is more convenient, our USA Office (np-usaoffice@lancaster.ac.uk)
- For submission instructions, subscription and all the latest information visit **www.newphytologist.com**