



1 **Spatial mapping of key plant functional traits in terrestrial**
2 **ecosystems across China**

3 Nannan An^{1,2,3}, Nan Lu^{2,3}, Weiliang Chen², Yongzhe Chen^{2,4}, Hao Shi^{2,3}, Fuzhong
4 Wu¹, Bojie Fu^{2,3}

5
6
7 ¹Key Laboratory for Humid Subtropical Eco-Geographical Processes of the Ministry of Education,
8 School of Geographical Sciences, Fujian Normal University, Fuzhou 350117, PR China

9 ²State Key Laboratory of Urban and Regional Ecology, Research Center for Eco-Environmental
10 Sciences, Chinese Academy of Sciences (CAS), Beijing 100085, PR China

11 ³University of Chinese Academy of Sciences, Beijing 101408, PR China

12 ⁴State Key Laboratory of Hydrosience and Engineering, Department of Hydraulic Engineering,
13 Tsinghua University, Beijing 100084, PR China

14
15 *Correspondence to:* Nan Lu (nanlv@rcees.ac.cn)



16 **Abstract**

17 Trait-based approaches are of increasing concern in predicting vegetation changes and linking
18 ecosystem structure to functions at large scales. However, a critical challenge for such approaches
19 is acquiring spatially continuous plant functional trait distribution. Here, eight key plant functional
20 traits were selected to represent two-dimensional spectrum of plant form and function, including
21 leaf area (LA), leaf dry matter content (LDMC), leaf N concentration (LNC), leaf P concentration
22 (LPC), plant height, seed mass (SM), specific leaf area (SLA) and wood density (WD). A total of
23 52477 trait measurements of 4291 seed plant species were collected from 1541 sampling sites in
24 China and were used to generate a spatial plant functional trait dataset (1 km), together with
25 environmental variables and vegetation indices based on two machine learning models (random
26 forest and boosted regression trees). The two models showed a good accuracy in estimating WD,
27 LPC and SLA, with average R^2 values ranging from 0.45 to 0.66. In contrast, both the two models
28 had a weak performance in estimating SM and LDMC, with average R^2 values below 0.25.
29 Meanwhile, LA, SM and plant height showed considerable differences between two models in some
30 regions. To obtain the optimal estimates, a weighted average algorithm was further applied to merge
31 the predictions of the two models to derive the final spatial plant functional trait dataset. The optimal
32 estimates showed that climatic effects were more important than those of edaphic factors in
33 predicting the spatial distribution of plant functional traits. Estimates of plant functional traits in
34 northeast China and the Qinghai-Tibet Plateau had relatively high uncertainties due to sparse
35 samplings, implying a need of more observations in these regions in future. Our trait dataset could
36 provide critical support for trait-based vegetation models and allows exploration into the
37 relationships between vegetation characteristics and ecosystem functions at large scales. The eight
38 plant functional traits datasets for China with 1 km spatial resolution are now available at
39 <https://figshare.com/s/c527c12d310cb8156ed2> (An et al., 2023).



40 **1 Introduction**

41 Climate change has been affecting vegetation distributions and biogeochemical cycling globally and
42 altering their feedbacks to the climate system (Kirilenko et al., 2000; Finzi et al., 2011; Jónsdóttir et
43 al., 2022). Dynamic global vegetation models (DGVMs) are powerful tools for predicting changes
44 in vegetation and ecosystem-atmosphere exchanges (e.g., water, carbon, and nutrient cycling) in a
45 changing climate (Foley et al., 1996; Peng, 2000). However, conventional DGVMs are still
46 insufficient realistic, largely due to their dependence on the plant functional types (PFTs) assumption
47 (Sitch et al., 2008; Yurova and Volodin, 2011; Scheiter et al., 2013). PFTs in conventional DGVMs
48 commonly have fixed attributes (mostly trait values) (Van Bodegom et al., 2012; Wullschlegler et
49 al., 2014) that do not reflect plant adaptation to environments, limiting the quantification of carbon-
50 water-nutrient feedback between terrestrial ecosystems and the atmosphere (Zaehle and Friend,
51 2010; Liu and Yin, 2013). Trait-based approaches can provide robust theoretical basis for developing
52 the next generation of DGVMs (Van Bodegom et al., 2012; Sakschewski et al., 2015; Matheny et
53 al., 2017). Plant functional traits, which are closely associated with ecosystem functions (Diaz et al.,
54 2004; Yan et al., 2023), can effectively reflect response and adaptation of plants to environmental
55 conditions (Myers-Smith et al., 2019; Qiao et al., 2023).

56 Attempts to predict spatially continuous trait data have been conducted at regional to global
57 scales (Madani et al., 2018; Moreno-Martínez et al., 2018; Boonman et al., 2020; Loozen et al.,
58 2020). Webb et al. (2010) proposed that the environment creates a filtered trait distribution along an
59 environmental gradient, and such trait-environment relationships offer fundamental supports to
60 predict the spatial distribution of plant functional traits through extrapolating local trait
61 measurements. Boonman et al. (2020) mapped the global patterns of specific leaf area (SLA), leaf
62 N concentration (LNC), wood density (WD) and plant height based on a set of climate and soil
63 variables. As the number of available global trait databases increase (Kattge et al., 2011; Wang et
64 al., 2018), trait-environment relationships are becoming increasingly quantitative and accurate
65 (Bruelheide et al., 2018; Myers-Smith et al., 2019). Alternatively, remote sensing approaches, such
66 as empirical methods and physical radiative transfer models (e.g., partial least squares regression,
67 PROPECT model), have been developed to estimate plant physiological, morphological, and
68 chemical traits (e.g., leaf chlorophyll content, SLA, LNC and leaf dry matter content (LDMC))
69 (Darvishzadeh et al., 2008; Romero et al., 2012; Ali et al., 2016). Vegetation indices, such as the
70 normalized difference vegetation index (NDVI) and the enhanced vegetation index (EVI), have been
71 successful in estimating plant functional traits of crops, grasslands and forests (Clevers and Gitelson,
72 2013; Li et al., 2018; Loozen et al., 2018). Loozen et al. (2020) demonstrated that EVI was the most
73 important predictor for mapping the spatial pattern of canopy nitrogen in European forests.
74 Admittedly, recent studies have suggested that combining environmental variables and vegetation
75 indices can improve the predictive accuracy of canopy N compared to those based on vegetation
76 indices alone (Loozen et al., 2020).



77 Although there have been reports on plant functional trait distribution in China in some global
78 or regional research (Yang et al., 2016; Butler et al., 2017; Madani et al., 2018; Moreno-Martínez et
79 al., 2018; Boonman et al., 2020), they are still of large uncertainties in characterizing the spatial
80 distribution of plant functional traits in China. First, global studies generally have relatively few,
81 unevenly distributed sampling sites in China (Butler et al., 2017; Madani et al., 2018; Boonman et
82 al., 2020), impeding our understanding of the true spatial characteristics of trait variability. Second,
83 these studies are usually inconsistent. For example, Moreno-Martínez et al. (2018) and Madani et
84 al. (2018) demonstrated that SLA values were low in the southeast areas but high in the southwest
85 areas of China, whereas Boonman et al. (2020) found the opposite. Third, most studies mainly
86 focused on leaf traits (Yang et al., 2016; Loozen et al., 2018; Moreno-Martínez et al., 2018), whereas
87 traits associated with the whole-plant and reproductive strategies, such as WD and seed mass (SM),
88 were ignored. Therefore, mapping and verifying the spatial patterns of key functional traits that
89 reflect the whole plant economics spectrum in China is a top priority.

90 In this study, our main objective was to generate a spatial dataset for several key plant
91 functional traits, through combining field measurements, environmental variables and vegetation
92 indices. To achieve this goal, we used a processing routine to predict the spatial distribution of plant
93 functional traits. First, eight plant functional traits (i.e., SLA, LDMC, LNC, LPC, LA, plant height,
94 WD and SM) were selected because they reflect plant adaptation to environment constraints and
95 trade-offs between plant form and function (Reich and Cornelissen, 2014; Diaz et al., 2016). Second,
96 we used random forest and boosted regression trees to predict the spatial patterns of plant functional
97 traits by training the relationships between plant functional traits and environmental variables and
98 vegetation indices. To obtain the optimal estimates, an ensemble model (i.e., weighted average
99 algorithm) was further applied to merge the predictions of the two models. Finally, plant species
100 were aggregated to PFTs, and the spatial abundance of PFTs at 1 km resolution was calculated using
101 land cover map (100 m). We derived the spatial trait datasets via calculating community-weighted
102 trait values within grid cells (1 km) based on these abundances of each PFT and predicted trait
103 values.

104 **2 Materials and Methods**

105 **2.1 Plant functional trait collection and data processing**

106 Westoby (1998) proposed the ‘leaf-height-seed’ (LHS) strategy scheme that describes three
107 functionally different strategy axes in relation to SLA, plant height and SM, which are also included
108 in our study. As key leaf economics traits, LNC, LPC and LDMC were selected because they are
109 closely linked to plant growth rate, resource acquisition, and ecosystem function (Wright et al.,
110 2004). LA is indicative of the trade-off between carbon assimilation and water-use efficiency
111 (Wright et al., 2017), and WD reflects the trade-off between growth rate and support cost, with a
112 higher WD linked to a lower growth rate but a higher biomass support cost (King et al., 2006). The



113 information on the eight plant functional traits and their ecological meanings are described in Table
114 1.

115 Plant trait data was obtained and collected via two main sources. The first source was public
116 trait databases, including the TRY database (Kattge et al., 2020) and the China Plant Trait Database
117 (Wang et al., 2018). The second source was from literature (listed in Appendix A). To ensure data
118 quality and comparability, we only included trait observations that met the following five criteria:
119 1) Measurements must be obtained from natural terrestrial fields in order to minimize the influences
120 of management disturbance, and observations from cropland, aquatic habitat, control experiments
121 or gardens were excluded; 2) According to the mass ratio hypothesis, the effect of plant species on
122 ecosystem functioning is determined to an overwhelming extent by the traits and functional diversity
123 of the dominant species and is relatively insensitive to the richness of subordinate species (Grime,
124 1998). Thus, we only included studies that measured plant trait observations from all species or
125 dominant species within a community; 3) In order to account for the trait variation within and
126 between communities, we only considered real measurements of traits from individual plants, and
127 not species-level averages (Jung et al., 2010; Siefert et al., 2015); 4) Plant trait observations must
128 be made on mature and healthy plant individuals, so some specific growth stages (e.g., seedling)
129 and size classes (e.g., sapling) were excluded to reduce the confounding effect of ontogeny (Thomas,
130 2010); 5) We only included studies with clear geographical coordinates to ensure alignment with
131 predictor variables. The sampling location and sample time information from the original studies
132 were also included in the dataset.

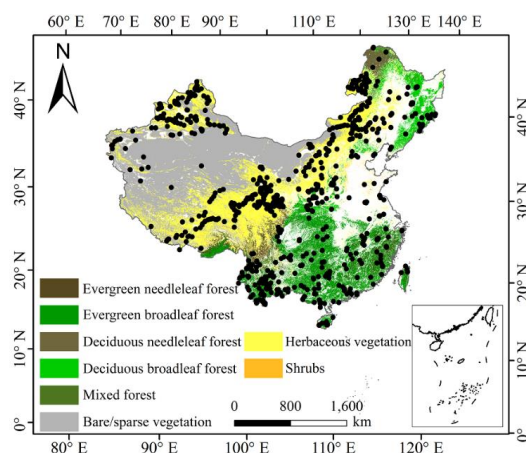
133 Plant functional traits must be sampled and measured according to standardized measurement
134 procedures (Perez-Harguindeguy et al., 2013) to reduce the variation and uncertainty among
135 different data sources. In this study, we included SLA measurements on both sun-leaves and shade-
136 leaves, WD measurements on both heartwood and sapwood of tree species, SM measurements on
137 both seeds and fruits, and plant height measurements on both vegetative and generative organs.



138 **Table 1** Description of plant functional traits selected in this study and their relevant ecosystem
 139 functions.

Trait	Abbreviation	Description	Relevant ecosystem functions
Specific leaf area	SLA	As a core leaf economics trait (Wright et al., 2004), it is related to trade-off between leaf lifespan and C acquisition as well as light competition (Reich et al., 1991)	Productivity, litter decomposition, competitive ability (Bakker et al., 2011; Smart et al., 2017)
Leaf dry matter content	LDMC	Strongly related to resource availability and potential growth rate (Hodgson et al., 2011)	Productivity, litter decomposition, herbivore resistance, and drought tolerance (Bakker et al., 2011; Smart et al., 2017; Blumenthal et al., 2020)
Leaf N concentration	LNC	As a core leaf economics trait, it is strongly related to photosynthetic capacity (Wright et al., 2004)	Productivity, nutrient cycling, litter decomposition (LeBauer and Treseder, 2008; Bakker et al., 2011)
Leaf P concentration	LPC	As a core leaf economics trait, it is strongly related to photosynthetic capacity (Wright et al., 2004)	Productivity, nutrient cycling, litter decomposition (LeBauer and Treseder, 2008; Bakker et al., 2011)
Leaf area	LA	Trade-off between C assimilation and water use efficiency, it is related to energy balance (Wright et al., 2017)	Productivity (Li et al., 2020)
Plant height	/	A major determinant of a plant's ability to compete for light (Moles et al., 2009)	C storage, animal diversity (Conti et al., 2013; Roll et al., 2015)
Wood density	WD	A measure of carbon investment, representing the trade-off between growth and mechanical support (Martínez-Vilalta et al., 2010)	Drought tolerance, productivity (Hoeber et al., 2014; Liang et al., 2021)
Seed mass	SM	Closely related to seed dispersal and seed predation, as well as seedling establishment, growth, and survival (Leishman et al., 2000)	Competitive ability (Zepeda and Martorell, 2019)

140 The plant trait data was checked for possible errors and corrected as per three steps as follows.
 141 First, species name and taxonomic nomenclature were corrected and standardized according to the
 142 Plant List (<http://www.theplantlist.org/>) using the “plantlist” package. Second, illogical values,
 143 repeated values and outliers were removed, which were defined by observations exceeding 1.5
 144 standard deviations of the mean trait value for a given species (Kattge et al., 2011). Third, we
 145 appended information on plant growth form (tree, shrub, and herb), leaf type (broadleaved and
 146 needle-leaved) and leaf phenology (evergreen and deciduous) from the TRY categorical traits
 147 database (<https://www.try-db.org/TRYWeb/Data.php#3>) and *Flora Reipublicae Popularis Sinicae*
 148 (<http://www.iplant.cn/frps>). After these treatments, we collected a total of 52477 trait measurements
 149 from 1541 sampling sites for our database, representing 4291 species from 212 families and 1230
 150 genera (Fig. 1). Information on the statistics for the eight plant functional traits collected in this
 151 study is shown in Table B1 in Appendix B.



152
153

Figure 1. Location distribution and land cover map in China.

154 2.2 Environmental data

155 2.2.1 Climate data

156 Twenty-one climate variables were used in this study, including 19 bioclimate variables, solar
157 radiation (RAD), and AI (Table B2 in Appendix B). The 19 bioclimate variables and RAD were
158 obtained from the WorldClim dataset (version 2.1) for the period from 1970 to 2000
159 (<https://www.worldclim.org/data/worldclim21.html>). The AI data was extracted from the CGIAR
160 Consortium of Spatial Information (CGIAR-CSI) website for the period from 1950 to 2000
161 (<http://www.csi.cgiar.org>) (Trabucco and Zomer, 2018). The spatial resolution of climate data was
162 1 km.

163 2.2.2 Soil data

164 Twelve soil variables were included in this study, representing the different aspects of soil properties,
165 i.e. soil texture, bulk density (BD), pH, and soil nutrients (Table B2 in Appendix B). All soil
166 variables were extracted from the Soil Database of China for Land Surface Modeling
167 (<http://globalchange.bnu.edu.cn/research/soil2>) (Shangguan et al., 2013). Given the importance of
168 topsoil properties on community composition (Bohner, 2005), the soil data was averaged to
169 represent the top 30 cm of soil in our study. The spatial resolution was 1 km.

170 2.2.3 Topography

171 The topographic variable was elevation. Elevation data was extracted from the STRM 90m dataset
172 in China, based on the SRTM V4.1 database (<https://www.resdc.cn/data.aspx?DATAID=123>). The
173 spatial resolution was 1 km.

174 Given the collinearity among climate and soil variables, we reduced the number of
175 environmental predictors based on Pearson's correlation coefficient (r) (Figs. B1 and B2 in
176 Appendix B). Among a set of highly correlated variables ($r > 0.75$), only one variable was retained
177 in subsequent analysis to ensure a combination of different environmental variables. The final
178 selection of environment predictors included nineteen variables: mean annual temperature (MAT),



179 mean diurnal range (MDR), min temperature of coldest quarter (Tmin), max temperature of coldest
180 quarter (Tmax), temperature seasonality (TS), mean annual precipitation (MAP), precipitation
181 seasonality (PS), precipitation of wettest quarter (PEQ), precipitation of driest quarter (PDQ), AI,
182 RAD, elevation, soil sand content (SAND), pH, BD, soil total N (STN), soil total P (STP), soil
183 alkali-hydrolysable N (SAN), and cation exchange capacity (CEC).

184 **2.3 Vegetation indices**

185 Three categories of vegetation indices were included in this study (Table B2 in Appendix B). The
186 first selected was EVI, which was extracted from the MOD13A3 V006 product
187 (<https://lpdaac.usgs.gov/products/mod13a3v006/>). This product is available as a monthly average
188 with spatial resolution of 1 km, ranging from January 2000 to December 2018. Second, MODIS
189 reflectance data was also extracted from the MOD13A3 V006 product. This included MIR
190 reflectance, NIR reflectance, red reflectance, and blue reflectance. Third, the MERIS terrestrial
191 chlorophyll index (MTCI) was extracted from the Natural Environment Research Council Earth
192 Observation Data Centre (NERC-NEODC, 2005) (<https://data.ceda.ac.uk/>). MTCI data is available
193 globally as a monthly average at 4.63 km spatial resolution, and ranges from June 2002 to December
194 2011. It is noted that valid MTCI values should be greater than 1, so our study deleted any values
195 less than 1.

196 To avoid collinearity, we also reduced the number of vegetation indices based on Pearson's
197 correlation coefficient (r) (Figs. B3 in Appendix B). Furthermore, given that most plant functional
198 traits were measured during the growing season, the variables related to the growing season were
199 determined to be important predictors. The final selection included 36 variables: annual EVI, EVI
200 (May, June, July, August and September), MTCI, MIR, NIR, red and blue (all for January, June,
201 July, August and September).

202 Both environmental variables and vegetation indices variables were resampled to a consistent
203 spatial resolution of 1 km using the nearest neighborhood method.

204 PFT is also an important factor in influencing the variation of plant functional traits (Verheijen
205 et al., 2016; Loozen et al., 2020), thus PFT was included as a predictor in this analysis. We used the
206 2015 land cover map at a 100 m spatial resolution from the Copernicus Global Land Service (CGLS-
207 LC100, Version 3) (<https://land.copernicus.eu/global/products/lc>) (Buchhorn et al., 2020). We
208 focused on natural terrestrial vegetation, so all artificial or crop areas were thus eliminated in our
209 dataset. Seven categories were included: evergreen needleleaf forest (ENF), evergreen broadleaf
210 forest (EBF), deciduous needleleaf forest (DNF), deciduous broadleaf forest (DBF), shrubland
211 (SHL), grassland (GRL) and bare/sparse vegetation. Furthermore, in order to match species names
212 to PFTs, we associated each species (i.e., plant growth form, leaf type and leaf phenology) with a
213 corresponding PFT. For example, the information on *Salix matsudana* is: tree, deciduous and
214 broadleaf, thus, we were able to associate the PFT of deciduous broadleaf forest (DBF) to this
215 species. The species that did not correspond to any PFT were discarded.



216 2.4 Model fitting and validation

217 To predict spatial patterns of plant functional traits, we used two machine learning models, i.e.,
218 random forest and boosted regression trees.

219 Random forest is an ensemble machine learning method based on classification and regression
220 trees using collections of regression trees to classify observations according to a set of predictive
221 variables (Breiman, 2001). This method repeatedly constructs a set of trees from random samples
222 of training data, and the final prediction is produced by integrating the results of all individual trees,
223 which makes it a robust method. The models are controlled by two main parameters: the number of
224 sampled variables (*mtry*) and the number of trees (*ntree*). The parameter *mtry* was set to range from
225 1 to 57 (at an interval of 1), and the *ntree* was set as 500, 1000, 2000, 5000 and 10000 in subsequent
226 runs. This analysis was performed using the ‘randomForest’ function in the ‘randomForest’ package
227 (Liaw and Wiener, 2002).

228 Boosted regression trees is a machine learning method based on generalized boosted regression
229 models, and using a boosting algorithm to combine many sample tree models to optimize predictive
230 performance (Elith et al., 2006). There is no need for prior data transformation or the elimination of
231 outliers, and this method can fit complex non-linear relationships while automatically handling
232 interaction effects between predictors (Elith et al., 2008). The four parameters to optimize in these
233 models are the number of trees, interaction depth, learning rate and bag fractions. We varied the
234 parameter settings to find the optimal parameter combination that achieves minimum predictive
235 error. The number of trees was set to 3000, the interaction depth varied from 1 to 7 (at an interval
236 of 1), the learning rate was set to 0.001, 0.01, 0.05 and 0.1, and the bag fraction was set to 0.5, 0.6,
237 0.7 and 0.75. PFT was used as a dummy variable in the boosted regression trees models. This
238 analysis was conducted using the ‘gbm’ function in the ‘gbm’ package (Ridgeway, 2006).

239 We used a 10-fold cross validation to select the optimal parameter combination and to evaluate
240 the final model performance for each trait. We split the data into two parts: 80% of the trait data was
241 used to train the models, and the remaining 20% was used to assess model’s performance. The fitting
242 performances of the random forest and boosted regression trees methods were evaluated using
243 determinate coefficient (R^2), root-mean-square error (RMSE), and mean absolute error (MAE).
244 These scores are calculated following Eq. (1), Eq. (2) and Eq. (3):

$$245 \quad R^2 = 1 - \frac{\sum_{i=1}^n (p_i - o_i)^2}{\sum_{i=1}^n (p_i - \hat{o}_i)^2} \quad (1)$$

$$246 \quad RMSE = \sqrt{\frac{1}{n} \sum_{i=1}^n (p_i - o_i)^2} \quad (2)$$

$$247 \quad MAE = \frac{1}{n} \sum_{i=1}^n |o_i - p_i| \quad (3)$$

248 where p_i and o_i are the predictive values and observed values, respectively, \hat{o}_i is the mean of
249 the observed values.

250 To quantify the relative importance of each predictor consistently across the two models, we



251 used the method proposed by Thuiller et al. (2009). The correlations between fitted values and
252 predictions were calculated using permuted values for the predictor of concern. This step was
253 repeated a user-defined number of times for each predictor, and the mean correlation coefficient
254 over runs was recorded. Then the relative importance of each predictor was quantified as one minus
255 the Spearman rank correlation coefficient (see Boonman et al. 2020). In addition, we used
256 generalized additive models to fit the relationships between plant functional traits and the most
257 important variables using the ‘gam’ function in the ‘mgcv’ package.

258 **2.5 Generation of plant functional trait maps and model performance**

259 To calculate community weighted mean trait values, the abundance of individual PFT within 1 km
260 grid cell was estimated using a land cover map with a spatial resolution of 100 m. The final
261 community weighted mean trait values were calculated according to the predicted trait values and
262 corresponding abundance of each PFT. To obtain the optimal estimates, the ensemble model was
263 further applied to merge the predictions of random forest and boosted regression trees according to
264 their cross-validated R^2 values. The accuracy of the ensemble model was calculated by regressing
265 the 20% of cross-validation data used for testing against the observed trait values.

266 To evaluate the model performance (i.e. the variability in the prediction across models), the
267 coefficient of variation (CV) was calculated as the difference between the predictions of random
268 forest and boosted regression trees methods and the ensemble prediction weighted by the predictive
269 performance of each of the models. CV is calculated following Eq. (4):

$$270 \quad CV_t = \frac{\sqrt{\frac{\sum_{m=1}^M (pred_{m,t} - obs_t)^2 + r_{m,t}^2}{\sum_{m=1}^M r_{m,t}^2}}}{obs_t} \quad (4)$$

271 where $pred_{m,t}$ is the predictive values of t trait in m model, obs_t is the values of t trait in the
272 ensemble model, $r_{m,t}^2$ is the cross-validated R^2 of t trait in m model.

273 **2.6 Uncertainty assessments**

274 Multivariate environmental similarity surface analysis (MESS) was used to identify the range of the
275 extrapolated predictor values across the locations in the plant trait dataset (Elith et al., 2010). This
276 method is often used to evaluate the extent of extrapolation and the applicability domain. If the
277 values are negative, this indicates that at a given grid cell, at least one predictor variable is outside
278 the extent of referenced predictor layer. This analysis was conducted using the ‘mess’ function in
279 the ‘dismo’ package.

280 All analyses were performed in R 4.0.2 (R Core Team, 2020).

281 **3 Results**

282 **3.1 Performances of prediction models**

283 Cross-validation showed that the performance of the predictive models differed greatly among the plant



284 functional traits (Table 2). WD had the best performance in all three models, with R^2 values of 0.64, 0.68
285 and 0.67 for random forest, boosted regression trees and ensemble model, respectively. LPC, height and
286 SLA had R^2 values greater than 0.45, while SM and LDMC performed the worst, with R^2 values
287 below 0.25. In addition, the ensemble model performed better than the random forest and boosted
288 regression trees alone (Tables C1 and C2 in Appendix C).

289 **Table 2** Results of plant functional traits for cross-validated R^2 , RMSE and MAE for random
290 forest, boosted regression trees, and ensemble model.

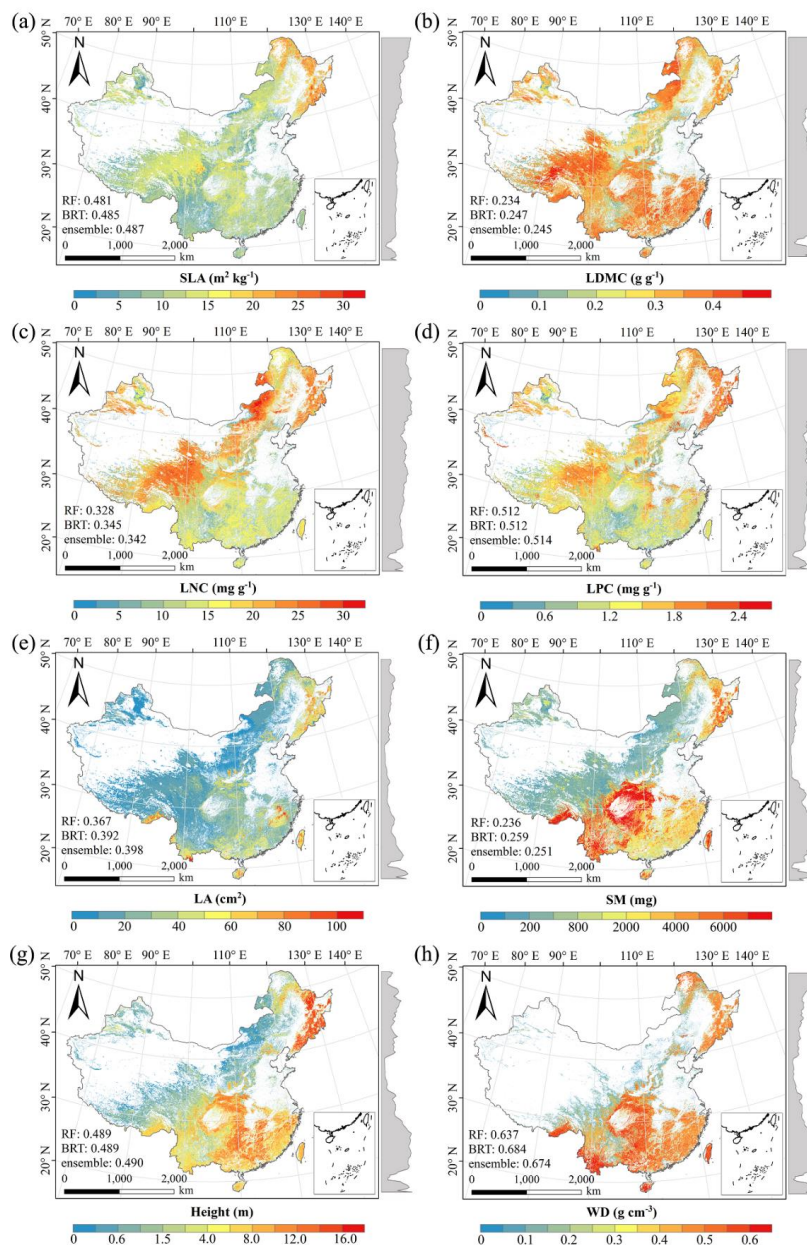
Traits	Random forest			Boosted regression trees			Ensemble model		
	R^2	RMSE	MAE	R^2	RMSE	MAE	R^2	RMSE	MAE
SLA	0.48	7.02	5.10	0.48	6.99	5.08	0.49	6.98	5.07
LDMC	0.23	0.10	0.07	0.28	0.09	0.07	0.24	0.09	0.07
LNC	0.33	6.64	4.92	0.34	6.52	4.85	0.34	6.54	4.85
LPC	0.51	0.80	0.53	0.51	0.80	0.53	0.51	0.80	0.53
LA	0.37	68.94	26.76	0.39	67.69	27.47	0.40	67.28	26.59
SM	0.24	4547.22	1228.07	0.26	4478.88	1183.61	0.25	4499.67	1201.83
Height	0.49	2.89	2.09	0.49	2.89	2.10	0.49	2.89	2.10
WD	0.64	0.13	0.10	0.68	0.12	0.10	0.67	0.13	0.10

291 SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf N concentration; LPC, leaf P
292 concentration; LA, leaf area; WD, wood density; SM, seed mass.

293 3.2 Spatial patterns of predicted plant functional traits

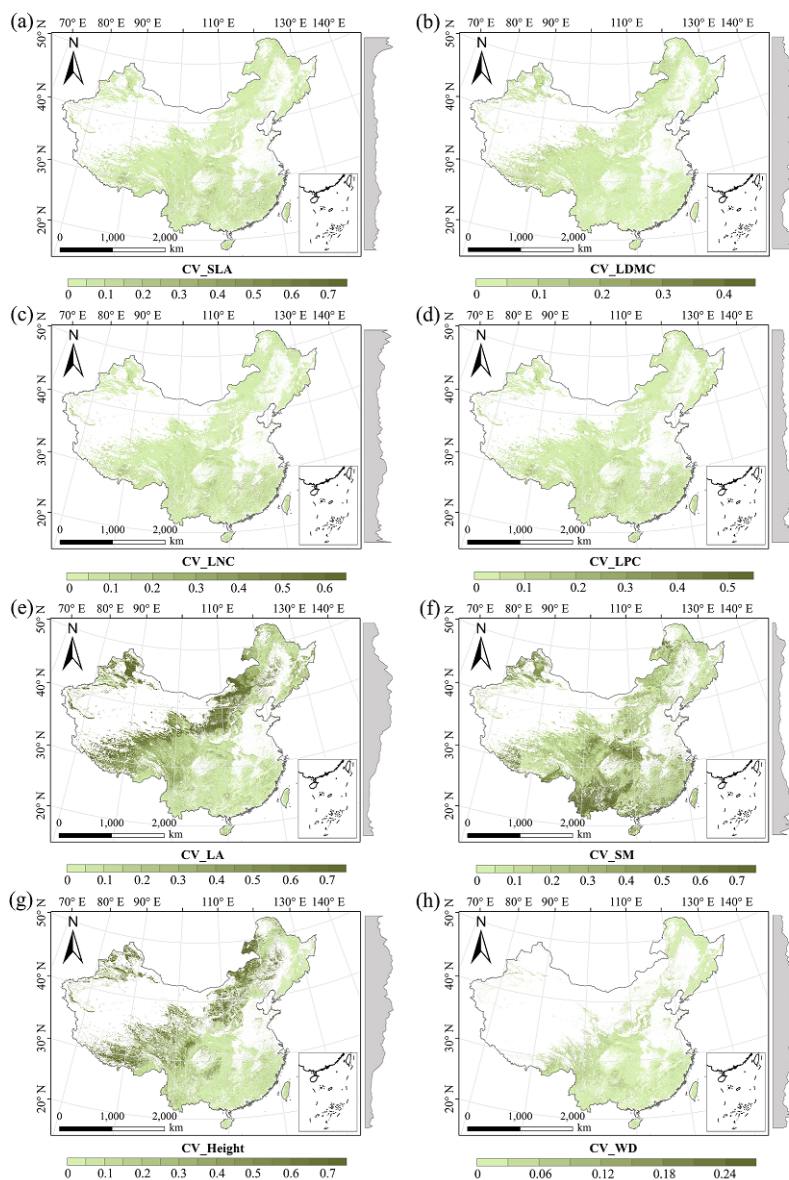
294 There were relatively consistent spatial patterns for SLA, LNC and LPC, with high values in the
295 northeastern and northwestern regions and the southeastern Qinghai-Tibet Plateau, and low values
296 in southwestern China (Figs. 2a, 2c and 2d, Figs. D1, D2 in Appendix D). SLA and LPC increased
297 with latitude, while LNC did not vary significantly along the latitudinal gradient. For SLA, LNC
298 and LPC, the variability was low among the random forest, boosted regression trees and ensemble
299 model, with an overall CV less than 0.3 (Figs. 3a, 3c, and 3d). LDMC values were relatively high
300 in most regions of China, and the low values were mainly located in eastern Yunnan and the Loess
301 Plateau (Fig. 2b, Figs. D1, D2 in Appendix D). LA and SM showed consistent spatial patterns, with
302 high values in the northeastern and southern regions (except for the Sichuan Basin), and the
303 southeastern Qinghai-Tibet Plateau (Figs. 2e and 2f, Figs. D1, D2 in Appendix D). The strong
304 latitudinal gradients were observed in LA and SM, where values decreased with latitude.

305 The CV values of LPC and SM decreased with latitude, but other traits did not show latitudinal
306 patterns (Figs. 3). The CV values were relatively high, especially in the northwestern region, the
307 Inner Mongolia Plateau-Loess Plateau region (only for LA) and Yunnan province (only for SM)
308 (Figs. 3e and 3f). Plant height and WD had consistent spatial patterns, with high values in the
309 northeastern and southern regions (Figs. 2g and 2h, Figs. D1, D2 in Appendix D). The CV values
310 across models for plant height were higher in northwestern China and Inner Mongolia Plateau-Loess
311 Plateau region, while CV values for WD in China were low throughout China (Figs. 3g and 3h).



312
 313 **Figure 2.** Spatial patterns of predicted plant functional traits in China based on the ensemble
 314 model. The grey curves to the right of the maps display trait distribution along with latitude. RF,
 315 random forest; BRT, boosted regression trees; ensemble, ensemble model; SLA, specific leaf area;
 316 LDMC, leaf dry matter content; LNC, leaf N concertation; LPC, leaf P concertation; LA, leaf area;
 317 WD, wood density; SM, seed mass.

318



319
320 **Figure 3.** The variability in plant functional trait predictions among random forest, boosted
321 regression trees and ensemble model. The grey curves to the right of the maps display coefficient of
322 variation along with latitude. SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf N
323 concentration; LPC, leaf P concentration; LA, leaf area; WD, wood density; SM, seed mass.

324 3.3 Relative importance of predictive variables

325 The dominant factors explaining spatial variation differed greatly among the eight plant functional



326 traits (Table 3). Overall, climate variables were more important for predicting plant functional traits
 327 than were soil variables. Temperature variables (i.e., MAT, MDR and TS) showed close
 328 relationships with SLA, LDMC, LPC and WD, while precipitation variables (i.e., PS, PEQ, MAP
 329 and PDQ) were more important for predicting the spatial patterns of LNC, LPC, LA and plant height.
 330 RAD was the fourth most dominant factor in predicting the spatial patterns of SLA, SM, WD and
 331 plant height. Elevation also play an important role in the LDMC and LPC predictions. Within soil
 332 variables, soil nutrients [i.e., pH and soil available P (SAP)] showed close associations with SLA,
 333 LNC and SM. In addition to the environmental variables, MTCI emerged as an important predictor
 334 for explaining SLA, LDMC, LA and plant height. Finally, EVI was the most important predictor for
 335 LA and SM, and MIR in January and May were the primary predictors of WD. The relationships
 336 between plant functional traits and the most important variables were shown in Figs. E1 and E2 in
 337 Appendix E.

338 **Table 3** List of the eight most important variables for plant functional trait predictions.

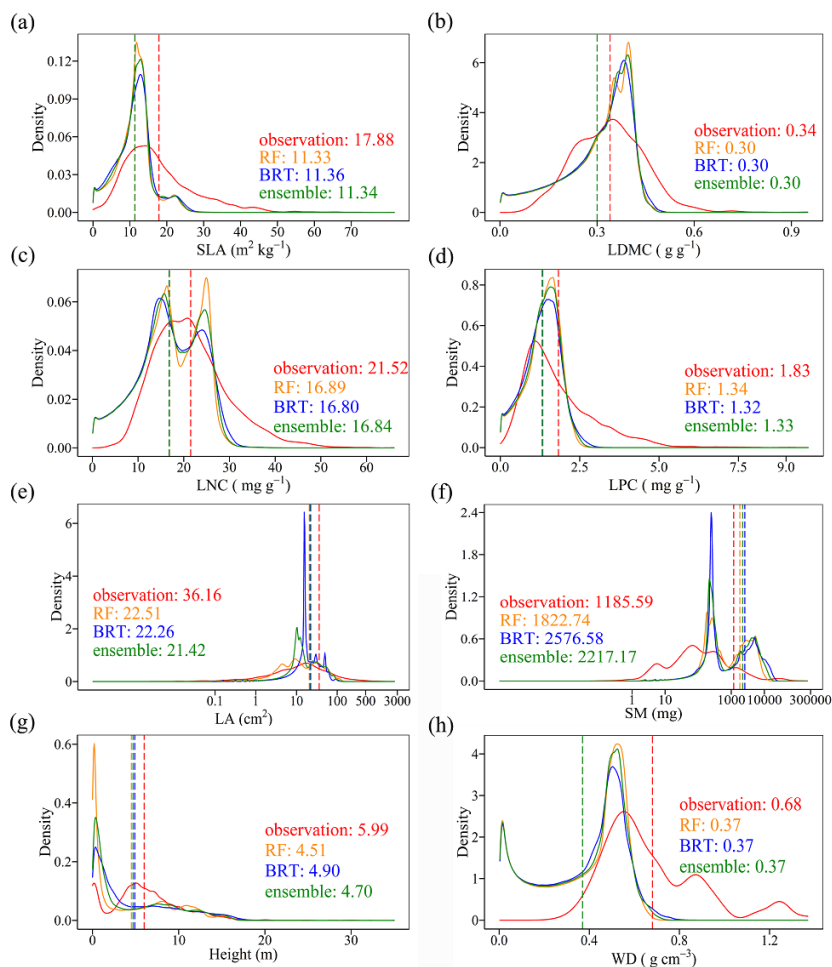
Rank	SLA	LDMC	LNC	LPC	LA	SM	Height	WD
1	SAP	MAT	PS	MDR	EVI5	EVI8	PEQ	MIR1
2	TS	Elevation	SAP	PDQ	PEQ	SAP	EVI6	TS
3	blue9	MTCI5	pH	Elevation	MTCI9	MAT	MTCI6	MIR5
4	RAD	blue8	MDR	MIR8	NIR9	RAD	RAD	RAD
5	MTCI4	MTCI4	MAP	Tmax	AI	NIR1	pH	MIR6
6	MTCI6	MTCI6	PEQ	MTCI6	MTCI6	NIR8	MAP	pH
7	Elevation	NIR1	MIR1	MIR7	MAP	SAND	red9	red5
8	MTCI7	CEC	Tmax	MIR9	red5	BD	red5	PS

339 SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf N concertation; LPC, leaf
 340 P concertation; LA, leaf area; WD, wood density; SM, seed mass; SAP, soil available P; TS,
 341 temperature seasonality; blue, blue reflectance; RAD, solar radiation; MTCI, MERIS terrestrial
 342 chlorophyll index; MAT, mean annual temperature; NIR, near-infrared reflectance; CEC, cation
 343 exchange capacity; PS, precipitation seasonality; MDR, mean diurnal range; MAP, mean annual
 344 precipitation; PEQ, precipitation of wettest quarter of a year; MIR, middle infrared reflectance;
 345 Tmax, max temperature of warmest month of a year; PDQ, precipitation of driest quarter of a year;
 346 EVI, enhanced vegetation index; AI, aridity index; red, red reflectance; SAND, soil sand content;
 347 BD, bulk density.

348 3.4 Model performance

349 The distributions of the predictive trait values based on random forest, boosted regression trees, and
 350 ensemble model were consistent with the original trait observations, especially the peak values (Fig.
 351 4). Except for SM, the mean values of trait observations were relatively higher than those of the
 352 predictive values.

353



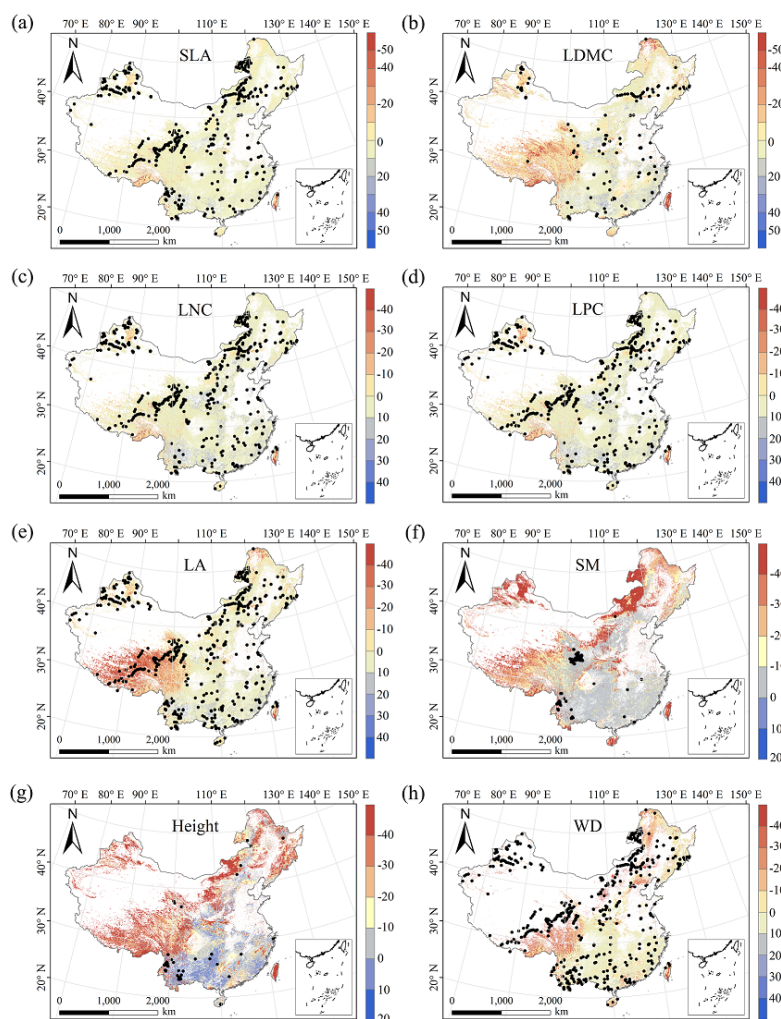
354
 355 **Figure 4.** Comparison of trait distribution between observations and predictive values in each
 356 of the different models. Each panel depicts the distribution of observations in solid red, of the
 357 random forest (RF) model in yellow, of the boosted regression trees (BRT) model in blue, and of
 358 the ensemble model in green. The dashed vertical lines indicate mean values. SLA, specific leaf
 359 area; LDMC, leaf dry matter content; LNC, leaf N concentration; LPC, leaf P concentration; LA, leaf
 360 area; WD, wood density; SM, seed mass.

361 3.5 Uncertainty assessments

362 The MESS values of five leaf traits and WD were positive in most regions, indicating a wide
 363 applicability domain of our models (Fig. 5). Nevertheless, trait predictions should be interpreted
 364 carefully for northeastern China and the Qinghai-Tibet Plateau due to the sparse samplings in these
 365 regions. In addition, spatial predictions for SM and plant height were extrapolated to a larger extent
 366 than were the other plant functional traits.



367



368

369 **Figure 5.** Multivariate environmental similarity surface (MESS) assessments for the eight
370 plant functional traits. The black dots represented the locations of trait observations. More intense
371 shades indicate greater similarity (blue) or difference (red) in environmental conditions of the
372 location compared to the predictive factors covered by the training dataset. SLA, specific leaf area;
373 LDMC, leaf dry matter content; LNC, leaf N concertation; LPC, leaf P concertation; LA, leaf area; WD,
374 wood density; SM, seed mass.

375 4 Discussion

376 4.1 Comparison with previous work

377 Our study predicted the spatial patterns of eight key plant functional traits across China using



378 machine learning methods and identified the applicability domain of the models. WD had the
379 highest precision with an R^2 of 0.66, which was higher than the global WD prediction (Boonman et
380 al., 2020). This improvement in precision may be attributed to the large number and dense
381 occurrence of sample sites as well as the inclusion of vegetation indices in our study. In addition,
382 SLA and LPC showed good accuracy with R^2 values of 0.50, which was higher than that of
383 Boonman et al. (2020) and consistent with that of Martínez et al. (2018). Our study also predicted
384 the spatial pattern of SM with an R^2 of 0.24, which was lower than in the global study of Madani et
385 al. (2018) in which environmental variables explained 45.5% of SM variation. The low precision of
386 SM may be explained in two ways. First, with few sampling sites included in our study, the
387 environmental gradients were narrow. Second, previous studies and our unpublished study have
388 suggested that SM variation is primarily controlled by a phylogenetic effect, whereas the
389 environmental effect is weak (Moles et al., 2006). Therefore, phylogenetic relatedness among
390 species should be considered to improve the predictive precision of the spatial pattern of SM in
391 further work.

392 There was no consensus in the spatial patterns of plant functional traits among the global
393 studies. Thus, we compared our results to the other studies focused on China. Yang et al. (2016)
394 predicted the spatial distribution of leaf mass per area (1/SLA) and LNC based on trait-environment
395 relationships in China and had an R^2 of 0.13-0.16. The lower predictive precision may be because
396 Yang et al. (2016) only used MAT, MAP, and RAD as predictors in estimating the spatial patterns
397 of leaf mass per area and LNC, which likely led to poor performance and low heterogeneity. These
398 results also demonstrate the advantage of our methods in mapping the spatial patterns of plant
399 functional traits at a regional scale.

400 **4.2 Spatial patterns of plant functional traits in China**

401 Our study revealed the spatial patterns of different plant functional traits across China, and the
402 variability among the two machine learning methods was relatively low. In some regions, there were
403 consistent patterns in plant functional traits between our study and the previous studies. For example,
404 our study showed high SLA in the southeastern Qinghai-Tibet Plateau, which concurred with the
405 global study of Boonman et al. (2020). Consistent with the global pattern (Wright et al., 2017), LA
406 was larger in southern regions than in northern regions and showed a decreasing trend along a
407 latitudinal gradient. Potapov et al. (2021) mapped global forest canopy height at a spatial resolution
408 of 30 m by integrating GEDI and Landsat data, and their resulting spatial pattern of plant height in
409 China was consistent with our study. This confirms the accuracy and reliability of predicting plant
410 height through spatial extrapolation as in our study. However, in some regions there were
411 contradictory patterns in the plant functional traits between our study and previous ones. Our study
412 showed high LNC values in the northern Inner Mongolia Plateau-Loess Plateau-eastern Qinghai-
413 Tibet Plateau and high heterogeneity in southern China, whereas Yang et al. (2016) predicted high
414 LNC values in northeastern and northwestern China, northern Inner Mongolia Plateau, and the entire



415 Qinghai-Tibet Plateau, but low heterogeneity overall. In addition, Yang et al. (2016) predicted low
416 SLA variability in China, especially in the Qinghai-Tibet Plateau. These discrepancies may be
417 attributed to spatial extrapolation based on trait-climate relationships with a low predictive precision.

418 Moreover, our study also identified the applicability domain of our models for predicting the
419 spatial patterns of plant functional traits across China. Five leaf traits and WD appeared to have poor
420 applicability in northeastern China and the Qinghai-Tibet Plateau, primarily due to sparse samplings.
421 Although the predictions of plant height and SM were obtained in most regions through spatial
422 extrapolation, the results were consistent with previous studies. This demonstrates the reliability of
423 our methods. Future studies predicting plant functional traits across a large scale through remote
424 sensing observations or other supplementary data will be needed to re-evaluate our results.

425 **4.3 The role of predictive variables**

426 Our study indicates that environmental variables are important for predicting the spatial patterns of
427 plant functional traits, especially climate variables. Temperature variables were primary predictors
428 for SLA, LDMC, LPC and WD. The relationships between leaf traits and temperature have been
429 widely discussed in global and regional studies (Reich and Oleksyn, 2004; Bruelheide et al., 2018).
430 The positive linkage between WD and temperature may be driven by changes in the viscosity of
431 water. Plants can adapt to the low water viscosity at high temperatures by reducing the diameter and
432 density of their vessels and by thickening cell walls (Roderick and Berry, 2002; Thomas et al., 2004).
433 Precipitation variables were important predictors for leaf nutrient traits, LA, and plant height. Water
434 availability emerged as the primary predictor of plant height, which may be explained by the
435 hydraulic limitation hypothesis. Relative to shorter plants, taller plants tend to be at a higher risk of
436 embolisms due to their increased xylem length and conduit width. Thus, tall plants may be forced
437 to close their stomata and reduce the amount of photosynthesis (Renninger et al., 2009; Wang et al.,
438 2019). Although the effects of soil on trait predictions were relatively weak, we found that SAP and
439 pH played key roles in SLA, LNC and SM predictions. These results were similar with the previous
440 studies that reported that soil pH was an important driver of trait variation at the global scale and in
441 tundra regions (Kemppinen et al., 2021; Maire et al., 2015). Additionally, from the perspective of
442 cost-efficient theory, the strong effects of SAP reflected that high SLA and small seeds may be an
443 adaptation for facilitating soil exploration more efficiently in fertile soils (Freschet et al., 2010).

444 Vegetation indices have recently been proposed as important predictors of spatial patterns of
445 plant functional traits (Loozen et al., 2018). Our results corroborate these findings and further
446 suggest that EVI, MTCI and MIR reflectance are important predictors in models. Here, the
447 underlying mechanisms between vegetation indices and plant functional traits are not further
448 discussed due to their complexity and uncertainty. However, our results indicated that vegetation
449 indices and NIR reflectance are not key predictors of LNC estimation, which contrasts the findings
450 from global and regional studies (Loozen et al., 2018; Moreno-Martínez et al., 2018; Wang et al.,
451 2016). This may be related to the multitude of factors that influence the relationship between LNC



452 and vegetation indices and NIR reflectance, such as forest type and canopy structure (Dahlin et al.,
453 2013).

454 **4.4 Uncertainties**

455 Although our study mapped the spatial patterns of key functional traits of seed plants in China
456 through large-scale field investigations and compared the predictions with previous studies
457 performed at global and regional scales, there persist some uncertainties in the interpretation of these
458 results. First, the predictive ability of machine learning methods was relatively worse for certain
459 traits, especially for SM and LDMC. Beyond the environmental effects, the variation in plant
460 functional traits is also regulated by phylogenetic structure among plant species (e.g., family, order
461 and phylogenetic clade) (Li et al., 2017). Consequently, incorporating the phylogenetic information
462 will be a promising avenue in future studies for further improving the accuracy of spatial predictions
463 of plant functional traits (Butler et al., 2017). A second potential issue is sampling bias; there were
464 major spatial gaps in field investigation in both the northeastern China and the Qinghai-Tibet Plateau,
465 especially for SM and plant height. There are an increasing number of available datasets and studies
466 on SM and plant height, but many did not provide the corresponding geographic coordinates, thus
467 rendering the data unusable. In addition, due to the challenges of measurements for small shrubs
468 and low vegetation, WD data is mainly confined to eastern forests (Perez-Harguindeguy et al., 2013),
469 and the overall quantity of WD data was much lower than that of leaf and reproductive traits, even
470 in the TRY database, which is the largest trait database in the world (Kattge et al., 2020). Finally,
471 additional key challenges in data availability must be resolved to scale up from the species to the
472 community levels, in particular with data surrounding species co-occurrence and their relative cover
473 or abundance in ecological communities (He et al., 2023). Global biodiversity data (e.g., sPlot and
474 Global Biodiversity Information Agency databases) that contains information on species occurrence
475 or the proportion of species in a community has the potential for enabling the calculation of
476 community-weighted trait values and the re-evaluation of our results in future work (Telenius, 2011;
477 Bruelheide et al., 2019). In addition, integrating satellite remote sensing monitoring methods with
478 in situ data collection can also provide an effective way to estimate and assess the species diversity
479 at a large scale (Cavender-Bares et al., 2022).

480 **4.5 Potential applications**

481 Maps of these key functional traits of seed plants highlighted large-scale variability in space, which
482 will significantly advance ecological analyses and future interdisciplinary research. First, using the
483 spatially continuous trait datasets, one can optimize and develop trait-flexible vegetation models,
484 which allows for the exploration of the community assembly rules based on how plants with
485 different trait combinations perform under a given set of environmental conditions (Berzaghi et al.,
486 2020). When trait-flexible vegetation models are available, incorporating trait maps into models
487 will bridge the gap for vegetation classifications and predictions of vegetation distribution under



488 global change, which is not feasible in conventional vegetation models (Van Bodegom et al., 2012;
489 Yang et al., 2019). Second, the assessments of China's terrestrial ecosystem carbon sink have had
490 large uncertainties so far (Piao et al., 2022), but the spatial continuous trait datasets will provide an
491 effective way to link ecosystem characteristics to ecosystem carbon sink estimates in China (Madani
492 et al., 2018; Šímová et al., 2019). These analyses will help shed light on the mechanisms underlying
493 plant functional traits and terrestrial ecosystem carbon storage at a large scale.

494 **5 Data availability**

495 The original eight plant functional traits dataset collected in this study that were used for machine
496 learning models (named by Data file used for machine learning models.csv) and final maps of eight
497 plant functional traits in terrestrial ecosystems in a GeoTIFF format across China (named by plant
498 functional trait category) are now available for the private link
499 <https://figshare.com/s/c527c12d310cb8156ed2> (An et al., 2023). Once the article is accepted, we
500 will publicly publish these datasets at the figshare website.

501 **6 Conclusions**

502 We created a set of spatial continuous trait datasets at a 1-km spatial resolution using machine
503 learning methods in combination with field measurements, environmental variables and vegetation
504 indices. Models for leaf traits (except for LDMC), WD and plant height showed good accuracy and
505 robustness, whereas models of SM and LDMC had relatively poor precision and robustness.
506 Temperature variables were the most important predictors for leaf traits (except for LA) and WD,
507 and precipitation variables were the most important predictors for leaf nutrient traits, LA and plant
508 height. We caution that plant functional trait predictions should be interpreted carefully for
509 northeastern China and the Qinghai-Tibet Plateau. The spatial continuous trait datasets generated in
510 our study are complementary to current terrestrial in-situ observations and offer new avenues for
511 predicting large-scale changes in vegetation and ecosystem function under climate scenarios in
512 China.

513

514 **Appendix A Data collection from literature**

- 515 An H. and Shanguan Z. P. Photosynthetic characteristics of dominant plant species at different succession stages of
516 vegetation on Loess Plateau. *Chinese Journal of Applied Ecology*, 2007, 18, 1175-1180.
- 517 Bai K. D., Jiang D. B., Wan C. X. Photosynthesis-nitrogen relationship in evergreen and deciduous tree species at
518 different altitudes on Mao'er Mountain, Guangxi. *Acta Ecologica Sinica*, 2013, 33, 4930-4938.
- 519 Bai W. J., Zheng F. L., Dong L. L., et al. Leaf traits of species in different habits in the water-wind erosion region of
520 the Loess Plateau. *Acta Ecologica Sinica*, 2010, 30, 2529-2540.
- 521 Chai Y F., Shang H. L., Zhang X. F., et al. Ecological variations of woody species along an altitudinal gradient in
522 the Qinling Mountains of Central China: area-based versus mass-based expression of leaf traits. *Journal of*
523 *Forestry Research*, 2021, 32, 599-608.



- 524 Chang Y. N., Zhong Q. L., Cheng D. L., et al. Stoichiometric characteristics of C, N, P and their distribution pattern
525 in plants of *Castanopsis carlesii* natural forest in Youxi. *Journal of Plant Resources and Environment*, 2013, 22,
526 1-10.
- 527 Chen F. Y., Luo T. X., Zhang L., et al. Comparison of leaf construction cost in dominant tree species of the evergreen
528 broadleaved forest in Jiulian Mountain, Jiangxi Province. *Acta Ecologica Sinica*, 2006, 26, 2485-2493.
- 529 Chen H. Y., Huang Y. M., He K. J., et al. Temporal intraspecific trait variability drives responses of functional
530 diversity to interannual aridity variation in grasslands. *Ecology and Evolution*, 2018, 9, 5731-5742.
- 531 Chen L. X., Xiang W. H., Wu H. L., et al. Tree growth traits and social status affect the wood density of pioneer
532 species in secondary subtropical forest. *Ecology and Evolution*, 2017, 7, 5366-5377.
- 533 Chen L., Yang X. G., Song N. P., et al. Leaf water uptake strategy of plants in the arid-semiarid region of Ningxia.
534 *Journal of Zhejiang University*, 2013, 39, 565-574.
- 535 Chen Y. H., Han W. X., Tang L. Y., et al. Leaf nitrogen and phosphorus concentrations of woody plants differ in
536 responses to climate, soil and plant growth form. *Ecography*, 2011, 36, 178-184.
- 537 Chen Y. S., Zhou S. B., Ou Z. L., et al. Seed mass variation in common plant species in Wanfoshan Natural
538 Reservation Region, Anhui, China. *Chinese Journal of Plant Ecology*, 2012, 36, 739-746.
- 539 Chen Z. H., Peng J. F., Zhang D. M., et al. Seed germination and storage of woody species in the lower subtropical
540 forest. *Acta Botanica Sinica*, 2002, 44, 1469-1476.
- 541 Cheng J. H., Chu P. F., Chen D. M., et al. Functional correlations between specific leaf area and specific root length
542 along a regional environmental gradient in Inner Mongolia grasslands. *Functional Ecology*, 2016, 30, 985-997.
- 543 Cheng W., Yu C. H., Xiong K. N., et al. Leaf functional traits of dominant species in karst plateau-canyon areas.
544 *Guihaia*, 2019, 39, 1039-1049.
- 545 Dong H. and Shekhar R. B. Negative relationship between interspecies spatial association and trait dissimilarity.
546 *Oikos*, 2019, 128, 659-667.
- 547 Dong T. F., Feng Y. L., Lei Y. B., et al. Comparison on leaf functional traits of main dominant woody species in wet
548 and dry habitats. *Chinese Journal of Ecology*, 2012, 31, 1043-1049.
- 549 Du H. D. Ecological responses of foliar anatomical structural & physiological characteristics of dominant plants at
550 different site conditions in north Shaanxi Loss Plateau. 2010, Graduation Thesis.
- 551 Fan Z. X., Zhang S. B., Hao G. Y., et al. Hydraulic conductivity traits predict growth rates and adult stature of 40
552 Asian tropical tree species better than wood density. *Journal of Ecology*, 2012, 100, 732-741.
- 553 Feng J. B., Fan S. X., Hou Y. F., et al. Interspecific and intraspecific variation of leaf function traits of herbaceous
554 plants in a forest-steppe zone, Hebei Province, China. *Journal of Northeast Forestry University*, 2021, 49, 23-
555 28.
- 556 Feng Q. H. The study on the response of foliar $\delta^{13}C$ of different life from plants to altitude in subalpine area of
557 Western Sichuan, China. 2011, Graduation Thesis.
- 558 Fu P. L., Zhu S. D., Zhang J. L., et al. The contrasting leaf functional traits between a karst forest and a nearby non-
559 karst forest in south-west China. *Functional Plant Biology*, 2019, 46, 907-915.
- 560 Gao S. P., Li J. X., Xu M. C., et al. Leaf N and P stoichiometry of common species in successional stages of the
561 evergreen broad-leaved forest in Tiantong National Forest Park, Zhejiang Province, China. *Acta Ecologica
562 Sinica*, 2007, 27, 947-952.
- 563 Geekyanage N., Goodale, U. M., Cao, K. F., et al. Leaf trait variations associated with habitat affinity of tropical
564 karst tree species. *Ecology and Evolution*, 2017, 8, 286-295.
- 565 Geng Y., Ma W. H., Wang L., et al. Linking above- and belowground traits to soil and climate variables: an integrated
566 database on China's grassland species. *Ecology*, 2017, 98, 1471.
- 567 Gong H. D., Tang C. Z. and Wang B. Post-dispersal seed predation and its relations with seed traits: a thirty-species-



- 568 comparative study. *Plant Species Biology*, 2015, 30, 193-201.
- 569 Guo F. C. The photosynthetic characteristics of precious broad-leaved tree species in south subtropics and their
570 relationship with leaf functional traits. 2015, Graduation Thesis.
- 571 Guo W. J. Exploring the relationship between arbuscular mycorrhizal fungi and plant based on phylogeny and plant
572 traits. 2015, Graduation Thesis.
- 573 Guo Z. W., Zhao W. X., Luo J. F., et al. The variation characteristics of plant functional traits among 16 woody plants
574 in subtropical broad-leaved forest at Dagang Mountain. *Journal of Fujian Normal University (Natural Science
575 Edition)*, 2019, 35, 82-87.
- 576 Hau C. H. Tree seed predation on degraded hillsides in Hong Kong. *Forest Ecology & Management*. 1997, 99, 215-
577 221.
- 578 He J. S., Wang Z. H., Wang X. P., et al. A test of the generality of leaf trait relationships on the Tibetan Plateau. *New
579 Phytologist*, 2006, 170, 835-848.
- 580 He P. C., Wright I. J., Zhu S. D., et al. Leaf mechanical strength and photosynthetic capacity vary independently
581 across 57 subtropical forest species with contrasting light requirements. *New Phytologist*, 2019, 223, 607-618.
- 582 He Y. T. Studies on physioecological traits of 30 plant species in the Subalpine Meadow of the Qinling Mountains.
583 2007, Graduation Thesis.
- 584 Hou M. M. Adaptive evolution of some species from sedges (*Carex Cyperaceae*) based on phylogeny and leaf
585 functional traits to habitat in the Poyang Lake Area. 2017, Graduation Thesis.
- 586 Hou Y., Liu M. X., Sun H. R., et al. Response of plant leaf traits to microhabitat change in a subalpine meadow on
587 the eastern edge of Qinghai-Tibetan Plateau, China. *Chinese Journal of Applied Ecology*, 2017, 28, 71-79.
- 588 Hu Z. Z., Michaletz S. T., Johnson D. J., et al. Traits drive global wood decomposition rates more than climate.
589 *Global Change Biology*, 2018, 24, 5259-5269.
- 590 Hua L., He P., Goldstein G., et al. Linking vein properties to leaf biomechanics across 58 woody species from a
591 subtropical forest. *Plant Biology*, 2019, 22, 212-220.
- 592 Huang J. J. and Wang X. H. Leaf nutrient and structural characteristics of 32 evergreen broad-leaved species. *Journal
593 of East China Normal University (Natural Science)*, 2003, 1, 92-97.
- 594 Huang Y. L. The research about the turnover patterns and moisture adaptation mechanism of major species on the
595 South-North-facing slope. 2012, Graduation Thesis.
- 596 Iida Y., Kohyama T. S., Swenson N. G., et al. Linking functional traits and demographic rates in a subtropical tree
597 community: the importance of size dependency. *Journal of Ecology*, 2014, 102, 641-650.
- 598 Jia Q. Q. Functional traits of fine roots and their relationship with leaf traits of 50 major species in a subtropical
599 forest in Gutianshan. 2011, Graduation Thesis.
- 600 Jiang Y., Chen X., Ma J., et al., Interspecific and intraspecific variation in functional traits of subtropical evergreen
601 and deciduous broadleaved mixed forests in karst topography, Guilin, Southwest China. *Tropical Conservation
602 Science*, 2016, 9.
- 603 Jin Y., Wang C. K., Zhou Z. H., et al. Co-ordinated performance of leaf hydraulics and economics in 10 Chinese
604 temperate tree species. *Functional Plant Biology*, 2016, 43, 1082-1090.
- 605 Jing G. H. Responses of grassland community structure and functions to management practices on the semi-arid area
606 of Loess Plateau. 2017, Graduation Thesis.
- 607 Kang M. Spatial distribution pattern and its causes of woody plant functional traits in Tiantong region, Zhejiang
608 Province. 2012, Graduation Thesis.
- 609 Krober W., Li Y., Hardtle W., et al. Early subtropical forest growth is driven by community mean trait values and
610 functional diversity rather than the abiotic environment. *Ecology and Evolution*, 2015, 5, 3541-3556.
- 611 Krober W., Bohnke M., Welk E., et al. Leaf trait-environment relationships in a subtropical broadleaved forest in



- 612 south-east China. *PloS One*, 2012, 7, e35742.
- 613 Krober W., Zhang, S. R. Ehmgig, M., et al. Linking xylem hydraulic conductivity and vulnerability to the leaf
614 economics spectrum—a cross-species study. *PloS One*, 2014, e109211.
- 615 Li F. Comparison of functional traits in semi-humid evergreen broad-leaved in Western Hill of Kunming. 2011,
616 Graduation Thesis.
- 617 Li H. Response of plant community functional traits to karst mountain tourism and its maintenance mechanism—A
618 case study of Shi Bing World Natural Heritage Site in Guizhou. 2019, Graduation Thesis.
- 619 Li K. and Xiang W. H. Comparison of specific leaf area, SPAD value and seed mass among subtropical tree species
620 in hilly area of Central Hunan, China. *Journal of Central South University of Forestry & Technology*, 2011, 31,
621 213-218.
- 622 Li L., McCormack M. L., Ma C.G., et al. Leaf economics and hydraulic traits are decoupled in five species-rich
623 tropical-subtropical forests. *Ecology Letters*, 2015, 18, 899-906.
- 624 Li Q. Leaf functional traits and their relationships with environmental factors in Beishan Mountain of Jinhua,
625 Zhejiang Province. 2020, Graduation Thesis.
- 626 Li S. J., Su P. X., Zhang H. N., et al. Characteristics and relationships of foliar water and leaf functional traits of
627 desert plants. *Plant Physiology Journal*, 2013, 49, 153-160.
- 628 Li W. H., Xu F. W., Zheng S. X., et al. Patterns and thresholds of grazing-induced changes in community structure
629 and ecosystem functioning: species-level responses and the critical role of species traits. *Journal of Applied
630 Ecology*, 2017, 54, 963-975.
- 631 Li W. Q., Xu Q., Li J., et al. Quantification of ecotone width of returned forest land from farmland based on specific
632 leaf area. *Journal of West China Forestry Science*, 2017, 46, 117-121.
- 633 Li X. F., Pei K. Q., Kery M., et al. Decomposing functional trait associations in a Chinese subtropical forest. *PloS
634 One*, 2017, 12, e0175727.
- 635 Li X. F., Schmid B., Wang F., et al. Net assimilation rate determines the growth rates of 14 species of subtropical
636 forest trees. *PloS One*, 2016, 11, e0150644.
- 637 Li X. L., Li X. H., Jiang D. M., et al. Leaf morphological characters of 22 compositae herbaceous species in Horqin
638 sandy land. *Chinese Journal of Ecology*, 2005, 24, 1397-1401.
- 639 Li Y. H., Luo T. X., Lu Q., et al. Comparisons of leaf traits among 17 major plant species in Shazhuyu Sand Control
640 Experimental Station of Qinghai Province. *Acta Ecologica Sinica*, 2005, 25, 994-999.
- 641 Li Y. L., Meng Q. T., Zhao X. Y., et al. Relationships of fresh leaf traits and leaf litter decomposition in Kerqin Sandy
642 Land. *Acta Ecologica Sinica*, 2008, 28, 2486-2494.
- 643 Li Y., Yao J., Yang S., et al. Trait differences research on leaf function of Liaodong oak forest main species in
644 Dongling mountain. *Guangdong Agricultural Sciences*, 2012, 23, 159-162, 171.
- 645 Liang X. Y., Ye Q., Liu H., et al. Wood density predicts mortality threshold for diverse trees. *New Phytologist*, 2021,
646 229, 3053-3057.
- 647 Li, R., Zhu, S., Chen, H. Y. H., et al. Are functional traits a good predictor of global change impacts on tree species
648 abundance dynamics in a subtropical forest? *Ecology Letters*, 2015, 18, 1181-1189.
- 649 Li Y. Y., Shi H., Shao M. A. Cavitation resistance of dominant trees and shrubs in Loess hilly region and their
650 relationship with xylem structure. *Journal of Beijing Forestry University*, 2010, 32, 8-13.
- 651 Lin G. G., Guo, D. L., Li, L., et al. Contrasting effects of ectomycorrhizal and arbuscular mycorrhizal tropical tree
652 species on soil nitrogen cycling: the potential mechanisms and corresponding adaptive strategies. *Oikos*, 2018,
653 127, 518-530.
- 654 Liu C. H. and Li Y. Y. Relationship between leaf traits and PV curve parameters in the typical deciduous woody
655 plants occurring in Southern Huanglong Mountain. *Journal of Northwest Forestry University*, 2013, 28, 1-5.



- 656 Liu G. F., Freschet G. T., Pan X., et al. Coordinated variation in leaf and root traits across multiple spatial scales in
657 Chinese semi-arid and arid ecosystems. *New Phytologist*, 2010, 188, 543-553.
- 658 Liu G. F., Wang L., Jiang L., et al. Specific leaf area predicts dryland litter decomposition via two mechanisms.
659 *Journal of Ecology*, 2017, 106, 218-229.
- 660 Liu J. H., Zeng D. H. and Don K. L. Leaf traits and their interrelationships of main plant species in southeast Horqin
661 sandy land. *Chinese Journal of Ecology*, 2006, 25, 921-925.
- 662 Liu J. X., Chen J., Jiang M. X., et al. Leaf traits and persistence of relict and endangered tree species in a rare plant
663 community. *Functional Plant Biology*, 2012, 39, 512-518.
- 664 Liu L. H. The traits and adaptive strategies of main herbaceous plants and lianas on micro-topographical units in
665 Huangcangyu reserves of Anhui Province. 2012, Graduation Thesis.
- 666 Liu M. C., Kong D. L., Lu X. R., et al. Higher photosynthesis, nutrient- and energy-use efficiencies contribute to
667 invasiveness of exotic plants in a nutrient poor habitat in northeast China. *Physiologia Plantarum*, 2017, 160,
668 373-382.
- 669 Liu R. H., Bai J. L., Bao H., et al. Variation and correlation in functional traits of main woody plants in the
670 *Cyclobalanopsis glauca* community in the karst hills of Guilin, southwest China. *Chinese Journal of Plant
671 Ecology*, 2020, 44, 828-841.
- 672 Liu W. D., Su J. R., Li S. F., et al. Stoichiometry study of C, N and P in plant and soil at different successional stages
673 of monsoon evergreen broad-leaved forest in Pu'er, Yunnan Province. *Acta Ecologica Sinica*, 2010, 30, 6581-
674 6590.
- 675 Liu X. C., Jia H. B., Wang Q. Y. Genetic variation and correlation in wood properties of *Betula platyphlla* in natural
676 Stands. *Journal of Northeast Forestry University*, 2018, 36, 8-10.
- 677 Liu Y. Y. Spatial distribution and habitat associations of trees in a typical mixed broad-leaved Korean pine (*Pinus
678 koraiensis*) forest. 2014, Graduation Thesis.
- 679 Liu Z. M., Li R. M., Li X. H., et al. A comparative study of seed weight of 69 plant species in Horqin sandyland,
680 China. *Acta Phytocologica Sinica*, 2004, 28, 225-230.
- 681 Luo Y. H., Cadotte M. W., Burgess K. S., et al. Greater than the sum of the parts: how the species composition in
682 different forest strata influence ecosystem function. *Ecology Letters*, 2019, 22, 1449-1461.
- 683 Lv J. Z., Miao Y. M., Zhang H. F., et al. Comparisons of leaf traits among different functional types of plant from
684 Huoshan Mountain in the Shanxi Province. *Plant Science Journal*, 2010, 28, 460-465.
- 685 Ma J., Wu L. F., Wei X., et al. Habitat adaptation of two dominant tree species in a subtropical monsoon forest: leaf
686 functional traits and hydraulic properties. *Guihaia*, 2015, 35, 261-268.
- 687 Mo J. M., Zhang D. Q., Huang Z. L., et al. Distribution pattern of nutrient elements in plants of Dinghushan Lower
688 Subtropical Evergreen Broad-Leaved Forest. *Journal of Tropical and Subtropical Botany*, 2000, 8, 198-206.
- 689 Niu C. Y., Meinzer F. C. and Hao G. Y. Divergence in strategies for coping with winter embolism among co-occurring
690 temperate tree species: the role of positive xylem pressure, wood type and tree stature. *Functional Ecology*,
691 2017, 31, 1550-1560.
- 692 Niu D. C., Li Q., Jiang S. G., et al. Seasonal variations of leaf C:N:P stoichiometry of six shrubs in desert of China's
693 Alxa Plateau. *Chinese Journal of Plant Ecology*, 2013, 37, 317-325.
- 694 Niu K. C., He J. S. and Lechowicz M. J. Grazing-induced shifts in community functional composition and soil
695 nutrient availability in Tibetan alpine meadows. *Journal of Applied Ecology*, 2016, 53, 1554-1564.
- 696 Niu K. C., Zhang S. and Lechowicz M. Harsh environmental regimes increase the functional significance of
697 intraspecific variation in plant communities. *Functional Ecology*, 2020, 34, 1666-1677.
- 698 Niu S. L. Photosynthesis research on the predominant legume species in Hunshandak Sandland. 2004, Graduation
699 Thesis.



- 700 Qi L. X. Response of leaf traits of *Pinus mongoliensis* and *Pinus massoniana* to elevation gradient in Daiyun
701 Mountain. 2015, Graduation Thesis.
- 702 Qian H., Niklas K. J., Yang D. M., et al. The effect of twig architecture and seed number on seed size variation in
703 subtropical woody species. *New Phytologist*, 2009, 183, 1212-1221.
- 704 Ren Q. J., Li Q. J., Bu H. Y., et al. Comparison of physiological and leaf morphological traits for photosynthesis of
705 the 51 plant species in the Maqu alpine swamp meadow. *Chinese Journal of Plant Ecology*, 2015, 39, 593-603.
- 706 Ren Y. T. The study of leaf functional traits of typical plants across the Alashan Desert. 2017, Graduation Thesis.
- 707 Ren Y., Wei C. G. and Guo X. Y. Comparison on leaf function traits of six kinds of plant in Ordos. *Journal of Inner
708 Mongolia Forestry Science & Technology*, 2019, 45, 43-46, 55.
- 709 Rios R. S., Salgado-Luarte C. and Gianoli E. Species divergence and phylogenetic variation of ecophysiological
710 traits in lianas and trees. *PloS One*, 2007, 9, e99871.
- 711 Shang K. K. Differentiation and maintenance of relict deciduous broad-leaved forest patterns along micro-
712 topographic gradient in subtropical area, East China. 2011, Graduation Thesis.
- 713 Song Y. T. Study on functional plant ecology in Songnen Grassland Northeast China. 2012, Graduation Thesis.
- 714 Song Y. T., Zhou D. W., Li Q., et al. Leaf nitrogen and phosphorus stoichiometry in 80 herbaceous plant species of
715 Songnen grassland in Northeast China. *Chinese Journal of Plant Ecology*, 2012, 36, 222-230.
- 716 Tan X. Y. Research on leaf functional diversity of forest communities in rainy area of south-west China. 2014,
717 Graduation Thesis.
- 718 Tang Q. Q. Variation in functional traits of plants in the Subtropical Evergreen and Deciduous Broad-leaved Mixed
719 Forest. 2016, Graduation Thesis.
- 720 Tang Y. Inter-specific variations and relationship in leaf traits of major temperate species in northern China. 2011,
721 Graduation Thesis.
- 722 Tao J. P., Zuo J., He Z., et al. Traits including leaf dry matter content and leaf pH dominate over forest soil pH as
723 drivers of litter decomposition among 60 species. *Functional Ecology*, 2019, 33, 1798-1810.
- 724 Tian M., Yu G. R., He N. P., et al. Leaf morphological and anatomical traits from tropical to temperate coniferous
725 forests: Mechanisms and influencing factors. *Scientific Reports*, 2016, 6, 19703.
- 726 Wang B. Analysis of leaf functional traits of 13 species trees in northwestern Fujian Province. 2019, Graduation
727 Thesis.
- 728 Wang B. B. A study on ecological stoichiometry of six kinds of dominant shrubs in Huangcangyu Nature Reserve.
729 2015, Graduation Thesis.
- 730 Wang G. H. Leaf trait co-variation, response and effect in a chronosequence. *Journal of Vegetation Science*, 2007,
731 18, 563-570.
- 732 Wang G. H., Liu J. L. and Meng T. T. Leaf trait variation captures climate differences but differs with species
733 irrespective of functional group. *Journal of Plant Ecology*, 2015, 8, 61-69.
- 734 Wang H. F. and Xu M. Individual size variation reduces spatial variation in abundance of tree community assemblage,
735 not of tree populations. *Ecology and Evolution*, 2017, 7, 10815-10828.
- 736 Wang J. H., Chen W., Baskin C. C., et al. Variation in seed germination of 86 subalpine forest species from the
737 eastern Tibetan Plateau: phylogeny and life-history correlates. *Ecological Research*, 2012, 27, 453-465.
- 738 Wang J. Y., Wang S. Q., Li R. L., et al. C:N:P stoichiometric characteristics of four forest types' dominant tree species
739 in China. *Chinese Journal of Plant Ecology*, 2011, 35, 587-595.
- 740 Wang K. B. Vegetation ecological features and net primary productivity simulation in Yanggou watershed in the
741 Loess hill-gully areas of China. 2011, Graduation Thesis.
- 742 Wang S. S. The traits and adaptive strategies of main herbaceous plants and lianas on micro-topographical units in
743 Longjishan reserves of Anhui Province. 2016, Graduation Thesis.



- 744 Wang X. J., Alvarez M., Donohue K., et al. Elevation filters seed traits and germination strategies in the eastern
745 Tibetan Plateau. *Ecography*, 2021, 44, 242-254.
- 746 Wei L. P. Variations in functional traits of main tree species along tree-crown in broadleaved Korean Pine Forest in
747 Jiaohe, Jilin Province. 2014, Graduation Thesis.
- 748 Wei L. P., Hou J. H. and Jiang S. S. Changes of leaf functional traits of two main species along tree height in broad-
749 leaved Korean pine forest. *Guangdong Agricultural Sciences*, 2014, 12, 55-58, 71.
- 750
- 751 Wei L. Y. and Shangguan Z. P. Relation between specific leaf areas and leaf nutrient contents of plants growing on
752 slopelands with different farming-abandoned periods in the Loess Plateau. *Acta Ecologica Sinica*, 2008, 28,
753 2526-2535.
- 754 Wei L. Y., Zhou J. W., Xiao H. G., et al. Variations in leaf functional traits among plant species grouped by growth
755 and leaf types in Zhenjiang, China. *Journal of Forestry Research*, 2011, 28, 241-248.
- 756 Wu D. H., Pietsch K. A., Staab M., et al. Wood species identity alters dominant factors driving fine wood
757 decomposition along a subtropical plantation forests tree diversity gradient in subtropical plantation forests.
758 *Biotropica*, 2021, 53, 643-657.
- 759 Wu T. G., Chen B. F., Xiao Y. H., et al. Leaf stoichiometry of trees in three forest types in Pearl River Delta, South
760 China. *Chinese Journal of Plant Ecology*, 2009, 34, 58-63.
- 761 Xie Y. J. The characteristics of 20 dominant plant functional traits in evergreen broad-leaf forest in Daming Mountain
762 Nature Reserve, Guangxi. 2013, Graduation Thesis.
- 763 Xu M. F., Ke X. H., Zhang Y., et al. Wood densities of six hardwood tree species in Eastern Guangdong and
764 influencing factors. *Journal of South China Agricultural University*, 2016, 37, 100-106.
- 765 Xu M. S., Zhao Y. T., Yang X. D., et al. Geostatistical analysis of spatial variations in leaf traits of woody plants in
766 Tiantong, Zhejiang Province. *Chinese Journal of Plant Ecology*, 2016, 40, 48-59.
- 767 Xu Y. Z. Biomass estimate and storage mechanisms in northern subtropical forest ecosystems, central China. 2016,
768 Graduation Thesis.
- 769 Xun Y. H., Di X. Y. and Jin G. Z. Vertical variation and economic strategy of leaf trait of major tree species in a
770 typical mixed broadleaved-Korean pine forest. *Chinese Journal of Plant Ecology*, 2020, 44, 730-741.
- 771 Yan E. R., Milla R., Aarssen L. W., et al. Functional relationships of leafing intensity to plant height, growth form
772 and leaf habit. *Acta Oecologica-International Journal of Ecology*, 2012, 41, 20-29.
- 773 Yan E. R., Wang X. H., Guo M., et al. C:N:P stoichiometry across evergreen broad-leaved forests, evergreen
774 coniferous forests and deciduous broad-leaved forests in the Tiantong region, Zhejiang Province, eastern China.
775 *Chinese Journal of Plant Ecology*, 2010, 34, 48-57.
- 776 Yang S. The adaptive strategies of main herbaceous plants traits to different micro-topographical units in Dashushan
777 Mountain, Hefei. 2017, Graduation Thesis.
- 778 Yang Y., Xu X., Xu M., et al. Adaptation strategies of three dominant plants in the trough-valley karst region of
779 northern Guizhou Province, Southwestern China, evidence from associated plant functional traits and
780 ecostochiometry. *Earth and Environment*, 2020, 48, 413-423.
- 781 Yang Z., Fan S. X., Zhou B. C., et al. Leaf function and soil nutrient differences of dominant tree species on different
782 slope aspects at the south foothills of Taihang Mountains. *Journal of Henan Agricultural University*, 2020, 54,
783 408-414.
- 784 Yi F Y., Wang Z. R., Baskin C. C., et al. Seed germination responses to seasonal temperature and drought stress are
785 species-specific but not related to seed size in a desert steppe: Implications for effect of climate change on
786 community structure. *Ecology and Evolution*, 2019, 9, 2149-2159.
- 787 Yin Q. L., Wang L., Lei, M. L., et al. The relationships between leaf economics and hydraulic traits of woody plants



- 788 depend on water availability. *Science of the Total Environment*, 2018, 621, 245-252.
- 789 Yu Y. H., Zhong X. P. and Chen W. Analysis of relationship among leaf functional traits and economics spectrum of
790 dominant species in northwestern Guizhou Province. *Journal of Forest and Environment*, 2018, 38, 196-201.
- 791 Yuan S. Preliminary research on plant functional traits and the capability of carbon sequestration of major tree species
792 in Changbai Mountain Area. 2011, Graduation Thesis.
- 793 Zhang H., Chen H. Y. H., Lian J. Y., et al. Using functional trait diversity patterns to disentangle the scale-dependent
794 ecological processes in a subtropical forest. *Functional Ecology*, 2018, 32, 1379-1389.
- 795 Zhang J. G., Fu S. L., Wen Z. D., et al. Relationship of key leaf traits of 16 woody plant species in Low Subtropical
796 China. *Journal of Tropical and Subtropical Botany*, 2009, 17, 395-400.
- 797 Zhang J. L., Poorter L., Cao K. F. Productive leaf functional traits of Chinese savanna species. *Plant Ecology*, 2012,
798 213, 1449-1460.
- 799 Zhang J. Y. Comparative study on the different plant functional groups leaf traits at the Maoershan Region. 2008,
800 Graduation Thesis.
- 801 Zhang Q. W., Zhu S. D., Jansen S., et al. Topography strongly affects drought stress and xylem embolism resistance
802 in woody plants from a karst forest in Southwest China. *Functional Ecology*, 2020, 35, 566-577.
- 803 Zhang S. B. and Cao K. F. Stem hydraulics mediates leaf water status, carbon gain, nutrient use efficiencies and
804 plant growth rates across dipterocarp species. *Functional Ecology*, 2009, 23, 658-667.
- 805 Zhang S. B., Cao K. F., Fan Z. X., et al. Potential hydraulic efficiency in angiosperm trees increases with growth-
806 site temperature but has no trade-off with mechanical strength. *Global Ecology and Biogeography*, 2013, 22,
807 971-981.
- 808 Zhang S. T., Du G. Z. and Chen J. K. Seed size in relation to phylogeny, growth form and longevity in a subalpine
809 meadow on the east of the Tibetan Plateau. *Folia Geobotanica*, 2004, 39, 129-142.
- 810 Zhang Y., Ren Y. X., Yao J., et al. Leaf nitrogen and phosphorous stoichiometry of trees in *Pinus tabulaeformis* Carr
811 stands, North China. *Journal of Anhui Agricultural University*, 2012, 39, 247-251.
- 812 Zhao Y. T., Ali, A. and Yan, E. R. The plant economics spectrum is structured by leaf habits and growth forms across
813 subtropical species. *Tree Physiology*, 2016, 37, 173-185.
- 814 Zheng X. J., Li S. and Li Y. Leaf water uptake strategy of desert plants in the Junggar Basin, China. *Chinese Journal*
815 *of Plant Ecology*, 2011, 35, 893-905.
- 816 Zheng Y. M. Carbon, nitrogen and phosphorus stoichiometry of plant and soil in the sandy hills of Poyang Lake.
817 2014, Graduation Thesis.
- 818 Zheng Z. X. Comparison of plant leaf, height and seed functional traits in dry-hot valleys. 2010, Graduation Thesis.
- 819 Zhou J. Y., He J. J., Guo Z. Y., et al. A study on specific leaf area and leaf dry matter content of five dominant species
820 in Xiangshan Mountain, Huaibei City, Anhui Province. *Journal of Huaibei Normal University (Natural*
821 *Sciences)*, 2013, 34, 51-54.
- 822 Zhou X., Zuo X. A., Zhao X. Y., et al. Plant functional traits and interrelationship of 34 plant species in south central
823 Horqin Sandy Land, China. *Journal of Desert Research*, 2015, 35, 1489-1495.
- 824 Zhu B. R., Xu B. and Zhang D. Y. Extent and sources of variation in plant functional traits in grassland. *Journal of*
825 *Beijing Normal University (Natural Science)*, 2011, 47, 485-489.
- 826 Zhu S. D., Song J. J., Li R. H., et al. Plant hydraulics and photosynthesis of 34 woody species from different
827 successional stages of subtropical forests. *Plant Cell and Environment*, 2013, 36, 879-891.
- 828 Zhu X B, Liu Y. M. and Sun S. C. Leaf expansion of the dominant woody species of three deciduous oak forests in
829 Nanjing, East China. *Chinese Journal of Plant Ecology*, 2005, 29, 125-136.



830 Appendix B

831 **Table B1** Summary of statistics in plant functional traits, environmental variables and geographical
832 distribution in China.

Trait	Unit	Range	Mean	CV (%)	No. of species	Entries	Sites
SLA	m ² kg ⁻¹	0.06–81.68	17.88	54.96	2463	8851	1032
LDMC	g g ⁻¹	0.06–0.95	0.34	100.00	1582	3549	193
LNC	mg g ⁻¹	3.41–66.02	21.52	37.44	2335	7060	567
LPC	mg g ⁻¹	0.09–9.70	1.83	62.19	2074	5968	515
LA	cm ²	0.0033–2553.33	36.16	259.64	1838	5899	691
Height	m	0.01–35.00	5.99	67.58	1171	16324	636
WD	g cm ⁻³	0.25–1.37	0.68	33.16	768	1476	639
SM	mg	0.10–201300.00	1185.59	562.32	1163	3080	134
Altitude	m	-144–5454					1541
MAT	°C	-12.07–24.32					1541
MAP	mm	15–2982					1541
Soil total N	g kg ⁻¹	0.11–10.25					1541
Bulk density	g cm ⁻³	0.83–1.45					1541

833 SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf N concentration; LPC, leaf P concentration; LA,
834 leaf area; WD, wood density; SM, seed mass; MAT, mean annual temperature; MAP, mean annual precipitation.



835 **Table B2** List of all the predictors including environment and remote sensing variables used in this study.

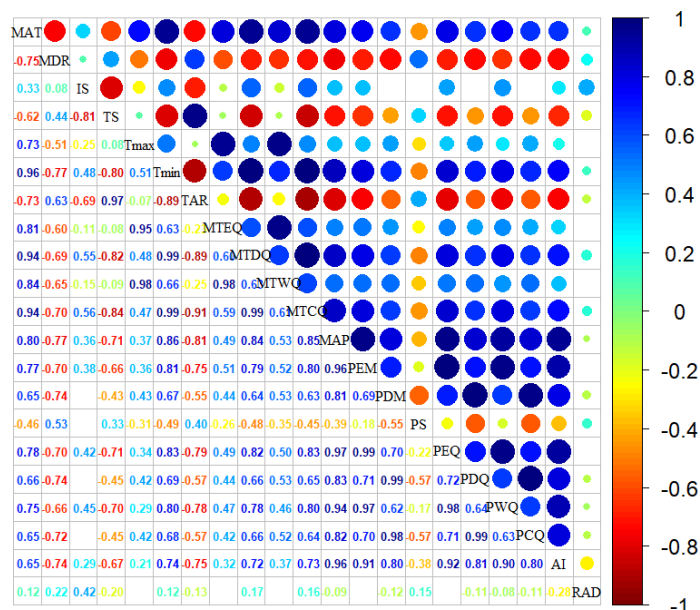
Type of variables	Variable name	Abbreviations	Units	Time periods	Spatial resolution	Source
Climate	Mean annual temperature	MAT	°C	1970-2000	1 km	WorldClim version 2.1
	Mean diurnal range	MDR	°C	1970-2000	1 km	WorldClim version 2.1
	Temperature seasonality	TS	°C	1970-2000	1 km	WorldClim version 2.1
	Max temperature of warmest month	Tmin	°C	1970-2000	1 km	WorldClim version 2.1
	Min temperature of coldest month	Tmax	°C	1970-2000	1 km	WorldClim version 2.1
	Temperature annual range	TAR	°C	1970-2000	1 km	WorldClim version 2.1
	Isothermality	IS	%	1970-2000	1 km	WorldClim version 2.1
	Mean temperature of wettest quarter	MTEQ	°C	1970-2000	1 km	WorldClim version 2.1
	Mean temperature of driest quarter	MTDQ	°C	1970-2000	1 km	WorldClim version 2.1
	Mean temperature of warmest quarter	MTWQ	°C	1970-2000	1 km	WorldClim version 2.1
	Mean temperature of coldest quarter	MTCQ	°C	1970-2000	1 km	WorldClim version 2.1
	Mean annual precipitation	MAP	mm	1970-2000	1 km	WorldClim version 2.1
	Precipitation of wettest month	PEM	mm	1970-2000	1 km	WorldClim version 2.1
	Precipitation of driest month	PDM	mm	1970-2000	1 km	WorldClim version 2.1
	Precipitation seasonality	PS	%	1970-2000	1 km	WorldClim version 2.1
	Precipitation of wettest quarter	PEQ	mm	1970-2000	1 km	WorldClim version 2.1
	Precipitation of driest quarter	PDQ	mm	1970-2000	1 km	WorldClim version 2.1
	Precipitation of warmest quarter	PWQ	mm	1970-2000	1 km	WorldClim version 2.1
	Precipitation of coldest quarter	PCQ	mm	1970-2000	1 km	WorldClim version 2.1
	Aridity index	AI	/	1970-2000	1 km	Global CGIAR-CSI
Solar radiation	RAD	kJ m ⁻² day ⁻¹	1970-2000	1 km	WorldClim version 2.1	
Topography	Elevation	/	m		1 km	SRTM 90m V4.1
Soil	Soil sand content	SAND	%	/	1 km	Shangguan et al. (2013)
	Soil silt content	SILT	%	/	1 km	Shangguan et al. (2013)
	Soil clay content	CLAY	%	/	1 km	Shangguan et al. (2013)
	Bulk density	BD	g cm ⁻³	/	1 km	Shangguan et al. (2013)
	Soil pH	pH	/	/	1 km	Shangguan et al. (2013)



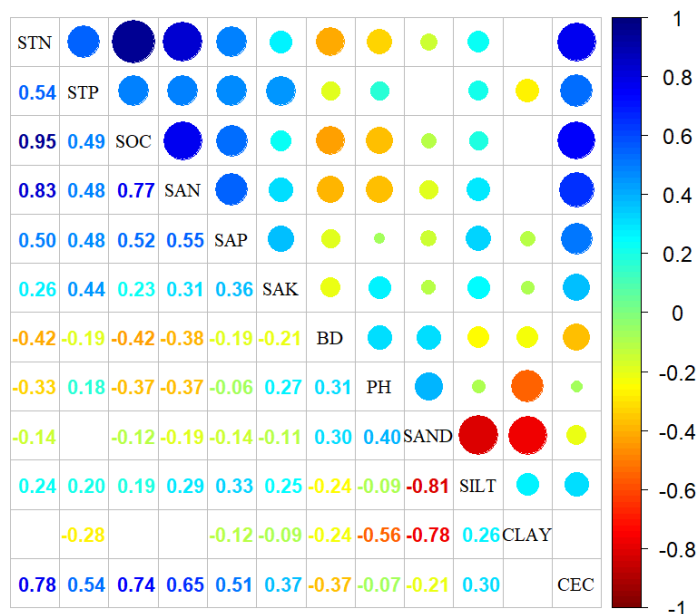
Continued

Type of variables	Variable name	Abbreviations	Units	Time periods	Spatial resolution	Source
	Soil organic matter	SOC	g kg ⁻¹ /		1 km	Shangguan et al. (2013)
	Soil total N	STN	g kg ⁻¹ /		1 km	Shangguan et al. (2013)
	Soil total P	STP	g kg ⁻¹ /		1 km	Shangguan et al. (2013)
	Soil alkali-hydrolysable N	SAN	mg /		1 km	Shangguan et al. (2013)
			kg ⁻¹			
	Soil available P	SAP	mg /		1 km	Shangguan et al. (2013)
			kg ⁻¹			
	Soil available K	SAK	mg /		1 km	Shangguan et al. (2013)
			kg ⁻¹			
	Cation exchange capacity	CEC	me /		1 km	Shangguan et al. (2013)
			kg ⁻¹			
EVI	MODIS EVI long-term monthly averages		/	2001-2018	1 km	MOD13A3 V006
NIR	MODIS NIR long-term monthly averages		/	2001-2018	1 km	MOD13A3 V006
MIR	MODIS MIR long-term monthly averages		/	2001-2018	1 km	MOD13A3 V006
Red	MODIS red long-term monthly averages		/	2001-2018	1 km	MOD13A3 V006
Blue	MODIS blue long-term monthly averages		/	2001-2018	1 km	MOD13A3 V006
MTCI	MTCI long-term monthly averages		/	2003-2011	4.63 km	MTCI level 3 product
Land cover	Land cover map		/	2015	100 m	Copernicus Global Land Service Collection 3

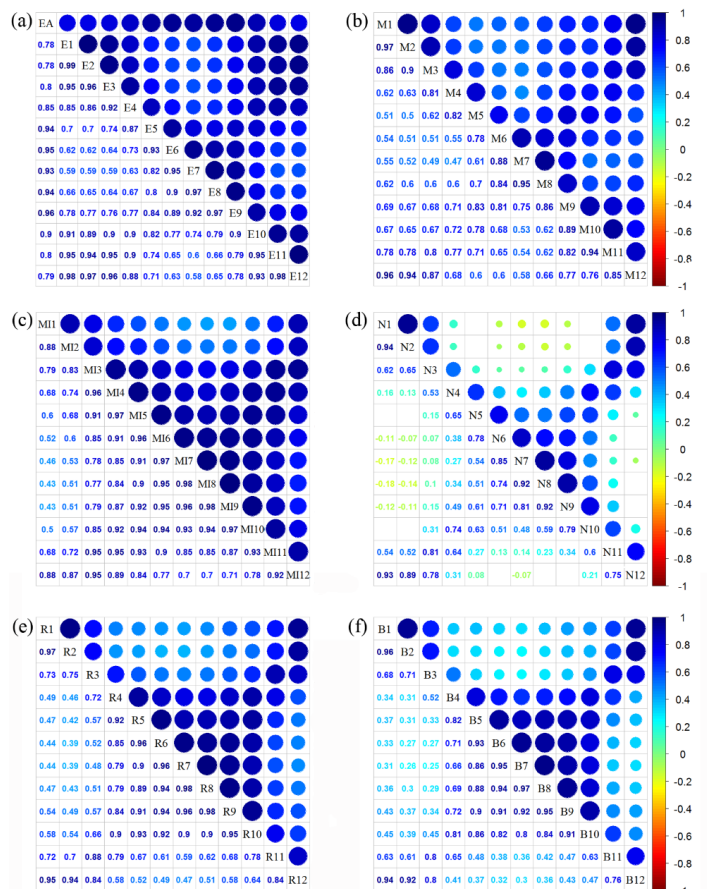
836 The remote sensing variables are calculated as long-term monthly averages from 2001 to 2018. Thus 12
 837 variables of each remote sensing category are obtained.



838
 839 **Figure B1.** Correlations among climate variables. The blank indicates that the correlations are not
 840 significant ($P > 0.05$). The size of the circles is proportional to the correlation coefficient. The
 841 abbreviation of climate variables is seen in Table B2.



842
 843 **Figure B2.** Correlations among soil variables. The blank indicates that the correlations are not significant
 844 ($P > 0.05$). The size of the circles is proportional to the correlation coefficient. The abbreviation of soil
 845 variables is seen in Table B2.



846

847 **Figure B3.** Correlations among monthly remote sensing variables. The blank indicates that the
 848 correlations are not significant ($P > 0.05$). The size of the circles is proportional to the correlation
 849 coefficient. (a) enhanced vegetation index (EVI); (b) MERIS terrestrial chlorophyll index (MTCI); (c)
 850 MIR reflectance; (d) NIR reflectance; (e) red reflectance; (f) blue reflectance.



851 **Appendix C**

852 **Table C1** Optimal parameter combination and model performance of random forest (RF) for plant
 853 functional traits

Traits	n _{tree}	m _{try}	R ²	RMSE	MAE
SLA	1000	24	0.476	7.049	5.134
LDMC	1000	11	0.234	0.095	0.072
LNC	1000	57	0.392	0.129	0.098
LPC	1000	20	0.587	0.176	0.129
LA	1000	18	0.278	72.996	26.622
Height	1000	38	0.871	0.234	0.178
WD	1000	9	0.531	0.092	0.072
SM	1000	22	0.197	6043.95	1290.866

854 SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf N concentration; LPC, leaf P
 855 concentration; LA, leaf area; WD, wood density; SM, seed mass.

856

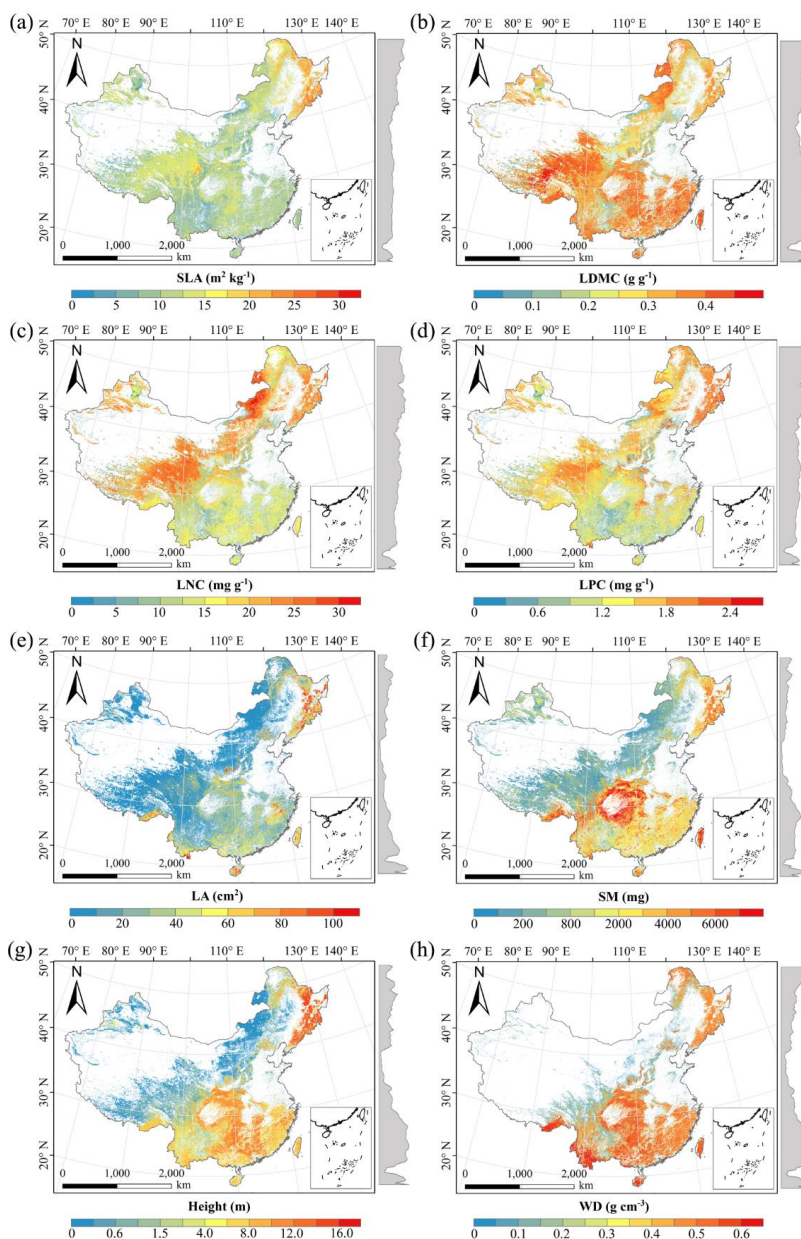
857 **Table C2** Optimal parameter combination and model performance of boosted regression trees (BRT) for
 858 plant functional traits

Traits	n _{tree}	interaction. depth	shrinkage	learning rate	bag fractions	R ²	RMSE	MAE
SLA	3000	6	0.01	10	0.75	0.486	6.986	5.082
LDMC	3000	2	0.01	10	0.75	0.247	0.094	0.071
LNC	3000	6	0.01	10	0.70	0.414	0.126	0.096
LPC	3000	7	0.01	10	0.75	0.591	0.175	0.129
LA	3000	3	0.001	10	0.75	0.282	72.308	27.556
Height	3000	3	0.05	10	0.6	0.871	0.234	0.178
WD	3000	4	0.01	10	0.70	0.627	0.082	0.066
SM	3000	7	0.001	10	0.50	0.192	6070.703	1268.386

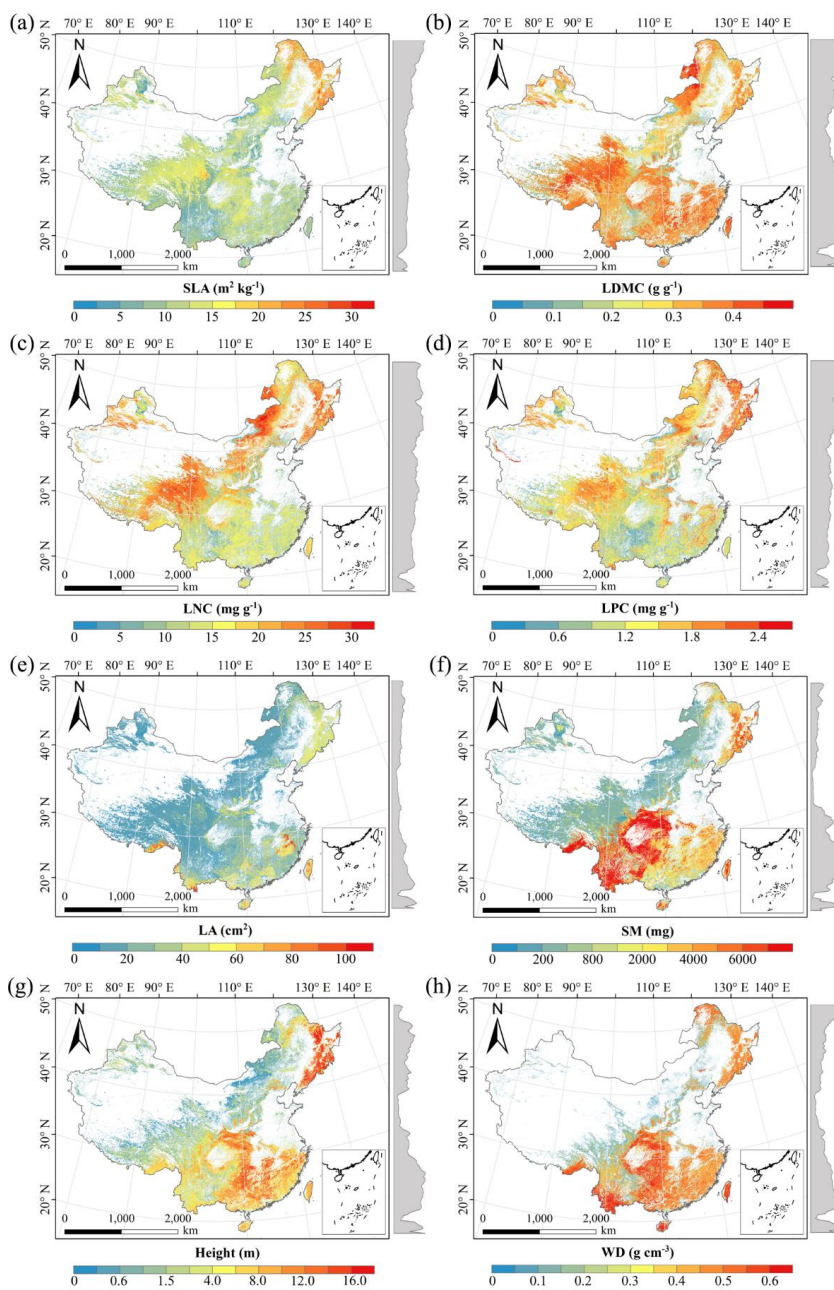
859 SLA, specific leaf area; LDMC, leaf dry matter content; LNC, leaf N concentration; LPC, leaf P
 860 concentration; LA, leaf area; WD, wood density; SM, seed mass.



861 **Appendix D**



862
863 **Figure D1.** Spatial distribution of plant functional traits based on random forest (RF). The grey curves
864 on the right of maps were trait distribution along with latitude. SLA, specific leaf area; LDMC, leaf dry
865 matter content; LNC, leaf N concentration; LPC, leaf P concentration; LA, leaf area; WD, wood density;
866 SM, seed mass.

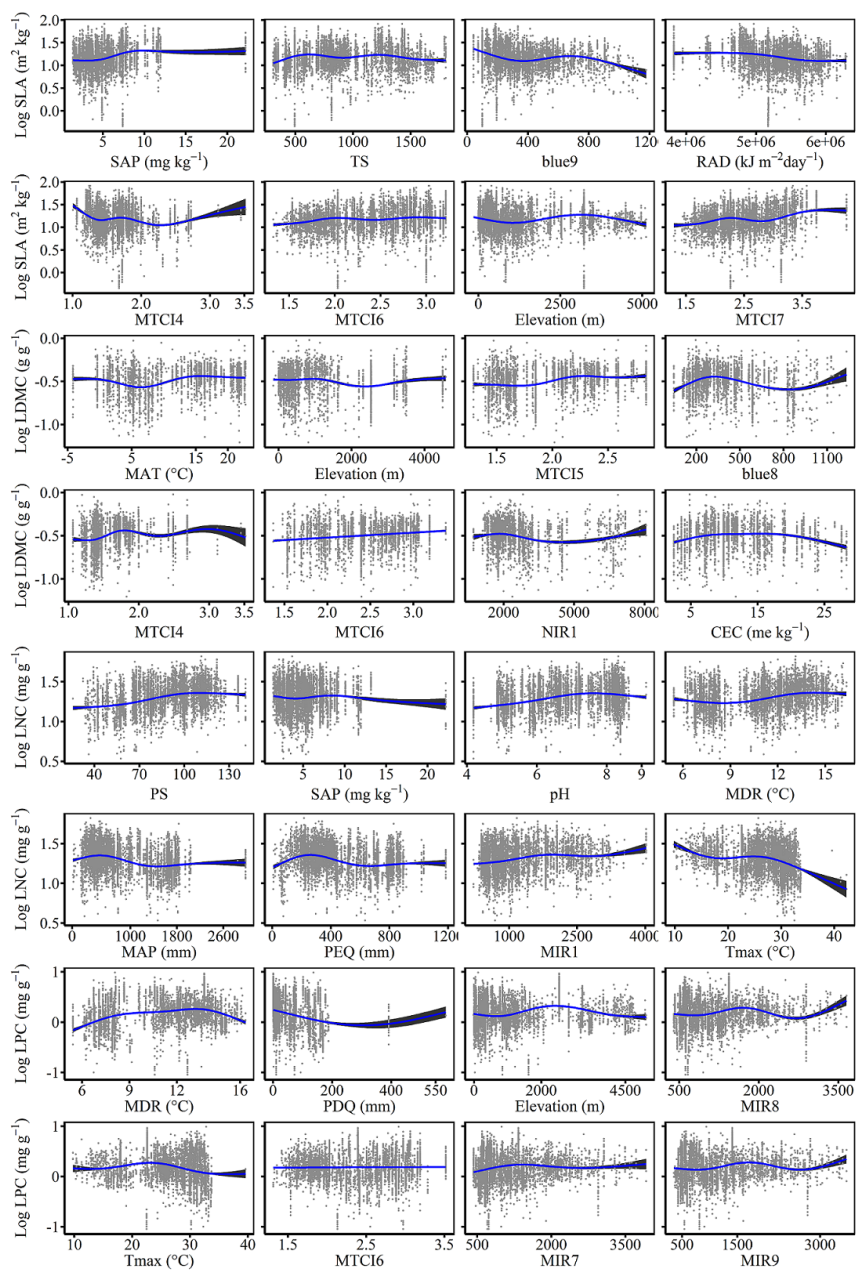


867

868 **Figure D2.** Spatial distribution of plant functional traits based on boosted regression trees (BRT). The
869 grey curves on the right of maps were trait distribution along with latitude. SLA, specific leaf area;
870 LDMC, leaf dry matter content; LNC, leaf N concertation; LPC, leaf P concertation; LA, leaf area; WD,
871 wood density; SM, seed mass.

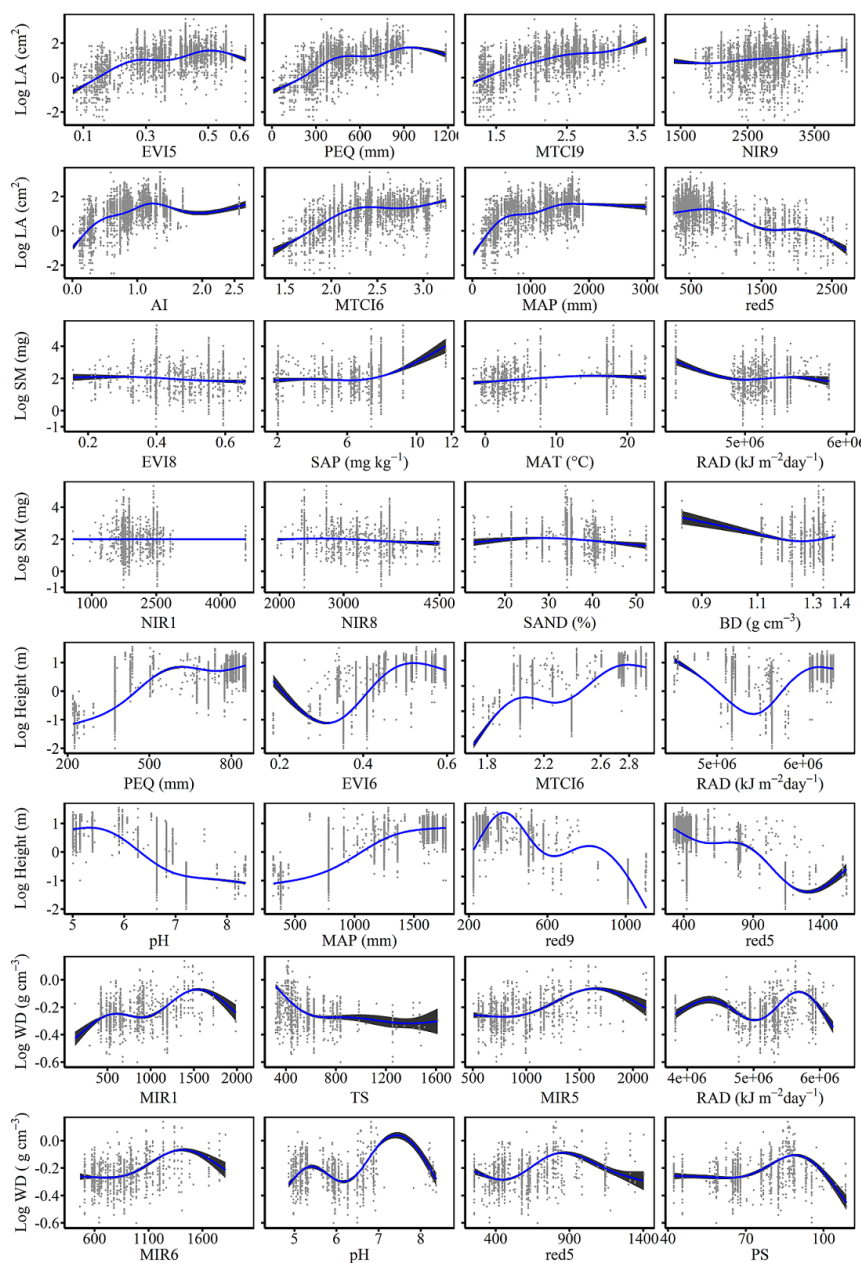


872 **Appendix E**



873

874 **Figure E1.** The relationships between SLA, LDMC, LNC, LPC and their eight most important predictors.



875

876

Figure E2. The relationships between LA, SM, Height, WD and their eight most important predictors.



877 **Author contributions.** NA and NL designed the research. NA did the analysis, processed the data
878 and wrote the draft of the paper. All co-authors commented on the manuscript and agreed upon the
879 final version of the paper.

880

881 **Competing interests.** The contact author has declared that none of the authors has any competing
882 interests.

883

884 **Disclaimer.** Publisher's note: Copernicus Publications remains neutral with regard to jurisdictional
885 claims in published maps and institutional affiliations.

886

887 **Acknowledgement.** We acknowledge financial supports from the National Natural Science
888 Foundation of China (41991234) and the Joint CAS-MPG Research Project (HZXM20225001MI).

889

890 **Financial support.** This work has been supported by the National Natural Science Foundation of
891 China (grant no. 41991234) and the Joint CAS-MPG Research Project (grant no.
892 HZXM20225001MI).

893

894 **References**

895 Ali, A. M., Darvishzadeh, R., Skidmore, A. K., Duren, I. v., Heiden, U., and Heurich, M.: Estimating
896 leaf functional traits by inversion of PROSPECT: assessing leaf dry matter content and specific
897 leaf area in mixed mountainous forest. *Int. J. Appl. Earth Obs. Geoinf.*, 45, 66–76,
898 <https://doi.org/10.1016/j.jag.2015.11.004>, 2016.

899 Bakker, M. A., Carreño-Rocabado, G., and Poorter, L.: Leaf economics traits predict litter
900 decomposition of tropical plants and differ among land use types. *Funct. Ecol.*, 25, 473–483,
901 <https://doi.org/10.1111/j.1365-2435.2010.01802.x>, 2011.

902 Berzaghi, F., Wright, I. J., Kramer, K., Oddou-Muratorio, S., Bohn, F. J., Reyer, C. P. O., Sabate, S.,
903 Sanders, T. G. M., and Hartig, F.: Towards a new generation of trait-flexible vegetation models.
904 *Trends Ecol. Evol.*, 35, 191–205, <https://doi.org/10.1016/j.tree.2019.11.006>, 2020.

905 Blumenthal, D. M., Mueller, K. E., Kray, J. A., Ocheltree, T. W., Augustine, D. J., Wilcox, K. R.,
906 and Cornelissen, H.: Traits link drought resistance with herbivore defence and plant economics
907 in semi-arid grasslands: The central roles of phenology and leaf dry matter content. *J. Ecol.*,
908 108, 2336–2351, <https://doi.org/10.1111/1365-2745.13454>, 2020.

909 Bohner, A. Soil chemical properties as indicators of plant species richness in grassland communities.
910 Integrating efficient grassland farming and biodiversity, Proceedings of the 13th International
911 Occasional Symposium of the European Grassland Federation, Tartu, Estonia, 29–31 August,
912 48-51, 2005.

913 Boonman, C. C. F., Benitez-Lopez, A., Schipper, A. M., Thuiller, W., Anand, M., Cerabolini, B. E.
914 L., Cornelissen, J. H. C., Gonzalez-Melo, A., Hattingh, W. N., Higuchi, P., Laughlin, D. C.,



- 915 Onipchenko, V. G., Penuelas, J., Poorter, L., Soudzilovskaia, N. A., Huijbregts, M. A. J., and
916 Santini, L.: Assessing the reliability of predicted plant trait distributions at the global scale.
917 *Glob. Ecol. Biogeogr.*, 29, 1034–1051, <https://doi.org/10.1111/geb.13086>, 2020.
- 918 Breiman, L.: Random forests. *Mach. Learn.*, 45, 5–32, <https://doi.org/10.1023/a:1010933404324>,
919 2001.
- 920 Bruelheide, H., Dengler, J., Purschke, O., Lenoir, J., Jimenez-Alfaro, B., Hennekens, S. M., Botta-
921 Dukat, Z., Chytry, M., Field, R., Jansen, F., Kattge, J., Pillar, V. D., Schrod, F., Mahecha, M.
922 D., Peet, R. K., Sandel, B., van Bodegom, P., Altman, J., Alvarez-Davila, E., Arfin Khan, M.
923 A. S., et al.: Global trait-environment relationships of plant communities. *Nat. Ecol. Evol.*, 2,
924 1906–1917, <https://doi.org/10.1038/s41559-018-0699-8>, 2018.
- 925 Bruelheide, H., Dengler, J., Jiménez-Alfaro, B., Purschke, O., Hennekens, S. M., Chytrý, M., Pillar,
926 V. D., Jansen, F., Kattge, J., Sandel, B., Aubin, I., Biurrun, I., Field, R., Haider, S., Jandt, U.,
927 Lenoir, J., Peet, R. K., Peyre, G., Sabatini, F. M., Schmidt, M., et al.: sPlot – A new tool for
928 global vegetation analyses. *J. Veg. Sci.*, 30, 161–186, <https://doi.org/10.1111/jvs.12710>, 2019.
- 929 Buchhorn, M., Bertels, L., Smets, B., De Roo, B., Lesiv, M., Tsendbazar, N. E., Masiliunas, D., and
930 Linlin, L.: Copernicus Global Land Service: Land Cover 100m: Version 3 Globe 2015-2019:
931 Algorithm Theoretical Basis Document. <https://doi.org/10.5281/zenodo.3938968>, 2020.
- 932 Butler, E. E., Datta, A., Flores-Moreno, H., Chen, M., Wythers, K. R., Fazayeli, F., Banerjee, A.,
933 Atkin, O. K., Kattge, J., Amiaud, B., Blonder, B., Boenisch, G., Bond-Lamberty, B., Brown,
934 K. A., Byun, C., Campetella, G., Cerabolini, B. E. L., Cornelissen, J. H. C., Craine, J. M.,
935 Craven, D., de Vries, F. T., Diaz, S., Domingues, T. F., Forey, E., Gonzalez-Melo, A., Gross,
936 N., Han, W., Hattingh, W. N., Hickler, T., Jansen, S., Kramer, K., Kraft, N. J. B., Kurokawa,
937 H., Laughlin, D. C., Meir, P., Minden, V., Niinemets, U., Onoda, Y., Penuelas, J., Read, Q.,
938 Sack, L., Schamp, B., Soudzilovskaia, N. A., Spasojevic, M. J., Sosinski, E., Thornton, P. E.,
939 Valladares, F., van Bodegom, P. M., Williams, M., Wirth, C., and Reich, P. B.: Mapping local
940 and global variability in plant trait distributions. *P. Nat. Acad. Sci. USA*, 114, 10937–10946,
941 <https://doi.org/10.1073/pnas.1708984114>, 2017.
- 942 Cavender-Bares, J., Schneider, F. D., Santos, M. J., Armstrong, A., Carnaval, A., Dahlin, K. M.,
943 Fatoyinbo, L., Hurtt, G. C., Schimel, D., Townsend, P. A., Ustin, S. L., Wang, Z. H., and Wilson,
944 A. M.: Integrating remote sensing with ecology and evolution to advance biodiversity
945 conservation. *Nat. Ecol. Evol.*, 6, 506–519, <https://doi.org/10.1038/s41559-022-01702-5>, 2022.
- 946 Clevers, J. G. P. W., and Gitelson, A. A.: Remote estimation of crop and grass chlorophyll and
947 nitrogen content using red-edge bands on Sentinel-2 and -3. *Int. J. Appl. Earth Obs. Geoinf.*,
948 23, 344–351, <https://doi.org/10.1016/j.jag.2012.10.008>, 2013.
- 949 Conti, G., Díaz, S., and Lavorel, S.: Plant functional diversity and carbon storage - an empirical test
950 in semi-arid forest ecosystems. *Journal of Ecology*, 101, 18–28, <https://doi.org/10.1111/1365-2745.12012>, 2013.
- 952 Dahlin, K. M., Asner, G. P., and Field, C. B.: Environmental and community controls on plant



- 953 canopy chemistry in a Mediterranean-type ecosystem. *P. Nat. Acad. Sci. USA*, 110, 6895–6900,
954 <https://doi.org/10.1073/pnas.1215513110>, 2013.
- 955 Darvishzadeh, R., Skidmore, A., Schlerf, M., and Atzberger, C.: Inversion of a radiative transfer
956 model for estimating vegetation LAI and chlorophyll in a heterogeneous grassland. *Remote
957 Sens. Environ.*, 112, 2592–2604, <https://doi.org/10.1016/j.rse.2007.12.003>, 2008.
- 958 Diaz, S., Kattge, J., Cornelissen, J. H., Wright, I. J., Lavorel, S., Dray, S., Reu, B., Kleyer, M., Wirth,
959 C., Prentice, I. C., Garnier, E., Bonisch, G., Westoby, M., Poorter, H., Reich, P. B., Moles, A.
960 T., Dickie, J., Gillison, A. N., Zanne, A. E., Chave, J., Wright, S. J., Sheremet'ev, S. N., Jactel,
961 H., Baraloto, C., Cerabolini, B., Pierce, S., Shipley, B., Kirkup, D., Casanoves, F., Joswig, J.
962 S., Gunther, A., Falczuk, V., Ruger, N., Mahecha, M. D., and Gorne, L. D.: The global spectrum
963 of plant form and function. *Nature*, 529, 167–171, <https://doi.org/10.1038/nature16489>, 2016.
- 964 Diaz, S., Hodgson, J. G., Thompson, K., Cabido, M., Cornelissen, J. H. C., Jalili, A., Montserrat-
965 Marti, G., Grime, J. P., Zarrinkamar, F., Asri, Y., Band, S. R., Basconcelo, S., Castro-Diez, P.,
966 Funes, G., Hamzehee, B., Khoshnevi, M., Perez-Harguindeguy, N., Perez-Rontome, M. C.,
967 Shirvany, F. A., Vendramini, F., Yazdani, S., Abbas-Azimi, R., Bogaard, A., Boustani, S.,
968 Charles, M., Dehghan, M., de Torres-Espuny, L., Falczuk, V., Guerrero-Campo, J., Hynd, A.,
969 Jones, G., Kowsary, E., Kazemi-Saeed, F., Maestro-Martinez, M., Romo-Diez, A., Shaw, S.,
970 Siavash, B., Villar-Salvador, P., and Zak, M. R.: The plant traits that drive ecosystems: evidence
971 from three continents. *J. Veg. Sci.*, 15, 295–304, [https://doi.org/10.1111/j.1654-
972 1103.2004.tb02266.x](https://doi.org/10.1111/j.1654-1103.2004.tb02266.x), 2004.
- 973 Elith, J., Leathwick, J. R., and Hastie, T.: A working guide to boosted regression trees. *J. Anim.
974 Ecol.*, 77, 802–813, <https://doi.org/10.1111/j.1365-2656.2008.01390.x>, 2008.
- 975 Elith, J., Kearney, M., and Phillips, S.: The art of modelling range-shifting species. *Methods Ecol.
976 Evol.*, 1, 330–342, <https://doi.org/10.1111/j.2041-210X.2010.00036.x>, 2010.
- 977 Elith, J., Graham, C. H., Anderson, R. P., Dudik, M., Ferrier, S., Guisan, A., Hijmans, R. J.,
978 Huettmann, F., Leathwick, J. R., Lehmann, A., Li, J., Lohmann, L. G., Loiselle, B. A., Manion,
979 G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J. M., Peterson, A. T., Phillips, S. J.,
980 Richardson, K., Scachetti-Pereira, R., Schapire, R. E., Soberon, J., Williams, S., Wisz, M. S.,
981 and Zimmermann, N. E.: Novel methods improve prediction of species' distributions from
982 occurrence data. *Ecography*, 29, 129–151, <https://doi.org/10.1111/j.2006.0906-7590.04596.x>,
983 2006.
- 984 Finzi, A. C., Austin, A. T., Cleland, E. E., Frey, S. D., Houlton, B. Z., and Wallenstein, M. D.:
985 Responses and feedbacks of coupled biogeochemical cycles to climate change: examples from
986 terrestrial ecosystems. *Front. Ecol. Environ.*, 9, 61–67, <https://doi.org/10.1890/100001>, 2011.
- 987 Foley, J. A., Prentice, I. C., Ramankutty, N., Levis, S., Pollard, D., Sitch, S., and Haxeltine, A.: An
988 integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation
989 dynamics. *Global Biogeochem. Cy.*, 10, 603–628, <https://doi.org/10.1029/96gb02692>, 1996.
- 990 Freschet, G. T., Cornelissen, J. H. C., van Logtestijn, R. S. P., and Aerts, R.: Evidence of the ‘plant



- 991 economics spectrum' in a subarctic flora. *J. Ecol.*, 98, 362–373, <https://doi.org/10.1111/j.1365->
992 2745.2009.01615.x, 2010.
- 993 Grime, J. P.: Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.*,
994 86, 902–910, <https://doi.org/10.1046/j.1365-2745.1998.00306.x>, 1998.
- 995 He, N., Yan, P., Liu, C., Xu, L., Li, M., Van Meerbeek, K., Zhou, G., Zhou, G., Liu, S., Zhou, X.,
996 Li, S., Niu, S., Han, X., Buckley, T. N., Sack, L., and Yu, G.: Predicting ecosystem productivity
997 based on plant community traits. *Trends Plant Sci.*, 28, 43–53,
998 <https://doi.org/10.1016/j.tplants.2022.08.015>, 2023.
- 999 Hodgson, J. G., Montserrat-Marti, G., Charles, M., Jones, G., Wilson, P., Shipley, B., Sharafi, M.,
1000 Cerabolini, B. E. L., Cornelissen, J. H. C., Band, S. R., Bogard, A., Castro-Diez, P., Guerrero-
1001 Campo, J., Palmer, C., Perez-Rontome, M. C., Carter, G., Hynd, A., Romo-Diez, A., Espuny,
1002 L. D., and Pla, F. R.: Is leaf dry matter content a better predictor of soil fertility than specific
1003 leaf area? *Ann. Bot.*, 108, 1337–1345, <https://doi.org/10.1093/aob/mcr225>, 2011.
- 1004 Hoeber, S., Leuschner, C., Köhler, L., Arias-Aguilar, D., and Schuldt, B.: The importance of
1005 hydraulic conductivity and wood density to growth performance in eight tree species from a
1006 tropical semi-dry climate. *Forest Ecol. Manag.*, 330, 126–136,
1007 <https://doi.org/10.1016/j.foreco.2014.06.039>, 2014.
- 1008 Jónsdóttir, I. S., Halbritter, A. H., Christiansen, C. T., Althuizen, I. H. J., Haugum, S. V., Henn, J. J.,
1009 Björnsdóttir, K., Maitner, B. S., Malhi, Y., Michaletz, S. T., Roos, R. E., Klanderud, K., Lee,
1010 H., Enquist, B. J., and Vandvik, V.: Intraspecific trait variability is a key feature underlying
1011 high Arctic plant community resistance to climate warming. *Ecol. Monogr.*, 93,
1012 <https://doi.org/10.1002/ecm.1555>, 2022.
- 1013 Jung, V., Violle, C., Mondy, C., Hoffmann, L., and Muller, S.: Intraspecific variability and trait-
1014 based community assembly. *J. Ecol.*, 98, 1134–1140, <https://doi.org/10.1111/j.1365->
1015 2745.2010.01687.x, 2010.
- 1016 Kattge, J., Diaz, S., Lavorel, S., Prentice, C., Leadley, P., Bonisch, G., Garnier, E., Westoby, M.,
1017 Reich, P. B., Wright, I. J., Cornelissen, J. H. C., Violle, C., Harrison, S. P., van Bodegom, P. M.,
1018 Reichstein, M., Enquist, B. J., Soudzilovskaia, N. A., Ackerly, D. D., Anand, M., Atkin, O., et
1019 al.: TRY - a global database of plant traits. *Glob. Change Biol.*, 17, 2905–2935,
1020 <https://doi.org/10.1111/j.1365-2486.2011.02451.x>, 2011.
- 1021 Kattge, J., Bonisch, G., Diaz, S., Lavorel, S., Prentice, I. C., Leadley, P., Tautenhahn, S., Werner, G.
1022 D. A., Aakala, T., Abedi, M., Acosta, A. T. R., Adamidis, G. C., Adamson, K., Aiba, M., Albert,
1023 C. H., Alcantara, J. M., Alcazar, C. C., Aleixo, I., Ali, H., Amiaud, B., et al.: TRY plant trait
1024 database - enhanced coverage and open access. *Global Change Biol.*, 26, 119–188,
1025 <https://doi.org/10.1111/gcb.14904>, 2020.
- 1026 King, D. A., Davies, S. J., Tan, S., and Noor, N. S. M.: The role of wood density and stem support
1027 costs in the growth and mortality of tropical trees. *J. Ecol.*, 94, 670–680,
1028 <https://doi.org/10.1111/j.1365-2745.2006.01112.x>, 2006.



- 1029 Kirilenko, A. P., Belotelov, N. V., and Bogatyrev, B. G.: Global model of vegetation migration:
1030 incorporation of climatic variability. *Ecol. Model.*, 132, 125–133,
1031 [https://doi.org/10.1016/S0304-3800\(00\)00310-0](https://doi.org/10.1016/S0304-3800(00)00310-0), 2000.
- 1032 LeBauer, D. S., and Treseder, K. K.: Nitrogen limitation of net primary productivity in terrestrial
1033 ecosystems is globally distributed. *Ecology*, 89, 371–379, <https://doi.org/10.1890/06-2057.1>,
1034 2008.
- 1035 Leishman, M. R., Wright, I. J., Moles, A. T., and Westoby, M. The evolutionary ecology of seed size
1036 in: *Seeds: the ecology of regeneration in plant communities*, 2nd edn, edited by: Fenner, M.
1037 CAB International, Wallingford, UK, 31–57, <https://doi.org/10.1079/9780851994321.0031>,
1038 2000.
- 1039 Li, C. X., Wulf, H., Schmid, B., He, J. S., and Schaepman, M. E.: Estimating plant traits of alpine
1040 grasslands on the Qinghai-Tibetan Plateau using remote sensing. *IEEE J. Sel. Top. Appl. Earth
1041 Obs. Remote Sens.*, 11, 2263–2275, <https://doi.org/10.1109/jstars.2018.2824901>, 2018.
- 1042 Li, D. J., Ives, A. R., and Waller, D. M.: Can functional traits account for phylogenetic signal in
1043 community composition? *New Phytol.*, 214, 607–618, <https://doi.org/10.1111/nph.14397>,
1044 2017.
- 1045 Li, Y. Q., Reich, P. B., Schmid, B., Shrestha, N., Feng, X., Lyu, T., Maitner, B. S., Xu, X., Li, Y. C.,
1046 Zou, D. T., Tan, Z. H., Su, X. Y., Tang, Z. Y., Guo, Q. H., Feng, X. J., Enquist, B. J., and Wang,
1047 Z. H.: Leaf size of woody dicots predicts ecosystem primary productivity. *Ecol. Lett.*, 23, 1003–
1048 1013, <https://doi.org/10.1111/ele.13503>, 2020.
- 1049 Liang, X. Y., Ye, Q., Liu, H., and Brodrribb, T. J.: Wood density predicts mortality threshold for
1050 diverse trees. *New Phytol.*, 229, <https://doi.org/10.1111/nph.17117>, 2021.
- 1051 Liaw, A., and Wiener, M.: Classification and Regression by randomForest. *R News*, 2, 18–22, 2002.
- 1052 Liu, H. Y., and Yin, Y.: Response of forest distribution to past climate change: an insight into future
1053 predictions. *Chinese Science Bulletin*, 58, 4426–4436, <https://doi.org/10.1007/s11434-013-6032-7>, 2013.
- 1055 Loozen, Y., Rebel, K. T., Karssenber, D., Wassen, M. J., Sardans, J., Peñuelas, J., and De Jong, S.
1056 M.: Remote sensing of canopy nitrogen at regional scale in Mediterranean forests using the
1057 spaceborne MERIS Terrestrial Chlorophyll Index. *Biogeosciences*, 15, 2723–2742,
1058 <https://doi.org/10.5194/bg-15-2723-2018>, 2018.
- 1059 Loozen, Y., Rebel, K. T., de Jong, S. M., Lu, M., Ollinger, S. V., Wassen, M. J., and Karssenber,
1060 D.: Mapping canopy nitrogen in European forests using remote sensing and environmental
1061 variables with the random forests method. *Remote Sens. Environ.*, 247, 111933,
1062 <https://doi.org/10.1016/j.rse.2020.111933>, 2020.
- 1063 Madani, N., Kimball, J. S., Ballantyne, A. P., Affleck, D. L. R., van Bodegom, P. M., Reich, P. B.,
1064 Kattge, J., Sala, A., Nazeri, M., Jones, M. O., Zhao, M., and Running, S. W.: Future global
1065 productivity will be affected by plant trait response to climate. *Sci. Rep.*, 8, 1–10,
1066 <https://doi.org/10.1038/s41598-018-21172-9>, 2018.



- 1067 Martínez-Vilalta, J., Mencuccini, M., Vayreda, J., and Retana, J.: Interspecific variation in functional
1068 traits, not climatic differences among species ranges, determines demographic rates across 44
1069 temperate and Mediterranean tree species. *J. Ecol.*, 98, 1462–1475,
1070 <https://doi.org/10.1111/j.1365-2745.2010.01718.x>, 2010.
- 1071 Matheny, A. M., Mirfenderesgi, G., and Bohrer, G.: Trait-based representation of hydrological
1072 functional properties of plants in weather and ecosystem models. *Plant Divers*, 39, 1–12,
1073 <https://doi.org/10.1016/j.pld.2016.10.001>, 2017.
- 1074 Moles, A. T., Warton, D. I., Warman, L., Swenson, N. G., Laffan, S. W., Zanne, A. E., Pitman, A.,
1075 Hemmings, F. A., and Leishman, M. R.: Global patterns in plant height. *J. Ecol.*, 97, 923–932,
1076 <https://doi.org/10.1111/j.1365-2745.2009.01526.x>, 2009.
- 1077 Moreno-Martínez, Á., Camps-Valls, G., Kattge, J., Robinson, N., Reichstein, M., van Bodegom, P.,
1078 Kramer, K., Cornelissen, J. H. C., Reich, P., Bahn, M., Niinemets, Ü., Peñuelas, J., Craine, J.
1079 M., Cerabolini, B. E. L., Minden, V., Laughlin, D. C., Sack, L., Allred, B., Baraloto, C., Byun,
1080 C., Soudzilovskaia, N. A., and Running, S. W.: A methodology to derive global maps of leaf
1081 traits using remote sensing and climate data. *Remote Sens. Environ.*, 218, 69–88,
1082 <https://doi.org/10.1016/j.rse.2018.09.006>, 2018.
- 1083 Myers-Smith, I. H., Thomas, H. J. D., and Bjorkman, A. D.: Plant traits inform predictions of tundra
1084 responses to global change. *New Phytol.*, 221, 1742–1748, <https://doi.org/10.1111/nph.15592>,
1085 2019.
- 1086 Peng, C. H.: From static biogeographical model to dynamic global vegetation model: a global
1087 perspective on modelling vegetation dynamics. *Ecol. Model.*, 135, 33–54,
1088 [https://doi.org/10.1016/S0304-3800\(00\)00348-3](https://doi.org/10.1016/S0304-3800(00)00348-3), 2000.
- 1089 Perez-Harguindeguy, N., Diaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte,
1090 M. S., Cornwell, W. K., Craine, J. M., Gurvich, D. E., Urcelay, C., Veneklaas, E. J., Reich, P.
1091 B., Poorter, L., Wright, I. J., Ray, P., Enrico, L., Pausas, J. G., de Vos, A. C., Buchmann, N.,
1092 Funes, G., Quetier, F., Hodgson, J. G., Thompson, K., Morgan, H. D., ter Steege, H., van der
1093 Heijden, M. G. A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M. V., Conti, G., Staver, A. C.,
1094 Aquino, S., and Cornelissen, J. H. C.: New handbook for standardised measurement of plant
1095 functional traits worldwide. *Aust. Bot.*, 61, 167–234, <https://doi.org/10.1071/bt12225>, 2013.
- 1096 Piao, S. L., He, Y., Wang, X. H., and Chen, F. H.: Estimation of China’s terrestrial ecosystem carbon
1097 sink: Methods, progress and prospects. *Science China Earth Sciences*, 65, 641–651,
1098 <https://doi.org/10.1007/s11430-021-9892-6>, 2022.
- 1099 Potapov, P., Li, X. Y., Hernandez-Serna, A., Tyukavina, A., Hansen, M. C., Kommareddy, A.,
1100 Pickens, A., Turubanova, S., Tang, H., Silva, C. E., Armston, J., Dubayah, R., Blair, J. B.,
1101 Hofton, M.: Mapping global forest canopy height through integration of GEDI and Landsat
1102 data, *Remote Sens. Environ.*, 253, 112165, <https://doi.org/10.1016/j.rse.2020.112165>, 2021.
- 1103 Qiao, J. J., Zuo, X. A., Yue, P., Wang, S. K., Hu, Y., Guo, X. X., Li, X. Y., Lv, P., Guo, A. X., and
1104 Sun, S. S.: High nitrogen addition induces functional trait divergence of plant community in a



- 1105 temperate desert steppe. *Plant and Soil*, <https://doi.org/10.1007/s11104-023-05910-1>, 2023.
- 1106 Reich, P. B., and Oleksyn, J.: Global patterns of plant leaf N and P in relation to temperature and
1107 latitude. *Proc. Natl. Acad. Sci. U. S. A.*, 101, 11001–11006,
1108 https://doi.org/10.1073/pnas.0403588101_2004.
- 1109 Reich, P. B., and Cornelissen, H.: The world-wide ‘fast-slow’ plant economics spectrum: a traits
1110 manifesto. *Journal of Ecology*, 102, 275–301, <https://doi.org/10.1111/1365-2745.12211>, 2014.
- 1111 Reich, P. B., Uhl, C., Waiters, M. B., and Ellsworth, D. S.: Leaf lifespan as a determinant of leaf
1112 structure and function among 23 Amazonian tree species. *Oecologia*, 86, 16–24,
1113 <https://doi.org/10.1007/BF00317383>, 1991.
- 1114 Renninger, H. J., Phillips, N., and Hodel, D. R.: Comparative hydraulic and anatomic properties in
1115 palm trees (*Washingtonia robusta*) of varying heights: implications for hydraulic limitation to
1116 increased height growth. *Trees*, 23, 911–921, <https://doi.org/10.1007/s00468-009-0333-0>,
1117 2009.
- 1118 Ridgeway, G.: Gbm: generalized boosted regression models. R package version 1.5-6, Available at:
1119 <http://cran.r-project.org/web/packages/gbm/index.html>, accessed 11/02/20092006.
- 1120 Roderick, M. L., and Berry, S. L.: Linking wood density with tree growth and environment: a
1121 theoretical analysis based on the motion of water. *New Phytol.*, 149, 473–485,
1122 <https://doi.org/10.1046/j.1469-8137.2001.00054.x>, 2002.
- 1123 Roll, U., Geffen, E., and Yom-Tov, Y.: Linking vertebrate species richness to tree canopy height on
1124 a global scale. *Glob. Ecol. Biogeogr.*, 24, 814–825, <https://doi.org/10.1111/geb.12325>, 2015.
- 1125 Romero, A., Aguado, I., and Yebra, M.: Estimation of dry matter content in leaves using normalized
1126 indexes and PROSPECT model inversion. *Int. J. Remote Sens.*, 33, 396–414,
1127 <https://doi.org/10.1080/01431161.2010.532819>, 2012.
- 1128 Sakschewski, B., von Bloh, W., Boit, A., Rammig, A., Kattge, J., Poorter, L., Penuelas, J., and
1129 Thonicke, K.: Leaf and stem economics spectra drive diversity of functional plant traits in a
1130 dynamic global vegetation model. *Global Change Biol.*, 21, 2711–2725,
1131 https://doi.org/10.1111/gcb.12870_2015.
- 1132 Scheiter, S., Langan, L., and Higgins, S. I.: Next-generation dynamic global vegetation models:
1133 learning from community ecology. *New Phytol.*, 198, 957–969,
1134 <https://doi.org/10.1111/nph.12210>, 2013.
- 1135 Shangguan, W., Dai, Y. J., Liu, B. Y., Zhu, A. X., Duan, Q. Y., Wu, L. Z., Ji, D. Y., Ye, A. Z., Yuan,
1136 H., Zhang, Q., Chen, D. D., Chen, M., Chu, J. T., Dou, Y. J., Guo, J. X., Li, H. Q., Li, J. J.,
1137 Liang, L., Liang, X., Liu, H. P., Liu, S. Y., Miao, C. Y., and Zhang, Y. Z.: A China data set of
1138 soil properties for land surface modeling. *J. Adv. Model. Earth Syst.*, 5, 212–224,
1139 <https://doi.org/10.1002/jame.20026>, 2013.
- 1140 Siefert, A., Violle, C., Chalmandrier, L., Albert, C. H., Taudiere, A., Fajardo, A., Aarssen, L. W.,
1141 Baraloto, C., Carlucci, M. B., Cianciaruso, M. V., de, L. D. V., de Bello, F., Duarte, L. D.,
1142 Fonseca, C. R., Freschet, G. T., Gaucherand, S., Gross, N., Hikosaka, K., Jackson, B., Jung, V.,



- 1143 Kamiyama, C., Katabuchi, M., Kembel, S. W., Kichenin, E., Kraft, N. J., Lagerstrom, A.,
1144 Bagousse-Pinguet, Y. L., Li, Y., Mason, N., Messier, J., Nakashizuka, T., Overton, J. M., Peltzer,
1145 D. A., Perez-Ramos, I. M., Pillar, V. D., Prentice, H. C., Richardson, S., Sasaki, T., Schamp, B.
1146 S., Schob, C., Shipley, B., Sundqvist, M., Sykes, M. T., Vandewalle, M., and Wardle, D. A.: A
1147 global meta-analysis of the relative extent of intraspecific trait variation in plant communities.
1148 *Ecol. Lett.*, 18, 1406–1419, <https://doi.org/10.1111/ele.12508>, 2015.
- 1149 Šímová, I., Sandel, B., Enquist, B. J., Michaletz, S. T., Kattge, J., Violle, C., McGill, B. J., Blonder,
1150 B., Engemann, K., Peet, R. K., Wisser, S. K., Morueta-Holme, N., Boyle, B., Kraft, N. J. B.,
1151 Svenning, J. C., and Hector, A.: The relationship of woody plant size and leaf nutrient content
1152 to large-scale productivity for forests across the Americas. *J. Ecol.*, 107, 2278–2290,
1153 <https://doi.org/10.1111/1365-2745.13163>, 2019.
- 1154 Sitch, S., Huntingford, C., Gedney, N., Levy, P. E., Lomas, M., Piao, S. L., Betts, R., Ciais, P., Cox,
1155 P., Friedlingstein, P., Jones, C. D., Prentice, I. C., and Woodward, F. I.: Evaluation of the
1156 terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five
1157 Dynamic Global Vegetation Models (DGVMs). *Global Change Biol.*, 14, 2015–2039,
1158 <https://doi.org/10.1111/j.1365-2486.2008.01626.x>, 2008.
- 1159 Smart, S. M., Glanville, H. C., Blanes, M. d. C., Mercado, L. M., Emmett, B. A., Jones, D. L., Cosby,
1160 B. J., Marrs, R. H., Butler, A., Marshall, M. R., Reinsch, S., Herrero-Jáuregui, C., Hodgson, J.
1161 G., and Field, K.: Leaf dry matter content is better at predicting above-ground net primary
1162 production than specific leaf area. *Funct. Ecol.*, 31, 1336–1344, <https://doi.org/10.1111/1365-2435.12832>, 2017.
- 1164 Telenius, A.: Biodiversity information goes public: GBIF at your service. *Nord. J. Bot.*, 29, 378–
1165 381, <https://doi.org/10.1111/j.1756-1051.2011.01167.x>, 2011.
- 1166 Thomas, D. S., Montagu, K. D., and Conroy, J. P.: Changes in wood density of *Eucalyptus*
1167 *camaldulensis* due to temperature—the physiological link between water viscosity and wood
1168 anatomy. *Forest Ecol. Manag.*, 193, 157–165, <https://doi.org/10.1016/j.foreco.2004.01.028>,
1169 2004.
- 1170 Thomas, S. C.: Photosynthetic capacity peaks at intermediate size in temperate deciduous trees. *Tree*
1171 *Physiol.*, 30, 555–573, <https://doi.org/10.1093/treephys/tpq005>, 2010.
- 1172 Trabucco, A., and Zomer, R. J.: Global Aridity Index and Potential Evapo-Transpiration (ET0)
1173 Climate Database v2. CGIAR Consortium for Spatial Information (CGIAR-CSI),
1174 <https://cgiarcsi.community>, 2018.
- 1175 Van Bodegom, P. M., Douma, J. C., Witte, J. P. M., Ordoñez, J. C., Bartholomeus, R. P., and Aerts,
1176 R.: Going beyond limitations of plant functional types when predicting global ecosystem-
1177 atmosphere fluxes: exploring the merits of traits-based approaches. *Glob. Ecol. Biogeogr.*, 21,
1178 625–636, <https://doi.org/10.1111/j.1466-8238.2011.00717.x>, 2012.
- 1179 Verheijen, L. M., Aerts, R., Bonisch, G., Kattge, J., and Van Bodegom, P. M.: Variation in trait trade-
1180 offs allows differentiation among predefined plant functional types: implications for predictive



- 1181 ecology. *New Phytol.*, 209, 563–575, <https://doi.org/10.1111/nph.13623>, 2016.
- 1182 Wang, H., Harrison, S. P., Prentice, I. C., Yang, Y. Z., Bai, F., Togashi, H. F., Wang, M., Zhou, S. X.,
1183 and Ni, J.: The China Plant Trait Database: toward a comprehensive regional compilation of
1184 functional traits for land plants. *Ecology*, 99, 500, <https://doi.org/10.1002/ecy.2091>, 2018.
- 1185 Wang, Z. H., Li, Y. Q., Su, X. Y., Tao, S. L., Feng, X., Wang, Q. G., Xu, X. T., Liu, Y. P., Michaletz,
1186 S. T., Shrestha, N., Larjavaara, M., and Enquist, B. J.: Patterns and ecological determinants of
1187 woody plant height in eastern Eurasia and its relation to primary productivity. *Journal of Plant
1188 Ecology*, 12, 791–803, <https://doi.org/10.1093/jpe/rtz025>, 2019.
- 1189 Webb, C. T., Hoeting, J. A., Ames, G. M., Pyne, M. I., and LeRoy Poff, N.: A structured and dynamic
1190 framework to advance traits-based theory and prediction in ecology. *Ecol. Lett.*, 13, 267–283,
1191 <https://doi.org/10.1111/j.1461-0248.2010.01444.x>, 2010.
- 1192 Westoby, M.: A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant Soil*, 199, 213–227,
1193 1998.
- 1194 Wright, I. J., Dong, N., Maire, V., Prentice, I. C., Westoby, M., Diaz, S., Gallagher, R. V., Jacobs, B.
1195 F., Kooyman, R., Law, E. A., Leishman, M. R., Niinemets, U., Reich, P. B., Sack, L., Villar, R.,
1196 Wang, H., and Wilf, P.: Global climatic drivers of leaf size. *Science*, 357, 917–921,
1197 <https://doi.org/10.1126/science.aal4760>, 2017.
- 1198 Wright, I. J., Reich, P. B., Westoby, M., Ackerly, D. D., Baruch, Z., Bongers, F., Cavender-Bares, J.,
1199 Chapin, T., Cornelissen, J. H. C., Diemer, M., Flexas, J., Garnier, E., Groom, P. K., Gulias, J.,
1200 Hikosaka, K., Lamont, B. B., Lee, T., Lee, W., Lusk, C., Midgley, J. J., Navas, M. L., Niinemets,
1201 U., Oleksyn, J., Osada, N., Poorter, H., Poot, P., Prior, L., Pyankov, V. I., Roumet, C., Thomas,
1202 S. C., Tjoelker, M. G., Veneklaas, E. J., and Villar, R.: The worldwide leaf economics spectrum.
1203 *Nature*, 428, 821–827, <https://doi.org/10.1038/nature02403>, 2004.
- 1204 Wullschleger, S. D., Epstein, H. E., Box, E. O., Euskirchen, E. S., Goswami, S., Iversen, C. M.,
1205 Kattge, J., Norby, R. J., van Bodegom, P. M., and Xu, X.: Plant functional types in earth system
1206 models: past experiences and future directions for application of dynamic vegetation models
1207 in high-latitude ecosystems. *Ann. Bot.*, 114, 1–16, <https://doi.org/10.1093/aob/mcu077>, 2014.
- 1208 Yan, P., He, N. P., Yu, K. L., Xu, L., and Van Meerbeek, K.: Integrating multiple plant functional
1209 traits to predict ecosystem productivity. *Commun Biol*, 6, 239, <https://doi.org/10.1038/s42003-023-04626-3>, 2023.
- 1211 Yang, Y. Z., Zhu, Q. A., Peng, C. H., Wang, H., Xue, W., Lin, G. H., Wen, Z. M., Chang, J., Wang,
1212 M., Liu, G. B., and Li, S. Q.: A novel approach for modelling vegetation distributions and
1213 analysing vegetation sensitivity through trait-climate relationships in China. *Sci. Rep.*, 6, 24110,
1214 <https://doi.org/10.1038/srep24110>, 2016.
- 1215 Yang, Y. Z., Zhao, J., Zhao, P. X., Wang, H., Wang, B. H., Su, S. F., Li, M. X., Wang, L. M., Zhu,
1216 Q. A., Pang, Z. Y., and Peng, C. H.: Trait-Based Climate Change Predictions of Vegetation
1217 Sensitivity and Distribution in China. *Front. Plant Sci.*, 10, 908,
1218 <https://doi.org/10.3389/fpls.2019.00908>, 2019.



- 1219 Yurova, A. Y., and Volodin, E. M.: Coupled simulation of climate and vegetation dynamics. *Izv.*,
1220 *Atmos. . Ocean. Phy.*, 47, 531-539, <https://doi.org/10.1134/s0001433811050124>, 2011.
- 1221 Zaehle, S., and Friend, A. D.: Carbon and nitrogen cycle dynamics in the O-CN land surface model:
1222 1. Model description, site-scale evaluation, and sensitivity to parameter estimates. *Global*
1223 *Biogeochem. Cy.*, 24, n/a-n/a, <https://doi.org/10.1029/2009gb003521>, 2010.
- 1224 Zepeda, V., and Martorell, C.: Seed mass equalises the strength of positive and negative plant-plant
1225 interactions in a semi-arid grassland. *Oecologia*, 190, 287–296,
1226 <https://doi.org/10.1007/s00442-018-04326-4>, 2019.