



RESEARCH ARTICLE

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Increasing Functional Diversity in a Global Land Surface Model Illustrates Uncertainties Related to Parameter Simplification

Key Points:

- We implemented distributions of leaf economic spectrum traits in a land surface model in 15 diverse landscapes
- Trait variation has a substantial influence on gross primary production (GPP)
- Phenology plays a key role in guiding where traits fall within the global trait distribution and hence trait-GPP relationships

Supporting Information:

Supporting Information may be found in the online version of this article.

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Citation:












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Abstract Simulations of the land surface carbon cycle typically compress functional diversity into a small set of plant functional types (PFT), with parameters defined by the average value of measurements of functional traits. In most earth system models, all wild plant life is represented by between five and 14 PFTs and a typical grid cell ($\approx 100 \times 100$ km) may contain a single PFT. Model logic applied to this coarse representation of ecological functional diversity provides a reasonable proxy for the carbon cycle, but does not capture the non-linear influence of functional traits on productivity. Here we show through simulations using the Energy Exascale Land Surface Model in 15 diverse terrestrial landscapes, that better accounting for functional diversity markedly alters predicted total carbon uptake. The shift in carbon uptake is as great as 30% and 10% in boreal and tropical regions, respectively, when compared to a single PFT parameterized with the trait means. The traits that best predict gross primary production vary based on vegetation phenology, which broadly determines where traits fall within the global distribution. Carbon uptake is more closely associated with specific leaf area for evergreen PFTs and the leaf carbon to nitrogen ratio in deciduous PFTs.

Plain Language Summary Plants play a critical role in the global carbon cycle, and diversity has been shown to influence vegetation productivity. However, when the land surface is simulated in a global model all wild plant life is reduced to a small number of plant functional types. Here we estimate how incorporating diversity influences ecosystem carbon uptake in 15 globe spanning landscapes. We find that diversity has a strong influence on modeled productivity, particularly in the arctic and tropics. Further, we find that whether plants shed their leaves annually has a strong influence on where traits fall within the global distribution and thus how traits and productivity interact.

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1. Introduction

The representation of the land surface in an earth system model (ESM) differs from other key components of the Earth system (e.g., atmosphere, ocean) in that biological processes play an equal, or even dominant, role which interacts with physical processes to determine the functioning of the system. Early representations of the

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land surface (Sellers et al., 1986) primarily provided a meaningful boundary condition with appropriate physical properties for the rest of the physical Earth System. However, as the importance of the carbon cycle in these models has grown, so too has the physiological sophistication of the biologically driven land surface, particularly photosynthesis (Albritton et al., 2001; Bonan et al., 2011; Oleson et al., 2013). Despite the increasing complexity of plant physiology in land surface models, the representation of vegetation as plant functional types (PFTs) compresses functional diversity into fewer than 20 aggregate types (Harrison et al., 2010; Oleson et al., 2013; Quillet et al., 2010; Wullschleger et al., 2014). Moreover, many grid cells (on the order of 100×100 km) are occupied by a single PFT, and thus have no diversity. While the quality of plant biochemistry in ESMs has provided a good first order approximation of the carbon state and fluxes of the land surface, it does not capture how plant functional diversity—known from experiments and observations (Isbell et al., 2018; Liang et al., 2016; Oehri et al., 2017; Reich, 2012; Tilman et al., 2012) to have a substantial influence on productivity—affects ESM predictions of gross primary productivity (GPP).

Representing plant life as PFTs essentially transforms diverse organisms, for example, different plant species, each with potentially contrasting traits and growth rates, adapted to varied micro-environments, into a single aggregate organism (Sellers et al., 1986). Historically, the simplistic representation of terrestrial plants at global scale was due to a lack of available data. Now, the existence of large aggregate databases (Iversen et al., 2017; Kattge et al., 2011, 2020) has allowed for the estimation of functional diversity across the global land surface (Butler et al., 2017; Harper et al., 2016; van Bodegom et al., 2014).

One of the outcomes of the simplified representation of functional diversity in PFTs is a restriction in the ways different plant life responds to both environmental variation and a directionally changing climate (Funk et al., 2017; Oehri et al., 2017; Pennekamp et al., 2018). The single PFT representation limits the phenotypic response to environmental variation to that of a single organism rather than the broader envelope of responses that a plant community will inhabit (Nicotra et al., 2010; Sakschewski et al., 2015, 2016; Scheiter et al., 2013). Ultimately, incorporating plant diversity into model analyses will enable a broader range of responses to a changing environment than the single organism response of a PFT (Sakschewski et al., 2016). Previous efforts to account for plant diversity in global vegetation models have built on community assembly theory (Pavlick et al., 2013), but had limited data to compare their results against. Other work has produced detailed regional studies of diversity's influence on carbon and water cycles (Pappas et al., 2014). A detailed study of the Amazon rainforest (Sakschewski et al., 2015, 2016) used a large database (Kattge et al., 2011) to build tightly constrained trait distributions; however, the trait distributions were ultimately constrained by theoretical competitive dynamics, and in global scale models this region may have as few as two PFTs and is thus an incomplete test of how a broader range of landscapes will be affected by the shift to trait distributions.

Here, we use an updated selection of plant traits central to the leaf economic spectrum, that is, to interspecific variation in traits related to carbon and nutrient uptake, processing and conservation (Wright et al., 2004), to estimate the influence of this diversity on carbon cycle simulations from the Energy Exascale Earth System Land Model (ELM) across a diverse array of regions spanning tropical to boreal ecosystems (Figure 1, Table 1). We demonstrate that the modeled response to identical environmental fluctuations can vary dramatically for different trait combinations, even within the range of values associated with a single PFT. Further, we evaluate how modeling a PFT as a distribution of trait values, as opposed to a single mean value, changes estimates of GPP. This is equivalent to envisioning extant PFTs as comprising a set of representative vegetation types across a region as opposed to being a single aggregate entity. This distinguishes the analysis presented here from a sensitivity study of the model to the distribution of trait values.

We take a three-step approach within and across 15 globally distributed grid cells, each of which includes a FLUXNET site (Falge et al., 2016), to assess whether and how increasing the functional diversity of model parameterization can lead to substantial differences in model output. Based on the trait records compiled in the TRY database (Kattge et al., 2020) we generate site-specific three-dimensional distributions of trait values for specific leaf area (leaf area per dry mass, SLA), leaf carbon-nitrogen (mass) ratio (LCN), and leaf lifespan (LLS), accounting for the well-known trait-trait covariance structure (joint distributions; Wright et al., 2004). In the ELM model, each of these traits has a substantial influence on model output: LCN is a major control of canopy nitrogen content, which influences photosynthesis rates (Thornton & Zimmermann, 2007); SLA determines carbon investment in leaf area; LLS controls the time over which a leaf will fix carbon. These three traits together describe the main carbon and nutrient economy, and growth strategy (from inherently “fast to slow”), of different

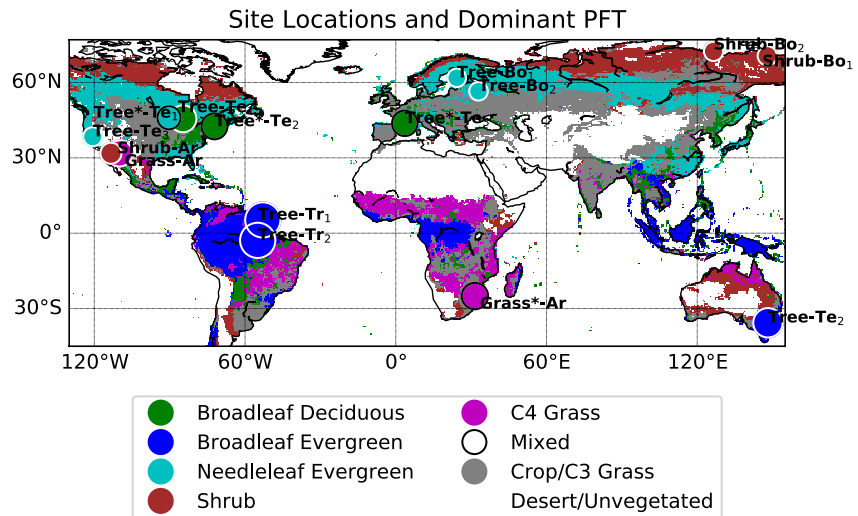


Figure 1. Site Locations and dominant plant functional types (PFT). Each circle is a site in the analysis, a white ring indicates a single PFT and a black ring indicates two PFTs co-dominating (Mixed). The size of the circle scales with the number of trait observations at each site. Background colors correspond to regions dominated by the corresponding PFTs. Note that Shrub-Ar in the Southwestern United States has been jittered slightly to distinguish it from Grass-Ar.

Table 1
Site Summaries

Name	Country	ID	T[C]	P[mm]	PFT
Chokurdakh	Russia	Shrub-Bo ₁	-12.4	163	Broadleaf Deciduous Boreal Shrub
Samoylov	Russia	Shrub-Bo ₂	-12.1	135	Broadleaf Deciduous Boreal Shrub
Hyytiala	Finland	Tree-Bo ₁	3.6	507	Needleleaf Evergreen Boreal Tree
Fyodorovskoye	Russia	Tree-Bo ₂	4.0	488	Needleleaf Evergreen Boreal Tree
U. of Michigan Bio. Station	USA	Tree-Te ₁	7.1	574	Broadleaf Deciduous Temperate Tree
Tumbarumba	Australia	Tree-Te ₂	7.5	856	Broadleaf Evergreen Temp. Tree
Blodgett	USA	Tree-Te ₃	8.8	1,159	Needleleaf Evergreen Temp. Tree
Park Falls	USA	Tree*-Te ₁	4.6	540	Bro. Deciduous Temp. Tree (50%), Nee. Evergreen Temp. Tree (50%)
Harvard Forest	USA	Tree*-Te ₂	5.1	980	Bro. Deciduous Temp. Tree (85%), Nee. Evergreen Temp. Tree (15%)
Puechabon	France	Tree*-Te ₃	13.3	901	Bro. Deciduous Temp. Tree (80%), Nee. Evergreen Temp. Tree (20%)
Kendall Grassland	USA	Grass-Ar	17.3	256	C4 Grass
Santa Rita Mesquite	USA	Shrub-Ar	19.6	320	Broadleaf Deciduous Temperate Shrub
Kruger Park	South Africa	Grass*-Ar	22.5	490	C4 Grass (70%), Broadleaf Deciduous Tropical Tree (30%)
Guyaflox	French Guiana	Tree-Tr ₁	24.6	3,158	Broadleaf Evergreen Tropical Tree
Santarem, km 67	Brazil	Tree-Tr ₂	24.7	2,670	Broadleaf Evergreen Tropical Tree

Note. This table contains detailed information for each FLUXNET tower site in the analysis according to the following categories: Name, the given name of the site in the FLUXNET Database; Country, the country that hosts the site; ID, the identification value defined by the dominant growth form (Tree, Shrub, Grass) with an asterisk (*) indicating a mixed site, and a two letter abbreviation for one of four climate types: Tr (tropical), Te (temperate), Bo (boreal), and Ar (arid), numerical suffixes are used to distinguish sites with repeated characteristics. Site climate was picked based on PFT, except for arid sites which are distinguished by being both hot (T[C] > 15C) and dry (P[mm] < 500); T[C]: The mean annual temperature of the site in degree Celsius; P[mm]: The mean annual precipitation at the site in millimeters; PFT: The PFT(s) present at the site as defined by ELM.

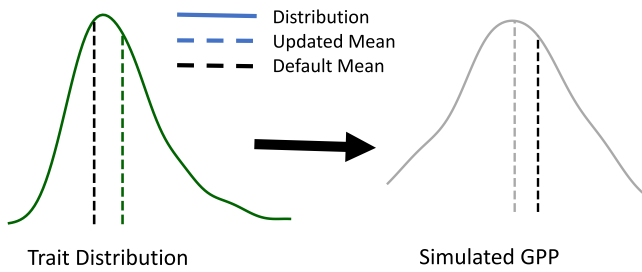


Figure 2. The three types of model simulations. There are three distinct model configurations analyzed in this study: two single runs with trait means, (i) the model default based on old species trait values (black vertical dashed line); (ii) an updated mean based on the trait distributions generated here (green vertical dashed line) and (iii) the distribution of traits (green solid line). These three model runs generate corresponding output from ELM as indicated by the black arrow and the gray distributions and vertical lines, where the line style of the trait input corresponds to the line style of the GPP output.

plant species and types; and thereby for productivity (Reich, 2014). Further, SLA and LCN directly influence V_{cmax} (the maximum velocity of carboxylation), a key parameter in photosynthesis. Using the joint distributions, we first evaluate the ranges of modeled GPP with a focus on generalizable characteristics between traits and GPP. Second, we evaluate how updating trait values changes GPP estimates relative to GPP based on FLUXNET measurements using three sets of model runs (Figure 2): (a) default parameterization; (b) updated mean trait parameterization, and (c) multiple model runs using the joint trait distributions. Third, we evaluate the non-linear relationship between traits and modeled GPP and summarize this using the updated mean trait values (b above) to the mean of GPP using the joint trait distributions (c above). Lastly, we analyze a subset of sites to better interpret how the trait-GPP relationship influences these differences. These approaches demonstrate the many ways that trait distributions drive differences in modeled GPP relative to a single trait value.

2. Materials and Methods

The model used throughout this analysis is the Energy Land Model (ELM, v1), the land component of the U.S. Department of Energy's Energy Exascale Earth System Model (E3SM), which may be run as a fully coupled ESM with atmosphere, land, ocean, sea ice, and land ice components. ELM is based on the Community Land Model version 4.5 (CLM4.5; Oleson et al., 2013), including canopy integrated leaf photosynthesis (Bonan et al., 2011, 2012), dynamically coupled carbon and nitrogen in vegetation and soil (Thornton et al., 2007), soil biogeochemistry resolved across vertical layers (Koven et al., 2013), and permafrost hydrology (Swenson et al., 2012). Further, it uses temperature revised Rubisco kinetics (Bernacchi et al., 2001, 2003) as well as a high temperature adjustment to photosynthesis (Leuning, 2002). More recently a prognostic phosphorus cycle has been added (Yang et al., 2014, 2019).

We modify the model by including a wider range of trait values based on observed functional diversity. Leveraging the global scale trait database, TRY (Kattge et al., 2011, 2020), the subset used for this analysis includes 83,585 measurements from 7,489 species across the 14 PFTs in ELM. Each trait measurement from TRY was assigned to one of the 14 natural PFTs in ELM based on its species and location. We estimate trait distributions from observations associated with the extant PFTs of ELM to explore how three key traits, SLA, leaf nitrogen concentration (LCN), and LLS, influence ELM's carbon cycle estimates as summarized by GPP. For consistency with ELM, mass based leaf nitrogen is converted to LCN ratio and SLA is converted to units of area per carbon mass by a simplifying assumption of 50% carbon content for each leaf.

These traits were selected for the central role they play in photosynthesis within ELM. A central parameter in the photosynthesis model used in ELM is the maximum velocity of carboxylation (V_{cmax}), which was modified in (Thornton & Zimmermann, 2007) to dynamically respond to changes in leaf SLA and LCN through the following relationship:

$$V_{\text{cmax}} = N_a F_{\text{LNR}} \frac{1}{F_{\text{NR}}} \alpha_R, \quad (1)$$

In Equation 1 N_a is area based leaf nitrogen content (gN m^{-2} one-sided leaf area), F_{LNR} is the fraction of leaf nitrogen in Rubisco (unitless), F_{NR} is the mass ratio of nitrogen in a Rubisco molecule to total molecular mass (unitless) and α_R is the specific activity of Rubisco ($\mu\text{mol CO}_2 \text{gRubisco}^{-1} \text{s}^{-1}$). The area based leaf nitrogen, N_a , may then be defined as:

$$N_a = \frac{1}{\text{SLA} \times \text{LCN}}, \quad (2)$$

with SLA and LCN being, SLA (m^2 one-sided leaf area gC^{-1}) and LCN ratio (gC gN^{-1}). Thus, the inverse value of SLA and LCN exert a linear control on V_{cmax} , whose components have been shown to be key parameters in controlling GPP (Ricciuto et al., 2018). The relationship between the inverse trait values and GPP is roughly consistent among sites; but, however, somewhat variable (Figure S1 in Supporting Information S1). For LLS,

its inclusion in the model is critical due to its covariance with these traits and its importance to evergreen PFTs (Reich et al., 2014), as deciduous PFTs are governed by a separate phenology module.

To determine an appropriate size for the distributions to simulate we conducted an extensive analysis using 1,000 simulations at two sites, one temperate deciduous (Tree-Te₁) and one tropical evergreen (Tree-Tr₂) to determine the requisite size of trait distribution. We expanded this pool of 1,000 simulations up to 100,000 using a simulation analysis (Castruccio et al., 2014), and tested subsets of simulations including between 20 and 1,000 samples in the distribution against the simulation with 100,000 samples. From this we determined that 100 samples, or subPFTs, were a sufficient balance between computational efficiency and accuracy. Please see Text S1 in Supporting Information S1: Supplemental Methods and Figures S2 and S3 in Supporting Information S1 for a complete description of the simulation analysis conducted to reach this conclusion.

Lastly, the distributions we report in the manuscript are from a screened subset of the original 100 trait values (Figure S4 in Supporting Information S1) because some trait combinations, generally with LLS, generated no carbon uptake at some of these sites (GPP values of 0) and others, with high LLS, produced highly unrealistic model output (e.g., Leaf Area Index (LAI) values > 1,000, Figure S5 in Supporting Information S1), this issue has been reported in other analyses where leaf life span was modified from model defaults (Reich et al., 2014). This screening reduced the included simulations to between 45% and 99% of the original 100 draws, with a mean of 68%. This leads to a unique set of trait values for each site from a previously identical distribution for each PFT.

We estimate formal non-linear trait-GPP relationships with the following form:

$$GPP_s = \beta_0 * TR_s^{\beta_1}, \quad (3)$$

here GPP_s is the annual average GPP at a site, s , for a given trait value, TR_s . All trait-GPP relationships are evaluated at each site, but generally a single trait shows a clear non-linear relationship. The β values are empirically fit constants using the Levenberg-Marquardt algorithm in SciPy (Virtanen et al., 2020).

3. Data Screening and Model Protocol

The data were screened for outliers after log transformation by removing entries greater than the 95th percentile, but only if the 95th percentile was more than three times (i.e., three orders of magnitude) the value of the fifth percentile. This criterion filtered entries that were outliers while leaving large trait values intact. Then, within each of the 14 PFTs each trait was summarized into a mean value (Table S1 in Supporting Information S1) and a pairwise covariance matrix was calculated across all PFTs (Table S2 in Supporting Information S1; Reich, 2014; Wright et al., 2004). In other words, we assume the distribution of traits to be a multi-variate log-normal for each PFT and that each PFT is, initially, identical at every site, per the current model logic. Trait values were then screened at each site based on leaf life span and producing non-zero GPP output, as noted above. This produces a set of trait values with a higher Pearson's correlation than a pairwise estimate from the raw data, but preserves the general covariance structure. Independent of this analysis PFTs have been assigned a percentage presence at each site (Table 1) and regardless of the size of the presence each PFT is assigned a unique draw from the trait distribution for each model run.

For each simulation ELM was fully spun-up under pre-industrial conditions using a 250 years accelerated decomposition spin-up (Koven et al., 2013; Thornton & Rosenbloom, 2005) followed by a 600 years final spin-up. The spin-ups are followed by a transient simulation from 1850-present forced by historically varying CO₂, nitrogen deposition (Lamarque et al., 2010), and site based meteorological observations. The observed meteorology at each site is recycled in a loop for the spin-ups and the period preceding observation, with the exact time frame rounded up to make an even multiple of the observed meteorological forcing. Site specific data are also used to update the soil texture and PFT presence. In total, we produce 102 model simulations at each of the sites. As each of the model runs is conducted independently, the subPFT simulations do not interact with each other and there is no competition between subPFTs. Thus, the modeling protocol assumes that the estimated subPFTs are present at each site and will remain static. This is in keeping with the logic that assigns the spatial location of PFTs across the land surface in most land surface models. This analysis is a simulation of how diversity influences the carbon cycle, not how that diversity arose in the first instance, as pioneered by community ecologists (Sakschewski et al., 2015, 2016; Scheiter et al., 2013).

Flux tower data are from the FLUXNET network, and we used mean annual GPP estimates (Falge et al., 2016). The flux towers were selected to cover a wide range of PFTs at sites with at least 10 years of data collected. We evaluated model output relative to flux tower data through a Kruskal-Wallis test in SciPy (Virtanen et al., 2020), by calculating the root mean square error and standard deviation across all sites, and the absolute difference between each model configuration and the flux tower estimated GPP.

4. Results and Discussion

4.1. Carbon Cycle Simulations From the Distribution of Traits

The individual runs within the distribution of traits generate GPP estimates that vary up to over an order of magnitude within a site (Figure 3). We find the greatest influence of functional trait variation on simulated productivity in the boreal zone. At one boreal shrub site in Russia (Shrub-Bo₂), the extreme trait combinations for GPP range from ≈ 100 to $\approx 1,300$ gC m⁻² yr⁻¹. There are suites of traits that produce much lower and much higher GPP in this environment than other suites, and use of a single “mean organism” in the model parameterization misses this heterogeneity. Other boreal sites show a similar range of GPP values; for example, a Finnish evergreen tree site (Tree-Bo₁) varies from ≈ 300 to 1,600 gC m⁻² yr⁻¹. At another climatic extreme, the magnitude of simulated GPP variation within tropical sites is also large, approximately a factor of five at both tropical evergreen sites. At both sites the least productive trait combination has a GPP of $\approx 1,000$ gC m⁻² yr⁻¹ and the most productive trait combination yields $\approx 5,000$ gC m⁻² yr⁻¹.

By contrast, environmentally constrained arid sites tend to show little influence on GPP from biological variation, with one arid grassland site in the US Southwest (Grass-Ar) varying as little as ≈ 200 –300 gC m⁻² yr⁻¹, only a factor of 1.5, across the trait distribution. Despite a comparable range of input trait values (Figure S4 in Supporting Information S1) the arid sites produce a narrower GPP distribution than other locations. In the environmentally constrained arid sites there is little room for greater productivity with the leaf economic spectrum traits selected for this analysis, but in highly productive tropical sites and environmentally variable boreal sites distinct trait combinations can yield vastly different outcomes.

These simulations are distinct from a parameter sensitivity analysis because all three traits are varied together and constrained by their trait-trait covariances (Table S2 in Supporting Information S1). In essence, these GPP distributions may be thought of as each representing a set of patches within the simulated grid cell. Each simulation and its estimated GPP is equivalent to the productivity of different coexisting species or individuals with varying trait values.

Most of the GPP distributions are approximately normal by both visual inspection and a D’Agostino K² normality test ($p < 0.05$, at 13 sites, Figure S6 in Supporting Information S1). However, the near normality of most of the GPP distributions is contrasted by net primary production (NPP, Figure S7 in Supporting Information S1) which fails the test at six sites ($p < 0.05$). Three sites fail the normality test for leaf maintenance respiration (Figure S8 in Supporting Information S1; $p < 0.05$). Temperate and arid sites most frequently show varying distribution shapes across these different components of the carbon cycle. The variation in shape of these distributions highlights the non-linear influence of leaf economic spectrum traits on the carbon cycle, and challenges reducing the distribution down to a single value as is currently done (Oleson et al., 2013).

4.2. Phenology, Trait Distributions, and GPP

We focus on the divergence between deciduous and evergreen phenology in terms of the influence of traits on GPP within the model. Phenology is a convenient division between SLA and LCN because these two groups, evergreen and deciduous, occupy markedly different components of the global trait distribution for these two traits, Figure 4. Deciduous PFTs cluster around the mean of both groups for SLA (Figure 4a), while evergreen PFTs occupy the low valued tail of the SLA distribution. For LCN it is the reverse, evergreen PFTs are more strongly clustered around the mean of the two groups while deciduous PFTs skew into the tail. Because of the relationship between these traits and V_{cmax} (Equations 1 and 2), and therefore GPP, we expect these traits to have variable influence on model behavior for these two groups.

As expected from the position of these phenological groups within the trait distributions, the trait-GPP relationships are quite different. The deciduous sites show a close coupling between LCN and GPP while the evergreen

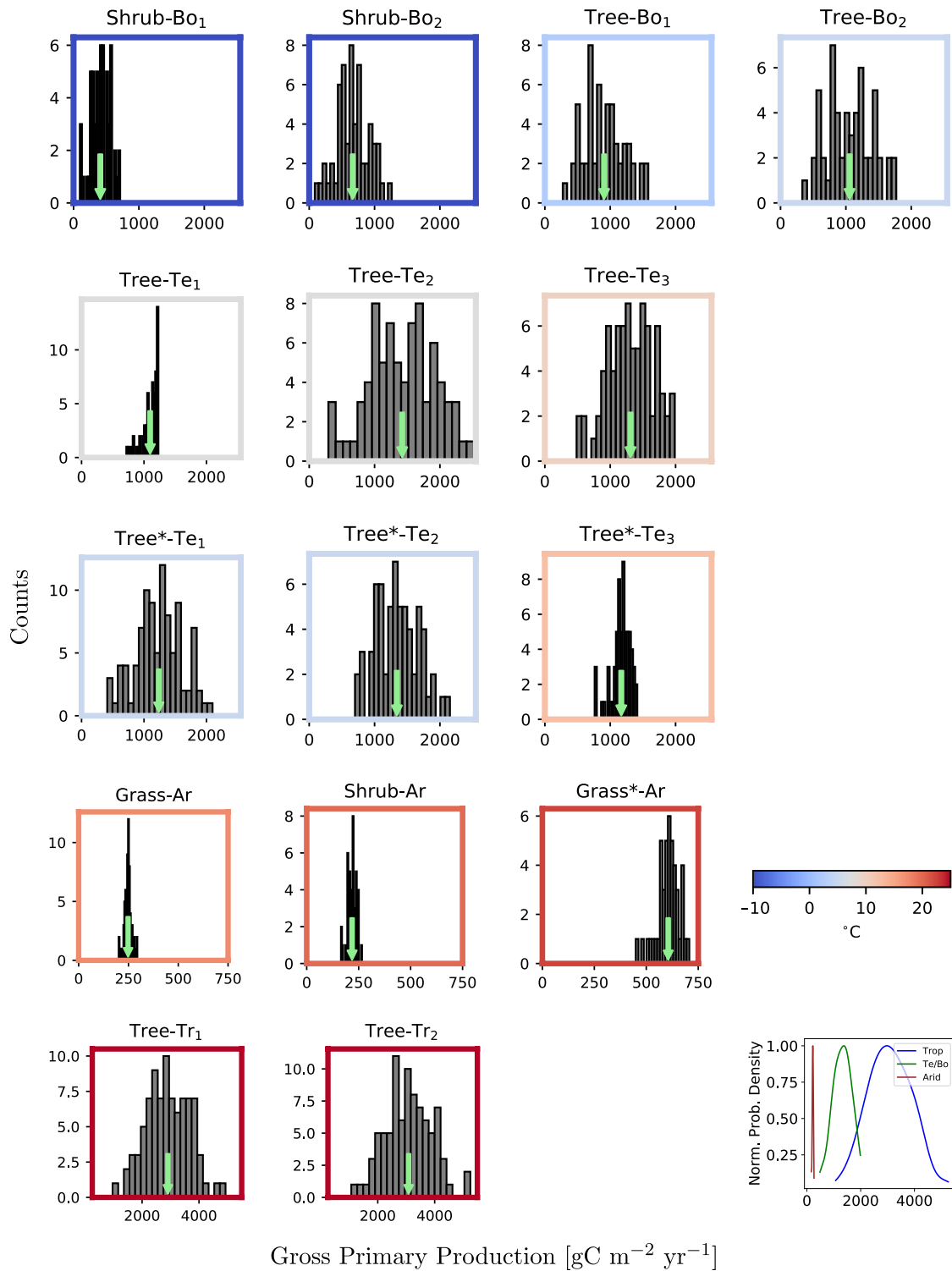


Figure 3. The distribution of gross primary production (GPP) estimates at each site. The distribution of GPP from the joint distribution of trait values is in gray, the green arrow indicates the mean of the distribution. Sites are ordered from coldest to hottest within rows which are determined by their climatic region, border colors display the annual average temperature per the color bar in the right column. The range of GPP values displayed on the x-axis is determined by the climatic region: boreal/temperate, arid, or tropical, the three are displayed on a common axis in the lower right corner.

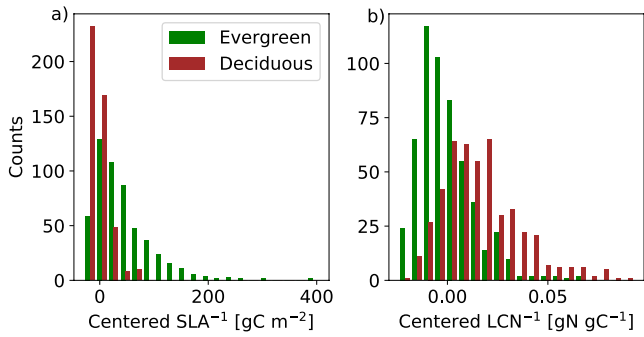


Figure 4. Distributions of inverse traits broken down by phenology. In both panels the inverse of specific leaf area (SLA) and leaf carbon-nitrogen (LCN) is shown to more easily visualize the impact on V_{cmax} (Equations 1 and 2), similarly both panels are centered on the mean value of both groups combined, this emphasizes deviation from a common value. Evergreen counts are shown in green, while deciduous values are in brown. In (a) the evergreen plant functional types (PFTs) skew toward high values of SLA^{-1} , while in (b) the deciduous PFTs skew toward high values of LCN^{-1} .

sites show a tighter relationship between SLA and GPP; to simplify across sites, GPP and traits are normalized across sites into z-scores (Figure 5). We focus on SLA and LCN because LLS covaries closely with SLA (Table S2 in Supporting Information S1) and thus the relationship between LLS and GPP is largely redundant (Figure S9 in Supporting Information S1). Further, SLA and LCN are directly coupled with V_{cmax} , as noted earlier. Last, LLS is only used with evergreen species as LLS is governed by a separate phenology module for deciduous PFTs. However, the inclusion of LLS is still critical for constraining model output for evergreen PFTs. Within ELM, phenological habit sorts PFTs into different portions of trait space, which then drives which trait will have a more predictable influence on GPP. However, as discussed below, apparent phenological habit is only a guide and not fully predictive of the model relationship between traits, environment, and productivity (see Section 4.4).

4.3. Comparing Model GPP Against Flux Data

We compare three estimates of model GPP to evaluate how the representation of functional diversity influences the prediction of GPP and how those compare to an external benchmark. The first used unmodified trait values from the prior version of the model (*default*). Second, we updated the default values to the mean of the draws from the trait distribution (*updated mean*). Third, we produced an estimate using the distribution of traits as input (*distrib-*

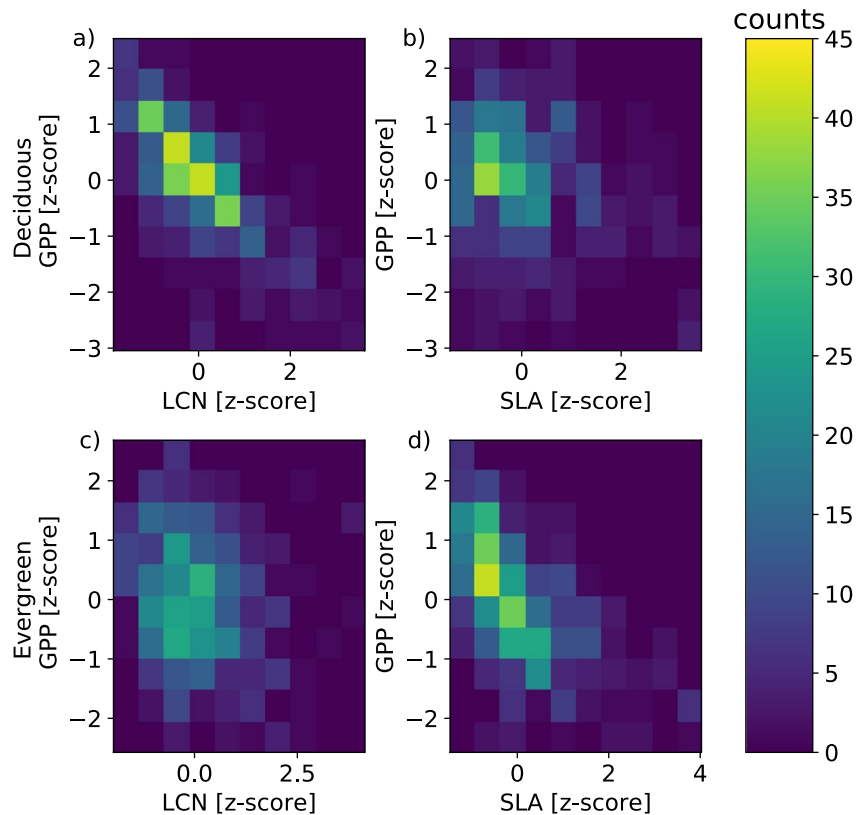


Figure 5. Relationships between traits and gross primary production (GPP). Panels (a and b) are for deciduous sites and panels (c and d) are for the evergreen sites. Within each 2D histogram lighter colors indicate more site-trait combinations that fall within the GPP-trait pixel, after normalization to z-scores. At the deciduous sites the relationship between leaf carbon-nitrogen (LCN) and GPP is constrained while specific leaf area (SLA) is more diffuse. The evergreen sites are the opposite, with a tight relationship between SLA and GPP and a more diffuse relationship with LCN.

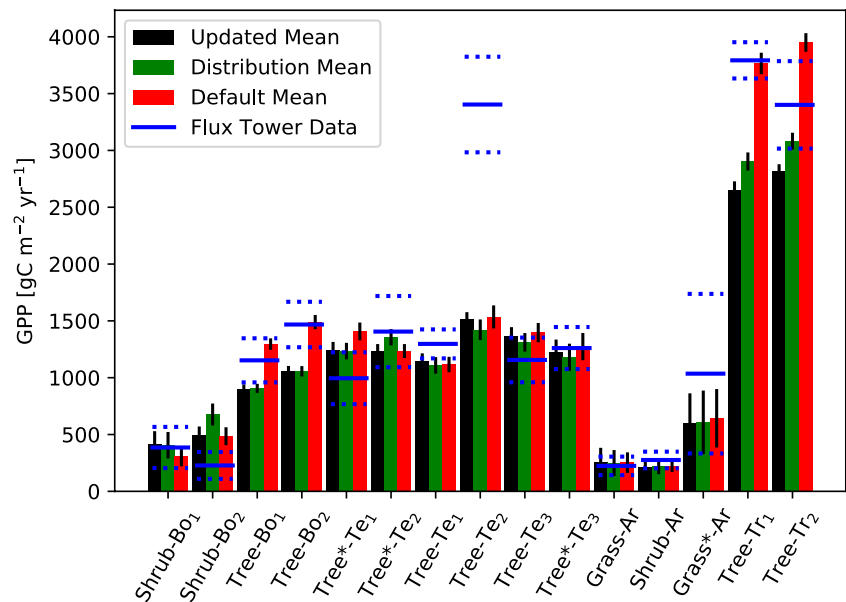


Figure 6. Each site's temporal mean annual gross primary production (GPP) estimated by four different methods. The x-axis is labeled with the site ID (Figure 1, Table 1). The colors of each bar indicate the method used to estimate GPP as indicated in the legend. Thin black lines are the temporal standard deviation at the site. The solid blue line across all bars at each site is the flux tower estimate of GPP and the dashed lines are the temporal standard deviation.

bution mean). Across all sites, the difference between flux tower GPP and any of the three estimates (Figure 6) were comparable. Formally, a Kruskal-Wallis test could not distinguish between the median differences of the flux tower GPP and all three GPP model estimates ($p < 0.05$). The default mean had a root mean squared error (\pm standard deviation, across sites) of $538 \pm 928 \text{ gC m}^{-2} \text{ yr}^{-1}$ versus $624 \pm 950 \text{ gC m}^{-2} \text{ yr}^{-1}$ using the updated mean. The mean of all runs from the trait distribution, the distribution mean, is intermediate to the default and updated mean simulations with a root mean squared error of $609 \pm 985 \text{ gC m}^{-2} \text{ yr}^{-1}$. As is clear from the difference at each site (Table S3 in Supporting Information S1), all three configurations have comparable differences (on average) relative to the flux tower data, so we consider these results to be inconclusive regarding which of these methods is the best match to a flux tower benchmark. We further note that flux tower footprints cover only a tiny proportion of any (roughly $100 \times 100 \text{ km}$) grid cell, and thus the vegetation in the flux footprint and the flux data are unlikely to represent the full diversity of the grid cell, so one should not necessarily expect a close match between tower flux data and grid cell model output. Despite this, we believe that comparisons with the flux tower data serve as a useful contextual framing, but not as validation of the models.

4.4. Evaluating the Difference Between GPP From the Trait Distribution and the Updated Mean Across Sites

A particular challenge to the single PFT representation that motivated this analysis is the non-linearity of the relationships between functional traits and carbon fluxes of ecosystems (Medvigy et al., 2009; Moorcroft et al., 2001). Jensen's Inequality (Cover & Thomas, 1991; Jensen, 1905) ensures that using the mean of the trait distribution as input to a convex function will give a lesser (or equal) result than taking the mean of the output of the function, and the opposite for a concave function (Figure S10 in Supporting Information S1). Here, Jensen's Inequality serves as an entry point to evaluate the magnitude of difference that a single extant PFT, the updated mean, compares to a diverse set of organisms or subPFTs, the distribution mean. To summarize the influence of the trait distribution we used the mean of the model output over the observation period at each site. This provides an estimate of the magnitude of Jensen's inequality at these sites, which we may write as:

$$f(E[x]) \leq E[f(x)], \quad (4)$$

for a convex function f . When a function is concave the less than (or equal to) relationship reverses to greater than (or equal to), so $f(E[x]) \geq E[f(x)]$. In this equation the function f , represents the whole set of algorithms

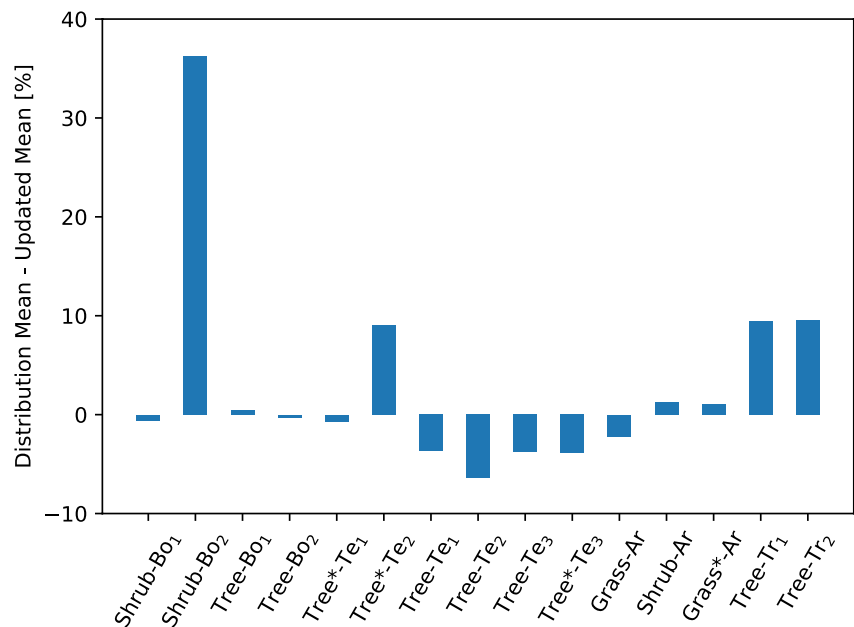


Figure 7. Difference in modeled gross primary production (GPP) between the updated mean and the distribution mean. The x-axis labels are the corresponding site IDs (Figure 1, Table 1) ordered from coldest to warmest. The largest percentage differences are in more extreme sites, with larger GPP estimates from the distribution at one boreal shrub site and both tropical evergreen sites but negligible differences at boreal tree sites. Temperate sites are mixed but generally negative. Phenological habit and the structure of the trait-GPP relationship provide some further insight into these differences, see Figures 4, 5 and 8.

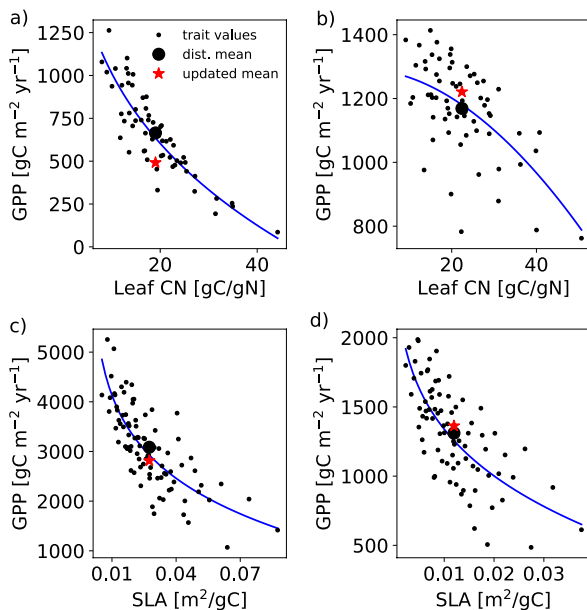


Figure 8. Non-linear trait-gross primary production (GPP) relationships at four sites. Two deciduous sites (a) Shrub-Bo₂ and (b) Tree*-Te₃ and two evergreen sites (c) Tree-Tr₂ and (d) Tree-Te₃ highlight how differences in the trait-GPP relationship can drive divergent responses in the updated mean and the distribution mean depending on how tight the correspondence is between GPP and the trait value as well as the nature of the non-linear relationship. Blue lines indicate a non-linear fit of the form described in Equation 3.

and equations that comprise the vegetation model in ELM, $E[x]$ indicates the expected value, and x is the distribution of trait values. In the context of this analysis the left-hand side of Equation 4 is the updated mean while the right-hand side is the distribution mean.

As already noted, using the updated (or for that matter, the default) mean masks considerable variation in projected GPP for the individual trait runs (Figures 2, 3 and 5). Beyond the distribution driven variation in model output the comparison of updated and distribution mean values between these sites reveals substantial differences, varying between a 36% increase and 6% decline when comparing the distribution mean of the trait distribution to the single updated mean value (Figure 7). Four of 15 sites show an increase of at least 9% in GPP when using the distribution, with the largest percentage increase in one boreal shrub site; whereas on an absolute basis, the largest magnitude increase occurred at the two tropical forest sites (Figure S11 in Supporting Information S1).

Interestingly, the contrasting results between the distribution mean and the updated mean show that incorporating the distribution of functional traits as evaluated here did not have a consistent influence on model GPP, and hence the constraint implied by Jensen's inequality is not a straightforward guide to how functional diversity will affect model behavior. In short, the set of algorithms denoted by $f(x)$ in Equation 4 does not respond consistently, even non-linearly, to trait input values (Figures 8, S9 in Supporting Information S1). However, there is some rough structure to the differences between the updated mean and the distribution mean. The phenological differences (Figures 4 and 5) are apparent here with a sharp contrast between increases at tropical evergreen sites and decreases in most deciduous angiosperm systems.

However, boreal systems show a mixed effect the output at one of the very cold deciduous shrub sites had a large increase using trait distributions whereas the other boreal shrub site and the two boreal evergreen conifer sites showed almost no effect. One explanation for the deviation between boreal and tropical evergreen systems is that the tropics are photosynthetically active year-round, but the evergreen conifers have a long dormant season.

The phenological differences noted earlier (Figures 4 and 5), coupled with a sub-set of four sites sheds some further light on the basis for the widely varying differences between the estimated GPP from the distribution mean relative to the updated mean. A suite of factors including how closely coupled each trait is with GPP as well as the non-linear structure of the relationship between the trait and GPP estimate both appear to influence this result. For example, in Shrub-Bo₂ there is a tight convex relationship between LCN and GPP (Figure 8a) and this site has a substantial difference between the updated and distribution mean. By contrast, Tree*-Te₃ (Figure 8b) shows a much looser relationship and the distribution and updated means show notably different results. Critically the relationship flips to concave, which - as Jensen's Inequality would predict - induces a sign change between these two sites. However, among evergreen sites the tropical site Tree-Tr₂ (Figure 8c) has only a slightly tighter relationship between SLA and GPP than Tree-Te₃ (Figure 8d). Because both have concave SLA-GPP relationships it is now the variation around this relationship that drives a sign change between the updated and distribution mean. The variation of GPP for a given trait value occurs because we draw trait combinations from a joint distribution, for example, there is a range of SLA values for a given LCN and vice versa. Even modest variation around the non-linear trait-GPP relationship can drive a substantial shift in the modeled output and in this case the trait variation appears to be a more dominant factor than the concavity of the trait-GPP relationship. The phenology still serves as a guide to the trait-GPP relationship, but Jensen's Inequality alone cannot predict how the distribution mean will vary relative to the updated mean.

5. Conclusions

Our analyses show that accounting for leaf functional diversity can have a substantial influence on modeled carbon fluxes. We focused our analysis on three approaches. First, we evaluated the distribution of modeled GPP when using a distribution of traits as input and found that GPP could vary over an order of magnitude at some sites among hypothetical "patches" differing in traits. We found that phenological habit was a guide to which trait appears to govern the GPP response within the model with a contrast between deciduous and evergreen habits driven by LCN and SLA, respectively. This contrast is likely to result from the portion of trait space occupied by the PFTs within these phenology groups where deciduous trees have values of LCN more favorable to high V_{cmax} and the same for evergreen trees and SLA. Second, we compared three different modeling schemes against flux tower data, and found that all were generally in rough agreement with tower data (except for one site), which we note represent only one of the myriad possible trait distributions within the large grid cells the model parameters are set to describe. Third, we evaluated how using updated mean trait values as input in modeling GPP compared to evaluating the distribution mean from the output of the distribution of trait values. A boreal shrub site and both tropical tree sites showed the greatest influence when modeling the trait distribution, with a notable but less pronounced effect at temperate tree sites. However, further work is needed to refine what drives both the non-linear structure and tightness of coupling between traits and modeled GPP. Until there is a stronger theoretical basis for these differences, explicitly modeling the trait distribution is the only means to ensure how varying traits will influence productivity.

By contrast with previous efforts to incorporate functional diversity into land surface models (Pavlick et al., 2013; Sakschewski et al., 2015, 2016), we developed an empirical method to derive representative trait combinations and use them for model ensemble runs, without explicit mechanisms for community assembly. This method is closer to the current framework applied in global vegetation models and could be implemented in future global simulations. There are competing ideas for both what can and should be improved in terrestrial vegetation models (Fatichi et al., 2019). Here, we have pioneered a method to incorporate empirical distributions of plant traits into the model structure as a method to simulate the functional diversity that occurs at the scales the models simulate ($\approx 100 \times 100$ km). The impact in tropical regions was consistently substantial and, while less consistent in boreal regions, the effect was potentially much greater in a proportional sense. Accurately simulating these vulnerable and rapidly changing regions is critical to improving projections of the global carbon cycle, and the magnitude of the response in these regions suggests that improving our understanding and modeling of trait diversity impacts on carbon cycling processes is of paramount importance.

Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

Data Availability Statement

Analysis code and model output are stored in a Zenodo repository: <https://zenodo.org/record/6127506>.

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