



**1 Enhancing the representation of African vegetation in the JULES land surface
 2 model (version 7.1) through trait-informed parameterisation**

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56 **Abstract:**

57 African ecosystems remain underrepresented in the plant trait datasets used to
58 parameterise land surface models (LSMs), limiting our confidence in simulations of African
59 landscapes. We assessed whether African plant trait data can improve parameterisation of
60 plant functional types (PFTs) in the Joint UK Land Environment Simulator (JULES vn 7.1)
61 model by updating two key photosynthetic traits: leaf mass per area (LMA) and leaf nitrogen
62 content (Nmass). First, we evaluated African-derived trait estimates relative to default JULES
63 parameters. We then analysed impact of mean annual temperature, mean annual
64 precipitation and an aridity index on variability in these traits using generalized additive
65 mixed models (GAMM), and tested the effect of updated trait parameter values on
66 simulated gross primary productivity (GPP) against data from 16 African eddy covariance
67 sites spanning different biomes. Comparison with JULES default parameters showed that
68 African trait values differed for several PFTs, highlighting the value of trait-informed regional
69 parameterization for representing African vegetation more realistically. GAMM analysis
70 showed that LMA and Nmass varied nonlinearly across climate space, indicating that African
71 leaf trait variation is shaped by interacting environmental gradients rather than single
72 climate drivers. Incorporating the revised trait values into JULES generally produced modest
73 improvements in simulated GPP. Improvements were expressed primarily through reduced
74 bias and root mean square error, with little effect on temporal correlation. Performance
75 gains were most evident at grassland sites, highlighting the limitations of representing
76 diverse vegetation using single PFT-level trait values. This study demonstrates that regionally
77 derived plant trait data can refine LSM parameterisation and can improve aspects of model
78 performance in African ecosystems. It also shows that regionally derived trait data provide a
79 practical basis for evaluating and updating default model parameters, while highlighting the
80 need for approaches that better represent within-PFT trait variability across environmental
81 gradients and biome types.

82 **Keywords:**

83 trait-based modelling, ecosystem processes, plant functional types, parameterisation,
84 vegetation dynamics, terrestrial biosphere



85 **1. Introduction**

86 Accurate simulation of gross primary productivity (GPP) is fundamental to representing
87 terrestrial carbon uptake and land–atmosphere feedback across the Earth. This is especially
88 crucial because African ecosystems are important component of the global terrestrial carbon
89 cycle, and include extensive semi-arid regions that contribute strongly to interannual
90 variability in the global land CO₂ sink, yet their carbon dynamics remain comparatively
91 poorly constrained (Ahlström et al., 2015; Ernst et al., 2024; C. A. Williams et al., 2007). In
92 land surface models (LSMs), vegetation is represented using plant functional types (PFTs),
93 with key physiological properties specified at the PFT level rather than resolved for the full
94 diversity of plant species (Clark et al., 2011; Harper et al., 2016). Consequently, confidence in
95 model predictions depends partly on whether these parameter values adequately represent
96 the functional diversity and adaptive strategies expressed in the simulated ecosystems.

97 The representation of vegetation in LSMs depends on both model structure and the
98 empirical evidence used to parameterise it. In the Joint UK Land Environment Simulator
99 (JULES), vegetation dynamics can be simulated using the dynamic global vegetation model
100 TRIFFID (Top-down Representation of Interactive Foliage and Flora Including Dynamics),
101 while surface cover may also be prescribed depending on the application (Clark et al., 2011;
102 Cox, 2001; Harper et al., 2016, 2018). The expansion from five to nine PFTs improved
103 representation of variation in leaf lifespan and metabolic capacity (Harper et al., 2016), but
104 PFTs necessarily compress substantial ecological variation within broad functional classes.
105 Many LSM parameter values were established using relatively limited empirical datasets,
106 and it remains unclear whether they continue to reflect the substantially expanded global
107 plant trait evidence now available. The TRY database (<https://www.try-db.org/>) now
108 contains approximately 15.4 million trait records spanning 2,661 traits and more than
109 305,000 plant taxa, providing an unprecedented resource for evaluating and refining model
110 parameterisation (Kattge et al., 2020; Lam et al., 2024). Despite this progress, African
111 ecosystems remain comparatively underrepresented within global trait datasets, and
112 important gaps persist for many traits relevant to vegetation modelling, particularly across
113 under-sampled regions and biomes (Akhavue et al., 2026a; Kattge et al., 2020).
114 Consequently, the extent to which current JULES parameters adequately represent African
115 vegetation remains uncertain.



116 Among these parameters, leaf mass per area (LMA) and leaf nitrogen content per unit mass
117 (N_{mass}) provide an effective link between plant ecological strategy and photosynthetic
118 function. Both traits occupy a central position within the leaf economics spectrum, spanning
119 a continuum from resource-acquisitive strategies characterised by low LMA and rapid
120 nutrient turnover to more conservative strategies with higher structural investment and
121 longer leaf lifespan (Reich, 2014; Wright et al., 2004). Leaf nitrogen (N) is closely associated
122 with photosynthetic capacity because a substantial proportion is allocated to the
123 photosynthetic apparatus, underpinning relationships with parameters such as the
124 maximum rate of Rubisco carboxylation (V_{cmax}) in biochemical photosynthesis models
125 (Dong et al., 2017). LMA further influences photosynthetic capacity by determining leaf
126 construction costs and the scaling of nitrogen from a mass basis to an area basis (Dong et al.,
127 2017). It also determines the amount of leaf area that can be deployed for a given
128 investment in leaf biomass and therefore influences LAI, canopy light interception and
129 absorbed photosynthetically active radiation (Poorter et al., 2009). Both traits vary
130 systematically across environmental gradients through climatic filtering driving acclimation
131 and adaptation (Dong et al., 2020). Mean annual temperature (MAT), mean annual
132 precipitation (MAP), and aridity index therefore provide a useful framework for examining
133 trait variation across African bioclimatic space. MAT and MAP capture broad thermal and
134 rainfall gradients, while aridity index integrates precipitation with potential
135 evapotranspiration to provide a more direct indicator of climatic moisture limitation.
136 Previous developments within JULES have demonstrated that incorporating environmentally
137 driven variation in photosynthetic traits, including thermal acclimation of parameters such
138 as V_{cmax} and the maximum rate of electron transport (J_{max}), can influence simulated
139 carbon uptake and land carbon storage (Mercado et al., 2018; Oliver et al., 2022). More
140 broadly, incorporating observed trait variation into vegetation models has been shown to
141 influence simulated carbon fluxes and vegetation dynamics and, in some cases, improve the
142 representation of observed vegetation distributions, providing a strong rationale for trait-
143 informed parameterisation (Verheijen et al., 2013, 2016).

144 Reducing parameter uncertainty is an important component of improving LSM performance.
145 Parameter uncertainty contributes substantially to uncertainty in simulated land-
146 atmosphere exchanges alongside structural limitations arising from missing or simplified



147 ecological processes (Flato et al., 2013; Raoult et al., 2016). Refining parameter values using
148 contemporary observations can improve ecological realism while helping to distinguish
149 genuine structural deficiencies from compensating parameter errors (Raoult et al., 2024).
150 This is particularly relevant in Africa, where ecosystems span exceptional climatic and
151 functional diversity but have historically been underrepresented in the empirical datasets
152 used for model parameterisation and evaluation (Akhavue et al., 2026a; Clements et al.,
153 2024). Regionally derived trait data therefore provide an opportunity both to evaluate
154 whether existing model parameters remain representative of current evidence and to assess
155 whether regionally informed parameterisations can improve model performance.

156 Here, we use African plant trait data to refine PFT-specific estimates of LMA and Nmass for
157 JULES, examine how these traits vary across African climatic gradients, and assess the
158 consequences of revised parameter values for simulated GPP. Specifically, we address three
159 questions:

- 160 1) How do JULES-default parameter values of LMA and Nmass compare with Africa TRY-
161 derived summaries?
- 162 2) How do two key leaf traits (LMA and Nmass) vary across African climatic gradients
163 defined by MAT, MAP and aridity index?
- 164 3) What is the effect of implementing Africa TRY-derived PFT parameter values on
165 simulated GPP across African eddy covariance sites representing diverse ecosystems?



166 2. Methods

167 2.1. Plant trait data and PFT classification

168 We focused on two leaf traits that directly inform photosynthetic capacity and associated
 169 carbon and water exchange processes in JULES: LMA and Nmass. Plant trait records were
 170 obtained from the TRY database through data requests completed on 6 December 2023, 7
 171 May 2024, and 27 August 2024. Across the full global TRY dataset, these traits comprised
 172 299,533 LMA observations from 17,449 species and 89,142 Nmass observations from 12,109
 173 species. The TRY dataset reflects the uneven taxonomic, geographic, and environmental
 174 distribution of available observations rather than a systematically balanced sampling of
 175 vegetation (Kattge et al., 2020). For this study, we restricted the dataset to geolocated
 176 observations within Africa, yielding 17,506 LMA observations from 1,109 species, and 7,078
 177 Nmass observations from 1,001 species.

178 Species were assigned to JULES PFTs using a harmonised classification framework that
 179 classified African plant species according to growth form, leaf type, phenology,
 180 photosynthetic pathway, and climatic zone (Akhavue et al., 2026a). We matched TRY species
 181 names to this lookup table and appended the corresponding PFT label to each trait record
 182 where a unique classification was available. Records lacking a reliable and complete PFT
 183 assignment were excluded from the subsequent analyses. After PFT assignment, the dataset
 184 retained 12,739 LMA observations from 860 species and 4,793 Nmass observations from 799
 185 species all observed within the Africa region. The final LMA observations retained include
 186 measurements made with and without petioles, to maximise the available sample while
 187 reflecting the range of measurement protocols represented in the database.

188 For each PFT, we summarised trait distributions to quantify within- and among-PFT
 189 variability and derive updated parameter values for JULES by calculating the median. To
 190 assess the spatial representativeness of the Africa dataset, we mapped the geographic
 191 distribution of trait observations across the continent, highlighting areas of comparatively
 192 higher sampling density and areas where observations remained sparse.

193



2.2. Climate gradient and trait-climate analysis (MAT-MAP-Aridity index space)

To examine how African plant trait values vary across climatic gradients, we analysed trait observations within climate space defined by MAT ($^{\circ}\text{C}$), MAP (mm yr^{-1}), and aridity index. For each trait record, MAT and MAP were extracted from the ERA5-Land monthly aggregated product at 0.1° spatial resolution using Google Earth Engine (Gorelick et al., 2017). We generated a 1991–2020 climatology by retrieving annual mean temperature and precipitation for each year and then averaged these values over the 30-year period.

Trait record coordinates (longitude and latitude) were used to sample the MAT and MAP climatology layers. Records for which MAT/MAP could not be retrieved (e.g., due to masked pixels in the ERA5-Land land-only domain, typically affecting coastal or water-adjacent locations) were excluded from subsequent trait–climate analyses. Following this new filtering step, the modelling dataset was reduced again, from 17,532 to 16,905 trait observations with complete climate information.

To represent climatic moisture limitation more directly, we derived aridity index using TerraClimate monthly precipitation and potential evapotranspiration (PET) data. TerraClimate provides monthly climate and climatic water-balance variables for global terrestrial surfaces, including precipitation and PET, at approximately $1/24^{\circ}$ spatial resolution (Abatzoglou et al., 2018). For each trait location, annual precipitation and annual PET were calculated for 1991–2020 and averaged across the 30-year period. Aridity index was then calculated as the ratio of MAP to PET, following the UNEP definition (United Nations Environment Programme, 1992). Lower aridity index values indicate more arid conditions, whereas higher values indicate wetter conditions. We used TerraClimate to derive aridity index because it provides precipitation together with Penman-Monteith reference evapotranspiration within a consistent climatic water-balance dataset (Abatzoglou et al., 2018). Although ERA5-Land also provides PET, its formulation assumes a well-watered crop surface and may be less reliable under strongly arid conditions (Muñoz-Sabater et al., 2021).

To characterise how leaf traits varied across the African climate space and quantify their relationships with climatic gradients, we analysed LMA and Nmass using Generalised Additive Mixed Models (GAMMs) (Wood, 2017). We mapped the density of trait observations within MAT-MAP climate space to assess sampling coverage across environmental conditions.



225 All statistical analyses were conducted in R (R Core Team, 2021). For statistical inference,
226 GAMMs were fitted separately for LMA and Nmass using the *mgcv* package (Wood, 2017).
227 Prior to modelling, trait values were $\log_{10}$ -transformed to reduce right-skew, stabilise
228 variance, and improve comparability between traits. MAT, MAP and aridity index were
229 retained together because they represent complementary dimensions of the climatic
230 environment relevant to plant function. MAT characterises the thermal regime, MAP
231 represents absolute precipitation input, and aridity index expresses precipitation relative to
232 atmospheric evaporative demand. Including both MAP and aridity index therefore allowed
233 trait variation to be characterised across gradients of both absolute water input and climatic
234 moisture limitation. Our objective was to characterise trait responses across their joint
235 multidimensional climate space. Each model represented $\log_{10}$ -transformed trait values as a
236 tensor-product smooth of MAT, MAP, and aridity index, allowing non-linear and interacting
237 effects of the three climatic variables to be represented across their joint climate space:

$$238 \quad \log_{10}(\text{trait}) \sim te(\text{MAT}, \text{MAP}, \text{aridity index}) + s(\text{species}, bs = "re")$$

239 To account for repeated observations within species and the resulting non-independence
240 among records, we included species identity as a random-effect smooth. Models were fitted
241 using restricted maximum likelihood (REML).

242 Model adequacy was assessed using standard diagnostic procedures (*gam.check*), including
243 inspection of residual patterns and evaluation of basis dimension sufficiency. Because MAT,
244 MAP and aridity index were represented jointly within a single tensor-product, the fitted
245 surface was interpreted as a multivariate climate–trait relationship rather than as
246 independent effects of the individual climatic variables. In particular, because aridity index
247 incorporates precipitation, we did not interpret the effects of MAP and aridity index
248 independently.

249

250 **2.3. Implementation of trait-informed parameterisation in JULES**

251 The version of JULES used in this study is version 7.1. The trait-informed parameterisation
252 was implemented by replacing the default JULES (version 7.1) values for LMA and Nmass
253 with PFT-specific median estimates derived from African trait observations. The default
254 values are described by Harper et al. (2016) and are widely used in offline and coupled



255 configurations of JULES (e.g., Sellar et al., 2019), including applications contributing to global
256 terrestrial carbon-cycle assessments (Friedlingstein et al., 2025; Sitch et al., 2024). All other
257 vegetation and biophysical parameters were retained from the baseline configuration to
258 isolate the effects of substituting African-derived estimates for these two traits.

259 JULES represents these traits using the trait-based physiology developed by Harper et al.
260 (2016), which reformulated the nine-PFT vegetation scheme by replacing the earlier
261 parameters of specific leaf density, expressed as leaf carbon per unit leaf area (σ_l) and top-
262 leaf nitrogen content, expressed as nitrogen per unit carbon (NI0) with LMA and Nmass.

263 Within this formulation, LMA and Nmass influence photosynthetic capacity as they
264 determine leaf nitrogen per unit area. Area-based leaf nitrogen is calculated by multiplying
265 mass-based leaf nitrogen by leaf mass per area and is subsequently used to estimate V_{cmax}
266 in JULES (Eq. S1-S2). Consequently, changes in LMA or Nmass can alter estimated V_{cmax} and,
267 consequently, simulated photosynthetic carbon uptake. However, V_{cmax} is not determined
268 solely by these two traits. Other PFT-dependent parameters, including the intercept and
269 slope of the V_{cmax} –leaf nitrogen relationship, canopy nitrogen distribution, and respiration-
270 related parameters, were not constrained by the African trait dataset and were therefore
271 retained from the baseline configuration of Harper et al. (2016).

272

273 **2.4. Site-level evaluation of trait-informed parameterisation in JULES**

274 To evaluate the effects of African trait-informed parameterisation on model performance,
275 we compared simulations from the default JULES configuration with those from a trait-
276 informed configuration that differed only in the values of LMA and Nmass. The default
277 configuration followed the JULES flux-tower evaluation setup described by Harper et al.
278 (2021), which was developed to evaluate JULES simulations of carbon and water fluxes
279 against flux-tower observations. Both configurations used identical meteorological forcing
280 and model settings (as described in Akhabue et al., 2026b), allowing differences in simulated
281 GPP to be attributed solely to the revised trait parameter values. This experimental design
282 therefore provided a direct test of whether African trait-informed parameterisation
283 improved the simulation of GPP in JULES.



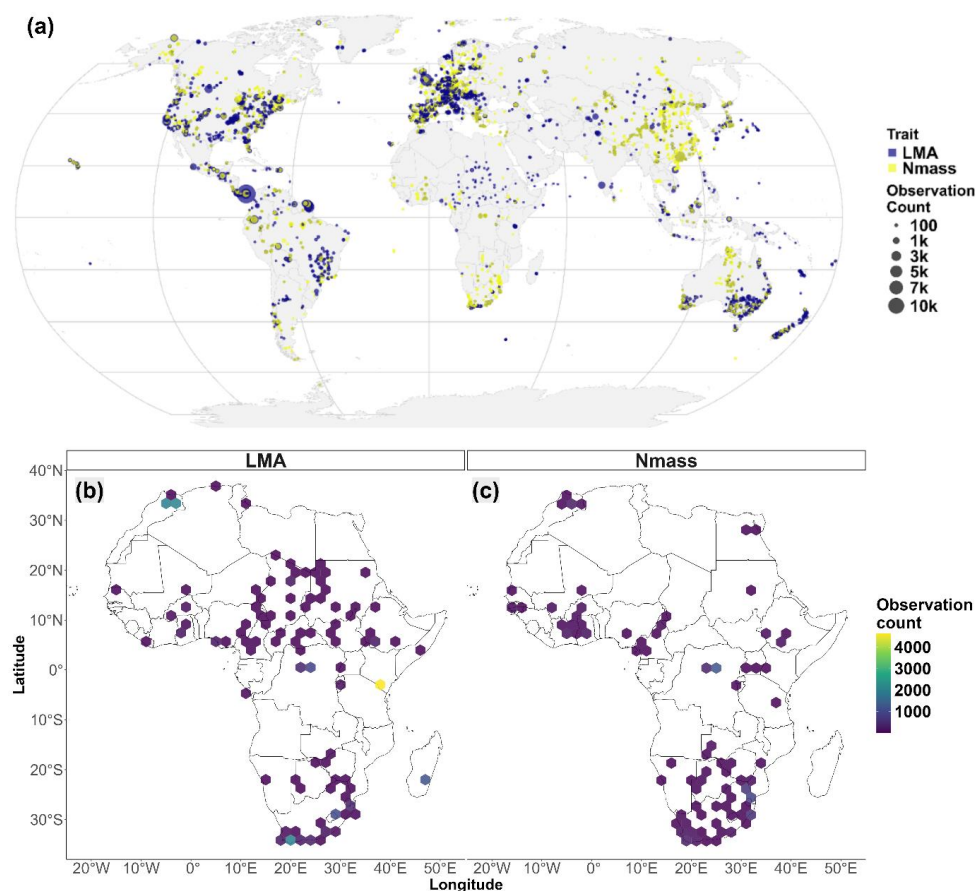
284 Model performance was evaluated against eddy covariance flux tower observations from 16
285 African sites (Figure S1) collated and prepared as described in Akhabue et al. (2026b). These
286 sites span a wide range of African bioclimatic domains and provide independent
287 measurements of carbon exchange for evaluating LSM performance under diverse
288 environmental conditions. The evaluation dataset comprises 110 site-years of observations
289 and, to our knowledge, represents the most extensive flux-based benchmark yet assembled
290 across Africa, corresponding to a fourfold increase in site-years and data relative to previous
291 comparable evaluations.

292

293 **3. Results**

294 **3.1. Trait dataset coverage and geographic distribution**

295 The TRY database showed a highly uneven global distribution of LMA and Nmass
296 observations (Figure 1a), with denser sampling in North America, Europe, and parts of Asia,
297 but comparatively sparse coverage across Africa. Within Africa, LMA observations were
298 concentrated primarily in southern and eastern Africa, whereas Nmass observations were
299 concentrated mainly in southern Africa, with substantially sparser coverage across Central
300 Africa and the northern parts of the continent (Figures 1b and 1c). Thus, although the
301 African dataset provides broad continental coverage, substantial geographic gaps remain,
302 particularly for Nmass and across Central and Northern Africa. The apparent concentration
303 of LMA observations in southeastern Africa reflects intensive spatial sampling around Mount
304 Kilimanjaro, with 2,938 observations from 152 species across 56 coordinates aggregated
305 within a single mapping bin in this continental-scale visualisation.



306

307 Figure 1. African plant trait observations are geographically uneven within a globally
 308 imbalanced evidence base. (a) Global observations of leaf mass per area (LMA; blue) and
 309 leaf nitrogen content per leaf dry mass (Nmass; yellow) are concentrated in North America,
 310 Europe, and parts of Asia, with comparatively sparse coverage across Africa. Point size is
 311 proportional to the number of records per location. Within Africa, LMA observations are
 312 concentrated primarily in southern and eastern regions, and Nmass in southern regions,
 313 with relatively sparse sampling across Central Africa and the Sahel. Panels (b) and (c) show
 314 the spatial density of observations for LMA and Nmass, respectively, across Africa.

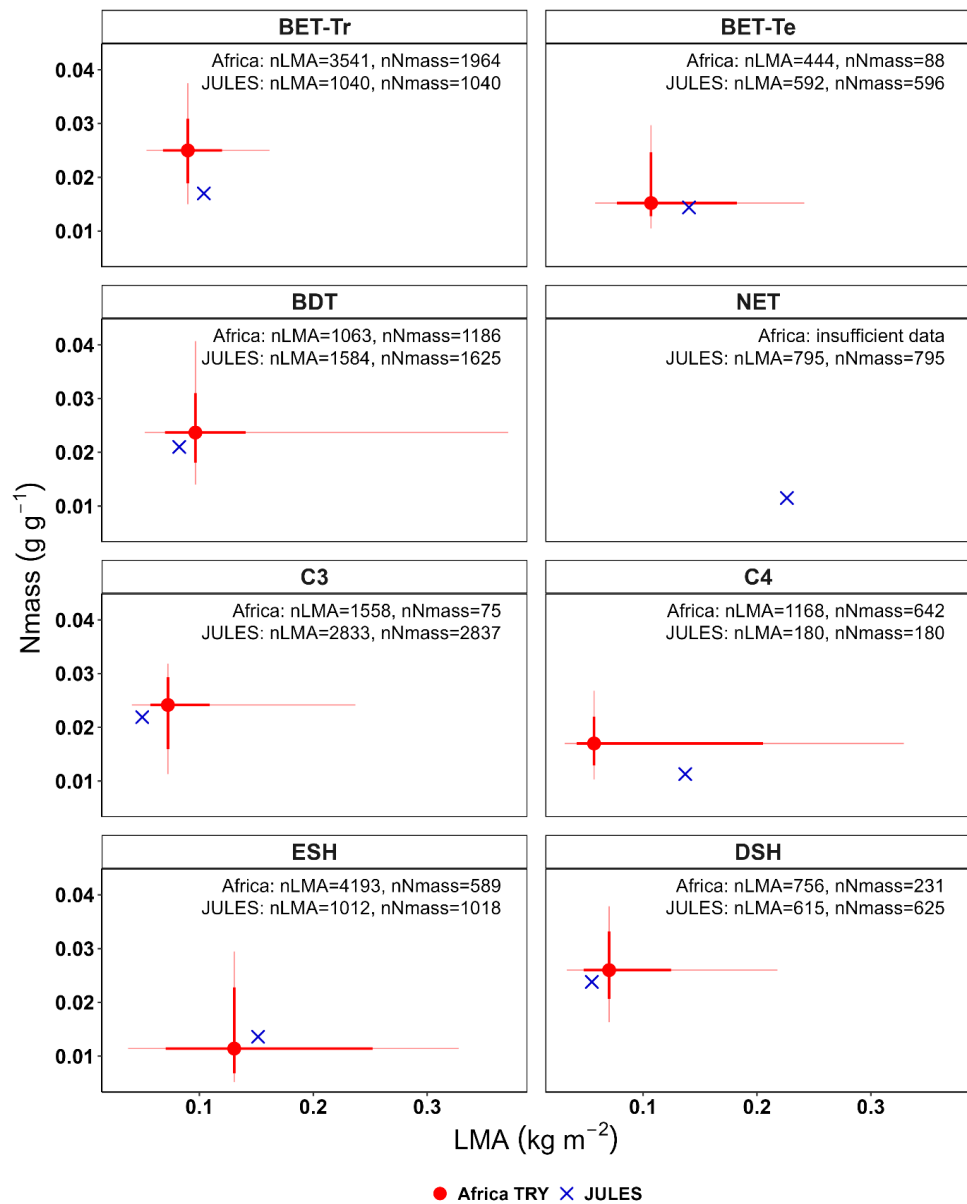
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316 **3.2. African PFT trait estimates differ from current JULES default values**

317 JULES default values for LMA and Nmass diverged from African TRY-derived trait estimates
318 for several PFTs (Figure 2). Differences were evident across tree, grass and shrub PFTs,
319 although some were small relative to within-PFT trait variability. African TRY-derived median
320 LMA was generally lower in grasses (C3 and C4) than in woody PFTs, while BET-Te, ESH, BET-
321 Tr and BDT showed among the highest median LMA values. Nmass also varied among PFTs,
322 with generally higher median values in BDT and BET-Tr than in C4 grass and shrubs. These
323 patterns broadly reflected functional differences among vegetation types.

324 Interpretation of these comparisons should be considered alongside the uneven
325 representation of individual PFTs across Africa (Figure S2). BET-Tr, BDT and ESH were
326 comparatively well represented across southern and eastern Africa, whereas NET and BET-Te
327 were more sparsely sampled. The African NET estimate is therefore not shown because the
328 available observations ($n = 34$) were insufficient to provide a reliable estimate. NET was also
329 absent from the PFT configurations used at the evaluation sites and therefore did not affect
330 the reparameterisation experiments.



331

332 Figure 2. JULES default values for leaf mass per area (LMA) and leaf nitrogen content per unit
333 mass (Nmass) diverge from African TRY-derived trait estimates for several plant functional
334 types (PFTs). Points show the median LMA and Nmass for each PFT derived from African TRY
335 observations (red), and the current JULES parameter values (blue). Horizontal and vertical
336 whiskers show the marginal distribution of each trait independently, with thin whiskers



337 indicating the 10th-90th percentile range and thick whiskers the interquartile range (25th-
 338 75th percentile). In-panel labels report the number of observations contributing to each
 339 summary for Africa and JULES, where nLMA and nNmass denote the sample sizes for LMA
 340 and Nmass, respectively. The African estimate for NET is not shown because of insufficient
 341 observations. PFTs are BET-Tr, broadleaf evergreen tropical tree; BET-Te, broadleaf evergreen
 342 temperate tree; BDT, broadleaf deciduous tree; NET, needleleaf evergreen tree; C3, C3 grass;
 343 C4, C4 grass; ESH, evergreen shrub; and DSH, deciduous shrub.

344

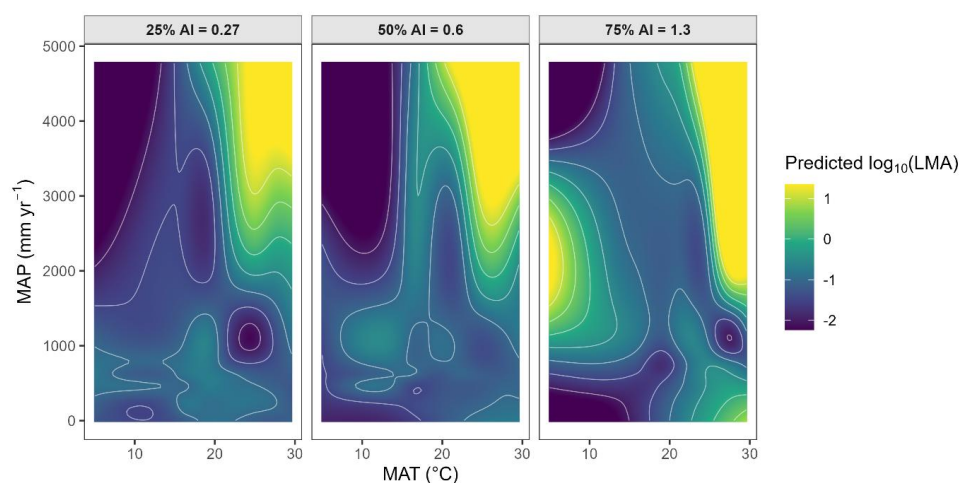
345 **3.3. LMA and Nmass vary nonlinearly across Africa climate space**

346 The trait observations spanned a broad but uneven African climate space, with particularly
 347 dense sampling in warm, moderately dry conditions (Figure S3). The LMA GAMM showed
 348 that LMA varied systematically across joint MAT–MAP–aridity index climate space, with both
 349 the climate smooth and species effect highly significant ($p < 0.001$). The fitted surface
 350 showed substantial nonlinear variation in predicted LMA across MAT–MAP space, with the
 351 pattern shifting across aridity-index levels (Figure 3). Higher predicted LMA generally
 352 occurred in warmer and wetter parts of climate space, particularly at high MAT and MAP, but
 353 localised regions of higher and lower LMA occurred across the different aridity-index levels.
 354 The response surface therefore showed localised regions of high and low LMA rather than a
 355 monotonic response along any single climatic gradient.

356 The Nmass GAMM similarly showed systematic variation across the joint MAT–MAP–aridity
 357 index space, with the tensor-product smooth highly significant ($p < 0.001$). Predicted Nmass
 358 varied strongly across MAT–MAP space and shifted substantially across aridity-index levels
 359 (Figure 4). At low aridity index, higher predicted Nmass occurred mainly in cooler to
 360 intermediate temperature regions with moderate to high MAP, whereas lower values were
 361 associated with warmer, high-MAP regions. At median aridity index, the response was more
 362 heterogeneous, with higher predicted Nmass occurring in parts of the low-MAP/high-MAT
 363 space and lower values in portions of the warm, wetter climate space. At high aridity index,
 364 relatively high predicted Nmass occurred across low-MAP regions and parts of cooler climate
 365 space, whereas lower values occurred in some warm and wetter regions. Summary model
 366 outputs and diagnostics are provided in Tables S1 and S4 and Figures S4-S5.



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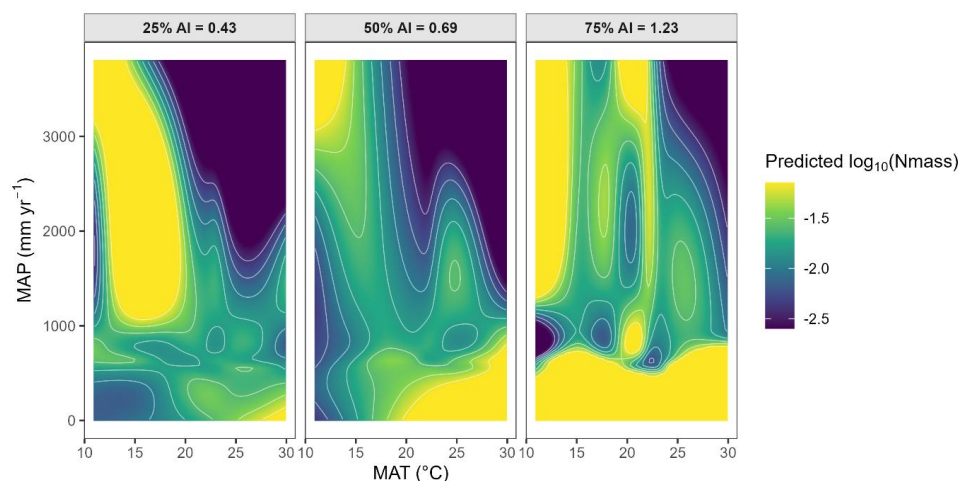


368

369 Figure 3. Predicted LMA increases nonlinearly across warmer and wetter parts of the MAT–
 370 MAP–aridity space. Predicted log₁₀ LMA from the GAMM with a three-way tensor smooth of
 371 MAT, MAP, and aridity index (AI). Panels show MAT–MAP response surfaces with AI = aridity
 372 index fixed at the 25th, 50th and 75th percentiles of LMA. Contour lines show equal
 373 predicted log₁₀(LMA) values. Aridity classes follow the UNEP/UNESCO classification: hyper-
 374 arid (<0.05), arid (0.05–<0.20), semi-arid (0.20–<0.50), dry sub-humid (0.50–<0.65), and
 375 humid (≥0.65) (United Nations Environment Programme, 1992).

376

377



378

379 Figure 4. Predicted Nmass shows a heterogeneous nonlinear response across the MAT–
 380 MAP–aridity space. Predicted $\log_{10}$ Nmass from the GAMM with a three-way tensor smooth
 381 of mean MAT, MAP, and aridity index (AI). Panels show MAT–MAP response surfaces with
 382 aridity index = AI fixed at the 25th, 50th and 75th percentiles of Nmass. Colour scales are
 383 constrained to the observed range of log-transformed Nmass values. Contour lines show
 384 equal predicted $\log_{10}$ (Nmass) values. Aridity classes follow the UNEP/UNESCO classification:
 385 hyper-arid (<0.05), arid ($0.05\text{--}<0.20$), semi-arid ($0.20\text{--}<0.50$), dry sub-humid ($0.50\text{--}<0.65$),
 386 and humid (≥ 0.65) (United Nations Environment Programme, 1992).

387

388 3.4. Site-level evaluations demonstrate modest improvements in LSM

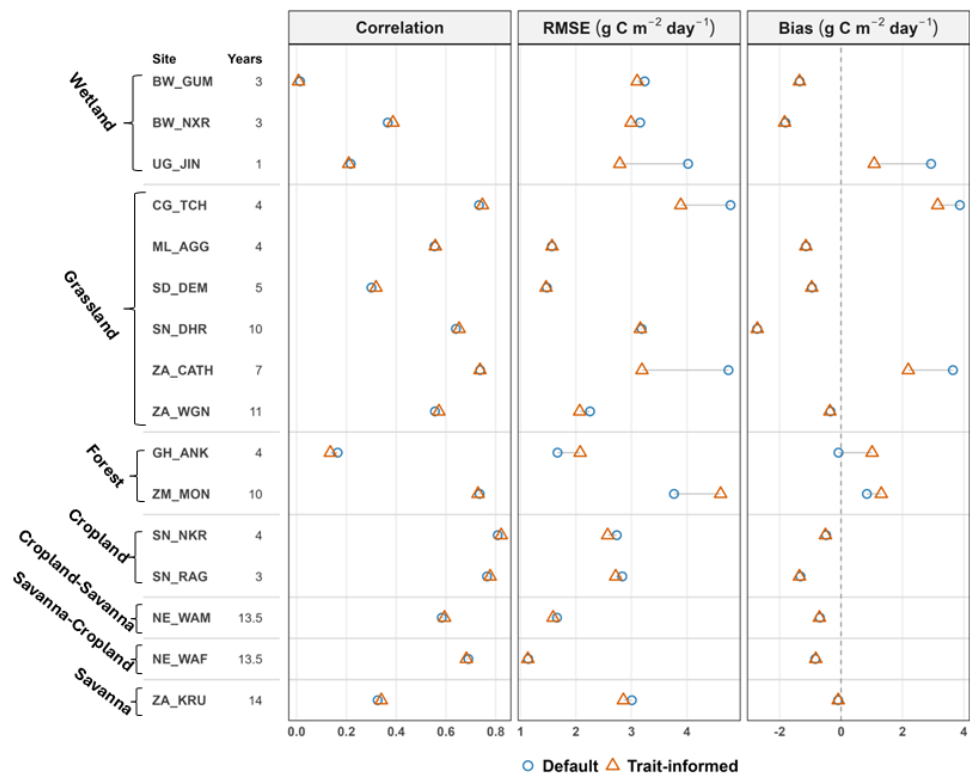
389 Trait-informed parameterisation produced heterogeneous changes in simulated GPP
 390 performance across sites and ecosystem types (Figure 5). Correlation between simulated
 391 and observed GPP changed little, indicating that both configurations captured temporal
 392 variability similarly, whereas RMSE and bias showed larger site-dependent responses. RMSE
 393 decreased at several sites, particularly in grassland and wetland ecosystems, but increased
 394 at the two forest sites. Bias also moved closer to zero at many sites, with the clearest
 395 improvements occurring in grassland and wetland systems. However, improvements were
 396 not universal, with some sites showing increased bias or little change in overall model
 397 performance.



398 When summarised across all sites using record length as weights, trait-informed
399 parameterisation produced a small increase in weighted mean correlation (+0.006),
400 alongside reductions in RMSE of $0.119 \text{ g C m}^{-2} \text{ day}^{-1}$ and absolute bias of $0.055 \text{ g C m}^{-2} \text{ day}^{-1}$,
401 indicating a modest improvement in network-level GPP simulation. Time series comparisons
402 between simulated and observed GPP further illustrate these site-level responses (Figure
403 S6).

404 To aid mechanistic interpretation, we calculated area-based leaf nitrogen (Narea) and the
405 implied $V_{\text{cmax}25}$ under the default and African trait-informed parameter values (Table S5).
406 African-derived parameters increased Narea and implied $V_{\text{cmax}25}$ for BET-Tr, BDT, C3
407 grasses, and DSH, but reduced them for BET-Te, C4 grasses, and ESH. These contrasting
408 responses indicate that the trait-informed parameterisation altered potential photosynthetic
409 capacity differently among PFTs, providing a mechanistic basis for the site-specific GPP
410 responses observed in JULES.

411



412

413 Figure 5. Trait-informed reparameterisation produces heterogeneous changes in simulated
414 GPP performance, with the largest improvements occurring in bias and RMSE rather than
415 temporal correlation. Model performance is compared between the default and Trait-
416 informed JULES configurations across 16 African eddy covariance flux tower sites. Panels
417 show (a) correlation, (b) root mean square error (RMSE; $\text{g C m}^{-2} \text{ day}^{-1}$), and (c) bias (g C m^{-2}
418 day^{-1}) between simulated and observed GPP. Circles denote the default configuration and
419 triangles the trait-informed configuration; connecting lines show the direction and
420 magnitude of change. For correlation, higher values indicate better performance, whereas
421 lower RMSE and bias values closer to zero indicate better performance.



422 4. Discussion

423 4.1. African trait data provide a basis for regional PFT parameterisation

424 The trait compilation highlights both the value and limitations of African plant trait data for
 425 LSM parameterisation. Trait records remain geographically uneven, with sparse coverage
 426 across parts of Central Africa, the Sahel, and other dryland regions relative to the denser
 427 coverage in Europe, North America, and parts of Asia. This persistent geographical bias in
 428 global trait datasets reinforces the underrepresentation of African vegetation in the
 429 evidence base used to parameterise Earth system and land surface models (Akhavue et al.,
 430 2026a; Grenié et al., 2025; Kattge et al., 2020). Despite these limitations, the TRY African
 431 dataset resolved clear differences in LMA and Nmass among PFTs, providing regionally
 432 specific information that can inform model parameterisation. These patterns are consistent
 433 with broader variation in leaf structure and nitrogen investment associated with plant
 434 functional strategies (Wright et al., 2004), while also demonstrating that broad PFT classes
 435 retain sufficient functional signal to support model parameterisation despite compressing
 436 substantial within-PFT variation (Butler et al., 2017, 2022; Wullschleger et al., 2014).

437 African TRY-derived medians differed from current JULES defaults for several PFTs, although
 438 the magnitude and direction of these differences varied among functional types. This
 439 indicates that existing JULES parameter values do not always capture the trait characteristics
 440 represented in the available African observations and supports the value of trait-informed
 441 regional parameterisation. Some of these differences may also reflect both the expansion of
 442 the TRY database since the original parameterisation and refinements in PFT classification
 443 and filtering workflows. The African estimates derived here use current species-level PFT
 444 lookup tables and retain only records with reliable PFT assignments (Akhavue et al., 2026a),
 445 whereas the default JULES parameterisation used broader classification rules, including
 446 latitude-based separation of tropical and temperate broadleaf evergreen trees and the
 447 allocation of herbaceous growth forms to grass categories (Harper et al., 2016). These
 448 highlight the value of regionally informed trait parameterisation while maintaining
 449 transparent links between species-level observations and the PFT-level values used in land-
 450 surface models.

451 The uneven trait coverage also has implications for representing vegetation adapted to
 452 disturbance. Fire and herbivory are important ecological filters in many African ecosystems



453 and can influence species composition, allocation strategies and vegetation structure
 454 (Archibald et al., 2019; Lehmann et al., 2011; Osborne et al., 2018). These processes are not
 455 explicitly represented through the LMA and Nmass parameterisation considered here,
 456 illustrating a broader limitation of PFT-based LSMs in capturing disturbance-mediated
 457 functional variation.

458 Together, these findings provide a rationale for regional parameterisation while highlighting
 459 its limits. African trait data contain sufficient functional information to refine PFT-level
 460 parameter estimates, but uneven geographical and taxonomic coverage means that the
 461 resulting medians should be regarded as improved regional estimates rather than definitive
 462 representations of continental trait variation. This provides both a basis for the trait-
 463 informed parameterisation tested here and important context for understanding why its
 464 effects on simulated GPP varied among ecosystems.

465

466 **4.2. Trait variability across climatic gradients**

467 The GAMM analysis showed that LMA and Nmass vary nonlinearly across joint gradients of
 468 temperature, precipitation and moisture availability, rather than following simple
 469 relationships with individual climatic variables. This indicates that plant trait variation is
 470 structured by combinations of environmental conditions, consistent with evidence that leaf
 471 traits respond to climate alongside species identity, growth form and local resource
 472 constraints (Díaz et al., 2016; Madani et al., 2018; Ordoñez et al., 2009; Poorter et al., 2009;
 473 Wright et al., 2004, 2005).

474 The contrasting response surfaces for LMA and Nmass provide further ecological insight.
 475 Predicted LMA was generally higher in warmer and wetter parts of climate space, although
 476 the response was heterogeneous across aridity-index levels, indicating that higher LMA is
 477 not confined to water-limited environments. Such patterns may reflect variation in leaf
 478 longevity, structural investment, nutrient limitation and disturbance-mediated adaptation
 479 across African forests, woodlands and savanna–forest transitions (Aleman & Fayolle, 2020; Li
 480 et al., 2021; Poorter et al., 2009; Sankaran et al., 2005). In contrast, Nmass exhibited a
 481 distinct response surface, suggesting that nitrogen investment was only partly coupled to
 482 LMA. Because mass-based leaf nitrogen and area-based nitrogen capture different aspects



483 of leaf investment and physiological function, LMA and Nmass provide complementary
 484 information for characterising plant strategies (Dong et al., 2022; Evans, 1989; John et al.,
 485 2017).

486 These relationships are directly relevant to JULES, where LMA and Nmass contribute to the
 487 estimation of area-based leaf nitrogen and photosynthetic capacity through V_{cmax} (Harper
 488 et al., 2016). The nonlinear climate responses help explain why a single PFT-level trait value
 489 cannot fully represent the range of physiological strategies expressed across African
 490 environments. Variations in LMA and Nmass may reinforce or offset one another, producing
 491 different effects on photosynthetic capacity and simulated carbon uptake among climates.
 492 This provides a complementary route to recent JULES developments in which physiological
 493 parameters such as V_{cmax} and J_{max} vary dynamically with thermal conditions (Kattge &
 494 Knorr, 2007; Mercado et al., 2018; Oliver et al., 2022), suggesting that environment–trait
 495 relationships could provide another means of increasing functional realism.

496 More broadly, these findings illustrate the limitations of fixed PFT-level parameterisation.
 497 PFTs provide a practical framework for land-surface modelling, but their fixed parameter
 498 values inevitably compress substantial within-PFT ecological variation (Griffith et al., 2020;
 499 Van Bodegom et al., 2012; Verheijen et al., 2013; Wullschlegel et al., 2014; Yang et al.,
 500 2019). The significant species effects retained in the GAMMs further indicate that climate
 501 alone does not explain trait variation. Regional median values therefore represent an
 502 intermediate step between globally fixed parameters and approaches that allow key traits to
 503 vary continuously with environmental conditions. For example, recent hybrid trait-based
 504 modelling studies have shown the potential for environment–trait relationships to improve
 505 representation of functional diversity and carbon–water exchange beyond conventional PFT-
 506 based approaches (Fang et al., 2026).

507 We recognise that alternative GAMM specifications could be used to investigate climate-trait
 508 relationships. We selected a three-dimensional tensor-product smooth because our
 509 objective was to characterise trait variation across joint MAT–MAP–aridity climate space
 510 rather than estimate independent effects of individual climatic variables. This formulation
 511 also reflects the inherent dependence between MAP and aridity index, meaning that their
 512 individual contributions cannot be disentangled. Within this framework, the results provide
 513 evidence that trait variation is structured across African climate space rather than



adequately represented by a single regional value. Future regional parameterisations could extend this framework by incorporating additional environmental controls, including edaphic gradients, as improved African soil datasets provide increasingly fine-grained, accurate and nuanced representations of soil properties (Hengl et al., 2021).

518

4.3. Trait-informed parameterisation improves GPP magnitude more than temporal dynamics

Using African plant trait data to refine PFT-specific values of LMA and Nmass produced modest but structured improvements in simulated GPP, with larger effects on flux magnitude than on temporal correspondence with observations. Across the site network, changes in correlation were generally small, whereas RMSE and bias responded more clearly. This indicates that trait-informed parameterisation primarily altered the overall level of simulated GPP rather than altering the timing of seasonal and/or short-term variability. This pattern is consistent with the role of Nmass and LMA in JULES, where they influence leaf nitrogen, photosynthetic capacity, and hence carbon uptake (Harper et al., 2016).

The clearest improvements occurred at grassland sites, where trait-informed parameterisation frequently reduced positive bias and RMSE. This suggests that trait representation contributed to part of the baseline model-observation mismatch in these ecosystems, alongside other sources of error. Open-canopy ecosystems such as grasslands and savannas may be particularly responsive to variation in leaf structural and bioclimatic traits because seasonal productivity is strongly influenced by the amount and activity of photosynthetic tissue (He et al., 2023; Whitley et al., 2016; Zhao et al., 2022). The reduction in bias at several grassland sites is therefore consistent with a more realistic representation of photosynthetic capacity following trait-informed parameterisation. However, the responses should be interpreted alongside broader limitations in JULES representation of hydrological boundary conditions, canopy development, and water-stress, which also influence GPP (Akhavue et al., 2026b; Harper et al., 2021; Slevin et al., 2015).

Forest sites showed a contrasting response, with RMSE generally increasing following reparameterisation. This likely reflects the greater structural and functional heterogeneity of forests, where a single PFT median captures only part of the variation in leaf strategy, canopy



position, nutrient availability, phenology, and species composition (Butler et al., 2017; Wu et al., 2017; Yu et al., 2021). More generally, performance can improve where the regional PFT median better matches local vegetation but deteriorate where it does not. The contrasting responses across ecosystems therefore highlight the limits of using a single parameter value to represent substantial within-PFT variation, while also demonstrating the importance of broad, heterogeneous evaluation networks for identifying such site-specific responses and reducing the risk of overinterpreting performance from a small number of sites (Akhavue et al., 2026b).

The limited change in temporal correlation provides further insight into the role of these traits. Because area-based leaf nitrogen is calculated from LMA and Nmass, changes in either trait alter the implied Vcmax25 and therefore potential photosynthetic capacity. The African-derived parameters increased implied Vcmax25 for BET-Tr, BDT, C3 grasses and DSH, but reduced it for BET-Te, C4 grasses and ESH. These contrasting PFT-level changes provide a mechanistic basis for the heterogeneous site responses and help explain why changes in trait parameters can alter the magnitude of simulated GPP without necessarily changing its temporal dynamics, which are additionally controlled by radiation, temperature, vapour pressure deficit, stomatal conductance, soil moisture stress, phenology and canopy development (Clark et al., 2011; Oliver et al., 2022). This limitation is also relevant where leaf nitrogen can vary substantially through the growing season rather than remaining constant as static trait parameters may not capture important temporal variation in plant physiology.

Improved agreement with GPP observations does not by itself demonstrate that the revised parameters are necessarily more accurate across all ecosystems and environmental conditions. For example, Hawkins et al. (2019) showed that multiple plausible TRIFFID parameterisations could reproduce contemporary vegetation patterns while producing substantially different responses under future climate conditions. In process-based models, improved performance can arise through compensation for errors elsewhere in the model, while changes that improve GPP may potentially worsen the representation of other state variables or fluxes (Verheijen et al., 2013). Because carbon, water and energy fluxes are tightly coupled within LSMs, improvements in GPP do not necessarily imply corresponding improvements in other state variables or fluxes. A broader evaluation of JULES across this



575 same African flux network identified limitations in seasonal canopy development and soil-
 576 moisture stress representation that also influence simulated GPP (Akhabue et al., 2026b).
 577 These results therefore provide evidence that African trait data add useful ecological
 578 information to JULES and can improve aspects of GPP simulation, while also demonstrating
 579 the limits of addressing model behaviour through changes to only two PFT parameters.

580 This limitation is also relevant when interpreting the site network, which includes cropland
 581 alongside natural and semi-natural ecosystems. Crop systems have distinct phenological and
 582 physiological controls, and previous work showed that JULES-Crop could reproduce aspects
 583 of productivity while failing to capture observed seasonal variation in leaf nitrogen in
 584 irrigated maize (K. Williams et al., 2017). The present study focused on LMA and Nmass
 585 because of their central roles in photosynthetic capacity and leaf functional strategy, but
 586 these traits represent only part of the functional variation shaping GPP. Residual differences
 587 in model performance, particularly in forest and transitional systems, are likely to reflect
 588 additional controls including phenology, rooting strategies, nutrient limitation, canopy
 589 structure and within-PFT trait variation. Thus, revising LMA and Nmass provides a targeted
 590 test of the contribution of leaf functional information to JULES rather than a comprehensive
 591 trait-based parameterisation. This is consistent with Harper et al. (2016), who showed that
 592 implementing trait-based physiology in JULES required coordinated changes across multiple
 593 physiological and phenological parameters rather than leaf traits alone. More
 594 comprehensive parameterisation approaches will therefore need to combine improved
 595 regional trait data with advances in representing other physiological and ecological
 596 processes.

597 The results therefore illustrate both the value and limits of trait-informed PFT
 598 parameterisation. LMA and Nmass represent only part of the functional variation influencing
 599 GPP, and residual errors, particularly in forest and transitional systems, are likely to reflect
 600 additional controls including phenology, rooting strategies, nutrient limitation, canopy
 601 structure and within-PFT trait variation. Future developments could consider greater
 602 functional differentiation within grass PFTs for example, whether annual and perennial
 603 grasses warrant greater functional distinction within JULES grass PFTs, as grass life-history
 604 strategies are associated with differences in leaf structural and physiological traits, while
 605 broad C3/C4 PFT classifications can obscure substantial functional diversity (Garnier &



606 Laurent, 1994; Griffith et al., 2020; Liu et al., 2019). Other avenues include
 607 parameterisations that allow key traits to vary with environmental conditions rather than
 608 relying solely on regional medians. The modest improvements demonstrated here suggest
 609 that incorporating regional trait evidence is a useful step towards improving African land-
 610 surface modelling, but larger gains are likely to require simultaneous advances in the
 611 representation of traits, water stress, phenology and other ecosystem processes.

612

613 5. Conclusion

614 This study demonstrates that African plant trait data can provide a useful basis for refining
 615 JULES vegetation parameterisation. African-derived estimates of LMA and Nmass differed
 616 from current JULES default values for several PFTs, highlighting the value of reassessing long-
 617 standing model parameterisations against contemporary and regionally representative
 618 evidence. Both traits also varied nonlinearly across African climate space defined by MAT,
 619 MAP and aridity, indicating that trait expression is structured by environmental conditions
 620 rather than uniform across the continent.

621 Replacing default Nmass and LMA values with African-derived PFT medians produced a
 622 modest overall improvement in simulated GPP across the African eddy covariance evaluation
 623 network, with the clearest gains reflected in reduced RMSE and mean bias error, particularly
 624 at grassland sites. However, contrasting responses among grassland, forest and transitional
 625 ecosystems show that updating PFT-level trait values alone cannot resolve all model
 626 deficiencies. The breadth of the flux-tower network was important in revealing this
 627 heterogeneity and reducing the risk of inferring broadly transferable improvements from a
 628 small environmentally narrow set of sites.

629 More broadly, the results indicate that some JULES GPP biases are sensitive to the
 630 vegetation trait parameterisation, while others reflect limitations in hydrology, phenology,
 631 and broader process representation. Further progress in African land-surface modelling will
 632 therefore require both continued expansion and improved coverage of African plant trait
 633 datasets and model developments that better represent within-PFT trait variation and other
 634 controls on vegetation function, including canopy development, rooting strategies, nutrient
 635 limitation, and disturbance regimes such as fire and herbivory. Regionally grounded trait



evidence, combined with broad and diverse model evaluation provides a practical pathway
for refining LSM parameterisation in Africa and other historically underrepresented regions.

638

639 **Author contributions**

Conceptualisation—E.F.A., A.M.C., K.W., A.H., P.H., and T.P.; funding — A.M.C. and T.P.;
supervision— A.M.C., K.W., A.H., P.H., and T.P.; data curation, and software—E.F.A.;
methodology— E.F.A., A.M.C., K.W., A.H., and P.H.; project administration, formal analysis,
and writing original draft—E.F.A.; visualisation — E.F.A. and A.M.C.; resources — A.M.C.;
data contribution — A.W., J.A., C.H., M.G., O.R., V.V., P.G.vZ., Y.N., M.A., T.T., J.D., M.S., S.J.V.R.;
investigation — all authors; writing review and editing— all authors; All authors contributed
to the final version of the paper.

647

648 **Code and data availability**

This study used JULES version 7.1. Data preparation, analysis code and the experiment-
specific Rose suite configurations are available at <https://doi.org/10.5281/zenodo.20528631>
(Akhabue & Cunliffe, 2026). The JULES model source code is available through the official
Met Office GitHub repository at <https://github.com/MetOffice/jules>, with accompanying
documentation available at <https://metoffice.github.io/jules>. The Google Earth Engine
repository for data preprocessing can be accessed by registered Earth Engine users at
https://code.earthengine.google.com/?accept_repo=users/akhasfaith/ClimateGradient_Trait_Variability_Extraction. ERA5-Land data are available at
<https://cds.climate.copernicus.eu/datasets/reanalysis-era5-land?tab=overview> (Muñoz
Sabater, 2019), TerraClimate data are available at http://developers.google.com/earth-engine/datasets/catalog/IDAHO_EPSCOR_TERRACLIMATE (Abatzoglou et al., 2018). While
we do not have permission to redistribute the flux datasets used in this study, data obtained
via FLUXNET and AMMA-CATCH remain available through their respective data portals
<https://fluxnet.org/data/fluxnet2015-dataset/> (Pastorello et al., 2020) and <http://bd.amma-catch.org/main.jsf> (AMMA-CATCH, 1990; Galle et al., 2018) (subject to registration and their
access conditions). For flux datasets provided directly by site data owners, we are happy to
facilitate discussions between prospective users and the relevant data owners. The TRY
dataset for plant traits can be accessed through the TRY data portal <http://www.try-db.org>.



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669 accordance with the University of Exeter's Rights Retention policy.

670

671 **Competing interests**

672 The authors declare that they have no conflict of interest.

673

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