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2 **Sensitivity and Uncertainty Analysis of China's Terrestrial Carbon-Water Cycle**

3 **Using a Dynamic Global Vegetation Model**

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11 Abstract

12 Parameter uncertainty in Dynamic Global Vegetation Models (DGVMs) substantially impacts
13 the reliability of carbon-water cycle simulations. Using the LPJ-GUESS model at 13 sites across
14 China's diverse ecosystems, this study employed a multi-method (Morris, eFAST, Sobol')
15 sensitivity analysis on 39 key parameters to assess their impacts on nine carbon-water cycle
16 variables. Our results revealed that the model's behavior is co-dominated by both core
17 physiological parameters, often hard-coded in the source, and plant functional type-specific traits.
18 This finding suggests limitations in the common practice of focusing calibration solely on user-
19 adjusted files. Furthermore, these parameter controls are highly context-dependent, shifting
20 based on both the target process (e.g., carbon uptake as opposed to water flux) and the regional
21 climate, where arid ecosystems respond most strongly to water-use parameters. The multi-
22 method approach also highlighted that the influence of many parameters is mediated through
23 complex interactions rather than direct effects alone. Consequently, this complex web of
24 sensitivities propagates into contrasting patterns of model uncertainty: arid ecosystems exhibit
25 the highest relative uncertainty, making predictions more uncertain, while humid, productive
26 ecosystems show the largest absolute uncertainty, posing a challenge for carbon budgeting.
27 These findings provide a scientific basis for developing targeted, region-specific
28 parameterization strategies to reduce model uncertainty and improve assessments of terrestrial
29 carbon sink functions.

30 Keywords

31 Sensitivity analysis; Uncertainty analysis; Carbon-water cycle; Parameterization; LPJ-GUESS



32 1 Introduction

33 Terrestrial ecosystems are an important component of the global carbon cycle and water cycle,
34 and play a crucial role in regulating climate change through land–atmosphere interactions
35 (Buster et al., 2024). Carbon uptake and water transport are tightly coupled through plant
36 physiological processes, especially via stomatal regulation, which simultaneously controls
37 carbon dioxide assimilation and water transpiration. In turn water availability directly restricts
38 photosynthetic efficiency, affecting carbon assimilation, vegetation structure, and then feedbacks
39 to soil moisture and evapotranspiration (Hickler et al., 2015). Together, these processes form a
40 complex and dynamic carbon-water coupling system linking terrestrial ecosystems and the
41 atmosphere (Buster et al., 2024; Zhao et al., 2025).

42 Dynamic Global Vegetation Models (DGVMs) are process-based tools that are widely used to
43 simulate ecosystem structure and function under varying climate conditions (Bonan et al., 2003;
44 Forster et al., 2024; Liu et al., 2024). Among them, the Lund-Potsdam-Jena General Ecosystem
45 Simulator (LPJ-GUESS) has become an important platform for carbon-water dynamic modeling
46 research due to its explicit representation of plant functional types, biogeochemical cycles and
47 hydrological processes (Smith et al., 2001). The model can simulate key ecological variables
48 such as gross primary productivity (GPP), evapotranspiration (ET), vegetation carbon storage,
49 and soil carbon storage, and has been widely used at both global and regional scales (Smith et al.,
50 2014; Smith et al., 2011).

51 Despite their broad applicability, the performance of DGVMs is strongly dependent on
52 parameter settings to describe ecological processes, and the selection of parameter values is
53 subject to uncertainty (Verrelst et al., 2019), especially in areas characterized by pronounced
54 ecological heterogeneity. China encompasses a wide range of climate zones and vegetation types
55 (Chen et al., 2022), spanning humid monsoon regions in the southeast to arid and semi-arid
56 inland regions in the northwest. This spatial heterogeneity poses a challenge to the adaptability
57 of model parameters (Guan et al., 2023; Wu, 2023; Ma et al., 2022b), and also provides an ideal
58 platform for exploring regional differences in parameter sensitivity of carbon-water coupling
59 processes.

60 Model parameter sensitivity analysis is a critical method to identify key parameters driving
61 model output and improve simulation accuracy and credibility (Yuxi et al., 2024). At present,



62 sensitivity analysis methods have evolved from traditional one-at-a-time (OTA) variation to
63 global sensitivity analysis techniques, such as Morris, eFAST and Sobol', which can identify
64 nonlinear relationships and parameter interaction effects (Ma et al., 2022b; Nossent et al., 2011;
65 Vazquez-Cruz et al., 2014). Although these methods have been increasingly applied in
66 ecosystem modeling studies (Pappas et al., 2013), most of them have focused on individual
67 carbon cycle processes or site-specific analyses, with relatively limited attention to the integrated
68 evaluation of carbon-water coupling processes (Oberpriller et al., 2022).

69 Previous studies have shown that LPJ-GUESS outputs are highly sensitive to parameters such
70 as photosynthetic efficiency, plant structure, and carbon allocation strategies. For instance,
71 Pappas et al. (2013) highlighted the influence of photosynthetic quantum efficiency and canopy
72 scale conversion coefficient on GPP and NPP, while Oberpriller et al. (2022) emphasized that the
73 parameters related to water processes and climatic drivers, such as temperature and precipitation,
74 substantially affects on forest simulations. However, these studies are largely confined to
75 temperate regions in Europe, and offer limited insights into the spatial variability of parameter
76 sensitivities across China's ecologically heterogeneous landscapes. Moreover, calibration and
77 sensitivity analyses in the DGVM community have traditionally focused on the more accessible
78 Plant Functional Type (PFT) parameters found in user-facing files, whereas the influence of core
79 physiological parameters embedded within the model's source code remains less well quantified,
80 potentially limiting a comprehensive understanding of model behavior (Peng et al., 2024).
81 Furthermore, different sensitivity analysis methods have their strengths and limitations. The
82 Morris method has high computational efficiency but is difficult to evaluate interaction effects,
83 whereas the Sobol' method can quantify both main effects and interaction effects but has high
84 computational costs. The extent to which these methods converge or diverge is not well
85 understood, particularly in their ability to untangle direct, linear parameter effects from the
86 complex, non-linear interactions that likely govern coupled systems. More importantly, most
87 existing studies focus on carbon cycle variables, often neglecting the critical role of water
88 dynamics and their feedbacks within ecosystem simulations (Oberpriller et al., 2022).

89 To address these gaps, this study selected 13 representative ecosystem sites across China,
90 covering a variety of typical vegetation types and climate zones. Based on the LPJ-GUESS
91 model, three complementary sensitivity analysis methods--Morris, eFAST and Sobol'--were used
92 to systematically evaluate the impact of 39 key ecological process parameters on the carbon and



water cycle simulation results. By assessing the sensitivity of nine carbon and water cycle variables and analyzing the spatial heterogeneity of parameter effects, this study aims to (1) identify the dominant parameters driving model outputs, (2) evaluate the regional variability of parameter sensitivities, (3) compare the consistency and complementarity of sensitivity analysis methods, and (4) quantify uncertainty propagation across ecosystems. The findings are intended to support the refinement of parameterization strategies in DGVMs and enhance the model's regional carbon–water cycle assessments under future climate scenarios.

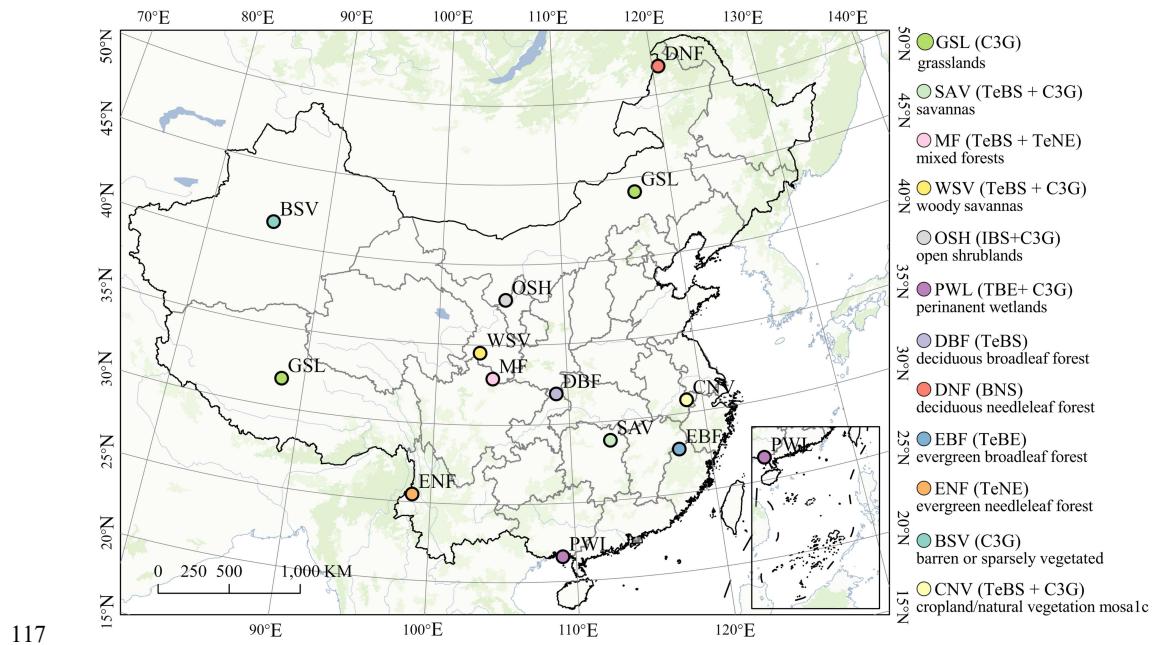
2 Materials and Methods

2.1 Study Area and Site Design

To assess the parameter sensitivity of the LPJ-GUESS model across diverse ecosystems, this study selected 13 representative sites spanning the major natural vegetation types and climate zones in China (Fig. 1; see Table S1 in the Supporting Information for site details). These sites, located within national nature reserves, were selected to minimize anthropogenic disturbances and ensure ecological representativeness.

Site selection was primarily based on the MODIS MCD12Q1 land cover product (2001-2023) (Friedl & Sulla-Menashe, 2022) and boundary data of Chinese nature reserves. Key criteria for the site selection included: ensuring the sites represent dominant regional vegetation types (e.g., forests, grasslands); excluding areas of significant anthropogenic land use; and verifying vegetation stability over time by assessing land cover consistency from 2001 to 2023.

To enhance national-scale representativeness, a two-stage sampling strategy was adopted, combining the International Geosphere–Biosphere Programme (IGBP) vegetation type classification with a spatial equilibrium algorithm to ensure a balanced geographical distribution. A detailed description of the site selection process is provided in Text S1 in the Supporting Information.



118 **Fig. 1. Spatial distribution of sample points used for sensitivity analysis**

119 **2.2 Model and Driving Data**

120 **2.2.1 LPJ-GUESS Model**

121 LPJ-GUESS is a process-based Dynamic Global Vegetation Model designed to simulate
122 terrestrial ecosystem dynamics under changing environmental conditions (Sitch et al., 2003;
123 Smith et al., 2014). It explicitly represents key water, carbon, and nitrogen processes within the
124 soil-plant-atmosphere continuum and simulates vegetation competition for light, water, and
125 space resources (Lindeskog et al., 2013; Lindeskog et al., 2021). The model classifies vegetation
126 into 12 PFTs characterized by specific growth forms (e.g., herbaceous, broadleaf tree, deciduous
127 tree), photosynthetic pathways (C3 or C4), phenological strategies (evergreen, summergreen, or
128 raingreen), tree biometrics and life-history traits, as well as bioclimatic constraints on
129 establishment and survival (Olin et al., 2015; Smith et al., 2014). It also accounts for the fire
130 sensitivity and disturbance responses among PFTs (Smith et al., 2014).

131 In this study, LPJ-GUESS version 4.1 was employed in cohort mode, in which woody
132 individuals of the same size and age within a local neighborhood or patch are grouped into a
133 representative average individual. Each PFT is simulated as a set of such cohorts, assuming



134 structural uniformity among individuals of the same age within a patch (Olin et al., 2015; Pugh et
135 al., 2019; Teckentrup, 2023). Establishment, mortality, and disturbance events are governed by
136 stochastic processes. Fire occurrence is simulated annually (stochastically) based on probabilistic
137 functions of temperature, fuel availability, and upper soil moisture content, which served as a
138 proxy for litter moisture (Thonicke et al., 2001).

139 **2.2.2 Driving Data**

140 The driving data required by the LPJ-GUESS model include monthly meteorological variables
141 (temperature, precipitation, and incoming shortwave radiation), soil texture (assumed static over
142 time), annual atmospheric CO₂ concentration, and nitrogen deposition rates.

143 In this study, meteorological forcing data were derived from the ERA5-Land reanalysis
144 dataset, which provides monthly data at a spatial resolution of 0.1° for the period 1980-2023
145 (Copernicus Climate Change Service, 2019). Specifically, monthly average temperature,
146 cumulative precipitation, and average incident shortwave radiation were extracted. Annual
147 atmospheric CO₂ concentration data, reflecting interannual variability, were derived from long-
148 term observations at the Mauna Loa Observatory, Hawaii (Lan et al., 2023). Soil texture data,
149 including sand and clay content, carbon-nitrogen ratio, pH, soil bulk density, and soil organic
150 carbon, were obtained from the National Tibetan Plateau Data Center (Shi et al., 2025). For
151 consistency, values from six standard soil layers within the 0-2 meters depth range were
152 averaged to generate a single representative soil profile for each site. Nitrogen deposition data
153 were adopted from the Lamarque dataset (default spatial resolution of 0.5°), with values from the
154 nearest grid cell assigned to each site as model input (Lamarque et al., 2013).

155 **2.2.3 Model Setup**

156 To ensure the stabilization of ecosystem carbon pools, the LPJ-GUESS model was initialized
157 with a 500-year spin-up period. This period employed repeated cycling of the first 20 years
158 (1980-2000) of climate forcing data, with temperature trends removed to maintain climatic
159 baseline. During the spin-up, stochastic processes such as fire and natural disturbances were
160 enabled to represent inherent ecological dynamics. However, anthropogenic land-use changes
161 were excluded, as all selected sites are located within national nature reserves, where direct
162 human impacts are minimal.



163 2.3 Parameter Selection and Value Ranges

164 For the sensitivity analysis, 39 key parameters of the LPJ-GUESS model were selected,
165 covering fundamental ecological processes such as photosynthesis, carbon allocation, and
166 vegetation structure. These parameters comprise 19 core physiological parameters, which are
167 applied uniformly across all vegetation types, and 20 PFT specific traits that characterize the
168 strategies of individual ecosystems. Detailed information on parameter definitions, functions,
169 and value ranges, is provided in Table 1.

170 Parameter value ranges were defined based on a combination of sources: (1) default values
171 and annotations within the model source code; (2) empirical ranges reported in peer-reviewed
172 LPJ-GUESS calibration studies; and (3) a $\pm 25\%$ deviation from the default value where direct
173 empirical constraints were unavailable. This strategy was adopted to ensure that the parameter
174 ranges are both sufficiently broad to support global sensitivity analysis and consistent with
175 current ecological understanding.

176 It is crucial to distinguish the objective of this study—Global Sensitivity Analysis (GSA)—
177 from that of parameter calibration. For several hard-coded internal parameters (e.g., *reprfrac*,
178 *turnover_root*), value ranges were defined using their technically permissible bounds [0, 1] as
179 specified in the model source code. We acknowledge that the extreme values within these
180 bounds may not always correspond to ecologically realistic conditions. However, retaining these
181 full technical ranges is appropriate in the context of GSA for two reasons. First, empirical
182 ecological constraints for these internal parameters are currently lacking, and restricting their
183 ranges without supporting evidence would introduce subjective assumptions. Second, GSA is
184 intended to examine model sensitivity across the technically allowable parameter space, rather
185 than to infer parameter realism. In this context, strong sensitivity associated with poorly
186 constrained parameters is interpreted as a diagnostic indicator of model behavior, rather than as a
187 direct measure of real-world uncertainty, and may point to priorities for future model
188 development and structural refinement. Finally, for all sampling procedures, parameter values
189 were drawn independently from uniform distributions within their specified minimum and
190 maximum ranges, reflecting the absence of prior information on parameter probability
191 distributions.



Table 1. Parameters for Sensitivity Analysis

Parameter Name	Default Value	Minimum Value	Maximum Value	Physical Meaning	Literature sources
THETA	0.7	0.2	0.996	colimation (shape) parameter	(Collatz et al., 1990; Leverenz, 1988)
ALPHAA	0.5	0.3	0.7	scaling factor for PAR absorption from leaf to plant projective area level	(Haxeltine & Prentice, 1996)
ALPHA_C3	0.08	0.02	0.125	intrinsic quantum efficiency of CO2 uptake, C3 plants	(Farquhar et al., 1980; Hallgren & Pitman, 2000)
ALPHA_C4	0.053	0.0477	0.0583	intrinsic quantum efficiency of CO2 uptake, C4 plants	(Ehleringer & Björkman, 1977)
BC3	0.015	0.01	0.021	leaf respiration as fraction of maximum rubisco, C3 plants	(Farquhar et al., 1980; Hallgren & Pitman, 2000)
BC4	0.02	0.018	0.022	leaf respiration as fraction of maximum rubisco, C4 plants	-
GM	3.26	2.5	18.5	Maximum canopy conductance equivalent	(Magnani et al., 1998)
ALPHAM	1.391	1.1	1.5	Empirical parameter in evapotranspiration process	(Monteith, 1995)
TAU_LITTER	2.85	1.23	5.26	Litter decomposition time at 10°C	(Meentemeyer, 1978)
ATMFRAC	0.7	0.5	0.9	Fraction of litter decomposition entering fast soil organic matter pool	(Pappas et al., 2013)
FASTFRAC	0.985	0.85	0.99	Fraction of bound litter decomposition entering intermediate soil pool	(Zachle et al., 2005)
PRIESTLEY_TAYLOR	1.32	1.08	1.6	Priestley-Taylor coefficient (converts equilibrium ET to potential ET)	(Pappas et al., 2013; Sumner & Jacobs, 2005)
BETA	0.17	0.15	0.19	Global average of shortwave albedo (not vegetation-specific)	(Li et al., 2022)
FRADPAR	0.5	0.4	0.7	Fraction of net incoming shortwave radiation that is photosynthetically active (PAR)	-
MINFUEL	0.2	0.01	0.4	Minimum aboveground litter mass required for fire occurrence	(Zachle et al., 2005)
K_MORT1	0.01	0.005	0.1	Constant in tree mortality equation	(Zachle et al., 2005)
K_MORT2	35	20	50	Constant in tree mortality equation based on annual NPP and growth efficiency	(Zachle et al., 2005)
R_GROWTH	0.25	0.15	0.4	Growth respiration	(Sprugel et al., 1995)



common_lambda_max	0.8	0.6	0.8	CO ₂ concentration under no water stress	(Haxeltine & Prentice, 1996)
common_emax	5	2.4	6.2	Maximum evapotranspiration rate	(Pappas et al., 2013; Whitehead et al., 1994)
common_refrac	0.1	0	1	Fraction of NPP allocated to reproduction	SourceCode
tree_turnover_root	0.7	0	1	Fine root turnover rate (annual fraction)	SourceCode
tree_k_rp	1.6	1.33	1.6	Constant in tree allometric growth equation	(Enquist & Niklas, 2002; Whitehead et al., 1994)
tree_crownarea_max	50	30	60	Maximum tree crown area (m ²)	-
tree_litterme	0.3	0.0225	0.375	Moisture flammability threshold of tree litter (as a fraction of available water capacity)	-
tree_k_allom2	60	5	60	Constant in tree allometric growth equation	-
tree_k_allom3	0.67	0.5	0.8	Constant in tree allometric growth equation	(Zaehle et al., 2005)
tree_kest_bg	0.1	0	1	Constant in tree establishment rate equation	SourceCode
broadleaved_gmin	0.5	0.42	0.58	Minimum stomatal conductance of broadleaved canopy	(Körner, 1995; Zaehle et al., 2005)
needleleaved_gmin	0.3	0.22	0.38	Minimum stomatal conductance of needleleaved canopy	(Körner, 1995; Zaehle et al., 2005)
broadleaved_k_allom1	250	225	275	Constant in broadleaved tree allometric growth equation	-
grass_gmin	0.5	0.22	0.38	Minimum stomatal conductance of grass canopy	(Körner, 1995)
needleleaved_k_allom1	150	112.5	187.5	Constant in needleleaved tree allometric growth equation	-
shade_tolerant_est_max	0.05	0.05	0.48	Maximum seedling establishment rate for shade-tolerant species	(Pappas et al., 2013; Zaehle et al., 2005)
shade_intolerant_est_max	0.2	0.05	0.48	Maximum seedling establishment rate for shade-intolerant species	(Pappas et al., 2013; Zaehle et al., 2005)
grass_litterme	0.2	0.15	0.25	Moisture flammability threshold of grass litter (as a fraction of available water capacity)	-
broadleaved_k_latosa	6000	2000	8000	Ratio of leaf area to sapwood area in broadleaved trees	(Oberpriller et al., 2022; Zaehle et al., 2005)
needleleaved_k_latosa	5000	2000	8000	Ratio of leaf area to sapwood area in needleleaved trees	(Oberpriller et al., 2022; Zaehle et al., 2005)

Note: sourcecode indicates that the range was derived from the source code



194 **2.4 Sensitivity Analysis Methods**

195 This study applies three complementary sensitivity analysis methods to assess the impact of
196 parameters on simulated outputs from different analytical perspectives.

197 **2.4.1 Morris Sensitivity Analysis Method**

198 The Morris method is an efficient global sensitivity analysis technique commonly designed
199 for preliminary parameter screening. It is based on a One-Factor-At-a-Time (OAT) perturbation
200 scheme, in which parameters are varied individually along predefined trajectories in the
201 parameter space while other parameters remain fixed for each elementary step (Morris, 1991).
202 By constructing multiple such trajectories, the method estimates the Elementary Effects (*EE*) of
203 parameters through successive single-parameter perturbations:

$$EE_i = \frac{f(x_1, \dots, x_{i-1}, x_i + \Delta, x_{i+1}, \dots, x_N) - f(x_1, \dots, x_i, \dots, x_N)}{\Delta} \quad (1)$$

204 where $f(\cdot)$ is the model output, and x and $x + \Delta$ represent the function values at points before
205 and after only the i -th parameter is changed, respectively. This definition reflects the impact on
206 the output results when only the i -th factor undergoes a minor perturbation.

207 The Morris method characterizes parameter importance using two summary statistics. The
208 mean of elementary effects (μ) represents the overall influence magnitude of a parameter on
209 model outputs, while the standard deviation of the elementary effects (σ) captures the variability
210 of this influence across the parameter space, which may arise from non-linear responses and
211 interactions with other parameters.

212 **2.4.2 eFAST Sensitivity Analysis Method**

213 The extended Fourier Amplitude Sensitivity Test (eFAST) is a variance-based global
214 sensitivity analysis method used to quantify the relative importance of model input parameters
215 (Saltelli et al., 1999; Andrea Saltelli, 2002). The method explores the parameter space by
216 assigning sinusoidal functions with distinct frequencies to each parameter, which allows the
217 decomposition of output variance into contributions associated with individual parameter:



$$V_Y = \sum_i V_i + \sum_{i < j} V_{ij} + \sum_{i < j < k} V_{ijk} + \dots + V_{12\dots k} \quad (2)$$

218 The eFAST method calculates two key types of sensitivity indices: First-order sensitivity
219 index S_i :
220 The proportion of contribution from the direct effect of the parameter:

$$S_i = \frac{V_i}{V(Y)} \quad (3)$$

221 Total sensitivity index ST_i : The overall contribution including all interaction effects:

$$ST_i = 1 - \frac{V_{-i}}{V(Y)} \quad (4)$$

222 This approach is well suited for the analysis of non-linear models behavior, as it can capture
223 both first-order (main effect) sensitivities and higher-order (interaction) contributions arising
224 from parameter interactions, while maintaining a relatively moderate computational cost (Saltelli
225 et al., 1999; Vazquez-Cruz et al., 2014).

226 **2.4.3 Sobol' Sensitivity Analysis Method**

227 The Sobol' method is a rigorous global sensitivity analysis framework that decomposes the
228 total variance of model outputs into contributions from individual input parameters and their
229 interactions through Monte Carlo sampling (Sobol', 2001). It provides a detailed quantification
230 of both first-order and higher-order sensitivity effects, making it particularly suitable for
231 complex, nonlinear, and non-monotonic models. In this method, two key sensitivity indices are
232 calculated (Verrelst et al., 2015; Wainwright et al., 2014)

233 First-order sensitivity index S_i represents the proportion of output variance that can be
234 attributed solely to variations in a single input parameter X_i , assuming all other parameters
235 remain unchanged (Song et al., 2012):

$$S_i = \frac{V_{X_i}(E_{\sim i}(Y|X_i))}{VY} \quad (5)$$

236 In contrast, the total sensitivity index ST_i accounts for the entire contribution of X_i to output
237 variance, including all its interaction effects with other parameters:



$$ST_i = S_i + \sum_{j \neq i} S_{ij} + \sum_{j \neq i, k \neq i, j < k} S_{ijk} + \dots \quad (6)$$

238 The Sobol' method provides the most comprehensive sensitivity assessment and is capable of
239 handling highly non-linear and non-monotonic models, but its computational cost is relatively
240 high compared to other methods (Nossent et al., 2011).

241 **2.5 Experimental Scheme and Design**

242 The study selected nine key carbon-water cycle variables as model output indicators: (1)
243 carbon flux variables, including Gross Primary Productivity (GPP), Net Ecosystem Exchange
244 (NEE), Soil Carbon Flux (Soil C Flux); (2) hydrological and structural variables, including Leaf
245 Area Index (LAI), and Actual Evapotranspiration (AET); and (3) carbon pool variables,
246 including Vegetation Carbon (Veg C), Litter Carbon (Litter C), Soil Carbon (Soil C), and Total
247 Carbon (Total C).

248 To systematically evaluate the performance of different sensitivity analysis methods and to
249 investigate the influence of various types of model parameters on carbon-water cycle simulations,
250 a comprehensive experimental framework was designed. First, the 39 parameters were divided
251 into two categories: 19 parameters related to plant physiological processes (hard-coded in the
252 source code), and 20 parameters related to PFT constitution. Second, each parameter group was
253 analyzed independently using three sensitivity analysis methods. Third, to capture the potential
254 interactions across parameter categories and evaluate their joint influence on model outputs, a
255 combined sensitivity analysis was conducted using all 39 parameters. The specific experimental
256 design is summarized in Table 2.

257 Table 2. Experimental Design Scheme

Parameter Category	Number of Parameter Sets	Number of Parameter Sets		
		Morris	eFast	Sobol'
Physiological processes	19	200	9899	10240
PFT parameters	20	200	9940	10752
Physiological + PFT	39	400	9711	10240

258 The generation of parameter sets (shown in Table 2) was guided by the specific requirements
259 of each method. As described in Section 2.4, the Morris method uses a specific One-Factor-at-a-



260 Time trajectory design, the eFAST method generates sample sets based on sinusoidal functions,
261 and the Sobol' method combinations were generated using standard Monte Carlo sampling.

262 For the eFAST and Sobol' methods, this resulted in approximately 10,000 parameter
263 combinations, which is sufficient to ensure robust and comprehensive variance decomposition.
264 To improve computational efficiency, parameter updating and model execution for all analyses
265 were fully automated and parallelized using Python process pools.

266 **2.6 Data Processing and Statistical Methods**

267 **2.6.1 Sensitivity Index Calculation and Standardization**

268 To ensure comparability of sensitivity analysis results across methods and target variables, a
269 standardized processing workflow was employed. First, for each parameter, raw sensitivity
270 indices were averaged across the 13 study sites—specifically, the mean of elementary effects (μ)
271 for the Morris method, and the total sensitivity index (ST_i) for eFAST and Sobol' methods. In
272 the first stage of standardization, the average sensitivity indices for each parameter p , method m
273 and target variable v , denoted as $S_{p,m,v}$ were normalized by dividing by the maximum sensitivity
274 value for the corresponding method and variable. This normalization ensured a consistent scale
275 for inter-method comparison. Next, to identify the most influential parameters, a preliminary
276 composite index $Combined_1$ was computed as the average of the normalized indices from the
277 three methods. Based on $Combined_1$, a subset of the top-N sensitive parameters was selected for
278 further analysis. These top parameters were then re-standardized across the three methods, and a
279 final comprehensive sensitivity score $Combined_2$ was calculated by averaging the re-
280 standardized values. This two-stage process enhances interpretability while preserving the
281 relative discriminative power of each sensitivity analysis method.

282 **2.6.2 Method Consistency Assessment**

283 To assess the consistency in parameter importance ranking among the Morris, eFAST, and
284 Sobol' methods, two complementary approaches were adopted. Spearman rank correlation
285 analysis (ρ) and corresponding p -values were used to evaluate monotonic agreement among
286 rankings. Additionally, pairwise linear regression analysis, expressed as $R_B = a + b \times R_A$ were
287 performed to examine systematic differences and relationships in parameter rankings between
288 methods.



289 **2.6.3 Uncertainty Quantification and Spatial Analysis**

290 Model output uncertainty was quantified using the Coefficient of Variation (*CV*), calculated
291 across all parameter samples. To evaluate the consistency of uncertainty estimates between the
292 eFAST and Sobol' methods, both Pearson and Spearman correlation analyses were conducted,
293 along with linear regression modeling. Results were visualized with scatter plots to identify
294 systematic deviations. Spatial patterns of model output uncertainty across sites and vegetation
295 types were further analyzed using Cumulative Distribution Functions (CDFs) and box plots,
296 enabling the identification of regions and vegetation types characterized by highly sensitive or
297 relatively stable model responses.

298 **3 Results**

299 **3.1 Co-dominance of Physiological and PFT Parameters in Model Sensitivity**

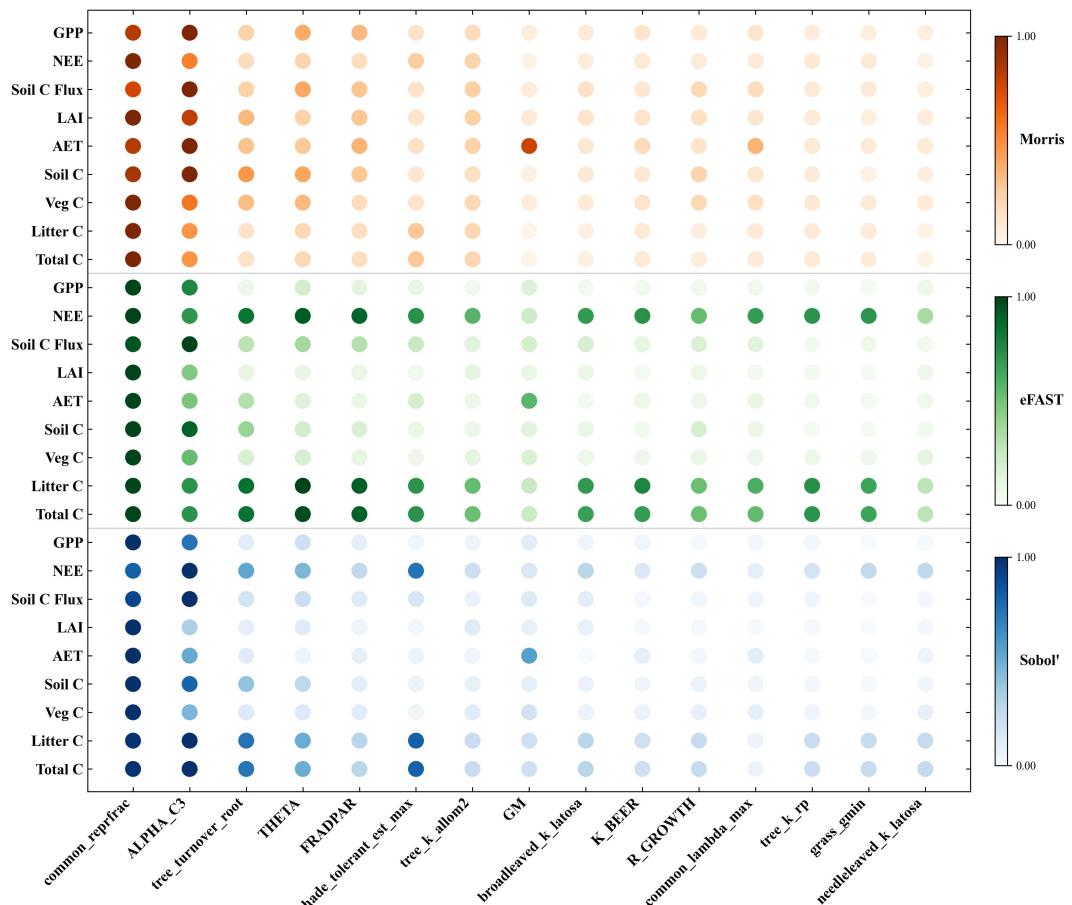
300 Our comprehensive sensitivity analysis, conducted using three global methods (Morris,
301 eFAST, Sobol'), reveals a fundamental characteristic of the LPJ-GUESS model: its outputs are
302 not driven by a single class of parameters, but are co-dominated by both core physiological
303 parameters, often hard-coded in the source code, and PFT-specific traits defined in user-facing
304 files. This finding suggests limitations in the common practice of focusing calibration efforts
305 solely on the more accessible PFT parameters (Oberpriller et al., 2022; Peng et al., 2024). A
306 detailed breakdown of sensitivities for physiological versus PFT parameters is provided in Text
307 S2.1 and S2.2.

308 This co-dominance is illustrated by the two most influential parameters identified across
309 nearly all nine output variables (Fig. 2; see Fig. S1 for full rankings). The highest overall
310 sensitivity was associated with *ALPHA_C3* (intrinsic quantum efficiency of CO₂ uptake), a
311 fundamental physiological parameter, which primarily governed carbon flux variables such as
312 GPP and Soil Carbon Flux. Closely ranked was *common_reprfrac* (proportion of NPP allocated
313 to reproduction), a key PFT trait parameter, which exerted dominant control over ecosystem
314 structure and the magnitude of major carbon stocks (Veg C, Litter C, Soil C, and Total C).

315 This pattern extends beyond the two most influential parameters. The subsequent group of
316 highly sensitive parameters also included a mixture of both parameter types: core physiological
317 parameters like *THETA* (photosynthesis co-limitation shape) and *FRADPAR* (fraction of PAR in



318 shortwave radiation) were critical for photosynthetic processes, while PFT-specific traits such as
 319 *tree_turnover_root* (fine root turnover rate) played a key role in regulating carbon residence time
 320 in litter and soil pools.



321

322 **Fig. 2: Union of the Top 10 Most Sensitive Parameters across All Target Variables for**
 323 **Different Methods**

324 While all three analysis methods consistently identified this overall hierarchy of control, minor
 325 discrepancies in rankings and sensitivity magnitude were observed for less dominant parameters,
 326 such as *shade_tolerant_est_max* (Fig. 2). These differences reflect methodological
 327 characteristics of individual approaches and underscore the value of applying multiple sensitivity
 328 analysis methods in parallel. Moreover, some parameters exhibited process-specific importance:



329 GM (maximum canopy conductance) was particularly influential for AET, whereas the
330 allometric constant $tree_k_allom2$ showed a distinct sensitivity signal for LAI.

331 Overall, these results refine the understanding of parameter influence in LPJ-GUESS. The
332 regulation of carbon-water cycle processes is not solely governed by adjustable PFT traits but is
333 also strongly constrained by core physiological parameters. This co-dependence underscores that
334 efforts to improve model calibration and reduce uncertainty would benefit from a more
335 comprehensive strategy that explicitly considers both parameter types.

336 **3.2 Dissecting Parameter Influence: Direct Physiological Control Versus
337 Interactive Allocation Effects**

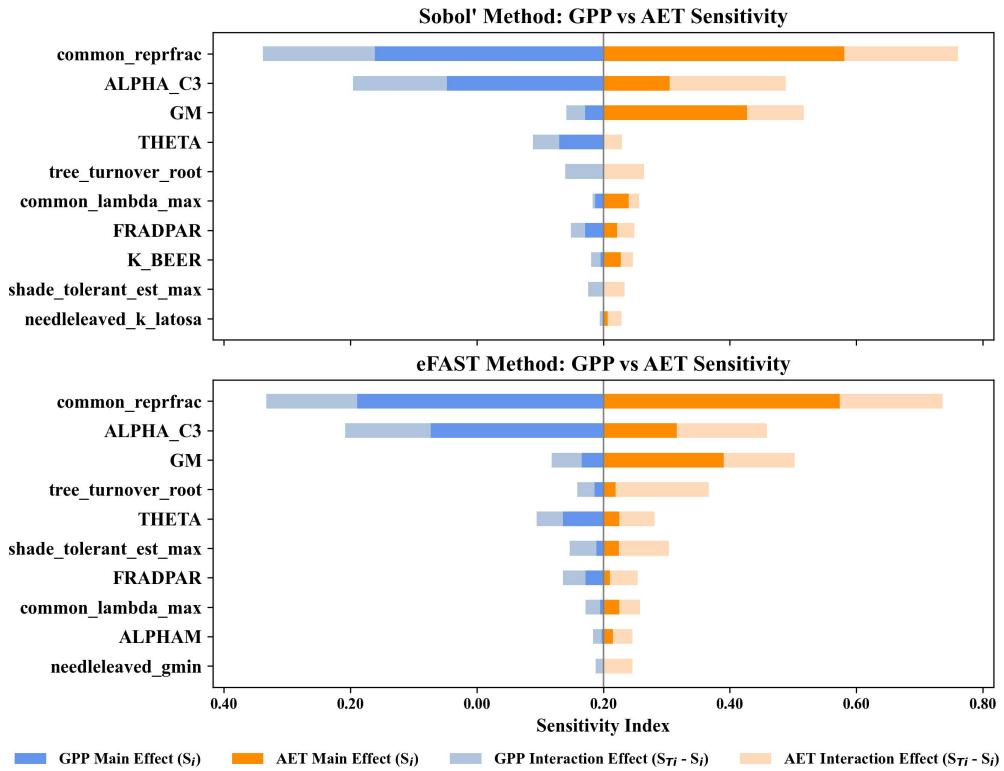
338 To examine the mechanisms governing the carbon and water cycles, we decomposed the total
339 sensitivity of parameters into direct main effects S_i and higher-order interaction effects $S_{Ti} - S_i$
340 using the Sobol' and eFAST methods (Fig. 3, Fig. S4-S5). This analysis reveals distinct
341 differences in the parameter control structures of GPP and AET, which are used as representative
342 fluxes.

343 For GPP, the controlling patterns differ markedly among parameters. The influence of the core
344 physiological constant $ALPHA_C3$ (intrinsic quantum efficiency) is dominated by its direct main
345 effect, with only a minor contribution from interaction effects (blue bars, Fig. 3). This suggests
346 that its influence on modeled photosynthetic capacity is largely independent of other parameters.
347 In contrast, the most influential GPP parameter, the PFT trait $common_reprfrac$ (NPP allocation
348 to reproduction), displays a substantial contribution from interaction effects, comparable in
349 magnitude to its main effect. This indicates that the impacts of carbon allocation are strongly
350 modulated by interactions with other parameters governing vegetation growth and turnover.

351 In contrast, the sensitivity of AET is dominated by interaction effects. For all key controlling
352 parameters—including $common_reprfrac$, $ALPHA_C3$, and GM (maximum canopy
353 conductance)—interaction effects constitute a substantial, and in several cases dominant, portion
354 of their total influence (orange bars, Fig. 3). This underscores that AET is not governed by
355 individual parameters in isolation, but rather emerges from the combined effects of soil water



356 availability, canopy properties, and atmospheric demand. Consequently, the influence of any
357 single parameter depends strongly on the overall state of the soil-plant-atmosphere system.



358
359 **Fig. 3. Decomposition of parameter sensitivity for GPP and AET into main effects (S_i) and**
360 **interaction effects ($S_{Ti} - S_i$) based on the Sobol' method.**

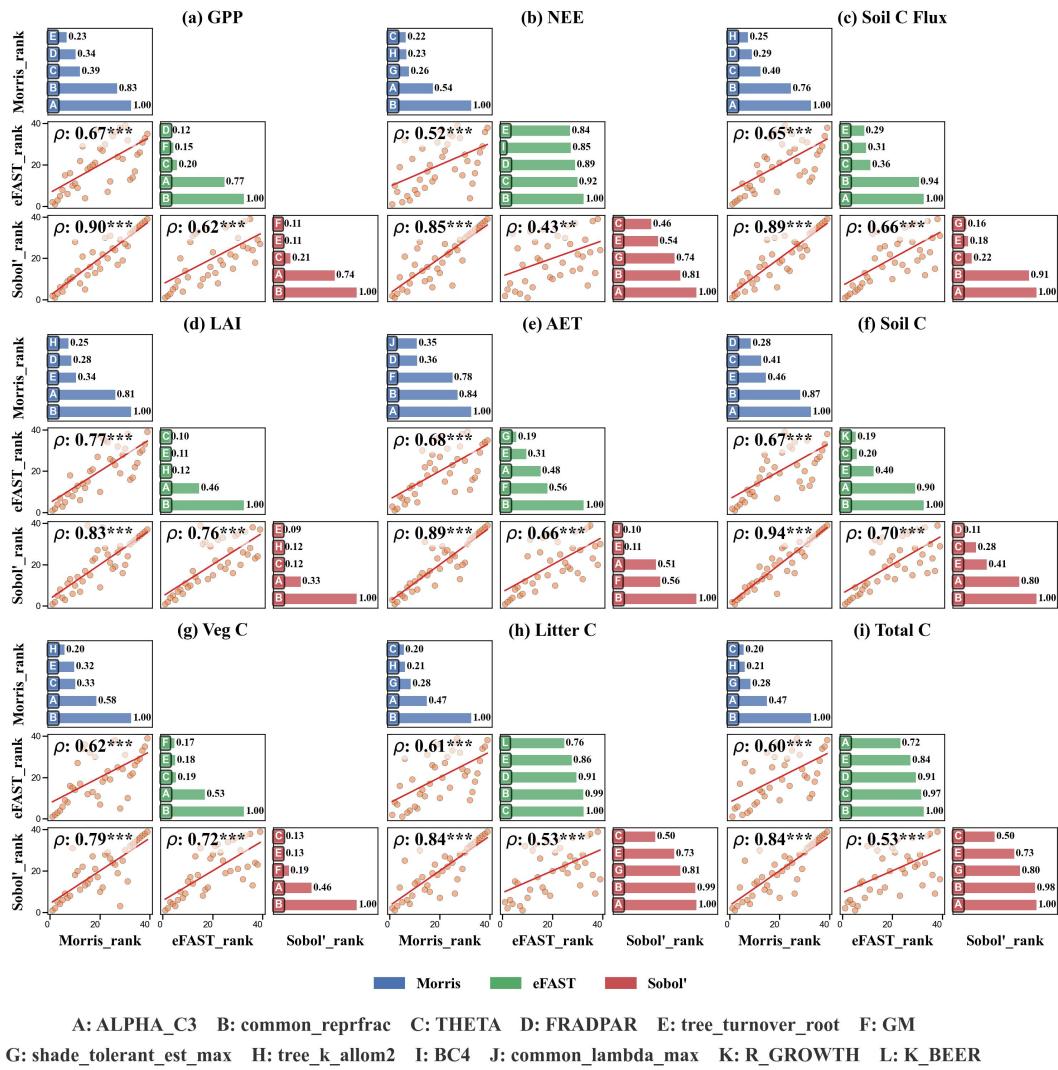
361 **3.3 Methodological Consensus and Complementarity in Sensitivity Rankings**

362 To evaluate the robustness of our findings, we assessed the consistency of parameter
363 importance rankings derived from the Morris, eFAST, and Sobol' methods across all nine output
364 variables (Fig. 4). Pairwise comparisons using Spearman rank correlation revealed strong and
365 statistically significant agreement ($p < 0.01$) among all methods, indicating a high degree of
366 consensus in identification of key model controls.

367 The agreement was particularly notable between the Morris and Sobol' methods, which
368 consistently yielded the strongest correlations, with coefficients (ρ) frequently exceeding 0.85 for
369 major outputs such as GPP ($\rho = 0.90$) and Soil C ($\rho = 0.94$). The other pairings, while still
370 showing substantial agreement, exhibited greater variability. For instance, the agreement



371 between eFAST and Sobol' was strong for structural and stock variables (e.g., $\rho = 0.76$ for LAI),
 372 but notably weaker for net fluxes such as NEE ($\rho = 0.43$). This reduced consistency for NEE is
 373 mechanistically plausible, as NEE represents a small residual between two large, opposing fluxes
 374 (GPP and ecosystem respiration), which can lead to a more complex and variable sensitivity
 375 structure.



376
 377 **Fig. 4: Consistency analysis of parameter sensitivity rankings identified by Morris, eFAST,**
 378 **and Sobol' methods across nine output variables. Each of the nine large panels corresponds**
 379 **to a specific model output variable. Within each large panel, the sub-panels compare the**
 380 **sensitivity rankings of the three methods: the diagonal sub-panels display the standardized**
 381 **sensitivity indices for the top-five ranked parameters from each method; the lower-left sub-**



382 panels show scatter plots comparing the parameter sensitivity ranks between pairs of
383 methods, annotated with the Spearman's rank correlation coefficient ρ and its statistical
384 significance (** represents significance < 0.001 , ** represents significance < 0.01). The
385 solid line represents the linear regression fit to the ranked scatter points.

386 Crucially, this consensus was strongest for the most influential parameters. Across all three
387 methods, *ALPHA_C3* and *common_reprfrac* were consistently identified as the two dominant
388 drivers of GPP. These parameters, along with *tree_turnover_root* and *THETA*, also consistently
389 appeared among the top five ranked parameters for a suite of variables, including Soil C Flux,
390 LAI, and Soil C, with only minor differences in their relative ordering.

391 Nevertheless, the analysis also highlighted key divergences that underscore the
392 complementarity of the methods. A representative example is *GM* (maximum canopy
393 conductance): while all methods agreed on its top-tier importance for AET, the Morris method
394 assigned it a much lower rank for NEE compared to eFAST and Sobol'. Such discrepancies
395 likely arise from the different mathematical formulations of the methods, particularly in how the
396 parameter space is sampled and how interaction effects are quantified.

397 In summary, although all three sensitivity analysis methods converge on the primary drivers of
398 the carbon-water cycle in LPJ-GUESS, the subtle variations in their rankings provide additional
399 insight into model behavior. This highlights the benefit of a multi-method framework for a more
400 comprehensive assessment of parameter influence.

401 **3.4 Divergent Parameter Controls Across Target Variables**

402 The influence of model parameters varied markedly across the nine output variables, revealing
403 distinct control structures for different components of the carbon-water cycle (Fig. 5).

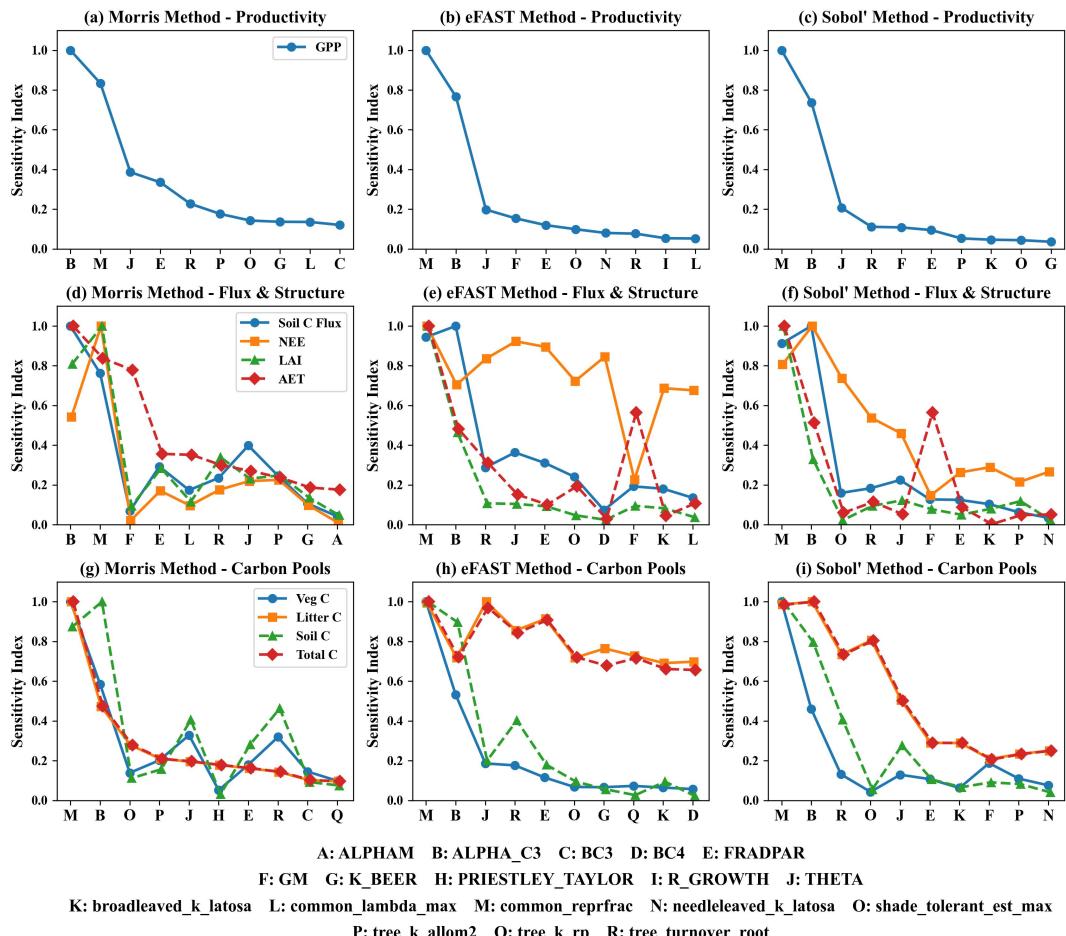
404 GPP displayed the most concentrated sensitivity profile. Its response was dominated by a
405 small cohort of photosynthetic parameters—primarily *ALPHA_C3*, followed by
406 *common_reprfrac* and *THETA*. This focused control structure highlights that modeled
407 productivity is largely governed by biochemical efficiency at the leaf level (Fig. 5, a-c).

408 In contrast, flux and vegetation structure variables exhibited more complex and diversified
409 control structures (Fig. 5, d-f). Soil Carbon Flux sensitivity largely resembled that of GPP,
410 reflecting the tight coupling between carbon input and heterotrophic respiration. NEE, as a net
411 balance, was sensitive to a broader range of physiological and structural parameters. LAI was co-
412 limited by carbon allocation (*common_reprfrac*), productivity (*ALPHA_C3*), and turnover



413 (*tree_turnover_root*), while AET was particularly sensitive to *GM* (maximum canopy
 414 conductance), underscoring the role of stomatal regulation in controlling water fluxes.

415 The major carbon pools (Vegetation, Litter, and Soil) were governed by a common set of
 416 parameters, reflecting shared controls on biomass dynamics. Their sensitivities were co-
 417 dominated by production (*ALPHA_C3*), allocation (*common_reprfrac*), and residence time
 418 (*tree_turnover_root*). The strong influence of these parameters was most pronounced for Litter C
 419 and Total C, where their combined Sobol' sensitivity indices approached 1.0, indicating near-
 420 complete model control by these three factors alone (Fig. 5, g-i).



421

422 **Fig. 5: Comparison of results from the Morris, eFAST, and Sobol sensitivity analysis**
 423 **methods. Each subplot shows the normalized sensitivity index (Y-axis) of different model**
 424 **parameters (X-axis, letter codes) for three groups of target variables. The rows represent**



425 **the variable groups of Productivity, Flux & Structure, and Carbon Pools, respectively; the**
426 **columns correspond to the three analysis methods.**

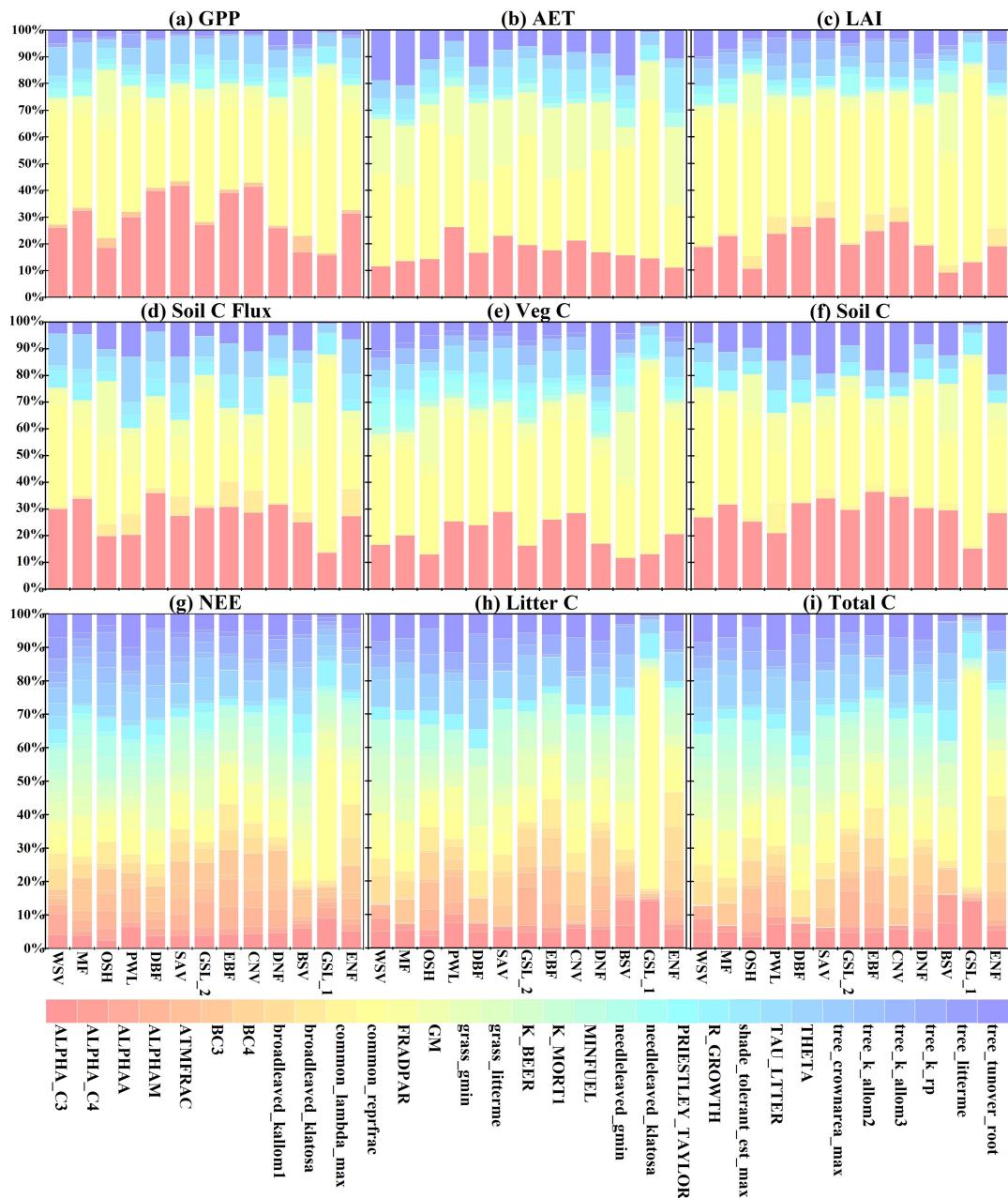
427 In summary, different groups of variables are governed by a distinct set of controlling
428 parameters. Productivity is primarily influenced by a small number of photosynthetic inputs,
429 fluxes and vegetation structure by a wider and more complex set of interacting factors, and
430 carbon stocks by the combined effects of production, allocation, and turnover. These findings
431 demonstrate that parameterization and calibration strategies should be aligned with the specific
432 processes of interest, as parameter sets optimized for one component of the system may not
433 perform equivalently for others.

434 **3.5 Spatial Heterogeneity of Parameter Controls Across Ecosystems**

435 Parameter sensitivities exhibited pronounced spatial heterogeneity across China's diverse
436 vegetation types, revealing distinct control structures between resource-rich and resource-limited
437 ecosystems (based on eFAST results; Fig. 6).

438 In humid forest ecosystems (e.g., DBF, EBF, CNV), model behavior was primarily governed
439 by parameters related to physiological efficiency and biomass turnover. GPP sensitivity was
440 highest for *ALPHA_C3*, while AET was most sensitive to stomatal regulation via *GM*. The large
441 carbon pools in these systems, particularly Litter C and Soil C, were strongly controlled by
442 *tree_turnover_root*, reflecting the dominant role of woody biomass turnover in regulating
443 detritus input and long-term carbon storage. Together, these patterns indicate that carbon and
444 water fluxes in humid forests are predominantly controlled by physiological processes operating
445 under relatively favorable resource conditions.

446 Conversely, arid and semi-arid ecosystems (e.g., BSV, GSL) displayed a distinctly different
447 sensitivity structure, characterized by a stronger influence of resource allocation and use
448 efficiency. The PFT trait *common_reprfrac* (carbon allocation to reproduction) emerged as a key
449 controlling parameter for GPP and LAI and also exerted a strong influence on AET. This
450 suggests that under conditions of severe water limitation, canopy structure, as shaped by carbon
451 allocation strategies, can exert a greater control over water loss in addition to direct stomatal
452 regulation. Furthermore, the net carbon balance (NEE) in these sensitive systems showed high
453 sensitivity to photosynthetic (*ALPHA_C3*, *BC3*) and radiation-use (*FRADPAR*) parameters,
454 indicating that relatively small changes in carbon assimilation efficiency can substantially affect
455 whether the ecosystem functions as a net carbon sink or source.



456

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Fig. 6: Spatial heterogeneity of parameter sensitivity across different vegetation types. Each of the nine panels corresponds to a specific output variable (e.g., GPP, AET). Within each panel, the x-axis represents the 13 different study sites. Each vertical bar is a stacked bar chart, illustrating the relative contribution of the most sensitive parameters (listed in the bottom legend) for that specific site. The color of each segment corresponds to a parameter, and its height represents that parameter's proportional contribution to the total



463 sensitivity (based on the eFAST method). Therefore, within a single panel, significant
464 variation in the color composition across the site bars indicates that the key controlling
465 parameters for that output variable differ greatly between locations. Conversely, similarity
466 in color composition suggests spatial consistency in the controlling parameters.

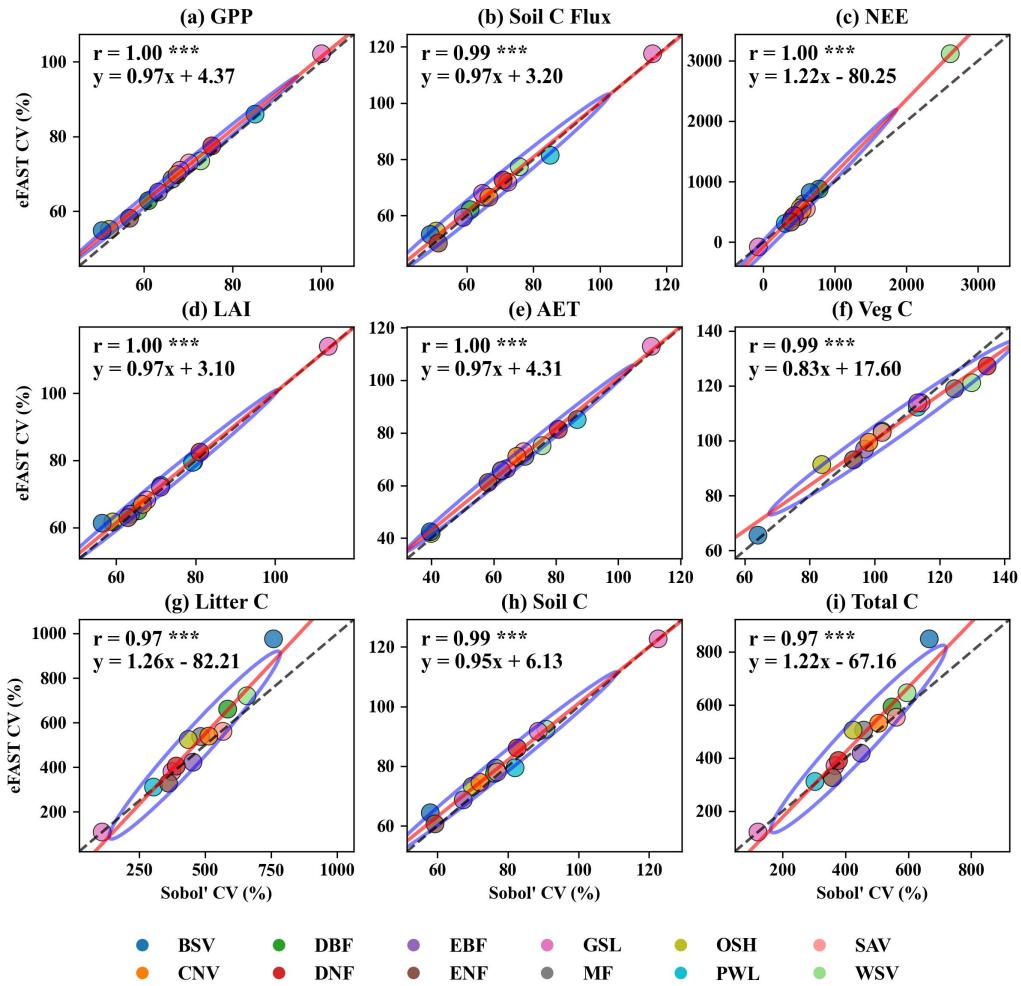
467 In summary, parameter sensitivities are strongly contingent on the ecosystem context. Humid
468 forests are primarily controlled by parameters of physiological process rates and biomass
469 turnover. In contrast, arid systems are more sensitive to parameters governing the strategic
470 allocation of scarce resources. This substantial spatial heterogeneity underscores that uniform
471 parameterization strategies are insufficient. Accurate regional and global modeling therefore
472 require ecosystem-specific calibration strategies to capture the diverse responses of terrestrial
473 ecosystems to environmental change.

474 **3.6 Impact of Parameter Uncertainty on Model Output**

475 Following the identification of sensitive parameters, this section investigates how the inherent
476 uncertainty (i.e., variability within their prescribed ranges) of these parameters collectively
477 propagates to affect the overall uncertainty and range of simulated values for key model output
478 variables. Furthermore, it examines whether the magnitude and spatial characteristics of this
479 output uncertainty vary across vegetation types and geographic regions.

480 **3.6.1 Consistency of Uncertainty Quantification**

481 To ensure the robustness of our uncertainty assessment, we compared the output Coefficient of
482 Variation (CV) derived from both the Sobol' and eFAST methods. The two methods yielded
483 nearly identical uncertainty estimates across all nine output variables (Fig. 7). This high
484 consistency is demonstrated by strong Pearson correlations ($r > 0.97$ for all variables), scatter
485 plots where data points for all vegetation types cluster tightly along the 1:1 line, and regression
486 models with slopes approaching 1.0 and intercepts near zero. These results indicate that both
487 methods provide consistent and comparable quantifications of output uncertainty, supporting the
488 subsequent spatial analysis.



489

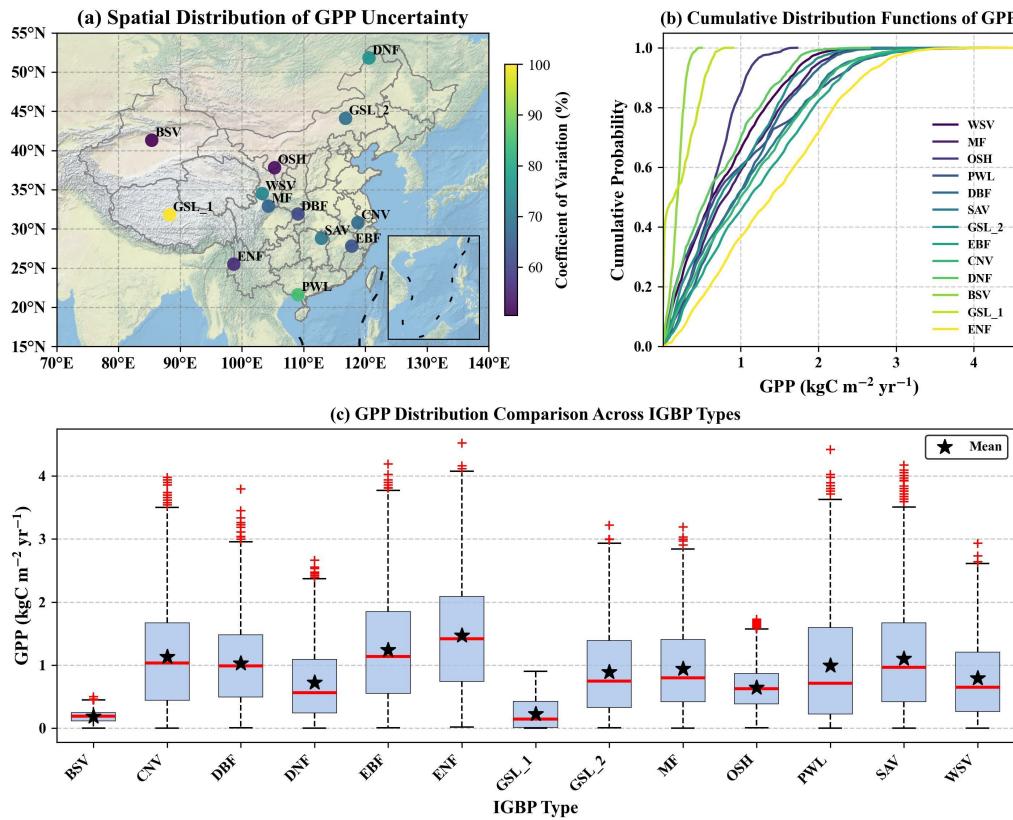
490 **Fig. 7: Uncertainty Assessment Using Sobol' and eFAST Methods**

491 **3.6.2 Opposing Gradients of Productivity and Uncertainty**

492 The propagation of parameter uncertainty into model outputs revealed strong and opposing
 493 spatial gradients across China. Using GPP as an illustrative example (Fig. 8), mean productivity
 494 increased systematically from the arid northwest to the humid southeast. Conversely, the relative
 495 uncertainty of simulated GPP, expressed as CV , showed an opposite pattern, with the highest
 496 values ($CV > 80\%$) occurring in the driest and least productive regions and the lowest values (CV



497 < 60%) in the most productive forest areas.



498

499 **Fig. 8: Spatial Distribution Pattern of GPP Uncertainty Across Different Sites**

500 Critically, this analysis uncovers a clear contrast between relative and absolute uncertainty
 501 (Fig. 8b, 8c). In the arid northwest, high relative uncertainty indicates strong sensitivity of
 502 modeled GPP to parameter variability, but the low baseline productivity results in a relatively
 503 small absolute range of simulated values (narrow box plots). In contrast, in the humid southeast,
 504 relative uncertainty is lower, yet the high baseline productivity causes even modest relative
 505 uncertainty to translate into a large absolute range of simulated GPP (wide box plots), which has
 506 important implications for regional carbon budget estimation. This contrast between relative
 507 uncertainty in low-productivity regions and absolute uncertainty in high-productivity regions is
 508 not unique to LPJ-GUESS, but likely represents a broader challenge for land surface models,
 509 including those used in TRENDY and CMIP6 intercomparisons. Similar spatial patterns were
 510 also observed for other variables, such as LAI and AET.



511 These findings underscore that effective uncertainty management requires region-specific
512 strategies. In resource-limited regions, reducing relative uncertainty depends primarily on
513 improving constraints on sensitive parameters. In productive regions, the key challenge lies in
514 constraining the absolute uncertainty of large fluxes, even when relative uncertainty is low, in
515 order to support reliable carbon accounting.

516 **4 Discussion**

517 **4.1 The Core Mechanisms of Model Control: From Parameter Co-**
518 **dominance to Spatial Divergence**

519 Our multi-method sensitivity analysis, whose robustness is supported by the strong consensus
520 among the Morris, eFAST, and Sobol' methods for top-ranking parameters (Section 3.3), reveals
521 a clear hierarchical and spatially contingent architecture of model control. At a broad level,
522 model behavior is not governed by a single process, but reflects the combined influence of
523 photosynthetic efficiency, carbon allocation strategies, and biomass turnover rates. The relative
524 importance of these processes is not static, but varies systematically across climate gradients,
525 consistent with differences in dominant ecological constraints observed in natural ecosystems
526 (Baral et al., 2014; Liu et al., 2022).

527 The dominant influence of photosynthetic efficiency—primarily represented by the
528 *ALPHA_C3* parameter—reinforces its role as the ultimate driver of carbon influx into the
529 ecosystem. This aligns with fundamental ecological theory, in which the efficiency of light-use
530 conversion constrains GPP (Farquhar et al., 1980; Thevasundaram et al., 2022). In the model,
531 this control is largely expressed through direct effects, as indicated by the decomposition of main
532 and interaction sensitivities (Section 3.2). However, what happens to this carbon post-
533 assimilation is equally critical. The high sensitivity associated with *common_reprfrac* (carbon
534 allocation) and *tree_turnover_root* (biomass turnover) underscores that patterns of carbon
535 investment among plant tissues and the residence time of biomass exert substantial influence on
536 long-term carbon storage, vegetation structure, and net ecosystem balance (Dong et al., 2024;
537 Wang et al., 2024). This finding suggests that photosynthesis alone is insufficient to explain
538 ecosystem carbon dynamics, and that allocation and turnover represent critical controls on the
539 persistence and distribution of assimilated carbon (Camargo et al., 2023; Kengdo et al., 2023;
540 Zandi et al., 2023).



541 Crucially, the dominance of these controlling processes is spatially contingent, leading to
542 distinct sensitivity patterns across environments gradients (Pappas et al., 2013). In humid,
543 productive forest ecosystems, model sensitivity is primarily driven by parameters of
544 physiological efficiency. Here, with water being less of a limiting factor, simulated ecosystems
545 operate closer to their maximum photosynthetic potential, making it highly sensitive to
546 *ALPHA_C3*. Furthermore, in structurally complex forest canopies, parameters related to
547 regeneration and light competition (e.g., *shade_tolerant_est_max*) also emerge as influential,
548 while large carbon stocks are primarily regulated by the slow turnover of woody biomass
549 (*tree_turnover_root*). This pattern reflects a system in which intrinsic growth rates competition
550 and biomass persistence play central roles (Bergkvist et al., 2023; Kühn et al., 2021; Pugh et al.,
551 2019).

552 In contrast, model control shifts towards parameters associated with resource acquisition and
553 allocation in arid and semi-arid ecosystems (Asargew et al., 2024; Lv et al., 2024). In these
554 water-limited environments, survival under stress becomes more influential than maximizing
555 productivity. Consequently, *GM* (stomatal conductance) and *common_reprfrac* (allocation) exert
556 strong control, including for fluxes like AET. This pattern indicates that, within the model
557 framework, conservative water use and allocation strategies play a greater role than
558 photosynthetic capacity alone in regulating ecosystem function under dry conditions (Liu et al.,
559 2022). The heightened sensitivity of NEE to a wider array of parameters in these arid sites
560 further illustrates their inherent sensitivity, where small perturbations in any number of processes
561 can shift the system from a net sink to a source (Liang et al., 2024; Mitchell et al., 2000). These
562 spatially divergent sensitivity patterns suggest that effective model parameterization should
563 reflect contrasting ecological constraints across environments. However, it is important to note
564 that these interpretations are based on the internal logic of LPJ-GUESS. In the absence of
565 systematic validation against site-level observations (e.g., eddy covariance data), these findings
566 should be viewed as model-dependent insights into potential dominant controls rather than direct
567 confirmation of ecosystem mechanisms. Nevertheless, the alignment of these sensitivity patterns
568 with general ecological theory supports the plausibility of the model's representation of key
569 controlling processes.



570 **4.2 Rethinking Model Uncertainty: From Spatial Patterns to an Inherent
571 Tradeoff**

572 The propagation of parameter uncertainty through the LPJ-GUESS model is not random but
573 instead follows a clear spatial logic that mirrors the hydro-thermal gradients across China. Our
574 results show that the highest relative uncertainty (CV) consistently occurs in the arid and semi-
575 arid ecosystems of the northwest. This pattern is a direct consequence of the mechanisms
576 discussed in the previous section: these water-stressed systems are critically sensitive to a few
577 dominant parameters controlling resource use and allocation (e.g., GM , *common_reprfrac*). As a
578 result, the model behavior in these regions is highly variable, where small parameter
579 perturbations can lead to large proportional changes in outputs (Liang et al., 2024). Conversely,
580 the humid and highly productive ecosystems in the southeast exhibit the lowest relative
581 uncertainty, suggesting a buffering effect where a more complex web of interacting, non-
582 dominant parameters creates a more robust and stable system response (Bello et al., 2021;
583 Gómez-Gras et al., 2021).

584 However, a deeper analysis reveals a fundamental—and critically important—tradeoff
585 between relative and absolute uncertainty. The low relative uncertainty in humid forests should
586 not be misconstrued as a lack of modeling challenge. While the model is robust in these regions
587 (low CV), the high baseline productivity and carbon fluxes imply that even small relative error
588 translates into substantial absolute uncertainty in terms of actual carbon mass ($\text{kgC m}^{-2} \text{ yr}^{-1}$). For
589 example, a 5% uncertainty associated with a GPP of $1.5 \text{ kgC m}^{-2} \text{ yr}^{-1}$ represents a much larger
590 quantity of unknown carbon than a 20% uncertainty associated with a GPP of $0.2 \text{ kgC m}^{-2} \text{ yr}^{-1}$ in
591 an arid ecosystem.

592 This tradeoff redefines the nature of model risk across different regions. In arid ecosystems,
593 the primary risk is relative instability: inaccurate parameterization can lead to qualitatively
594 incorrect predictions of ecosystem functioning (e.g., predicting a sink when it is a source). In
595 humid, productive ecosystems, the risk shifts to quantitative magnitude. Even for a well-
596 calibrated and structurally robust model, the resulting absolute uncertainty range can be enough
597 to substantially impact regional or global carbon budget calculations. This finding demonstrates
598 that managing and interpreting model uncertainty requires ecosystem-specific perspectives,
599 moving beyond reliance on a single metric like CV and toward an integrated understanding of



600 both relative sensitivity and absolute uncertainty across contrasting environmental contexts (Ma
601 et al., 2022b).

602 **4.3 Outlook: From Model Optimization to Future Directions**

603 The findings of this study provide a scientific basis for improving the application and
604 parameterization of DGVMs such as LPJ-GUESS. Our results argue against one-size-fits-all
605 calibration strategies and instead support the adoption of more nuanced, targeted approaches.
606 First, model calibration should follow a hierarchical strategy. Priority should be given to globally
607 sensitive parameters that govern core ecosystem processes (e.g., *ALPHA_C3*, *common_reprfrac*),
608 followed by targeted tuning for specific variables or regions where additional sensitivity emerges
609 (Gong & Duan, 2017; Yu et al., 2022). Second, calibration must be spatially explicit. The
610 distinctly different sensitivity signatures observed between humid and arid ecosystems clearly
611 indicate that region-specific parameter sets are required to reflect their contrasting environmental
612 constraints and limiting factors (Ma et al., 2022a). Third, given the tradeoff between relative and
613 absolute uncertainty, a multi-objective framework that simultaneously constrains both fluxes
614 (e.g., GPP) and stocks (e.g., Soil C) is essential for robust carbon accounting (Arbolino et al.,
615 2021; Rahimi et al., 2023).

616 Despite the comprehensive nature of our analysis, this study has limitations that define the
617 scope for future research. First, this study relies exclusively on model simulations to diagnose the
618 intrinsic behavior of LPJ-GUESS. While we acknowledge the lack of systematic validation
619 against observational benchmarks (e.g., FLUXNET data), this was a deliberate methodological
620 choice. Conducting GSA prior to calibration is critical to avoid equifinality—getting acceptable
621 model performance for the wrong reasons. By mapping the model's unconstrained sensitivity
622 first, we identify exactly which parameters require observational constraints, thus serving as a
623 necessary prerequisite for robust, data-driven calibration in future works.

624 Second, we focused primarily on parameter uncertainty, while other important uncertainty
625 sources, such as errors in climate forcing data and model structural assumptions, were not
626 explicitly quantified. Future research should therefore move towards an integrated assessment
627 that combines parameter, driver, and structural uncertainties, aiming to enhance model credibility
628 within the context of global efforts such as TRENDY and CMIP6.



629 Third, and importantly, our sensitivity analysis assumed parameter independence. However, in
630 reality, many physiological parameters often exhibit covariance due to underlying biological
631 trade-offs (e.g., between photosynthetic capacity and leaf nitrogen). Ignoring these correlations
632 may overestimate the effective parameter space and the resulting model sensitivity. Future
633 studies should aim to incorporate parameter correlation matrices into the sampling design to
634 provide a more constrained estimate of uncertainty.

635 These limitations directly inform our vision for the future of ecosystem modeling. An
636 important next step is to extend this analysis to a spatially continuous grid, allowing for the
637 creation of national-scale sensitivity maps that explicitly capture geographic variability in model
638 behavior (Ma et al., 2022a). In parallel, a key priority should be given to fully integrated
639 uncertainty frameworks that explicitly address the interplay of parameter, structural, and driver
640 uncertainties (Oberpriller et al., 2022). Moreover, the increasing availability of multi-source data
641 streams (e.g., eddy covariance, remote sensing, soil inventories) offers unprecedented
642 opportunities to validate sensitivity analyses and to develop more advanced data assimilation
643 schemes (Tao et al., 2020). Finally, exploring the dynamic behavior of these parameter
644 sensitivities under future climate change scenarios, potentially aided by machine learning
645 techniques, will be crucial for enhancing the predictive power of terrestrial ecosystem models in
646 a rapidly changing world (Buster et al., 2024; Gou & Soja, 2024; Hagenauer & Helbich, 2022;
647 Jung & Lee, 2021; Love et al., 2024; Reichstein et al., 2019).

648 5 Conclusions

649 This study provides a comprehensive assessment of parameter controls and uncertainty
650 propagation in the LPJ-GUESS model across China's diverse ecosystems. By integrating three
651 complementary sensitivity analysis methods, we reveal a clear, hierarchical architecture of model
652 control. The simulated carbon-water cycle is co-dominated by a few key parameters governing
653 photosynthetic efficiency (*ALPHA_C3*), carbon allocation (*common_reprfrac*), and biomass
654 turnover. Critically, the dominance of these controls is spatially contingent, shifting from a
655 system governed by physiological efficiency in humid forests to systems constrained by strategic
656 resource allocation and water use in arid and semi-arid ecosystems.

657 Furthermore, our analysis uncovers a fundamental tradeoff in how parameter uncertainty
658 propagates. Arid ecosystems exhibit the highest relative uncertainty, yet their low productivity



659 results in a comparatively small absolute uncertainty range. Conversely, humid and highly
660 productive ecosystems, despite showing greater robustness and low relative uncertainty, are
661 associated with the largest absolute uncertainty in carbon fluxes. This finding highlights distinct
662 modeling challenges across different environments.

663 Collectively, these findings support a move away from one-size-fits-all parameterization
664 towards hierarchical, spatially-explicit, and multi-objective optimization strategies. Future
665 research should focus on extending these analyses to continuous grids and integrating multiple
666 sources of uncertainty (e.g., driver data, model structure) to enhance the predictive reliability of
667 terrestrial biosphere models under ongoing and future environmental change.



668 **CRediT authorship contribution statement**

669 **Fulai Feng:** Conceptualization, Validation, Formal analysis, Writing – original draft, Writing
670 – review & editing, Visualization. **Jianwu Yan:** Writing – review & editing, Methodology,
671 Funding acquisition, Conceptualization. **Wei Liang:** Writing review & editing. **Xiaohong Liu:**
672 Writing review & editing. **Bo Liu:** Writing review & editing. **Xiaoru Liang:** Visualization,
673 Writing review & editing. **Jia Wei:** Writing review & editing. **Yangcan Bao:** Visualization,
674 Writing review & editing.

675 **Acknowledgments**

676 This work was performed with financial support from National Natural Science Foundation of
677 China (42330501, 42071144), and in part by Natural Science Basic Research Plan of Shaanxi
678 Province (2023JC-YB-275).

679 **Conflict of Interest**

680 The authors declare that they have no competing interests.

681 **Data Availability Statement**

682 The LPJ-GUESS model (version 4.1.1), an open-access software available under the Mozilla
683 Public License v. 2.0, was used to generate the results of this study and can be downloaded from
684 <https://zenodo.org/records/8065737> (Nord et al., 2021). Climate data (temperature, precipitation,
685 and shortwave radiation) are available from <https://cds.climate.copernicus.eu/datasets/reanalysis->
686 [era5-land-monthly-means?tab=download](https://cds.climate.copernicus.eu/datasets/reanalysis-) (Copernicus Climate Change Service, 2019). Soil data
687 were obtained from <https://data.tpdc.ac.cn/en/data/46ddd893-3b2b-4bb3-b9e6-b043f3c5c3a2>
688 (Shi et al., 2025). Land cover data for site selection were based on the NASA MODIS
689 MCD12C1 product (2001-2023), downloaded from
690 <https://e4ftl01.cr.usgs.gov/MOTA/MCD12C1.061/> (Friedl & Sulla-Menashe, 2022). Carbon
691 dioxide data were obtained from the NOAA Global Monitoring Laboratory
692 (<https://gml.noaa.gov/ccgg/trends/>) (Lan et al., 2023), and nitrogen deposition data can be
693 downloaded from <https://data.isimip.org/search/product/InputData/subcategory/n-deposition/>
694 (Lamarque et al., 2013).



695 **References**

696 Arbolino, R., Boffardi, R., De Simone, L., and Ioppolo, G.: Multi-objective optimization
697 technique: A novel approach in tourism sustainability planning, *J. Environ. Manage.*, 285,
698 112016, <https://doi.org/10.1016/j.jenvman.2021.112016>, 2021.

699 Asargew, M. F., Masutomi, Y., Kobayashi, K., and Aono, M.: Water stress changes the
700 relationship between photosynthesis and stomatal conductance, *Sci. Total Environ.*, 907,
701 167886, <https://doi.org/10.1016/j.scitotenv.2023.167886>, 2024.

702 Baral, B. R., Kuyper, T. W., and Van Groenigen, J. W.: Liebig's law of the minimum applied to
703 a greenhouse gas: Alleviation of P-limitation reduces soil N₂O emission, *Plant Soil*, 374,
704 539–548, <https://doi.org/10.1007/s11104-013-1913-8>, 2014.

705 Bello, F. de, Lavorel, S., Hallett, L. M., Valencia, E., Garnier, E., Roscher, C., Conti, L., Galland,
706 T., Goberna, M., Májeková, M., Montesinos-Navarro, A., Pausas, J. G., Verdú, M., E-
707 Vojtkó, A., Götzenberger, L., and Lepš, J.: Functional trait effects on ecosystem stability:
708 Assembling the jigsaw puzzle, *Trends Ecol. Evol.*, 36, 822–836,
709 <https://doi.org/10.1016/j.tree.2021.05.001>, 2021.

710 Bergkvist, J., Lagergren, F., Linderson, M.-L. F., Miller, P., Lindeskog, M., and Jönsson, A. M.:
711 Modelling managed forest ecosystems in Sweden: An evaluation from the stand to the
712 regional scale, *Ecol. Model.*, 477, 110253,
713 <https://doi.org/10.1016/j.ecolmodel.2022.110253>, 2023.

714 Bonan, G. B., Levis, S., Sitch, S., Vertenstein, M., and Oleson, K. W.: A dynamic global
715 vegetation model for use with climate models: concepts and description of simulated
716 vegetation dynamics, *Glob. Change Biol.*, 9, 1543–1566, <https://doi.org/10.1046/j.1365-2486.2003.00681.x>, 2003.

718 Buster, G., Benton, B. N., Glaws, A., and King, R. N.: High-resolution meteorology with climate
719 change impacts from global climate model data using generative machine learning, *Nat. Energy*,
720 <https://doi.org/10.1038/s41560-024-01507-9>, 2024.

721 Camargo, A. P., de Souza, R. S. C., Jose, J., Gerhardt, I. R., Dante, R. A., Mukherjee, S.,
722 Huntemann, M., Kyrpides, N. C., Carazzolle, M. F., and Arruda, P.: Plant microbiomes
723 harbor potential to promote nutrient turnover in impoverished substrates of a brazilian
724 biodiversity hotspot, *ISME J.*, 17, 354–370, <https://doi.org/10.1038/s41396-022-01345-1>,
725 2023.

726 Chen, S.-P. and Hu, Z.-M.: Ecosystem carbon and water fluxes in ecological vulnerable areas in
727 China, *Chin. J. Plant Ecol.*, 46, 1433–1436, <https://doi.org/10.17521/cjpe.2022.0404>,
728 2022.

729 Collatz, G. J., Berry, J. A., Farquhar, G. D., and Pierce, J.: The relationship between the rubisco
730 reaction mechanism and models of photosynthesis, *Plant Cell Environ.*, 13, 219–225,
731 <https://doi.org/10.1111/j.1365-3040.1990.tb01306.x>, 1990.

732 Copernicus Climate Change Service: ERA5-land monthly averaged data from 1950 to present,
733 <https://doi.org/10.24381/CDS.68D2BB30>, 2019.



734 Dong, R., Li, N., Li, M.-H., Cong, Y., Du, H., Gao, D., and He, H. S.: Carbon allocation in *pinus*
735 *jezoensis*: Adaptation strategies of a non-treeline species at its upper elevation limit,
736 *Forest Ecosystems*, 11, 100188, <https://doi.org/10.1016/j.fecs.2024.100188>, 2024.

737 Ehleringer, J. and Björkman, O.: Quantum yields for CO₂ uptake in C₃ and C₄ plants:
738 Dependence on temperature, CO₂ , and O₂ concentration, *Plant Physiol.*, 59, 86–90,
739 <https://doi.org/10.1104/pp.59.1.86>, 1977.

740 Enquist, B. J. and Niklas, K. J.: Global allocation rules for patterns of biomass partitioning in
741 seed plants, *Science*, 295, 1517–1520, <https://doi.org/10.1126/science.1066360>, 2002.

742 Farquhar, G. D., Von Caemmerer, S., and Berry, J. A.: A biochemical model of photosynthetic
743 CO₂ assimilation in leaves of C₃ species, *Planta*, 149, 78–90,
744 <https://doi.org/10.1007/BF00386231>, 1980.

745 Forster, P. M., Smith, C., Walsh, T., Lamb, W. F., Lamboll, R., Hall, B., Hauser, M., Ribes, A.,
746 Rosen, D., Gillett, N. P., Palmer, M. D., Rogelj, J., von Schuckmann, K., Trewin, B.,
747 Allen, M., Andrew, R., Betts, R. A., Borger, A., Boyer, T., Broersma, J. A., Buontempo,
748 C., Burgess, S., Cagnazzo, C., Cheng, L., Friedlingstein, P., Gettelman, A., Gütschow, J.,
749 Ishii, M., Jenkins, S., Lan, X., Morice, C., Mühle, J., Kadow, C., Kennedy, J., Killick, R.
750 E., Krummel, P. B., Minx, J. C., Myhre, G., Naik, V., Peters, G. P., Pirani, A., Pongratz,
751 J., Schleussner, C.-F., Seneviratne, S. I., Szopa, S., Thorne, P., Kovilakam, M. V. M.,
752 Majamäki, E., Jalkanen, J.-P., van Marle, M., Hoesly, R. M., Rohde, R., Schumacher, D.,
753 van der Werf, G., Vose, R., Zickfeld, K., Zhang, X., Masson-Delmotte, V., and Zhai, P.:
754 Indicators of global climate change 2023: Annual update of key indicators of the state of
755 the climate system and human influence, *Earth Syst. Sci. Data*, 16, 2625–2658,
756 <https://doi.org/10.5194/essd-16-2625-2024>, 2024.

757 Friedl, M. and Sulla-Menashe, D.: MODIS/terra+aqua land cover type yearly L3 global 500m
758 SIN grid V061, <https://doi.org/10.5067/MODIS/MCD12Q1.061>, 2022.

759 Gómez-Gras, D., Linares, C., Dornelas, M., Madin, J. S., Brambilla, V., Ledoux, J., López-
760 Sendino, P., Bensoussan, N., and Garrabou, J.: Climate change transforms the functional
761 identity of mediterranean coralligenous assemblages, *Ecol. Lett.*, 24, 1038–1051,
762 <https://doi.org/10.1111/ele.13718>, 2021.

763 Gong, W. and Duan, Q.: An adaptive surrogate modeling-based sampling strategy for parameter
764 optimization and distribution estimation (ASMO-PODE), *Environ. Modell. Softw.*, 95,
765 61–75, <https://doi.org/10.1016/j.envsoft.2017.05.005>, 2017.

766 Gou, J. and Soja, B.: Global high-resolution total water storage anomalies from self-supervised
767 data assimilation using deep learning algorithms, *Nat. Water*, 2, 139–150,
768 <https://doi.org/10.1038/s44221-024-00194-w>, 2024.

769 Guan, Q., Tang, J., Feng, L., Olin, S., and Schurgers, G.: Long-term changes of nitrogen
770 leaching and the contributions of terrestrial nutrient sources to lake eutrophication
771 dynamics on the Yangtze Plain of China, *Biogeosciences*, 20, 1635–1648,
772 <https://doi.org/10.5194/bg-20-1635-2023>, 2023.

773 Hagenauer, J. and Helbich, M.: A geographically weighted artificial neural network, *Int. J. Geogr.
774 Inf. Sci.*, 36, 215–235, <https://doi.org/10.1080/13658816.2021.1871618>, 2022.



775 Hallgren, W. S. and Pitman, A. J.: The uncertainty in simulations by a global biome model
776 (BIOME3) to alternative parameter values, *Glob. Change Biol.*, 6, 483–495,
777 <https://doi.org/10.1046/j.1365-2486.2000.00325.x>, 2000.

778 Haxeltine, A. and Prentice, I. C.: A general model for the light-use efficiency of primary
779 production, *Funct. Ecol.*, 10, 551, <https://doi.org/10.2307/2390165>, 1996.

780 Hickler, T., Rammig, A., and Werner, C.: Modelling CO₂ Impacts on Forest Productivity, *Curr*
781 *Forestry Rep.*, 1, 69–80, <https://doi.org/10.1007/s40725-015-0014-8>, 2015.

782 Jung, Y. and Lee, I.: Optimal design of experiments for optimization-based model calibration
783 using fisher information matrix, *Reliab. Eng. Syst. Saf.*, 216, 107968,
784 <https://doi.org/10.1016/j.ress.2021.107968>, 2021.

785 Kengdo, S. K., Ahrens, B., Tian, Y., Heinzle, J., Wanek, W., Schindlbacher, A., and Borken, W.:
786 Increase in carbon input by enhanced fine root turnover in a long-term warmed forest soil,
787 *Sci. Total Environ.*, 855, 158800, <https://doi.org/10.1016/j.scitotenv.2022.158800>, 2023.

788 Körner, Ch.: Leaf diffusive conductances in the major vegetation types of the globe, in:
789 *Ecophysiology of Photosynthesis*, edited by: Schulze, E.-D. and Caldwell, M. M.,
790 Springer Berlin Heidelberg, Berlin, Heidelberg, 463–490, https://doi.org/10.1007/978-3-642-79354-7_22, 1995.

792 Kühn, N., Tovar, C., Carretero, J., Vandvik, V., Enquist, B. J., and Willis, K. J.: Globally
793 important plant functional traits for coping with climate change, *Front. Biogeogr.*, 13,
794 <https://doi.org/10.21425/F5FBG53774>, 2021.

795 Lamarque, J.-F., Dentener, F., McConnell, J., Ro, C.-U., Shaw, M., Vet, R., Bergmann, D.,
796 Cameron-Smith, P., Dalsoren, S., Doherty, R., Faluvegi, G., Ghan, S. J., Josse, B., Lee, Y.,
797 H., MacKenzie, I. A., Plummer, D., Shindell, D. T., Skeie, R. B., Stevenson, D. S., Strode,
798 S., Zeng, G., Curran, M., Dahl-Jensen, D., Das, S., Fritzsche, D., and Nolan, M.: Multi-
800 model mean nitrogen and sulfur deposition from the Atmospheric Chemistry and Climate
801 Model Intercomparison Project (ACCMIP): evaluation of historical and projected future
802 changes, *Atmos. Chem. Phys.*, 13, 7997–8018, <https://doi.org/10.5194/acp-13-7997-2013>,
2013.

803 Lan, X., Tans, P., Thoning, K., and NOAA Global Monitoring Laboratory: Trends in globally-
804 averaged CO₂ determined from NOAA global monitoring laboratory measurements.,
805 <https://doi.org/10.15138/9N0H-ZH07>, 2023.

806 Leverenz, J. W.: The effects of illumination sequence, CO₂ concentration, temperature and
807 acclimation on the convexity of the photosynthetic light response curve, *Physiol. Plant.*,
808 74, 332–341, <https://doi.org/10.1111/j.1399-3054.1988.tb00639.x>, 1988.

809 Li, Y., Wang, Y., Sun, Y., and Li, J.: Global Sensitivity Analysis of the LPJ Model for *Larix*
810 *olgensis* Henry Forests NPP in Jilin Province, China, *Forests*, 13, 874,
811 <https://doi.org/10.3390/f13060874>, 2022.

812 Liang, X., Yan, J., Liang, W., Li, B., Liu, X., Feng, F., and Wei, J.: Ecosystem water limitation
813 shifts driven by soil moisture in the loess plateau, China, *Glob. Planet. Change.*, 243,
814 104625, <https://doi.org/10.1016/j.gloplacha.2024.104625>, 2024.



815 Lindeskog, M., Arneth, A., Bondeau, A., Waha, K., Seaquist, J., Olin, S., and Smith, B.:
816 Implications of accounting for land use in simulations of ecosystem carbon cycling in
817 Africa, *Earth Syst. Dynam.*, 4, 385–407, <https://doi.org/10.5194/esd-4-385-2013>, 2013.

818 Lindeskog, M., Smith, B., Lagergren, F., Sycheva, E., Ficko, A., Pretzsch, H., and Rammig, A.:
819 Accounting for forest management in the estimation of forest carbon balance using the
820 dynamic vegetation model LPJ-GUESS (v4.0, r9710): implementation and evaluation of
821 simulations for Europe, *Geosci. Model Dev.*, 14, 6071–6112,
822 <https://doi.org/10.5194/gmd-14-6071-2021>, 2021.

823 Liu, C., Li, C., and Li, L.: Climate Warming Benefits Plant Growth but Not Net Carbon Uptake:
824 Simulation of Alaska Tundra and Needle Leaf Forest Using LPJ-GUESS, *Land*, 13, 632,
825 <https://doi.org/10.3390/land13050632>, 2024.

826 Liu, X., Liu, C., Fan, B., Li, L., Tan, B., Jin, Z., Lu, H., and Liu, T.: Spatial responses of
827 ecosystem water-use efficiency to hydrothermal and vegetative gradients in alpine
828 grassland ecosystem in drylands, *Ecol. Indic.*, 141, 109064,
829 <https://doi.org/10.1016/j.ecolind.2022.109064>, 2022.

830 Love, R., Milne, G. A., Ajourlou, P., Parang, S., Tarasov, L., and Latychev, K.: A fast surrogate
831 model for 3D earth glacial isostatic adjustment using tensorflow (v2.8.0) artificial neural
832 networks, *Geosci. Model Dev.*, 17, 8535–8551, <https://doi.org/10.5194/gmd-17-8535-2024>, 2024.

833 Lv, S., Wang, Z., Yan, B., Liu, H., Han, G., Wang, Z., Li, Z., Wang, Z., Song, X., and Kang, S.:
834 The relationships between structure and function of plant communities in the desert
835 steppe, *BMC Plant Biol.*, 24, 983, <https://doi.org/10.1186/s12870-024-05659-4>, 2024.

836 Ma, H., Zhang, K., Ma, C., Wu, X., Wang, C., Zheng, Y., Zhu, G., Yuan, W., and Li, X.:
837 Research progress on parameter sensitivity analysis in ecological and hydrological
838 models of remote sensing, *Natl. Remote Sens. Bull.*, 26, 286–298,
839 <https://doi.org/10.11834/jrs.20219089>, 2022a.

840 Ma, R., Xiao, J., Liang, S., Ma, H., He, T., Guo, D., Liu, X., and Lu, H.: Pixel-level parameter
841 optimization of a terrestrial biosphere model for improving estimation of carbon fluxes
842 with an efficient model–data fusion method and satellite-derived LAI and GPP data,
843 *Geosci. Model Dev.*, 15, 6637–6657, <https://doi.org/10.5194/gmd-15-6637-2022>, 2022b.

844 Magnani, F., Leonardi, S., Tognetti, R., Grace, J., and Borghetti, M.: Modelling the surface
845 conductance of a broad-leaf canopy: Effects of partial decoupling from the atmosphere,
846 *Plant Cell Environ.*, 21, 867–879, <https://doi.org/10.1046/j.1365-3040.1998.00328.x>,
847 1998.

848 Meentemeyer, V.: Macroclimate and lignin control of litter decomposition rates, *Ecology*, 59,
849 465–472, <https://doi.org/10.2307/1936576>, 1978.

850 Mitchell, R. J., Auld, M. H. D., Le Duc, M. G., and Robert, M. H.: Ecosystem stability and
851 resilience: A review of their relevance for the conservation management of lowland
852 heaths, *Perspect. Plant Ecol. Evol. Syst.*, 3, 142–160, <https://doi.org/10.1078/1433-8319-00009>, 2000.

853 Monteith, J. L.: Accommodation between transpiring vegetation and the convective boundary
854 layer, *J. Hydrol.*, 166, 251–263, [https://doi.org/10.1016/0022-1694\(94\)05086-D](https://doi.org/10.1016/0022-1694(94)05086-D), 1995.



857 Morris, M. D.: Factorial sampling plans for preliminary computational experiments,
858 *Technometrics*, 33, 161–174, <https://doi.org/10.1080/00401706.1991.10484804>, 1991.

859 Nord, J., Anthoni, P., Gregor, K., Gustafson, A., Hantson, S., Lindeskog, M., Meyer, B., Miller,
860 P., Nieradzik, L., Olin, S., Papastefanou, P., Smith, B., Tang, J., Wårliind, D., and Past
861 LPJ-GUESS Contributors: LPJ-GUESS release v4.1.1 model code, ,
862 <https://doi.org/10.5281/ZENODO.8065736>, 2021.

863 Nossent, J., Elsen, P., and Bauwens, W.: Sobol' sensitivity analysis of a complex environmental
864 model, *Environ. Modell. Softw.*, 26, 1515–1525,
865 <https://doi.org/10.1016/j.envsoft.2011.08.010>, 2011.

866 Oberpriller, J., Herschlein, C., Anthoni, P., Arneth, A., Krause, A., Rammig, A., Lindeskog, M.,
867 Olin, S., and Hartig, F.: Climate and parameter sensitivity and induced uncertainties in
868 carbon stock projections for European forests (using LPJ-GUESS 4.0), *Geosci. Model
869 Dev.*, 15, 6495–6519, <https://doi.org/10.5194/gmd-15-6495-2022>, 2022.

870 Olin, S., Schurgers, G., Lindeskog, M., Wårliind, D., Smith, B., Bodin, P., Holmér, J., and Arneth,
871 A.: Modelling the response of yields and tissue C: N to changes in atmospheric
872 CO₂ and N management in the main wheat regions of western
873 Europe, *Biogeosciences*, 12, 2489–2515, <https://doi.org/10.5194/bg-12-2489-2015>, 2015.

874 Pappas, C., Faticchi, S., Leuzinger, S., Wolf, A., and Burlando, P.: Sensitivity analysis of a
875 process-based ecosystem model: Pinpointing parameterization and structural issues, *JGR
876 Biogeosciences*, 118, 505–528, <https://doi.org/10.1002/jgrg.20035>, 2013.

877 Peng, S., Terrer, C., Smith, B., Ciais, P., Han, Q., Nan, J., Fisher, J. B., Chen, L., Deng, L., and
878 Yu, K.: Carbon restoration potential on global land under water resource constraints, *Nat.
879 Water*, <https://doi.org/10.1038/s44221-024-00323-5>, 2024.

880 Pugh, T. A. M., Lindeskog, M., Smith, B., Poulter, B., Arneth, A., Haverd, V., and Calle, L.:
881 Role of forest regrowth in global carbon sink dynamics, *Proc. Natl. Acad. Sci. U.S.A.*,
882 116, 4382–4387, <https://doi.org/10.1073/pnas.1810512116>, 2019.

883 Rahimi, I., Gandomi, A. H., Chen, F., and Mezura-Montes, E.: A review on constraint handling
884 techniques for population-based algorithms: From single-objective to multi-objective
885 optimization, *Arch. Comput. Methods Eng.*, 30, 2181–2209,
886 <https://doi.org/10.1007/s11831-022-09859-9>, 2023.

887 Reichstein, M., Camps-Valls, G., Stevens, B., Jung, M., Denzler, J., Carvalhais, N., and Prabhat:
888 Deep learning and process understanding for data-driven Earth system science, *Nature*,
889 566, 195–204, <https://doi.org/10.1038/s41586-019-0912-1>, 2019.

890 Saltelli, A.: Making best use of model evaluations to compute sensitivity indices, *Comput. Phys.
891 Commun.*, 145, 280–297, [https://doi.org/10.1016/S0010-4655\(02\)00280-1](https://doi.org/10.1016/S0010-4655(02)00280-1), 2002.

892 Saltelli, A., Tarantola, S., and Chan, K. P.-S.: A quantitative model-independent method for
893 global sensitivity analysis of model output, *Technometrics*, 1999.

894 Shi, G., Sun, W., Shangguan, W., Wei, Z., Yuan, H., Li, L., Sun, X., Zhang, Y., Liang, H., Li, D.,
895 Huang, F., Li, Q., and Dai, Y.: A China dataset of soil properties for land surface
896 modelling (version 2, CSDLv2), *Earth Syst. Sci. Data*, 17, 517–543,
897 <https://doi.org/10.5194/essd-17-517-2025>, 2025.



898 Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S.,
899 Lucht, W., Sykes, M. T., Thonicke, K., and Venevsky, S.: Evaluation of ecosystem
900 dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global
901 vegetation model, *Glob. Change Biol.*, 9, 161–185, <https://doi.org/10.1046/j.1365-2486.2003.00569.x>, 2003.

903 Smith, B., Prentice, I. C., and Sykes, M. T.: Representation of vegetation dynamics in the
904 modelling of terrestrial ecosystems: comparing two contrasting approaches within
905 European climate space, *Glob. Ecol. Biogeogr.*, 10, 621–637, 2001.

906 Smith, B., Samuelsson, P., Wramneby, A., and Rummukainen, M.: A model of the coupled
907 dynamics of climate, vegetation and terrestrial ecosystem biogeochemistry for regional
908 applications, *Tellus B*, 63, 87–106, <https://doi.org/10.1111/j.1600-0870.2010.00477.x>,
909 2011.

910 Smith, B., Wårldin, D., Arneth, A., Hickler, T., Leadley, P., Siltberg, J., and Zaehle, S.:
911 Implications of incorporating N cycling and N limitations on primary production in an
912 individual-based dynamic vegetation model, *Biogeosciences*, 11, 2027–2054,
913 <https://doi.org/10.5194/bg-11-2027-2014>, 2014.

914 Sobol', I. M.: Global sensitivity indices for nonlinear mathematical models and their monte carlo
915 estimates, *Math. Comput. Simul.*, 55, 271–280, [https://doi.org/10.1016/S0378-4754\(00\)00270-6](https://doi.org/10.1016/S0378-4754(00)00270-6), 2001.

917 Song, X., Bryan, B. A., Paul, K. I., and Zhao, G.: Variance-based sensitivity analysis of a forest
918 growth model, *Ecol. Model.*, 247, 135–143,
919 <https://doi.org/10.1016/j.ecolmodel.2012.08.005>, 2012.

920 Sprugel, D. G., Ryan, M. G., Brooks, J. R., Vogt, K. A., and Martin, T. A.: Respiration from the
921 organ level to the stand, in: *Resource Physiology of Conifers*, Elsevier, 255–299,
922 <https://doi.org/10.1016/B978-0-08-092591-2.50013-3>, 1995.

923 Sumner, D. M. and Jacobs, J. M.: Utility of penman–monteith, priestley–taylor, reference
924 evapotranspiration, and pan evaporation methods to estimate pasture evapotranspiration,
925 *J. Hydrol.*, 308, 81–104, <https://doi.org/10.1016/j.jhydrol.2004.10.023>, 2005.

926 Tao, F., Zhou, Z., Huang, Y., Li, Q., Lu, X., Ma, S., Huang, X., Liang, Y., Hugelius, G., Jiang,
927 L., Doughty, R., Ren, Z., and Luo, Y.: Deep Learning Optimizes Data-Driven
928 Representation of Soil Organic Carbon in Earth System Model Over the Conterminous
929 United States, *Front. Big Data*, 3, 17, <https://doi.org/10.3389/fdata.2020.00017>, 2020.

930 Teckentrup, L.: The future of terrestrial carbon in australia, UNSW Sydney,
931 <https://doi.org/10.26190/UNSWORKS/24738>, 2023.

932 Thevasundaram, K., Gallagher, J. J., Cherng, F., and Chang, M. C. Y.: Engineering
933 nonphotosynthetic carbon fixation for production of bioplastics by methanogenic archaea,
934 *Proc. Natl. Acad. Sci. U.S.A.*, 119, e2118638119,
935 <https://doi.org/10.1073/pnas.2118638119>, 2022.

936 Thonicke, K., Venevsky, S., Sitch, S., and Cramer, W.: The role of fire disturbance for global
937 vegetation dynamics: Coupling fire into a dynamic global vegetation model, *Glob. Ecol.
938 Biogeogr.*, 10, 661–677, <https://doi.org/10.1046/j.1466-822X.2001.00175.x>, 2001.



939 Vazquez-Cruz, M. A., Guzman-Cruz, R., Lopez-Cruz, I. L., Cornejo-Perez, O., Torres-Pacheco,
940 I., and Guevara-Gonzalez, R. G.: Global sensitivity analysis by means of EFAST and
941 sobol' methods and calibration of reduced state-variable TOMGRO model using genetic
942 algorithms, *Comput. Electron. Agric.*, 100, 1–12,
943 <https://doi.org/10.1016/j.compag.2013.10.006>, 2014.

944 Verrelst, J., Rivera, J. P., Van Der Tol, C., Magnani, F., Mohammed, G., and Moreno, J.: Global
945 sensitivity analysis of the SCOPE model: What drives simulated canopy-leaving sun-
946 induced fluorescence?, *Remote Sens. Environ.*, 166, 8–21,
947 <https://doi.org/10.1016/j.rse.2015.06.002>, 2015.

948 Verrelst, J., Vicent, J., Rivera-Caicedo, J. P., Lumbierres, M., Morcillo-Pallarés, P., and Moreno,
949 J.: Global Sensitivity Analysis of Leaf-Canopy-Atmosphere RTMs: Implications for
950 Biophysical Variables Retrieval from Top-of-Atmosphere Radiance Data, *Remote Sens.*,
951 11, 1923, <https://doi.org/10.3390/rs11161923>, 2019.

952 Wainwright, H. M., Finsterle, S., Jung, Y., Zhou, Q., and Birkholzer, J. T.: Making sense of
953 global sensitivity analyses, *Comput. Geosci.*, 65, 84–94,
954 <https://doi.org/10.1016/j.cageo.2013.06.006>, 2014.

955 Wang, B., Smith, B., Waters, C., Feng, P., and Liu, D. L.: Modelling changes in vegetation
956 productivity and carbon balance under future climate scenarios in southeastern Australia,
957 *Sci. Total Environ.*, 924, 171748, <https://doi.org/10.1016/j.scitotenv.2024.171748>, 2024.

958 Whitehead, D., Kelliher, F. M., Lane, P. M., and Pollock, D. S.: Seasonal partitioning of
959 evaporation between trees and understorey in a widely spaced *pinus radiata* stand, *J. Appl.*
960 *Ecol.*, 31, 528, <https://doi.org/10.2307/2404448>, 1994.

961 Wu, S.: A systematic review of climate policies in China: Evolution, effectiveness, and
962 challenges, *Environ. Impact Assess. Rev.*, 99, 107030,
963 <https://doi.org/10.1016/j.eiar.2022.107030>, 2023.

964 Yu, E., Ma, J., and Sun, J.: Developing a climate prediction system over southwest China using
965 the 8-km weather research and forecasting (WRF) model: System design, model
966 calibration, and performance evaluation, *Weather Forecast.*, 37, 1703–1719,
967 <https://doi.org/10.1175/WAF-D-21-0188.1>, 2022.

968 Yuxi, W., Li, P., Yuemin, Y., and Tiantian, C.: Global vegetation-temperature sensitivity and its
969 driving forces in the 21st century, *Earth's Future*, 12, e2022EF003395,
970 <https://doi.org/10.1029/2022EF003395>, 2024.

971 Zaehle, S., Sitch, S., Smith, B., and Hatterman, F.: Effects of parameter uncertainties on the
972 modeling of terrestrial biosphere dynamics, *Glob. Biogeochem. Cycles*, 19,
973 2004GB002395, <https://doi.org/10.1029/2004GB002395>, 2005.

974 Zandi, P., Xia, X., Yang, J., Liu, J., Remusat, L., Rumpel, C., Bloem, E., Krasny, B. B., and
975 Schnug, E.: Speciation and distribution of chromium (III) in rice root tip and mature zone:
976 The significant impact of root exudation and iron plaque on chromium bioavailability, *J.*
977 *Hazard. Mater.*, 448, 130992, <https://doi.org/10.1016/j.jhazmat.2023.130992>, 2023.

978 Zhao, A., Li, Z., Zou, L., Wu, J., Stan, K., and Sanchez-Azofeif, A.: Evaluating dynamic global
979 vegetation models in China: Challenges in capturing trends in leaf area and gross primary



980 productivity, but effective seasonal variation representation, *Earth Syst. Dynam.*,
981 <https://doi.org/10.5194/esd-2024-44>, 2025.

982