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RESEARCH PAPER

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Assessing earth system model predictions of C_4 grass cover in North America: From the glacial era to the end of this century

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Abstract

Aim: C_4 grasses are distinct from C_3 grasses, because C_4 grasses respond in a different manner to light, temperature, CO_2 and nitrogen and often have higher resource-use efficiencies. C_3 and C_4 grasses are typically represented in earth system models (ESMs) by different plant functional types (PFTs). The ability of ESMs to capture C_4 grass biogeography and ecology across differing time periods is important to assess, given the crucial role they play in ecosystems and their divergent responses to global change.

Location: North America.

Time periods: Last Glacial Maximum (LGM), historical modern period (*ca*. 1850) and end of this century.

Major taxa studied: C_4 grasses.

Methods: Proxy data representing relative cover and productivity of C_4 grasses were collated, including carbon isotope ratios of soil carbon and animal grazer tissue, and vegetation plot data in undisturbed grasslands. We selected available model predictions of C_4 PFT percentage cover. Models were compared against one another and assessed against proxy data at key time points: the LGM, the historical modern period before widespread grassland conversion to agriculture, and the end of this century.

Results: We highlight large differences among model predictions of percentage C_4 grass cover across North America: all pairwise combinations have correlations $< .5$, and most are $< .2$. Models also do not capture spatial patterns of the percentage C_4 grass cover from proxy data, during either the LGM or the historical modern period. Models generally under-predict percentage C_4 grass cover, particularly during the historical modern period.

Main conclusions: Earth system models do not accurately represent the biogeography of C_4 grasses across a range of time-scales, and their outputs do not agree with one another. We suggest model improvements to represent this crucial functional type better, including more collection and greater integration of C_3 and C_4 grass trait data, explicit representations of tree–grass competition for water, and a greater focus on disturbance ecology.

KEYWORDS

C_4 grasses, CMIP5, DGVM, earth system model, grassland, plant functional type

1 | INTRODUCTION

Grasses that use the C_4 photosynthetic pathway often dominate cover and productivity in grasslands and savannas. These grasses are extremely important as food crops and biofuels, and often become aggressive weeds. C_4 grasses also account for a large fraction of carbon and water cycling (Miranda et al., 1997; Ratnam et al., 2011; Still, Berry, Collatz & DeFries, 2003). Grasslands and savannas where C_4 grasses most commonly occur are recognized to dominate the trend and interannual variability of the global land carbon sink (Ahlström et al., 2015). Palaeoevidence suggests that these grasses were also dominant in many tropical and subtropical regions during glacial cycles (Bond, 2008) and ecologically important since at least the late Miocene (Edwards et al., 2010). C_4 grasses also critically influence and are influenced by disturbances, particularly through fire interactions in the tropics and subtropics (Bond, Woodward, & Midgley, 2005; Randerson et al., 2005). Finally, C_4 grasses strongly influence (sub)tropical tree cover via competition for soil water, impacts on tree seedling recruitment and acceleration of the fire cycle (Bond, 2008; Higgins & Scheiter, 2012; Scheiter et al., 2012).

Given the influences of C_4 grasses on many aspects of the earth system, accurately predicting their cover and productivity should be a priority for global-scale modelling. Simulation of large-scale vegetation patterns and processes is accomplished with dynamic global vegetation models (DGVMs). The DGVMs represent a wide variety of physiological, ecological, hydrological, biophysical and biogeochemical processes occurring on the land surface (Cramer et al., 2001; Jiang et al., 2015; Piao et al., 2013; Shao, Zeng, Sakaguchi, Monson & Zeng, 2013; Sitch et al., 2008; Wullschleger et al., 2014). As such, DGVMs are a crucial component of earth system models (ESMs), which are used for predictions of a future warming climate and its attendant impacts on humanity and natural ecosystems.

A central component of most DGVMs is the use of the plant functional type (PFT) approach to represent a wide range of biological properties and traits. The PFT approach has been used to represent essential processes and properties of terrestrial vegetation required for earth system modelling (Sitch et al., 2003; Wullschleger et al., 2014), but the accuracy of modelled biogeography, cover and productivity across a range of temporal scales is crucially important to evaluate. One challenge to such an evaluation is having relevant empirical data on vegetation characteristics against which to compare model predictions at the appropriate spatial and temporal scales. Aspects of the C_4 photosynthetic pathway lead to lower carbon isotope fractionation compared with C_3 plants (Cernusak et al., 2013), creating a natural tracer of carbon inputs from C_4 grasses in plant and soil organic matter and carbon fluxes. This has been exploited in a range of applications to quantify C_4 plant contributions (i.e., $\%C_4$) to ecosystem respiration (Still, Berry, Ribas-Carbo, & Helliker, 2003), soil organic matter (Cerling, 1984; von Fischer, Tieszen, & Schimel, 2008), grazer tissue (Cotton, Cerling, Hoppe, Mosier, & Still, 2016) and food webs (Cerling et al., 2013).

In the present study, we compiled available data from isotope ratios preserved in soil organic matter and animal grazer tissues to create proxy information on $\%C_4$ grass cover and productivity during the Last Glacial Maximum (LGM) and historical modern period in North America. We also included information from vegetation plot surveys that measure plant cover. We assessed DGVM performance by comparing simulations of $\%C_4$ grass PFT cover with these proxy datasets for the LGM and historical modern time periods. We also compared model predictions for the end of the century. For this analysis, we focused on North America, where the distributions of C_3 and C_4 grasses are relatively well characterized based on proxy isotope data and modern vegetation plot measurements (e.g., Cotton et al., 2016; Griffith et al., 2015). We provide quantitative comparisons and recommendations for improvement in models in better capturing essential aspects of C_4 grass ecology and biogeography.

2 | METHODS

2.1 | Glacial, modern and future C_4 distributions from the Coupled Model Intercomparison Project Phase 5

We obtained outputs from a subset of models participating in the Coupled Model Intercomparison Project Phase 5 (CMIP5; Taylor, Stouffer, & Meehl, 2012). Model outputs included proportional cover in each grid cell of all grass PFTs, all tree PFTs and all C_4 plant PFTs (including grasses and crops) from the Earth System Grid Federation. Of the 40+ individual CMIP5 models, only a subset of modelling groups provided C_4 PFT cover fraction predictions for all time periods (Table 1). Although this is a small subset, the selected models do represent a range of approaches from well-respected modelling centres. For the LGM, monthly model outputs were averaged to produce $\%C_4$ layers for the simulated period, which was *ca*. 100 years for each model. For the historical modern period, we used the modelled percentage cover of tree PFTs, grass PFTs and C_4 grass PFTs from the oldest model run year, which corresponds to approximately the mid-1800s. This represents a time before extensive land cover change in the Great Plains and other regions replaced prairies and savannas with croplands (e.g., Hurtt et al., 2006; Ramankutty & Foley, 1999a, 1999b). We selected model outputs from the 'historical' experiment, because that is the experiment for which models simulated all components of the earth system through time. The other model experiments have different parts of the earth system removed, such as the 'historicalGHG' experiment, which is a simulation of the historical period, but with forcings other than anthropogenic greenhouse gases removed. For future scenarios, we used simulations based on the 'business as usual' scenario, RCP 8.5 (i.e., corresponding to a *ca*. 4 °C global temperature increase by 2100).

TABLE 1 Listing of earth system models compared in this study, along with relevant details about resolution and vegetation models used for simulations of different time periods

Time period of simulation	MPI-ESM	IPSL-CM5A	MIROC-ESM	GFDL-ESM2G
Last Glacial Maximum	MPI-ESM-P 1.875 × 1.85	IPSL-CM5A-LR ORCHIDEE DGVM 3.75 × 1.875	MIROC-ESM SEIB DGVM 2.81 × 1.77	
Historical modern period	MPI-ESM-MR JSBACH DGVM 1.875 × 1.85	IPSL-CM5A-MR ORCHIDEE DGVM 2.5 × 1.875	MIROC-ESM SEIB DGVM 2.81 × 1.77	GFDL-ESM2G GFDL DGVM 2.5 × 2.0
Future	MPI-ESM-MR JSBACH DGVM 1.875 × 1.85	IPSL-CM5A-MR ORCHIDEE DGVM 2.5 × 1.875	MIROC-ESM SEIB DGVM 2.81 × 1.77	GFDL-ESM2G GFDL DGVM 2.5 × 2.0

Note. Model metadata come from literature and Web resources for each individual model: MPI-ESM (Giorgetta et al., 2013), IPSL-CM5A (Dufresne et al., 2013), MIROC (Watanabe et al., 2011) and GFDL-ESM2G (Dunne et al., 2012). Resolutions are expressed as longitude × latitude.

2.2 | Observed C_4 proxy data: LGM and modern

We compiled independent datasets that document the %C_4 of herbaceous vegetation in North America during glacial and historical modern periods for comparison with model simulations. We used plot data from Griffith et al. (2015), resampled to a 100-km grid (available in Griffith, Cotton, Powell, Sheldon & Still, 2017), spanning the conterminous USA and representing C_3 and C_4 relative grass cover from survey plots (< 1,000 m^2) located in relatively undisturbed grassland remnants. Given that plot data were not collected in crops or farmlands, they are broadly comparable to model predictions for the mid-1800s, when natural vegetation predominated. Indeed, plot data and carbon isotope ratio proxies suggest little change in relative C_3/C_4 abundances from the mid-1800s (Griffith, Cotton, et al., 2017). We also collated glacial and modern observations of the carbon isotopic composition (δ^{13}C) of soil and palaeosol organic carbon and grazer (bison and mammoth) tissue. Differences between photosynthetic pathways drive variations in the δ^{13}C of modern C_3 and C_4 grasses (*ca*. −27‰ and *ca*. −12‰, respectively). The δ^{13}C values of soil carbon largely reflect the proportion of C_3 and C_4 biomass during soil formation (Cerling, 1984; Koch, 1998; von Fischer et al., 2008). We obtained 55 previously published modern soil δ^{13}C values from von Fischer et al. (2008). Given that bison (*Bison bison*) and Columbian mammoth (*Mammuthus columbi*) are predominately grazers, their tissues record the mean δ^{13}C of their diets (Cotton et al., 2016; Griffith, Cotton, et al., 2017; Hoppe, Paytan & Chamberlain, 2006). Previous work has shown that browsing constitutes a small proportion of modern bison diet and that they accurately record the abundance of C_4 grasses within *ca*. 10% (Hoppe et al., 2006). Additionally, analysis of Columbian mammoth diet in the late Pleistocene using carbon isotopes shows substantial inputs from C_4 vegetation, indicating a diet rich in grasses (Koch, Hoppe, & Webb, 1997). Modern and fossil bison and mammoth data (measurements from 281 individual modern bison and 95 LGM individual bison and mammoth) were obtained from Cotton et al. (2016). Additionally, five palaeosol δ^{13}C measurements of LGM age derived from the literature were added to the palaeo-proxy dataset.

We converted soil and animal grazer δ^{13}C values to %C_4 using linear mixing models and C_3 and C_4 isotopic endmembers. Owing to the Suess effect, the δ^{13}C values of mammal tissues and palaeosols were corrected to a preindustrial atmospheric value of −6.3‰ based on their age (Francey et al., 1999) and then converted to %C_4 with endmembers of −25.3 and −11.3‰ (Cotton et al., 2016; Koch, 1998). This correction results in the following equation for grazer tissues:

$$\%C_4 = 7.1429\delta^{13}C_{\mathrm{grazer}} + 180.71 \qquad (1)$$

In fossil localities where bison and mammoth coexisted, their δ^{13}C values are similar, although mammoth δ^{13}C values tend to be more negative, reflecting more input of C_3 vegetation (Connin, Betancourt, & Quade, 1998). This difference in δ^{13}C values could be interpreted as a larger component of C_3 browse vegetation in the mammoth diet compared with bison. Therefore, the abundance of C_4 vegetation derived from mammoth can be interpreted as a minimum estimate.

Soil samples were collected from the A horizon (von Fischer et al., 2008), which is the uppermost, organic-rich soil layer and reflects more recent carbon inputs (tens to hundreds of years; Leavitt, Follett, Kimble, & Pruessner, 2007). Here, we assumed that the A horizon carbon has a mean age of *ca*. 100 years and assigned a corresponding atmospheric δ^{13}C value of −6.6‰. We also assumed a uniform enrichment of 1‰ from plant matter to soil organic matter (von Fischer et al., 2008). We then converted soil δ^{13}C to %C_4 with endmembers of −25.6 and −11.6‰ using the following equation for soil carbon:

$$\%C_4 = 7.1429\delta^{13}C_{\text{soil}} + 182.86 \tag{2}$$

2.3 | Assessing model agreement

To assess agreement among models in %C_4 cover predictions, we calculated single score intraclass correlation coefficient (ICC) values for each of the three time periods ('two-way' ICC analyses as described by Shrout & Fleiss, 1979). Intraclass correlation coefficient values are similar in interpretation to Cohen's κ (Fleiss & Cohen, 1973) and range from minus one to plus one. Based on the inter-rater reliability literature (e.g., McHugh, 2012; McGraw & Wong, 1996) we conclude that ICC values < .6 are indicative of poor reliability, that is, poor model–model agreement, whereas values between .6 and 1 indicate moderate to excellent reliability. All ICC values were calculated using the 'icc' function (using type = 'agreement') in the 'irr' package (Gamer, Lemon, Fellows, & Singh, 2012) in R (version 3.4.2). We also calculated (using R) Pearson's product–moment correlations for each model pair combination and each time period, with values ranging from minus one to plus one; a value of zero indicates that there is no association between the two model pair predictions. We restricted all our model-to-model comparisons to grid cells with non-zero values, reasoning that the inclusion of the much more numerous zero %C_4 grid cells would artificially inflate model–model correlations. Finally, we assessed model predictions of %C_4 cover with proxy data for each time period by calculating Pearson's product–moment correlations.

3 | RESULTS

3.1 | Last Glacial Maximum period

In terms of simulated %C_4 PFT grass cover, the models diverge widely in their predictions relative to one another. For the LGM, only three modelling groups made C_4 grass PFT cover predictions available: MPI, IPSL and MIROC. Among these, modelled C_4 cover at the LGM varied tremendously, from minimal C_4 cover in the IPSL model to fairly extensive C_4 PFT cover in the MPI model, particularly in the Great Plains region of North America (Figure 1). The MIROC model (Watanabe et al., 2011) also predicted a fairly extensive amount of C_4 grass cover, but only in a tier across the southern part of North America. During the LGM, the ICC score was .27 (Table 2), a value which reflects the poor agreement among model predictions apparent in Figure 1. The Pearson's correlation coefficients (Table 3) for model pair predictions vary from .17 (MPI and IPSL) to .47 (MIROC and MPI). Despite relatively low values, this time period has the highest level of model–model agreement based on both the ICC and the correlation coefficients (Tables 2 and 3). Compared with available palaeodata for the LGM (δ^{13}C of fossil bison and mammoth tissues, and palaeosols), predictions from the MPI and MIROC models are visually superior to those from the IPSL model (Figure 1). Indeed, Pearson's correlation coefficients, relating proxy and model data, range from .46 (IPSL) to .78 (MPI), and all are statistically significant (Table 4). Notably, the proxy data sample a major gradient in %C_4, and model predictions range from a low of 0–30%C_4 in IPSL to a high of 0–70%C_4 in MPI.

3.2 | Historical modern period

A key aspect of simulating %C_4 grass cover during any time period is accurately capturing the relative cover of trees and grasses, given that C_4 grasses commonly occur in regions with low-to-moderate tree cover in the tropics and subtropics (i.e., savannas and woodlands). There is wide divergence in modelled tree and grass cover fractions during the historical modern period in North America (Figure 2). Within the Great Plains ecoregion, grass fractions are under-predicted and tree cover fractions over-predicted in the GFDL and MIROC models compared with potential natural vegetation distributions for this time period, which are reasonably well constrained by historical data (Ellis, Klein Goldewijk, Siebert, Lightman, & Ramankutty, 2010; Ramankutty & Foley, 1999b). The MPI and IPSL models generally have greater skill in predicting tree and grass cover fractions, although tree cover is still under-predicted and grass cover over-predicted by the MPI model.

During the historical modern period, model predictions of %C_4 grass PFT cover are likewise variable (Figure 3). Indeed, this time period has the lowest level of model–model agreement among the three time periods (Table 2). The ICC score is even lower for this time period (.05) than for the LGM. Pearson's correlation coefficients (Table 3) for model pair predictions vary from .02 (IPSL and MIROC) to .38 (IPSL and MPI). Only one model, MIROC, predicts extensive C_4 grass cover in the Great Plains and in the southwest and Texas. This agrees fairly well with available data from vegetation plots and with proxy data from soil carbon and bison tissue δ^{13}C. MIROC also predicts extensive C_4 cover in the upper Great Plains and into northern Canada, and into the upper Midwest and New England states of the USA. There are no plant or isotope proxy data to support extensive C_4 grass cover in these latter regions, which were mostly forested in the mid-1800s. All other models greatly under-predict C_4 grass cover in this time period compared with data. The IPSL model predicts moderate C_4 cover only in the southern USA and northern Mexico. Likewise, the MPI model predicts extensive C_4 grass PFT cover only in parts of southern Mexico, and in areas of the Gulf Coast and New England, although this ESM predicts extensive overall grass cover in the Great Plains (Figure 2). The GFDL model predicts very high C_4 cover across the arid Mojave Desert, and in parts of the cooler Great Basin and wetter Sonoran deserts and central California (Figure 3). This agrees somewhat with a prominent C_4 grass component in the summer-active grasses of desert regions that receive monsoon

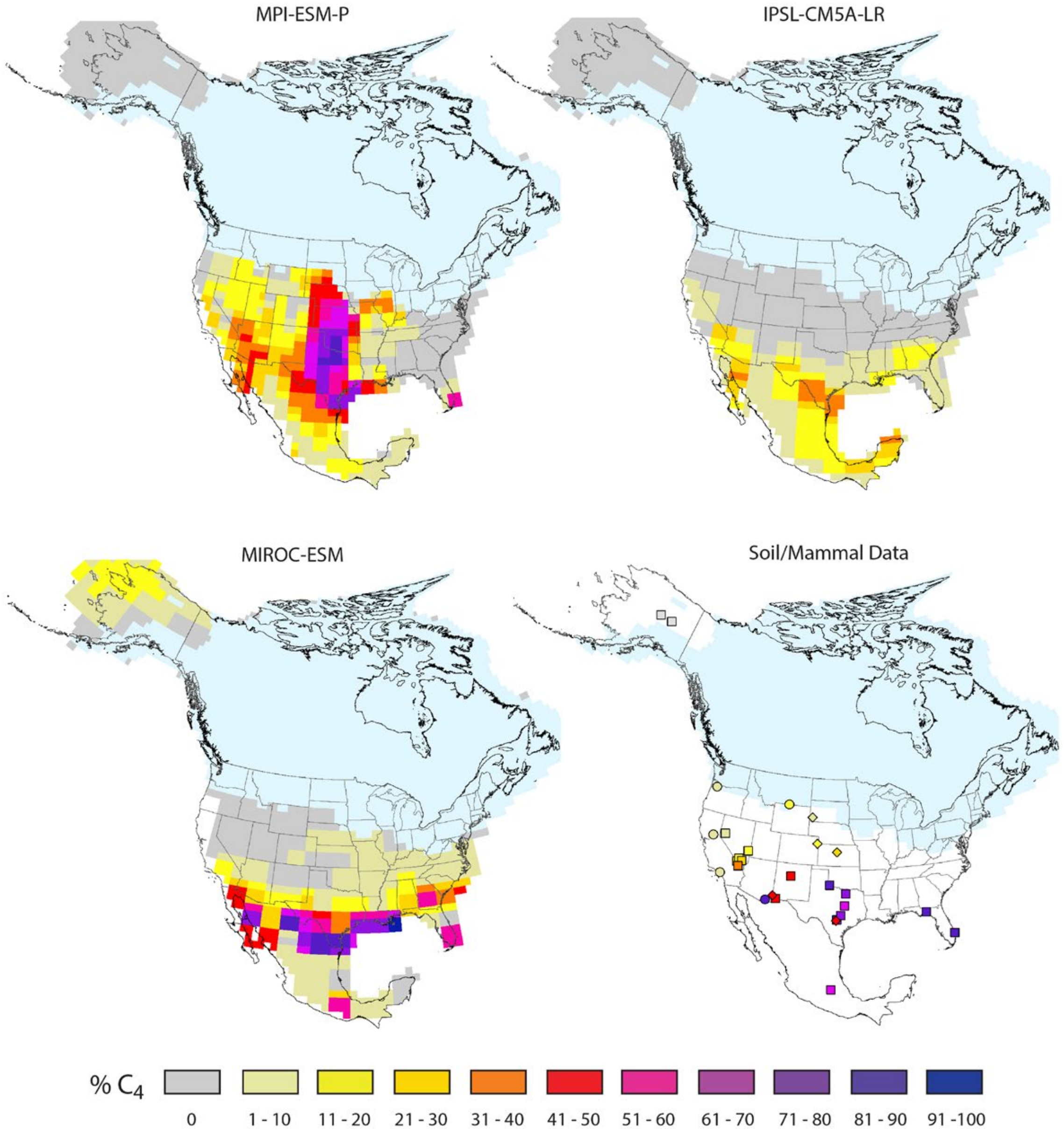

FIGURE 1 Modelled C_4 plant functional type cover at the Last Glacial Maximum compared with available proxy data (palaeosol and animal tissue δ^{13}C; Cotton et al., 2016) in the lower right panel. Light blue colour represents areas covered by glaciers during the Last Glacial Maximum. Circles represent C_4 abundance estimates derived from fossil bison isotope data, squares represent C_4 abundance estimates derived from fossil mammoth isotope data, and diamonds represent C_4 abundance estimates derived from palaeosol isotope data

TABLE 2 Comparison of agreement across models based on intraclass correlation coefficient values

Statistic of agreement	LGM (1,161, 363)	Historical modern (2,595, 1,062)	Future RCP 8.5 (not including GFDL model) (2,665, 208)
ICC values (95% confidence interval for ICC population values). All *p*-values < .001	.21 < .27 < .33	.02 < .05 < .08	.07 < .12 < .17

Note. Degrees of freedom are provided in the uppermost panels for each time period (*F* test, so two types of degrees of freedom are provided). ICC = intraclass correlation coefficient.

precipitation (Ehleringer, 1978). However, only the MIROC model accurately predicts extensive C_4 grass cover in the Great Plains during the period before large-scale agriculture. However, this model also over-predicts C_4 cover in north-central and northeastern North America. Relative to the LGM comparisons of model prediction against proxy data, the correlation coefficients for this

TABLE 3 Comparison of agreement across models based on Pearson's product–moment correlations

Pairwise Pearson's product–moment correlations between model predictions (*p << .001)	MPI	IPSL	MIROC
LGM			
MPI	1		
IPSL	.17* (799)	1	
MIROC	.32* (1,174)	.47* (1,141)	1
Historical			
MPI	1		
IPSL	.38* (1,046)	1	
MIROC	.08* (2,595)	.02 (2,758)	1
Future			
MPI	1		
IPSL	.41* (1,050)	1	
MIROC	.13* (2,672)	.14* (2,954)	1

Note. Degrees of freedom for each test are provided in parentheses.

TABLE 4 Comparison of agreement between model predictions and proxy data based on Pearson's product–moment correlations

Pairwise Pearson's product–moment correlations between proxy data and model prediction of %C_4 ($^*p$ << .001)	LGM	Historical
MPI	.78* (93)	.12* (661)
IPSL	.46* (93)	.42* (680)
MIROC	.58* (92)	.33* (646)

Note. The historical modern model comparison is against vegetation plot proxy data, because bison proxy data are highly correlated with plot data (Griffith, Cotton, et al., 2017). Degrees of freedom for each test are provided in parentheses.

period are much lower, ranging from a low of .12 for the MIROC model to a high of .42 for the IPSL model. These correlations are still statistically significant, but the sample sizes are much larger than for the LGM comparisons (Table 4).

3.3 | Future (end of century) period

Predictions for the end of this century further highlight the mismatch among models in predicting C_4 grass cover (Figure 4) The ICC score is also low (.13) for this time period, and correlation coefficients vary from .13 (MIROC and MPI) to .41 (IPSL and MPI) (Tables 2 and 3). The simulated future patterns largely mimic those for the mid-1800s, although all models predict increases in C_4 cover. It is difficult to disentangle how much of the predicted increase results from C_4 grasses interacting with a changing climate, atmospheric CO_2, disturbance patterns and other PFTs, because the future %C_4 cover in these models includes crops. Although models vary in their algorithms, crop cover predictions should be related to economic decisions, in addition to ecological and biophysical factors (Porfirio, Newth, Harman, Finnigan, & Cai, 2017).

4 | DISCUSSION

4.1 | Modelled vegetation distributions: Potential biases from climate models

C_4 abundance predicted by vegetation models will be influenced by the accuracy of the atmospheric models that simulate climate forcing data. Many recent studies have assessed climate model accuracy by comparing model outputs with palaeoclimatic proxy data for historical time periods, such as the LGM. Much of this model–proxy data comparison work for the historical periods has been focused on sea surface temperature (e.g., Bakker et al., 2014; Hossain, Zhang, & Lohmann, 2018) and has found that models are in broad agreement with proxy data from the LGM and mid-Holocene, although deviations do occur in some regions, such as the mid-latitudes of the Southern Hemisphere (Bakker et al., 2014). However, comparisons between proxy-based terrestrial climatic reconstructions and models are more variable. For instance, Braconnot et al. (2012) and Jiang, Tian, and Land (2013) found discrepancies between predictions from Paleoclimate Modelling Intercomparison Project (PMIP) outputs and proxy-based mean annual precipitation data for the eastern portion of the northern hemisphere and China, respectively, during the mid-Holocene. Otto-Bleisner et al. (2013) showed that the CCSM3 model has difficulties reproducing last interglacial warming over the terrestrial arctic and suggested that the simulation is missing crucial feedbacks. It is possible that greater model–proxy data mismatch occurs over the land compared with the ocean, especially if precipitation is driving deviations between modelled and proxy-based reconstructions of C_4 abundance at the LGM.

Global vegetation models are often driven by observed or modelled climate data in so-called 'offline simulations', and many vegetation models have been tested using this approach (Bonan & Levis, 2006). Importantly, vegetation model performance can be strongly

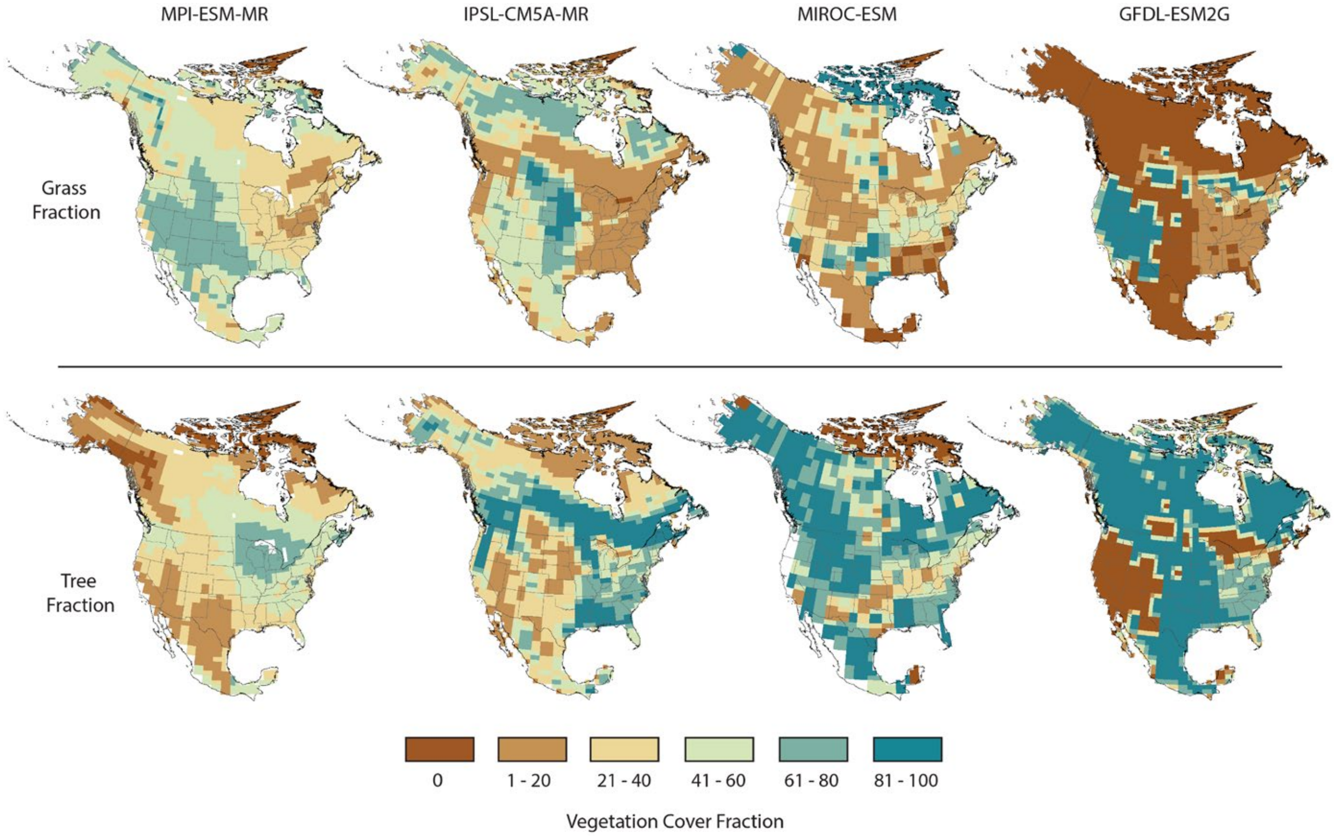

FIGURE 2 Relative cover fractions for tree and grass plant functional types as represented in various earth system models from historical simulations for the earliest model year (1850–1861, depending on the model)

affected by biases in the climate model forcing. For example, Ahlström, Schurgers, and Smith (2017) showed that climate model biases could be responsible for up to 40% of the range in simulated terrestrial carbon storage across 18 of the CMIP5 models. Global vegetation models that are coupled to climate models, as is the case for the simulations highlighted here, may also be biased from the coupling itself. Bonan and Levis (2006) highlighted problems that might arise when coupling two highly nonlinear systems. However, the advantage of the coupled approach is that feedbacks between the land and atmosphere can be captured. In sum, some of the model–model discrepancies and lack of agreement with proxy data we highlight here is very likely to be a result of poor performance of the atmospheric models that drive the vegetation models, in addition to potential feedbacks inherent in the model coupling process.

4.2 | Improving simulated C_4 grass biogeography: Missing processes and properties

Despite the importance of atmosphere model influences on simulated PFT biogeography and carbon cycle dynamics, the vegetation models are also very likely to be missing essential processes that influence the cover and productivity of C_4 grasses. The importance of capturing the photosynthetic physiologies of C_3 and C_4 grass types, and their variation with CO_2 and climate, has long been recognized (Collatz, Berry, & Clark, 1998; Sellers et al., 1997; Still, Berry, et al., 2003). However, additional ecological and hydrological factors control C_3 and C_4 distributions and can interact in complex ways, producing offsetting effects driven by interactions with hydrological cycles (Griffith, Lehmann, et al., 2017) or by driving systems towards deterministically woody states (Bond, 2008; Moncrieff, Scheiter, Bond, & Higgins, 2013; Oliveras, & Malhi, 2016). For example, in an experimental study conducted in a semi-arid, mixed C_3/C_4 grassland in North America, Morgan et al. (2011) showed that C_4 grasses were counterintuitively outperforming C_3 grasses owing to increases in water-use efficiency driven by interacting effects of higher CO_2 and warming on soil moisture and plant physiological responses.

Another key difference important to capture in models is the seasonal offset in cover and productivity between C_3 and C_4 grasses (Collatz et al., 1998). This is especially important in the Great Plains region of North America, where temporal mixtures of these grass types have been well studied. For example, in the shortgrass and upland mixed grass prairie ecosystem, C_3 grasses generally grow in spring and early summer, whereas C_4 grasses predominate during mid- and late summer (Kemp & Williams, 1980; Ode, Tieszen, & Lerman, 1980). The tallgrass prairie ecosystems are also characterized by seasonal C_3 and C_4 mixtures, although the variation is greatly dampened and C_4 grasses assimilate most of the carbon on an annual basis (Nippert, Knapp, & Briggs, 2006; Still, Berry, Ribas-Carbo, &

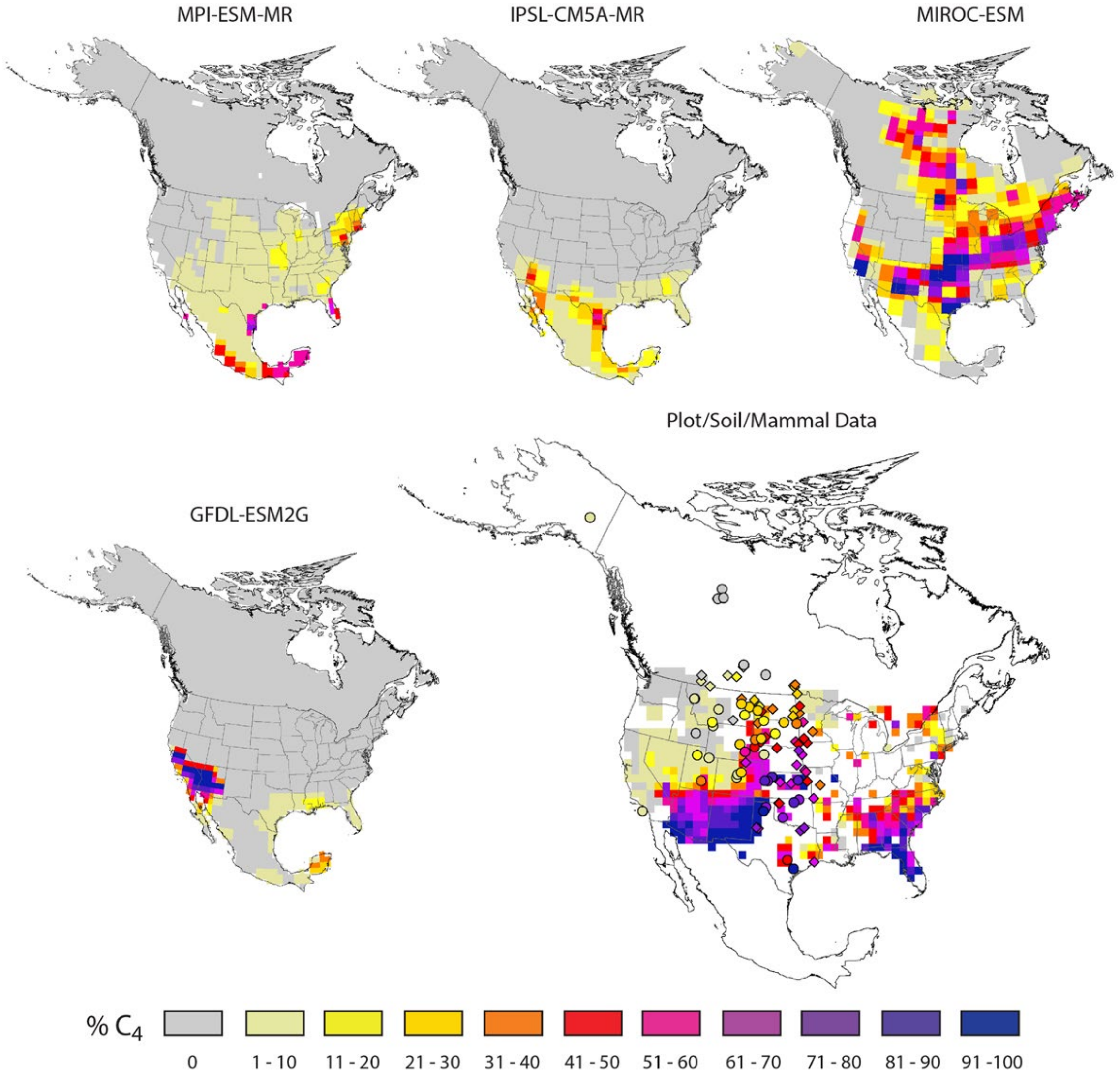

FIGURE 3 Modelled C_4 plant functional type cover in the historical modern period (*ca.* 1850 CE) compared with available data (soil $\delta^{13}C$, bison tissue $\delta^{13}C$ and plot data; Cotton et al., 2016; Griffith et al., 2015) in the lower right panel. Circles represent modern grazer isotope data, and diamonds represent soil isotope data

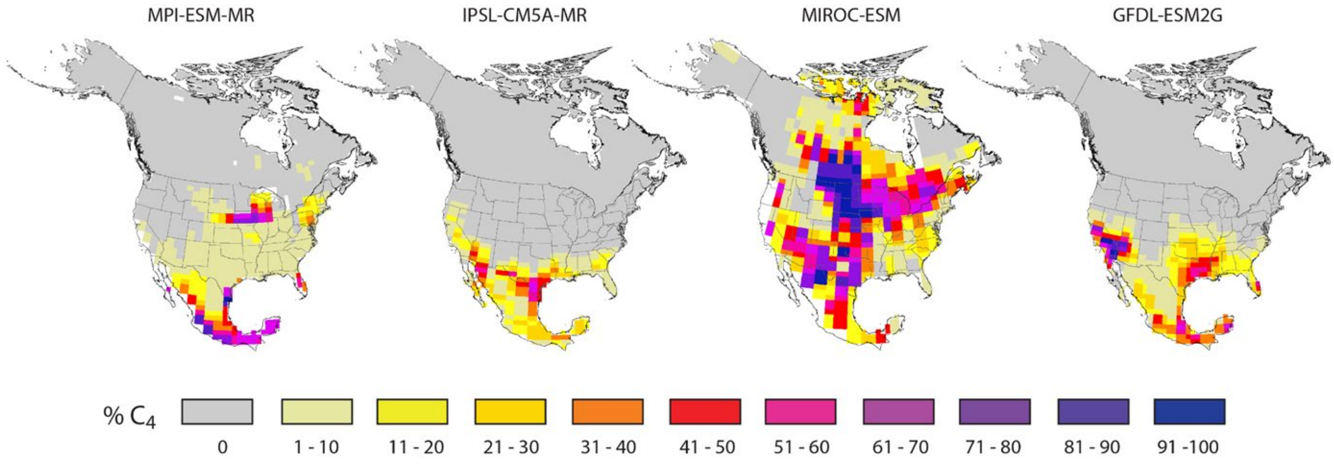

FIGURE 4 Modelled C_4 cover (sum of C_4 natural grass and crop plant functional types) for the mean of years 2071–2100 based on Representative Concentration Pathway 8.5

Helliker, 2003). Importantly, the proxy data we have collated here should generally capture such mixing, because soil organic matter and grazer hair tissue represent a weighted average of carbon inputs from each photosynthetic pathway type over seasonal and interannual time-scales.

Despite such complexities, global vegetation models driven by offline climate forcing data capture broad biogeographical patterns, generating reasonable tree–grass ecotones (Brovkin et al., 2013) and predicting primarily C_3 grasses in temperate zones and C_4 grasses in the tropics and subtropics. However, in our comparison, errors in simulating %C_4 cover in North America highlight challenges that are model specific. The GFDL model misplaced the grassland biome at a continental scale in the historical modern period. In contrast, the MIROC, MPI and IPSL models predicted somewhat realistic continental-scale grassland distributions, but very different C_4 grass distributions. The MPI grass distribution is based on the JSBACH model (Raddatz et al., 2007), which has been partly validated against satellite-based estimates of modern tree and grass cover (Brovkin et al., 2013). The LGM C_4 predictions from MPI were reasonable, whereas the MPI model underestimated C_4 grass cover in the historical period, indicating that other factors might need to be incorporated into the models, including aspects of disturbance ecology or competitive effects (e.g., Griffith et al, 2015). The MIROC natural grass distribution is based on the SEIB-DGVM (Sato, Itoh, & Kohyama, 2007), which simulates light competition among trees and a range of processes including population, community and ecosystem dynamics. Notably, this model seemed to match C_4 grass cover distributions best in the LGM and historical modern periods, although it also strongly over-predicted C_4 cover in northern and northeastern North America in the latter period.

The grass family is one of the most species-rich Angiosperm families and is easily one of the most dominant plant functional groups. Nevertheless, grasses are remarkably under-represented in trait databases (Engemann et al., 2016; Kattge et al., 2011; Wright et al., 2004), which are being used increasingly to enhance the ecological realism of DGVMs. For example, of the 2,548 species in the GLOPNET leaf trait database analysed by Wright et al. (2004), only 134 were grasses or sedges (5.3% of the total), and only 16 were C_4 grasses (.6% of the total database). Grasses are frequently ignored or minimized in global syntheses and meta-analyses, such as a recent study of plant respiration and its temperature response, which did not include a single grass species in the dataset used for analysis (Heskel et al., 2016). Likewise, meta-analyses of photosynthetic traits and leaf C and N dynamics do not include any C_4 grass species (Walker et al., 2014; Wullschleger, 1993). These gaps surely result from a lack of available trait data, not intentional exclusion of grasses, although missing information can result in environmental policies that endanger grassy ecosystems (Griffith, Lehmann, et al., 2017). This lack of data further highlights the challenges inherent in global modelling and synthesis analyses that fundamentally do not represent the functional diversity of grass-dominated biomes, in particular those dominated by an herbaceous layer of C_4 grass species.

A model improvement that would benefit from additional grass-specific trait data is explicit representation of different life-history and allocation strategies in grass PFTs. Most grass species are perennial (Atkinson et al., 2016), but a number of important invasive species are annuals, including cheat grass (*Bromus tectorum*) (D'Antonio & Vitousek, 1992). Key traits such as leaf lifespan (Lemaire, Da Silva, Agnusdei, Wade, & Hodgson, 2009) and seed mass (Bergmann, Ryo, Prati, Hempel, & Rillig, 2017; Liu, Edwards, Freckleton, & Osborne, 2012) vary greatly among grass lineages and across plant families in general (Davies et al., 2013). These traits represent key axes of variation in plant ecological and allocation strategies (Westoby, 1998) that should greatly contribute to intra-annual productivity and distributions of plants. Furthermore, phenological and reproductive traits are frequently associated with disturbance regimes such as fire and grazing (e.g., D'Antonio & Vitousek, 1992; Lemaire et al., 2009). These influence grass and tree coexistence (Higgins, Bond, & Trollope, 2000), resulting in major variation in nutrient cycling and productivity (Lehmann et al., 2014).

We suggest that, in addition to the need for more collection and greater integration of C_3 and C_4 grass trait data, other model improvements are needed to capture better the important ecological and biogeographical processes that influence distributions of grasses and their photosynthetic pathways, cover and productivity. Chief among these improvements should be more accurate representation of tree and grass cover distributions (Figure 2); these distributions should be reasonably well constrained by pollen data for the historical modern period (Whitmore et al., 2005). Accurate tree and grass cover distributions are crucial for predicting C_4 grass cover and a wide variety of biophysical and biogeochemical processes. Models can differ strongly in how they capture mechanisms that influence tree and grass distributions (Sitch et al., 2008, 2003), especially the representation of competition for water and response to disturbance. Tropical tree cover is often overestimated at the expense of savanna and grass cover in ESMs (Bonan, Levis, Sitch, Vertenstein & Oleson, 2003; Sitch et al., 2003). Models that more accurately capture disturbance responses and aspects of tree–grass competition have been successful at simulating C_4 grass cover and productivity across Africa (Higgins et al., 2000; Higgins & Scheiter, 2012; Ratnam et al., 2011; Scheiter, Langan, & Higgins, 2013). Capturing the competition for water between trees and grasses is especially important (Quijano, Kumar, Drewry, Goldstein, & Misson, 2012). At regional scales, such as those observed in the present study, the representation of C_4 cover and grass-dominated vegetation often contrasts with observations. This contrast may be because the distribution of grassy vegetation is often modified by ecosystem ecology and disturbance (Griffith et al., 2015; Moncrieff et al., 2013), and biome patterns may not be deterministic but instead contingent on biogeographical and evolutionary history (Higgins, Buitenwerf,

& Moncrieff, 2016; Lehmann et al., 2014; Moncrieff et al., 2016, 2016).

5 | CONCLUSIONS

We highlight important disagreement among global vegetation models, in addition to generally poor agreement between model predictions and observations of C_3 and C_4 grass cover and productivity. This lack of agreement occurs at a range of climates and atmospheric CO_2 concentrations, and it is unlikely that the same factors explain disagreement across models. Future improvements in grass modelling will require close collaborations between modellers and grassland ecologists and physiologists. We suggest that approaches integrating additional grass trait data and evolutionary history, in addition to approaches from community and disturbance ecology, are required to capture C_4 grass ecology and biogeography more accurately.

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DATA ACCESSIBILITY

Proxy data on C_4 cover and biomass were published at https://advances.sciencemag.org/content/suppl/2016/03/22/2.3.e1501346.DC1. CMIP5 model outputs are available at https://cmip-pcmdi.llnl.gov/cmip5/availability.html. The 100-km grid representing vegetation plot data is available in Griffith et al. (2017).

AUTHOR CONTRIBUTIONS

C.J.S., J.M.C. and D.M.G. planned and designed the research. C.J.S., J.M.C. and D.M.G. analysed data. J.M.C. created all figures. C.J.S., J.M.C. and D.M.G. wrote the manuscript.

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REFERENCES

Ahlström, A., Raupach, M. R., Schurgers, G., Smith, B., Arneth, A., Jung, M., … Kato, E. (2015). The dominant role of semi-arid ecosystems in the trend and variability of the land CO_2 sink. *Science*, *348*(6237), 895–899.

Ahlström, A., Schurgers, G., & Smith, B. (2017). The large influence of climate model bias on terrestrial carbon cycle simulations. *Environmental Research Letters*, *12*(1), 014004. https://doi.org/10.1088/1748-9326/12/1/014004

Atkinson, R. R. L., Mockford, E. J., Bennett, C., Christin, P.-A., Spriggs, E. L., Freckleton, R. P., … Osborne, C. P. (2016). C_4 photosynthesis boosts growth by altering physiology, allocation and size. *Nature Plants*, *2*, 16038. https://doi.org/10.1038/nplants.2016.38

Bakker, P., Masson-Delmotte, V., Martrat, B., Charbit, S., Renssen, H., Groger, M., … Varma, V. (2014). Temperature trends during the Present and Last Interglacial periods – a multi-model-data comparison. *Quaternary Science Reviews*, *99*, 224–243. https://doi.org/10.1016/j.quascirev.2014.06.031

Bergmann, J., Ryo, M., Prati, D., Hempel, S., & Rillig, M. C. (2017). Root traits are more than analogues of leaf traits: The case for diaspore mass. *New Phytologist*, *216*, 1130–1139. https://doi.org/10.1111/nph.14748

Bonan, G. B., & Levis, S. (2006). Evaluating aspects of the community land and atmosphere models (CLM3 and CAM3) using a dynamic global vegetation model. *Journal of Climate*, *19*, 2290–2301. https://doi.org/10.1175/JCLI3741.1

Bonan, G. B., Levis, S., Sitch, S., Vertenstein, M., & Oleson, K. W. (2003). A dynamic global vegetation model for use with climate models: Concepts and description of simulated vegetation dynamics. *Global Change Biology*, *9*, 1543–1566. https://doi.org/10.1046/j.1365-2486.2003.00681.x

Bond, W. J. (2008). What limits trees in C_4 grasslands and savannas? *Annual Review of Ecology, Evolution, and Systematics*, *39*, 641–659.

Bond, W. J., Woodward, F. I., & Midgley, G. F. (2005). The global distribution of ecosystems in a world without fire. *New Phytologist*, *165*, 525–538. https://doi.org/10.1111/j.1469-8137.2004.01252.x

Braconnot, P., Harrison, S. P., Kageyama, M., Bartlein, P. J., Masson-Delmotte, V., Abe-Ouchi, A., … Zhao, Y. (2012). Evaluation of climate models using paleoclimatic data. *Nature Climate Change*, *2*, 417–424.

Brovkin, V., Boysen, L., Raddatz, T., Gayler, V., Loew, A., & Claussen, M. (2013). Evaluation of vegetation cover and land-surface albedo in MPI-ESM CMIP5 simulations. *Journal of Advances in Modeling Earth Systems*, *5*, 48–57. https://doi.org/10.1029/2012MS000169

Cerling, T. E. (1984). The stable isotopic composition of modern soil carbonate and its relationship to climate. *Earth and Planetary Science Letters*, *71*, 229–240. https://doi.org/10.1016/0012-821X(84)90089-X

Cerling, T. E., Manthi, F. K., Mbua, E. N., Leakey, L. N., Leakey, M. G., Leakey, R. E., … Roche, H., (2013). Stable isotope-based diet reconstructions of Turkana Basin hominins. *Proceedings of the National Academy of Sciences*, *110*(26), 10501-10506.

Cernusak, L. A., Ubierna, N., Winter, K., Holtum, J. A., Marshall, J. D., & Farquhar, G. D. (2013). Environmental and physiological determinants of carbon isotope discrimination in terrestrial plants. *New Phytologist*, *200*, 950–965. https://doi.org/10.1111/nph.12423

Collatz, G. J., Berry, J. A., & Clark, J. S. (1998). Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C_4 grasses: Present, past, and future. *Oecologia*, *114*, 441–454. https://doi.org/10.1007/s004420050468

Connin, S. L., Betancourt, J., & Quade, J. (1998). Late Pleistocene C_4 plant dominance and summer rainfall in the Southwestern United States from isotopic study of herbivore teeth. *Quaternary Research*, *50*, 179–193. https://doi.org/10.1006/qres.1998.1986

Cotton, J. M., Cerling, T. E., Hoppe, K. A., Mosier, T. M., & Still, C. J. (2016). Climate, CO_2, and the history of North American grasses since the Last Glacial Maximum. *Science Advances*, *2*, e1501346–e1501346. https://doi.org/10.1126/sciadv.1501346

Cramer, W., Bondeau, A., Woodward, F. I., Prentice, I. C., Betts, R. A., Brovkin, V., … Young-Molling, C. (2001). Global response of terrestrial ecosystem structure and function to CO_2 and climate change: Results from six dynamic global vegetation models. *Global Change Biology*, *7*, 357–373.

D'Antonio, C. M., & Vitousek, P. M. (1992). Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of*

Ecology and Systematics, *23*, 63–87. https://doi.org/10.1146/annurev.es.23.110192.000431

Davies, T. J., Wolkovich, E. M., Kraft, N. J. B., Salamin, N., Allen, J. M., Ault, T. R., … Cook, B. I. (2013). Phylogenetic conservatism in plant phenology. *Journal of Ecology*, *101*, 1520–1530. https://doi.org/10.1111/1365-2745.12154

Dufresne, J.-L., Foujols, M.-A., Denvil, S., Caubel, A., Marti, O., Aumont, O., … Vuichard, N. (2013). Climate change projections using the IPSL-CM5 earth system model: From CMIP3 to CMIP5. *Climate Dynamics*, *40*, 2123–2165. https://doi.org/10.1007/s00382-012-1636-1

Dunne, J. P., John, J. G., Adcroft, A. J., Griffies, S. M., Hallberg, R. W., Shevliakova, E., … Zadeh, N. (2012). GFDL's ESM2 global coupled climate–carbon earth system models. Part I: Physical formulation and baseline simulation characteristics. *Journal of Climate*, *25*, 6646–6665. https://doi.org/10.1175/JCLI-D-11-00560.1

Edwards, E. J., Osborne, C. P., Stromberg, C. A. E., Smith, S. A., & C4 Grasses Consortium (2010). The origins of C_4 grasslands: Integrating evolutionary and ecosystem science. *Science*, *328*, 587–591. https://doi.org/10.1126/science.1177216

Ehleringer, J. R. (1978). Implications of quantum yield differences on the distributions of C_3 and C_4 grasses. *Oecologia*, *31*, 255–267.

Ellis, E. C., Klein Goldewijk, K., Siebert, S., Lightman, D., & Ramankutty, N. (2010). Anthropogenic transformation of the biomes, 1700 to 2000: Anthropogenic transformation of the biomes. *Global Ecology and Biogeography*, *19*, 589–606. https://doi.org/10.1111/j.1466-8238.2010.00540.x

Engemann, K., Sandel, B., Enquist, B. J., Jørgensen, P. M., Kraft, N., Marcuse-Kubitza, A., … Svenning, J.-C. (2016). Patterns and drivers of plant functional group dominance across the Western Hemisphere: A macroecological re-assessment based on a massive botanical dataset. *Botanical Journal of the Linnean Society*, *180*, 141–160. https://doi.org/10.1111/boj.12362

Fleiss, J. L., & Cohen, J. (1973). The equivalence of weighted kappa and the intraclass correlation coefficient as measures of reliability. *Educational and Psychological Measurement*, *33*, 613–619. https://doi.org/10.1177/001316447303300309

Francey, R. J., Allison, C. E., Etheridge, D. M., Trudinger, C. M., Enting, I. G., Leuenberger, M., … Steele, L. P. (1999). A 1000-year high precision record of $\delta^{13}C$ in atmospheric CO_2. *Tellus B: Chemical and Physical Meteorology*, *51*, 170–193.

Gamer, M., Lemon, J., Fellows, I., & Singh, P. (2012). irr: Various coefficients of interrater reliability and agreement. R package version 0.84, 137. https://cran.r-project.org/web/packages/irr/irr.pdfa

Giorgetta, M. A., Jungclaus, J., Reick, C. H., Legutke, S., Bader, J., Böttinger, M., … Stevens, B. (2013). Climate and carbon cycle changes from 1850 to 2100 in MPI-ESM simulations for the coupled model intercomparison project phase 5: Climate changes in MPI-ESM. *Journal of Advances in Modeling Earth Systems*, *5*, 572–597. https://doi.org/10.1002/jame.20038

Griffith, D. M., Anderson, T. M., Osborne, C. P., Strömberg, C. A. E., Forrestel, E. J., & Still, C. J. (2015). Biogeographically distinct controls on C_3 and C_4 grass distributions: Merging community and physiological ecology. *Global Ecology and Biogeography*, *24*, 304–313.

Griffith, D. M., Cotton, J. M., Powell, R. L., Sheldon, N. D., & Still, C. J. (2017). Multi-century stasis in C_3 and C_4 grass distributions across the contiguous United States since the industrial revolution. *Journal of Biogeography*, *44*, 2564–2574.

Griffith, D. M., Lehmann, C. E., Strömberg, C. A., Parr, C. L., Pennington, R. T., Sankaran, M., … Bond, W. J. (2017). Comment on 'The extent of forest in dryland biomes'. *Science*, *358*, eaao1309. https://doi.org/10.1126/science.aao1309

Heskel, M. A., O'Sullivan, O. S., Reich, P. B., Tjoelker, M. G., Weerasinghe, L. K., Penillard, A., … Atkin, O. K. (2016). Convergence in the temperature response of leaf respiration across biomes and plant functional types. *Proceedings of the National Academy of Sciences of the USA*, *113*, 3832–3837. https://doi.org/10.1073/pnas.1520282113

Higgins, S. I., Bond, W. J., & Trollope, W. S. W. (2000). Fire, resprouting and variability: A recipe for grass–tree coexistence in savanna. *Journal of Ecology*, *88*, 213–229. https://doi.org/10.1046/j.1365-2745.2000.00435.x

Higgins, S. I., Buitenwerf, R., & Moncrieff, G. R. (2016). Defining functional biomes and monitoring their change globally. *Global Change Biology*, *22*, 3583–3593.

Hoppe, K. A., Paytan, A., & Chamberlain, P. (2006) Reconstructing grassland vegetation and paleotemperatures using carbon isotope ratios of bison tooth enamel. *Geology*, *34*, 649–652.

Higgins, S. I., & Scheiter, S. (2012). Atmospheric CO_2 forces abrupt vegetation shifts locally, but not globally. *Nature*, *488*, 209–212. https://doi.org/10.1038/nature11238

Hossain, A., Zhang, X., & Lohmann, G. (2018). A model-data comparison of the Last Glacial Maximum surface temperature changes. *Climate of the Past*, 1–18. https://doi.org/10.5194/cp-2018-9

Hurtt, G. C., Frolking, S., Fearon, M. G., Moore, B., Shevliakova, E., Malyshev, S., … Houghton, R. A. (2006). The underpinnings of land-use history: Three centuries of global gridded land-use transitions, wood-harvest activity, and resulting secondary lands. *Global Change Biology*, *12*, 1208–1229. https://doi.org/10.1111/j.1365-2486.2006.01150.x

Jiang, D., Tian, Z., & Land, X. (2013). Mid-Holocene net precipitation changes over China: Model–data comparison. *Quaternary Science Reviews*, *82*, 104–120. https://doi.org/10.1016/j.quascirev.2013.10.017

Jiang, L., Yan, Y., Hararuk, O., Mikle, N., Xia, J., Shi, Z., … Luo, Y. (2015). Scale-dependent performance of CMIP5 earth system models in simulating terrestrial vegetation carbon. *Journal of Climate*, *28*, 5217–5232. https://doi.org/10.1175/JCLI-D-14-00270.1

Kattge, J., Díaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Bönisch, G., … Wirth, C. (2011). TRY – a global database of plant traits. *Global Change Biology*, *17*, 2905–2935. https://doi.org/10.1111/j.1365-2486.2011.02451.x

Kemp, P. R., & Williams, G. J. (1980). A physiological basis for niche separation between *Agropyron smythii* (C_3) and *Bouteloua gracilis* (C_4). *Ecology*, *6*, 846–858.

Koch, P. L. (1998). Isotopic reconstruction of past continental environments. *Annual Review of Earth and Planetary Sciences*, *26*, 573–613. https://doi.org/10.1146/annurev.earth.26.1.573

Koch, P. L., Hoppe, K. A., & Webb, S. D. (1997). The isotope ecology of late Pleistocene mammals in North America Part 1. Florida. *Chemical Geology*, *152*, 119–138.

Leavitt, S. W., Follett, R. F., Kimble, J. M., & Pruessner, E. G. (2007). Radiocarbon and $\delta^{13}C$ depth profiles of soil organic carbon in the U.S. Great Plains: A possible spatial record of paleoenvironment and paleovegetation. *Quaternary International*, *162–163*, 21–34.

Lehmann, C. E. R., Anderson, T. M., Sankaran, M., Higgins, S. I., Archibald, S., Hoffmann, W. A., … Bond, W. J. (2014). Savanna vegetation-fire-climate relationships differ among continents. *Science*, *343*, 548–552. https://doi.org/10.1126/science.1247355

Lemaire, G., Da Silva, S. C., Agnusdei, M., Wade, M., & Hodgson, J. (2009). Interactions between leaf lifespan and defoliation frequency in temperate and tropical pastures: A review. *Grass and Forage Science*, *64*, 341–353. https://doi.org/10.1111/j.1365-2494.2009.00707.x

Liu, H., Edwards, E. J., Freckleton, R. P., & Osborne, C. P. (2012). Phylogenetic niche conservatism in C4 grasses. *Oecologia*, *170*, 835–845. https://doi.org/10.1007/s00442-012-2337-5

McGraw, K. O., & Wong, S. P. (1996). Forming inferences about some intraclass correlation coefficients. *Psychological Methods*, *1*, 30. https://doi.org/10.1037/1082-989X.1.1.30

McHugh, M. L. (2012). Interrater reliability: The kappa statistic. *Biochemia Medica*, *22*, 276–282. https://doi.org/10.11613/BM.2012.031

Miranda, A. C., Miranda, H. S., Lloyd, J., Grace, J., Francey, R. J., McIntyre, J. A., … Brass, J. (1997). Fluxes of carbon, water and energy over Brazilian cerrado: An analysis using eddy covariance and stable isotopes. *Plant*, *Cell & Environment*, *20*, 315–328. https://doi.org/10.1046/j.1365-3040.1997.d01-80.x

Moncrieff, G. R., Bond, W. J., & Higgins, S. I. (2016). Revising the biome concept for understanding and predicting global change impacts. *Journal of Biogeography*, *43*, 863–873.

Moncrieff, G. R., Scheiter, S., Bond, W. J., & Higgins, S. I. (2013). Increasing atmospheric CO_2 overrides the historical legacy of multiple stable biome states in Africa. *New Phytologist*, *201*, 908–915.

Moncrieff, G. R., Scheiter, S., Langan, L., Trabucco, A., & Higgins, S. I. (2016). The future distribution of the savannah biome: Model-based and biogeographic contingency. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150311.

Morgan, J. A., LeCain, D. R., Pendall, E., Blumenthal, D. M., Kimball, B. A., Carrillo, Y., … West, M. (2011). C_4 grasses prosper as carbon dioxide eliminates desiccation in warmed semi-arid grassland. *Nature*, *476*, 202–205. https://doi.org/10.1038/nature10274

Nippert, J. B., Knapp, A. K., & Briggs, J. M. (2006). Intra-annual rainfall variability and grassland productivity: Can the past predict the future? *Plant Ecology*, *184*, 65–74. https://doi.org/10.1007/s11258-005-9052-9

Ode, D. J., Tieszen, L. L., & Lerman, J. C. (1980). The seasonal contribution of C_3 and C_4 plant species to primary production in a mixed prairie. *Ecology*, *61*, 1304–1311. https://doi.org/10.2307/1939038

Oliveras, I., & Malhi, Y. (2016). Many shades of green: The dynamic tropical forest–savannah transition zones. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*, 20150308.

Otto-Bleisner, B., Rosenbloom, N., Stone, E. J., McKay, N. P., Lunt, D. J., Brady, E. C., & Overpeck, J. T. (2013). How warm was the last interglacial? New model–data comparisons. *Philosophical Transactions of the Royal Society A: Mathematical*, *Physical and Engineering Sciences*, *371*, 20130097. https://doi.org/10.1098/rsta.2013.0097

Piao, S., Sitch, S., Ciais, P., Friedlingstein, P., Peylin, P., Wang, X., … Zeng, N. (2013). Evaluation of terrestrial carbon cycle models for their response to climate variability and to CO_2 trends. *Global Change Biology*, *19*, 2117–2132.

Porfirio, L. L., Newth, D., Harman, I. N., Finnigan, J. J., & Cai, Y. (2017). Patterns of crop cover under future climates. *Ambio*, *46*, 265–276. https://doi.org/10.1007/s13280-016-0818-1

Quijano, J. C., Kumar, P., Drewry, D. T., Goldstein, A., & Misson, L. (2012). Competitive and mutualistic dependencies in multispecies vegetation dynamics enabled by hydraulic redistribution: Multispecies vegetation dynamics. *Water Resources Research*, *48*, https://doi.org/10.1029/2011WR011416

Raddatz, T. J., Reick, C. H., Knorr, W., Kattge, J., Roeckner, E., Schnur, R., … Jungclaus, J. (2007). Will the tropical land biosphere dominate the climate–carbon cycle feedback during the twenty-first century? *Climate Dynamics*, *29*, 565–574. https://doi.org/10.1007/s00382-007-0247-8

Ramankutty, N., & Foley, J. A. (1999a). Estimating historical changes in global land cover: Croplands from 1700 to 1992. *Global Biogeochemical Cycles*, *13*, 997–1027.

Ramankutty, N., & Foley, J. A. (1999b). Estimating historical changes in land cover: North American croplands from 1850 to 1992. *Global Ecology and Biogeography*, *8*, 381–396.

Randerson, J. T., van der Werf, G. R., Collatz, G. J., Giglio, L., Still, C. J., Kasibhatla, P., … Kasischke, E. S. (2005). Fire emissions from C_3 and C_4 vegetation and their influence on interannual variability of atmospheric CO_2 and $\delta^{13}CO_2$. *Global Biogeochemical Cycles*, *19*, GB2019.

Ratnam, J., Bond, W. J., Fensham, R. J., Hoffmann, W. A., Archibald, S., Lehmann, C. E. R., … Sankaran, M. (2011). When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography*, *20*, 653–660. https://doi.org/10.1111/j.1466-8238.2010.00634.x

Sato, H., Itoh, A., & Kohyama, T. (2007). SEIB–DGVM: A new Dynamic Global Vegetation Model using a spatially explicit individual-based approach. *Ecological Modelling*, *200*, 279–307. https://doi.org/10.1016/j.ecolmodel.2006.09.006

Scheiter, S., Higgins, S. I., Osborne, C. P., Bradshaw, C., Lunt, D., Ripley, B. S., … Beerling, D. J. (2012). Fire and fire-adapted vegetation promoted C_4 expansion in the late Miocene. *New Phytologist*, *195*, 653–666. https://doi.org/10.1111/j.1469-8137.2012.04202.x

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

Sellers, P. J., Dickinson, R. E., Randall, D. A., Betts, A. K., Hall, F. G., Berry, J. A., … Henderson-Sellers, A. (1997). Modeling the exchanges of energy, water, and carbon between continents and the atmosphere. *Science*, *275*, 502–509. https://doi.org/10.1126/science.275.5299.502

Shao, P., Zeng, X., Sakaguchi, K., Monson, R. K., & Zeng, X. (2013). Terrestrial carbon cycle: Climate relations in eight CMIP5 earth system models. *Journal of Climate*, *26*, 8744–8764. https://doi.org/10.1175/JCLI-D-12-00831.1

Shrout, P. E., & Fleiss, J. L. (1979). Intraclass correlations: Uses in assessing rater reliability. *Psychological Bulletin*, *86*, 420. https://doi.org/10.1037/0033-2909.86.2.420

Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., … 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). *Global Change Biology*, *14*, 2015–2039. https://doi.org/10.1111/j.1365-2486.2008.01626.x

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., … Venevsky, S. (2003). Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology*, *9*, 161–185. https://doi.org/10.1046/j.1365-2486.2003.00569.x

Still, C. J., Berry, J. A., Collatz, G. J., & DeFries, R. S. (2003). Global distribution of C_3 and C_4 vegetation: Carbon cycle implications. *Global Biogeochemical Cycles*, *17*, 1006.

Still, C. J., Berry, J. A., Ribas-Carbo, M., & Helliker, B. R. (2003). The contribution of C_3 and C_4 plants to the carbon cycle of a tallgrass prairie: An isotopic approach. *Oecologia*, *136*, 347–359.

Taylor, K. E., Stouffer, R. J., & Meehl, G. A. (2012). An overview of CMIP5 and the experiment design. *Bulletin of the American Meteorological Society*, *93*, 485–498. https://doi.org/10.1175/BAMS-D-11-00094.1

von Fischer, J. C., Tieszen, L. L., & Schimel, D. S. (2008). Climate controls on C_3 vs. C_4 productivity in North American grasslands from carbon isotope composition of soil organic matter. *Global Change Biology*, *14*, 1141–1155.

Walker, A. P., Beckerman, A. P., Gu, L., Kattge, J., Cernusak, L. A., Domingues, T. F., … Woodward, F. I. (2014). The relationship of leaf photosynthetic traits – V_{cmax} and J_{max} – to leaf nitrogen, leaf phosphorus, and specific leaf area: A meta-analysis and modeling study. *Ecology and Evolution*, *4*, 3218–3235.

Watanabe, S., Hajima, T., Sudo, K., Nagashima, T., Takemura, T., Okajima, H., … Kawamiya, M. (2011). MIROC-ESM 2010: Model description and basic results of CMIP5-20c3m experiments. *Geoscientific Model Development*, *4*, 845–872. https://doi.org/10.5194/gmd-4-845-2011

Westoby, M. (1998). A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, *199*, 213–227.

Whitmore, J., Gajewski, K., Sawada, M., Williams, J. W., Shuman, B., Bartlein, P. J., … Anderson, P. (2005). Modern pollen data from North America and Greenland for multi-scale paleoenvironmental applications. *Quaternary Science Reviews*, *24*(16), 1828–1848. https://doi.org/10.1016/j.quascirev.2005.03.005

Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., … Villar, R. (2004). The worldwide leaf economics spectrum. *Nature*, *428*(6985), 821–827.

Wullschleger, S. D. (1993). Biochemical limitations to carbon assimilation in C_3 plants—A retrospective analysis of the A/C_i curves from 109 species. *Journal of Experimental Botany*, *44*(5), 907–920.

Wullschleger, S. D., Epstein, H. E., Box, E. O., Euskirchen, E. S., Goswami, S., Iversen, C. 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

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