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_3 grasses and (sub)tropical C_4 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_{cmax}) 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

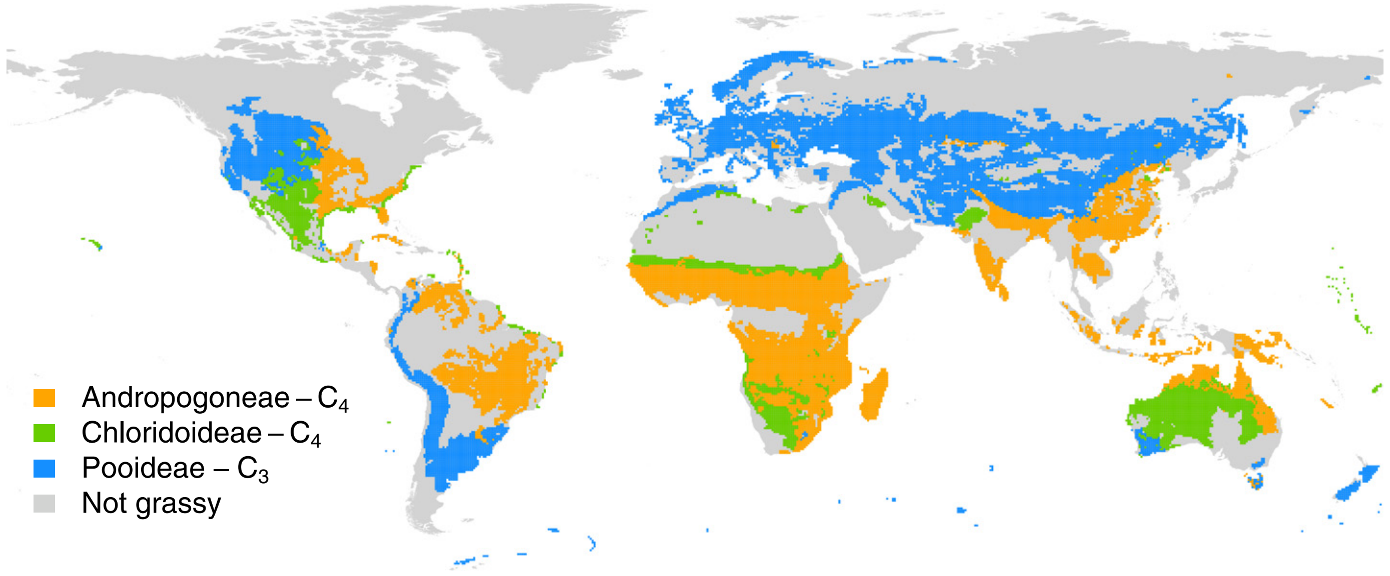

Fig. 1 Distributions of the three globally dominant grass lineages in the herbaceous layer. These data come from Lehmann *et al*. (2019) and show where each lineage is more abundant compared with the other two lineages based on a 0.5-degree grid.

RuBisCO in higher CO_2 environments (Collatz *et al.*, 1998). The Chloridoideae (C_4) grasses have intermediate V_{cmax} and J_{max} compared with the Andropogoneae (C_4) and the Pooideae (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 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; Heskel *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, C_3 grass PFTs have higher or similar SLA values as C_4 PFTs are likely to bias predictions. By contrast, we found that the C_4 LFTs had higher SLA than the C_3 LFT, but SLA did not differ between the two dominant 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 C_3 and C_4 grass lineages (Reich, 2014; Díaz *et al.*, 2016; Archibald *et al.*, 2019). Furthermore, the 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 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 C_4 photosynthesis (Sage, 2004; Ueno *et al.*, 2006). We describe next key hydraulic differences between the two dominant C_4 lineages that correspond to the 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 Chlordoideae 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_{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.

		PFT			LFT[†]		
Category	Parameter	C_4	C_3	Source	Andropogoneae	Chloridoideae	Pooideae
Physiological	V_{cmax} ($\mu mol\ m^{-2}\ s^{-1}$)	39	90	1, 2	38	45.6 (4.4)	63.6 (28)
	J_{max} ($\mu mol\ m^{-2}\ s^{-1}$)	400	100	3	180	108.1 (43)	128.8 (45)
	Rd ($\mu mol\ m^{-2}\ s^{-1}$)	0.8	1.1	1, 2	**0.9a (0.2)**	**2a (1.4)**	**0.9a (0.7)**
	Phi ($\mu mol\ \mu mol^{-1}$)	0.06	0.085	4, 5	0.06	0.06	0.09
	Trange (°C)	< 15.5	> 15.5	6	> 5[‡]	> –5[‡]	> –30 and < 5[‡]
Structural	SLA ($m^2\ kg^{-1}$)	16	33	7	**33b (11)**	**29b (14)**	**25a (12)**
	LDMC ($g\ g^{-1}$)	–	–		–	–	–
	SRL ($m\ g^{-1}$)	–	–		–	–	–
	Culm height (cm)	–	–		**150c (150)**	**80b (50)**	**60a (60)**
	R : S ($g\ g^{-1}$)	2	2	7	**0.4b (0.07)**	**0.3a (0.07)**	**0.4b (0.1)**
Biogeochemical/spectral	C : N ($g\ g^{-1}$)	10	17	7	**66.1b (14.7)**	**39.9a (22.2)**	**55.7ab (10)**
	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 (μm)	–	–		**85.7a (25.2)**	**136.8b (40)**	**242.1c (58)**
	Xylem dia. (μm)	–	–	7	**21.4b (12.2)**	**16.8a (10.7)**	**19.3a (6.7)**
	K*leaf*	–	–		–	–	–
	Vein hierarchy (Primary vein secondary $vein^{-1}$)	–	–		**0.11a (0.09)**	**0.29b (0.2)**	**0.58c (0.6)**
	Leaf width : Length	–	–		**0.04b (0.05)**	**0.03a (0.04)**	**0.03a (0.02)**
Life history	LL (months)	1.68	12	7	2 (0.4)	1.1	2 (1.8)
	1000-seed mass (g)	–	–	7	**1.4b (2.4)**	**0.2a (0.4)**	**1.4b (3.8)**
	Life history (% annual)	–	–	7	0.25	0.28	0.15
Disturbance	Curing rate (%)	80	20	8	80	50[‡]	20
	Bud bank	–	–		–	–	–
	Flammability ($g\ s^{-1}$)	–	–		–	–	–

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_{max}, light saturated rate of electron transport; K*leaf*, 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_{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_3 and C_4 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_3 and C_4 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; Forrestel *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.

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

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Methods S1 Description of data and code for Table 1.

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