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# Linking seed size and number to trait syndromes in trees

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### 134 **Author contributions**

135 MB and JSC performed analyses and co-wrote the paper, MB and JSC designed the study, JSC  
136 compiled the MASTIF network, and wrote the MASTIF model and software, BC, GK, VJ, and  
137 TQ co-wrote the paper, and all authors contributed data and revised the paper.

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## 155 **Data availability statement**

156 The data supporting the results are attached in the Online Supplement.

## 157 **Summary**

158 **Aim** : Understanding mechanisms that maintain forest diversity under changing climate can  
159 benefit from the knowledge of traits that are closely linked to fitness. We tested whether the link  
160 between traits and seed number and seed size is consistent with two hypotheses, termed the leaf  
161 economics spectrum and the plant size syndrome, or if reproduction represents an independent  
162 dimension related to a seed size and number trade-off.

163 **Location** : The majority of the data comes from Europe, North and Central America, and East  
164 Asia. A majority of the data comes from South America, Africa, and Australia.

165 **Time period** : 1960-2022.

166 **Major taxa studied** : Trees.

167 **Methods** : We gathered 12 million observations of the number of seeds produced in 784 tree  
168 species. We estimated the number of seeds produced by individual trees and scaled it up to  
169 the species level. Next, we used PCA and Generalized Joint Attribute Modeling to map seed  
170 number and size on the tree traits spectrum.

171 **Results** : Incorporating seed size and number into trait analysis while controlling for environ-  
172 ment and phylogeny with the GJAM exposes relationships in trees that might otherwise remain  
173 hidden. Production of the large total biomass of seeds (product of seed number and seed size  
174 hereafter species seed productivity, SSP) is associated with high leaf area, low foliar nitrogen,  
175 low specific leaf area (SLA), and dense wood. Production of high seed numbers is associated  
176 with small seeds produced by nutrient-demanding species with softwood, small leaves, and high  
177 SLA. Trait covariation is consistent with opposing strategies, one fast-growing, early succes-  
178 sional, with high dispersal and the other slow-growing, stress-tolerant, that recruit in shaded  
179 conditions.

180 **Main conclusion** : Earth system models currently assume that reproductive allocation is  
181 indifferent among plant functional types. Easily measurable seed size is a strong predictor of  
182 the seed number and species seed productivity. The connection of SSP with the functional traits  
183 can form the first basis of improved fecundity prediction across global forests.

184 —  
185 *keywords:* fecundity | functional traits | life history strategies | size syndrome | leaf economics  
186 | tree recruitment |

## 188 **Introduction**

189 Understanding the mechanisms that promote and maintain forest tree diversity under a warming  
190 climate can benefit from the knowledge of traits that are closely linked to fitness (Adler *et al.*,

191 2014; Paine *et al.*, 2015; Yang *et al.*, 2018; Kelly *et al.*, 2021). Adaptive evolution operates on  
192 the variation that affects survival and reproduction. Leaf traits, wood density, and plant height  
193 are clearly important for trees, yet their connections to fitness are indirect (Wright *et al.*, 2004;  
194 Violle *et al.*, 2007; Chave *et al.*, 2009; Díaz *et al.*, 2016). For example, large, thin, short-lived  
195 leaves with high nitrogen content confer clear benefits in high-resource environments where  
196 long-lived, highly lignified leaves are less advantageous (Shreve, 1925; Field & Mooney, 1986;  
197 Reich, 2014). Fitness is the quantitative representation of individual reproductive success, an  
198 organism's ability to pass its genetic material to its offspring. Thus, interpreting the fitness  
199 implications of traits often requires broad extrapolation, such as ecophysiological measurements  
200 describing minute-scale responses of leaves, roots, or xylem elements that are integrated with  
201 many other responses to determine survival and/or reproduction over the lifetimes of whole  
202 plants. While no trait links directly to fitness in trees, many are so weakly tied to fitness  
203 that their utility for comparative studies remains uncertain. In that light, seedling recruitment  
204 at tropical Barro Colorado Island provides a more direct link to fitness (Rüger *et al.*, 2018,  
205 2020). Nonetheless, given that recruitment varies for each species at each site, the species-level  
206 reproductive effort could be a valuable extension for trait understanding. Only recently have  
207 long-term and geographically extensive measurements of the number of seeds produced by trees  
208 needed for species-level synthesis become available (Clark *et al.*, 2021; Journé *et al.*, 2022; Qiu  
209 *et al.*, 2022; Sharma *et al.*, 2022). Here, we re-examine the hypotheses that describe the seed  
210 number and size as part of an omnibus syndrome that explains all traits (e.g., fast-slow plant  
211 economics spectrum) or, alternatively, as a separate axis of variation.

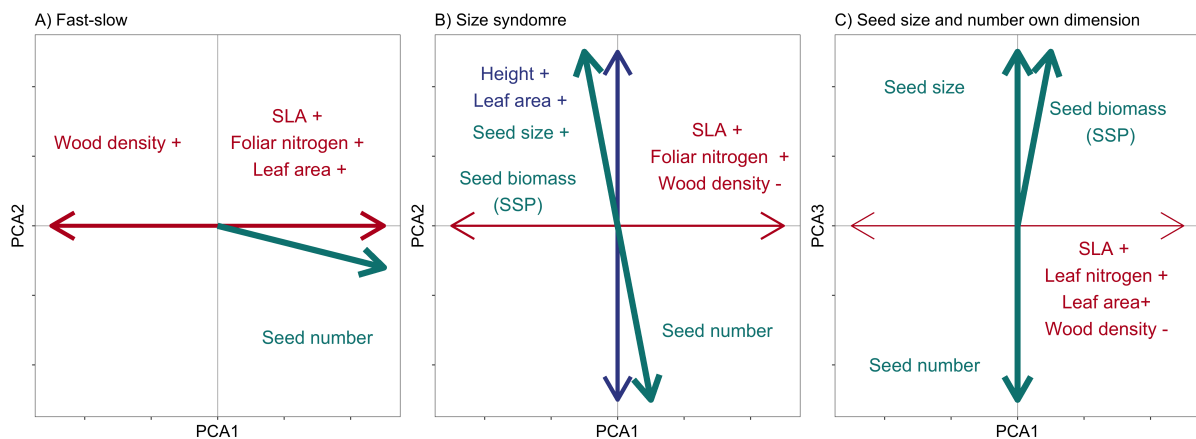
212 Principal components analysis (PCA) has been a primary tool for exploring combined trait  
213 variation, contributing to at least three interpretations for forest trees. One view sees the number  
214 of seeds produced and their size together with leaf traits as part of a “fast-slow” continuum  
215 of plant strategies (Reich, 2014). That dimension represents the trade-off between resource  
216 acquisition and processing, and it could be linked to a growth-survival trade-off (Poorter *et al.*,  
217 2008; Wright *et al.*, 2010; Rüger *et al.*, 2018). Cheaply constructed leaves that assimilate carbon  
218 quickly, together with low wood density, characterize species that are resource-demanding, grow  
219 fast, and die young (Westoby *et al.*, 2002; Moles, 2018). In such species, the production of a  
220 large number of seeds may offset mortality losses (Muller-Landau, 2010; Reich, 2014). Species  
221 with some or all of these traits might dominate early successional stages through effective  
222 colonization, and they might not persist under intense competition (Poorter *et al.*, 2008; Wright  
223 *et al.*, 2010).

224 Alternatively, the size hypothesis suggests that the seed number and seed size is part of  
225 a stature-recruitment trade-off (Kohyama, 1993; Díaz *et al.*, 2016; Rüger *et al.*, 2018, 2020).  
226 According to this hypothesis, large plant size maximizes canopy performance at the expense  
227 of recruitment, and vice versa. The analysis of 282 co-occurring tree species at tropical Barro  
228 Colorado Island (BCI) emphasized a leaf-trait axis and a size-recruitment axis, with species  
229 characterized by small stature, small leaves, and small seeds having high recruitment (Rüger  
230 *et al.*, 2018). Follow-up studies indicated that stature-recruitment trade-off extends to tropical  
231 forests more generally Kambach *et al.* (2022).

232 Finally, seed number and seed size may represent a third, largely independent, dimension of  
233 variation, as proposed by the twin-filter (TF) hypothesis (Grime & Pierce, 2012). According  
234 to the TF, primary strategies such as fast-slow determine persistence for the climate/habitat  
235 norms, while traits involved in episodic events, which might include reproduction, affect fitness  
236 independent of other traits (Grime & Pierce, 2012; Pierce *et al.*, 2014). The leaf-height-seed  
237 (LHS) scheme of Westoby (1998) hypothesizes that seed size plays a role similar to reproduction  
238 in the TF model. In both hypotheses, plants can produce either many or few seeds (TF) or small

239 or large seeds (LHS), largely independent of other plant traits. All three of the foregoing  
 240 hypotheses imply an important role of seed number and seed size, and they assume that all traits  
 241 have some connection to fitness. The availability of species-level seed numbers can lend novel  
 242 insight to trait analysis due to its close connection to recruitment, a major demographic and  
 243 fitness indicator.

244 A limitation of summaries available from PCA comes from the fact that correlations include  
 245 all the indirect ways that traits could be associated. For example, a correlation between seed size  
 246 and wood density could occur if there was a need for high wood density in order to produce large  
 247 seeds. If true, this would be a direct relationship. Alternatively, both variables might be driven  
 248 by climate for reasons that do not depend on one another. In such a case, that would be an indirect  
 249 relationship. Another indirect relationship is represented by phylogenetic conservatism. Some  
 250 species groups tend to produce larger seeds or denser wood than others, even if environments that  
 251 might select for one or both traits change. The correlation structure exposed by PCA does not  
 252 discriminate between direct (conditional) and indirect (marginal) relationships. If relationships  
 253 are indirect, then conditional estimates offer the most transparent view of their connections  
 254 (Seyednasrollah & Clark, 2020). To quantify direct links between traits, the traditional study  
 255 with PCA is supplemented here with conditional relationships between traits using Generalized  
 256 Joint Attribute Modeling (GJAM) (Clark *et al.*, 2017). Including environment as fixed effects  
 257 and phylogenetic groups as random effects, GJAM decomposes trait relationships into direct  
 258 and indirect relationships. While we believe GJAM is a valuable extension, we present results  
 259 of PCA as well to facilitate comparison with past studies.



**Figure 1:** Hypothetical associations between dimensions of plant life strategies represented by functional traits and the seed number, seed size, and species seed productivity (the product of seed number and seed size, SSP developed by Qiu *et al.* (2022)). Seed production can be associated with: A) fast life syndrome (slow-fast resource turnover axis); B) size syndrome; C) its own, largely independent axis of seed size-seed number trade-off. Both seed number and SSP are divided by tree basal area in our analyses.

260 In this study, we analyze trait syndromes in trees from a perspective that includes the number  
 261 of seeds produced and seed size. The Masting Inference and Forecasting (MASTIF) network  
 262 includes 12 million tree-year observations of the number of seeds produced by 775,991 trees  
 263 from 784 species from a broad range of biomes (Journé *et al.*, 2022; Qiu *et al.*, 2022). To control  
 264 for variation within species and, thus, to sharpen our understanding of interspecific differences,  
 265 we estimate seed numbers produced by trees with an analytical framework that includes trees'  
 266 condition (species, size, shading), habitat (soils), and climate (temperature and moisture deficit),  
 267 while accommodating dependence between and within trees across years (Clark *et al.*, 2019).

268 This large sample size is important for the notoriously noisy seed production in trees (Kelly  
269 *et al.*, 2021), where tree-to-tree and year-to-year variation in seed number span several orders of  
270 magnitude (Clark *et al.*, 2004; Journé *et al.*, 2022). By combining seed number with seed size into  
271 species seed productivity (seed size x seed number, SSP, developed by Qiu *et al.* (2022)), we show  
272 how reproductive traits relate to one another separately and in combination. Combining seed  
273 number and seed size into SSP brings more exhaustive information on reproductive investment  
274 because species that invest in large seeds are producing more seeds than expected from the 1:1  
275 trade-off (Qiu *et al.*, 2022). For this reason, SSP should be more strongly aligned with seed size  
276 than seed number. By standardizing these metrics for the tree size we account for the variation in  
277 size distribution within the data and facilitate comparisons. For example, the SSP is the average  
278 annual species seed productivity per m<sup>2</sup> basal area at average environmental conditions across  
279 the species' range in the data (Qiu *et al.*, 2021a, 2022). If large seeds confer an advantage in  
280 competitive, shaded understories, while many small seeds allow colonization of distant sites,  
281 then SSP provides a direct link to fitness. The hypothesized relationships between seed number,  
282 seed size, SSP, and traits are summarized in Figure 1.

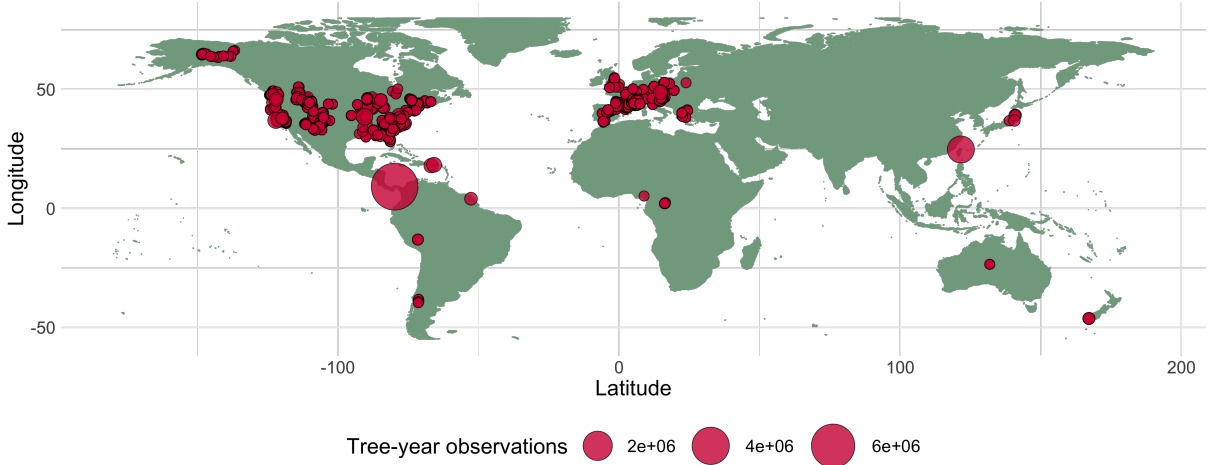
## 283 **Methods**

284 **Seed number, species seed productivity (SSP) and MASTIF model** Estimating the number  
285 of seeds produced in perennial plants suffers from extreme signal-to-noise problem, created  
286 by orders of magnitude variation from year to year and tree to tree (Pesendorfer *et al.*, 2021;  
287 Pearse *et al.*, 2020; Clark *et al.*, 2004) that can bury any trend (Clark *et al.*, 2021). There are as  
288 many time series as there are trees that must be modeled together because there is dependence  
289 created by among-trees synchrony in masting variation (Crone *et al.*, 2011; Bogdziewicz *et al.*,  
290 2021). Masting patterns are further complicated by the spatio-temporal variation in habitat and  
291 climate (Pesendorfer *et al.*, 2021; Pearse *et al.*, 2020). The many sources of variation mean that  
292 estimation of a seed number produced by trees can only be achieved from broad coverage and  
293 large sample sizes while accounting for individual trees' condition, local habitat, and climate  
294 (Clark *et al.*, 2021; Qiu *et al.*, 2021a; Sharma *et al.*, 2022). This is here achieved with the  
295 MASTIF model (Clark *et al.*, 2019).

296 The MASTIF model and data from the MASTIF network are summarized here, and exten-  
297 sively described in recent papers (Clark *et al.*, 2019, 2021; Qiu *et al.*, 2021a; Sharma *et al.*,  
298 2022; Journé *et al.*, 2022). The tree-year observations of seed numbers in the network come  
299 from seed traps and from crop counts. Data include longitudinal (repeated) observations on  
300 individual trees (99%) and opportunistic observations that come through the iNaturalist project  
301 (Clark *et al.*, 2019). Seed trap data consists of numbers of seeds that accumulate annually in  
302 mapped seed traps on forest inventory plots. A fitted dispersal kernel relates seed counts to  
303 mapped trees, accounting for uncertainty in seed transport and Poisson seed counts (Clark *et al.*,  
304 2019). Crop counts include counts of reproductive structures with estimates of the fraction of  
305 the crop observed, and beta-binomial distribution accounts for uncertainty in the crop-fraction  
306 estimates (Clark *et al.*, 2019). This study includes 12,008,722 tree-years from North America,  
307 South and Central America, Europe, Africa, Asia, and Oceania, which is gathered over 5,115  
308 sites and 787,444 trees (Fig. 2). The MASTIF model jointly estimates the number of seeds  
309 produced based on all the observations. The seed number (SN) and species seed productivity  
310 (SSP) (Qiu *et al.*, 2022) used in the analysis are calculated based on 297,690 mature individuals  
311 and 3,730,381 tree-years. The MASTIF model uses the whole dataset to estimate seed numbers  
312 produced annually, but the SN and SSP are calculated based on a mature tree subset of these  
313 estimates. The list of species included in the analysis is given in the Online Supplement as a csv



314 file.



**Figure 2:** Map of raw data used to estimate the number of seeds produced by trees with the MASTIF model.

315 The MASTIF model, detailed in Clark *et al.* (2019), is a dynamic biophysical model for  
 316 year-to-year and tree-to-tree seed production. The MASTIF model is a Bayesian hierarchical,  
 317 state–space model that allows for conditional independence in crop-count and seed-trap data  
 318 through latent states. The model estimates the number of seeds produced with conditional  
 319 fecundity, which depends on the probability that the tree is sexually mature, tree size, shading  
 320 (five classes from full sun to full shade), local climate, and soil conditions. Random effects  
 321 on individual and year allow for wide variation between trees and over time that is typical of  
 322 seed production. The posterior covariance between trees and years can take any form, avoiding  
 323 assumptions of standard time-series models, important due to the quasiperiodic variation in time  
 324 and varying levels of synchronicity between individual trees (Pesendorfer *et al.*, 2021). Model  
 325 structure and methodology were implemented with R, version 4.0 (R Core Team, 2020) and the  
 326 R package Mast Inference and Forecasting (MASTIF) (Clark *et al.*, 2019).

327 **Seed number and species seed productivity (SSP) at the tree and the species level** The  
 328 MASTIF model incorporates the effects of tree attributes with the environment on maturation  
 329 and conditional fecundity. To allow for an uncertain identification of seeds from trees of the  
 330 same genus and for dependence within trees over time and between trees, all three-years of a  
 331 genus are modeled jointly (Clark *et al.*, 2019, 2021). For each tree  $i$  of species  $s$  at stand  $j$   
 332 in year  $t$ , the expected seed number is the product of maturation probability  $\hat{\rho}$  and conditional  
 333 fecundity  $\hat{\psi}$ ,

$$E(f_{ijs,t}) = \hat{f}_{ijs,t} = \hat{\rho}_{ijs,t} \hat{\psi}_{ijs,t} \quad (1)$$

334 Conditional fecundity depends on predictors, individual effects, year effects, and error,

$$\log(\hat{\psi}_{ijs,t}) = \mathbf{x}'_{ijs,t} \boldsymbol{\beta}^{(x)} + \beta_{ijs}^{(w)} + \gamma_{g[ij]s,t} + \epsilon_{ijs,t} \quad (2)$$

335 where  $\mathbf{x}_{it}$  is a matrix holding individual attributes and environmental conditions (see *Gener-*  
 336 *alized joint attribute modeling* below), and  $\boldsymbol{\beta}^{(x)}$  are fixed-effects coefficients.  $\beta_{ijs}^{(w)}$  is the random  
 337 effect for tree  $i$  of species  $s$  at stand  $j$ .  $\gamma_{g[ij]s,t}$  are year effects that are random across groups  $g$   
 338 and fixed for the year  $t$  to account for interannual variation that is not fully captured by climate

339 anomalies. Group membership for year effects ( $g[ij]_s$ ) is defined by species-ecoRegion (Clark  
 340 *et al.*, 2019). There is a noise term  $\epsilon_{ijs,t}$ . Maturation probability  $\hat{\rho}_{ijs,t}$  accounts for the immature  
 341 state (for small trees) and failed crop in larger trees. The model implementation is open-access  
 342 with R package MASTIF, with algorithm details provided in Clark *et al.* (2019).

343 We estimated species investment into reproduction using two metrics, both scaled to the tree  
 344 basal area: annual seed number (SN), and annual species seed productivity (SSP; seed number  
 345  $\times$  seed mass) Qiu *et al.* (2022). Estimation of both SN and SSP starts with the estimation of  
 346 individual tree mean number of produced seeds that depends on each tree location that accounts  
 347 for effects of the environment and includes uncertainty for each year. Individual trees' number  
 348 of seeds produced over a species is then summarized as SN or SSP, as explained below. The  
 349 tree-level estimate of seed number, i.e., individual seed production (ISP), is the product of seed  
 350 size (its mass)  $m_s$  and seed number, scaled to tree basal area per year (Journé *et al.*, 2022).  
 351 We quantify ISP as the mass of a tree's seed production relative to its basal area to standardize  
 352 for tree size (intermediate trees produce more seeds than smaller ones Qiu *et al.* (2021a)). All  
 353 estimates are time averages across annual estimates, so we hereafter omit  $\text{yr}^{-1}$  from dimensions.  
 354 Therefore, ISP has the units of  $g/m^2$ . Following Qiu *et al.* (2022), species seed productivity  
 355 (SSP) comes from the expectation of all ISP for a given species. The detailed calculations of  
 356 ISP and SSP are provided in Online Supplement. Analyses of SSP are done on the proportionate  
 357 (log) scale to avoid dominance of results by the few species that produce the highest seed number.  
 358 The seed number is estimated following the same steps, but the calculations omit seed size (mass  
 359 of individual seed).

360 **Traits** We selected six functional plant traits previously shown to capture plant life strategies  
 361 well (Díaz *et al.*, 2016; Carmona *et al.*, 2021): plant height (measured in m), leaf area (measured  
 362 in  $\text{mm}^2$ ), specific leaf area (SLA; measured in  $\text{mm}^2/\text{mg}$ ; the inverse of leaf mass per area),  
 363 leaf nitrogen concentration (measured in  $\text{mg/g}$ ), wood density (measured in  $\text{g/m}^3$ ) and seed size  
 364 (measured in g). The data was obtained from primary sources and supplemented with publicly  
 365 available data from the latest version of the TRY Plant Trait Database [TRY Plant Trait Database](#)  
 366 (Kattge *et al.*, 2020) extracted from the Carmona *et al.* (2021). Missing values for the six traits  
 367 were filled with genus-level means. Bivariate relationships are summarized in Fig. S4).

368 **Trait relationships** PCA summarizes correlation in the joint distribution of traits, written in  
 369 bracket notation as  $[\mathbf{T}] = [T_1, \dots, T_M]$ . If the relationship between traits depends on phylogeny,  
 370 summarized by phylogenetic groups  $P_{g=1\dots G}$  (taxonomic, e.g., genus or family), and on the  
 371 environment  $X$ , then there is a joint distribution  $[\mathbf{T}, P, X]$ . The indirect environment and  
 372 phylogeny effects may dominate the relationships between some or many traits. An alternative  
 373 approach uses conditional distribution,

$$[\mathbf{T}|P, X] = \frac{[\mathbf{T}, P, X]}{[P, X]} \quad (3)$$

374 where the distribution of groups and environments  $[P, X]$  is that which occurs in the data set.

375 To determine trait relationships we fit a joint model to the conditional distribution  $[\mathbf{T}|P, X]$ ,  
 376 which provides estimates of the phylogeny as random groups  $\mathbf{g}[s]$ ,  $g = 1, \dots, M$  for species  $s$   
 377 and  $X$  as a  $Q \times M$  matrix of coefficients  $\mathbf{B}$  for  $Q$  predictors of  $M$  traits. We then decompose  
 378 the distribution into (conditional) effects of other traits and the environment (Seyednasrollah &  
 379 Clark, 2020; Qiu *et al.*, 2021b). The effect of trait  $m$  on the remaining  $-m$  traits is the conditional  
 380 distribution  $[\mathbf{T}_{-m}|T_m, P, X]$ . Using the fitted model in GJAM (see below), we decompose the  
 381 conditional effect of  $m$  on other traits as,

$$E(\mathbf{T}_{-m}|T_m, P, X) = E(\mathbf{T}_{-m}|T_m) + E(\mathbf{T}_{-m}|P, X) \quad (4)$$

382 The first term is a conditional influence of  $m$  as distinct from  $(P, X)$ .

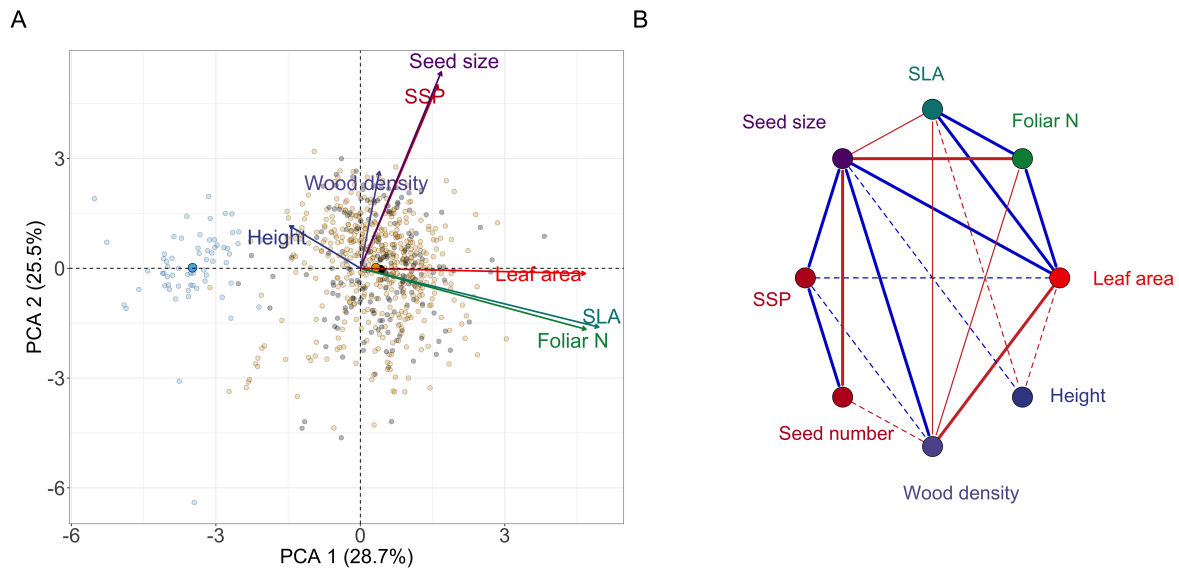
383 **Generalized joint attribute modeling** To incorporate the effects of environment and phy-  
 384 logeny on the distribution of traits, we use GJAM (Clark *et al.*, 2016). Environmental covariates  
 385 include soil fertility (Cation Exchange Capacity), mean annual temperature, and annual ac-  
 386 cumulative moisture deficit (difference between potential evapotranspiration and precipitation)  
 387 averaged at the species level for the MASTIF data set. GJAM allowed us to accommodate the  
 388 dependence between traits and phylogeny as random groups. A more detailed description of  
 389 GJAM fitting is given in Online Supplement. GJAM fitting is open-access with R package [GJAM](#)  
 390 on CRAN.

## 391 Results

392 Across the 784 species, foliar traits, wood density, and seed number and size are the dominant  
 393 sources of variation. In the principal components analysis (PCA) of our data that include  
 394 species seed productivity (SSP), 54.2% of variation is concentrated in two principal components  
 395 of equal importance (Fig. 3A, Fig. S1). PCA1 is associated with leaf traits. At one end are  
 396 species with thin, large, acquisitive leaves (large SLA, high area, high foliar nitrogen). Common  
 397 examples include heaven lotus (*Gustavia superba*), Panama tree (*Sterculia apetala*), pawpaw  
 398 (*Asimina triloba*), and eastern walnut (*Juglans nigra*). At the other end are species with low  
 399 SLA, low foliar nitrogen, and low leaf area, including evergreen conifers like giant sequoia  
 400 (*Sequoiadendron giganteum*), California redwood (*Sequoia sempervirens*), monkey puzzle tree  
 401 (*Araucaria araucana*), Fraser fir (*Abies fraseri*), and white cedar (*Thuja occidentalis*). PCA2  
 402 is dominated by seed size, SSP, and wood density. Large seeds are associated with high SSP  
 403 because species that produce large seeds tend to produce proportionally more of them than  
 404 predicted the strict trade-off between seed size and number (Qiu *et al.*, 2022). Dense wood is  
 405 associated with both seed size and SSP, with examples including African crabwood (*Carapa*  
 406 *procera*) and Fagales such as chestnuts (*Castanea*) and oaks (*Quercus*). At the opposite end  
 407 with low-density wood and small seeds are willows (*Salix*), fuchsia (*Fuchsia excorticata*), and  
 408 trumpet tree (*Cecropia obtusa*). Tree height is weakly associated with foliar attributes: small  
 409 trees tend to have large, thin leaves.

410 A second PCA in which SSP is replaced with seed number yields similar results (Fig. S2).  
 411 As with the PCA using SSP (fig. 3A), the first axis of this second PCA is associated with  
 412 foliar traits with no contributions from seed numbers. The second PCA axis separates species  
 413 according to seed size, seed number, and wood density. Tree height is again weakly associated  
 414 with foliar attributes but also with reproduction: small trees tend to produce small seeds in large  
 415 numbers (Fig. S2).

416 Using conditional prediction to control for the environment and taxonomic relatedness  
 417 shows that seed size is positively related to SSP and negatively related to seed number (Fig. 3B).  
 418 Conditional prediction allows for uncertainty and the effects of the environment on all traits,  
 419 but then isolates their direct (conditional) relationships to one another (see Methods). Nutrient-  
 420 demanding species with high foliar nitrogen concentrations, high SLA, and low-density wood,  
 421 produce small seeds in high numbers, a relationship that is not apparent in PCA. Large seeds  
 422 are produced by trees with dense wood, few seeds, high leaf area, low foliar N, and low SLA  
 423 (Fig. 4B-G). The relationship between high SSP and dense wood is suggested by PCA (Fig.

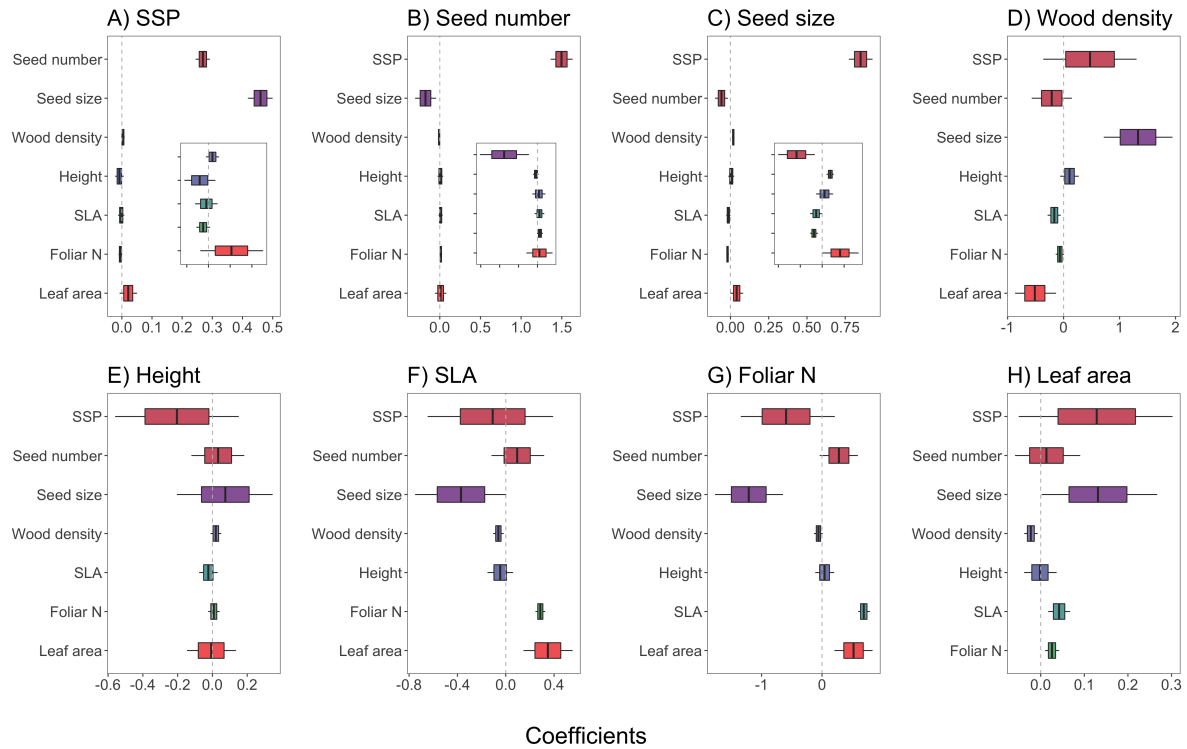


**Figure 3:** Seed size, seed number, and species seed productivity (SSP) on the spectrum of tree form. A) Biplot; arrow length indicates the loading of each considered trait onto the first two PCA axes. Points represent the position of species, coded blue for the needle, black for broad-deciduous, and yellow for broad evergreen leaf habit. Larger points indicate means for the groups. An extended version of that graph is given in Fig. S1. B) Summary of GJAM coefficients presented in Fig. 4. Significant associations between traits are highlighted by lines, coded red for negative and blue for positive relationships. Dashed lines highlight associations that are significant only in the model without phylogenetical control (see Fig. S3). Extended PCA plots are available in supplement Fig. S2. SSP stands for species seed productivity and is the product of seed size  $\times$  seed number (Qiu *et al.*, 2022). Both SSP and seed number are standardized to a tree basal area. Thicker lines qualitatively separate main relationships from the minute correlations among some foliar and other traits. Each trait has a unique color to improve comparisons between A and B.

424 3A), but that relationship is not significant after accounting for environment and phylogeny (Fig.  
 425 3B). Rather, the PCA can be driven by indirect links between traits. Although the links between  
 426 wood density and foliar traits are significant, they are weaker than the relationship between wood  
 427 density and seed size (Fig. 4D).

## 428 Discussion

429 Across 784 species spanning tropical to boreal environments, estimation of the number of seeds  
 430 produced by trees brings new insight to trait analysis with a strong connection to fitness. Seed  
 431 size and number make a dominant contribution to trait syndromes in trees, but one that is not  
 432 strictly consistent with the fast-slow or stature trade-offs. Controlling for common ancestry  
 433 and environment with GJAM indicates that large seed size is weakly associated with high leaf  
 434 area, low foliar nitrogen, low SLA, and dense wood. These associations were not detected by  
 435 conventional PCA that does not condition on environmental dependencies. Thus, there is a  
 436 weak, indirect link between these traits to SSP. Fast strategies, as captured by leaf traits, were  
 437 not coupled with high seed numbers, even though nutrient-demanding trees show a tendency to  
 438 produce small seeds. Seed size and number were also not associated with tree height as in the  
 439 stature-recruitment hypothesis at the tropical BCI (Rüger *et al.*, 2018, 2020). Across all species  
 440 and sites in this study, trees with dense wood, large leaves, and low nutrient demands produce  
 441 large but few seeds. These species invest heavily in SSP. In contrast, a high seed number is



**Figure 4:** Conditional relationships between traits after accounting for climate and phylogeny. Posterior distributions are shown as boxes that contain median vertical lines and are bounded by 68% credible intervals (CI), with 95% CI whiskers. Coefficients are evaluated on a standardized scale. The inset plots at A highlight the relationships between species seed productivity (SSP) and other traits after removing the effects of seed number and seed size that are part of SSP. Insets at B and C are analogous. Fig. 3 summarizes the significant relationships. See Fig. S3 for conditional relationships derived from GJAM without the phylogenetical control. SSP stands for species seed productivity and is the product of seed size x seed number. Both SSP and seed number are standardized to a tree basal area.

442 associated with small seeds, most common in species with low-density wood, low leaf area, high  
 443 foliar N, and high SLA.

444 Trait relationships identified here are consistent with some traditional trait concepts, including  
 445 change of traits associated with species turnover through succession (Bazzaz, 1979; Falster &  
 446 Westoby, 2005; Wilfahrt *et al.*, 2014). Production of a large number of small seeds  
 447 increases recruitment in distant, disturbed habitats (Muller-Landau, 2010). The *r* strategy of  
 448 the *r-K* spectrum is associated with fast growth and high nutrient requirements (Bazzaz, 1979;  
 449 Huston & Smith, 1987; Henery & Westoby, 2001; Muller-Landau *et al.*, 2008). By including  
 450 seed size and number, our analysis indicates that the traditional *r* strategy, which might include  
 451 low-density wood that often comes with fast growth (Chave *et al.*, 2009), also includes the  
 452 production of small seeds. High foliar nitrogen and cheap leaf construction (high SLA) align  
 453 with high photosynthetic rates (Reich & Oleksyn, 2004; Reich, 2014; Moles, 2018). On the  
 454 *K* side are species with dense wood and slow growth (Westoby, 1998; Poorter *et al.*, 2005).  
 455 Low foliar nitrogen and low SLA can align with low foliar Rubisco content, low photosynthetic  
 456 capacity, and, thus, low maintenance respiration in low light (Reich *et al.*, 1998; Poorter, 2015;  
 457 Moles, 2018). Species with such conservative leaves are also selected for large seeds needed  
 458 for seedling establishment in shade, at the expense of the many small seeds that would promote  
 459 colonization of distant sites (Westoby *et al.*, 2002; Muller-Landau, 2010).

460 Species seed productivity (SSP) is more strongly driven by seed size than seed number, which

461 follows from the observation that the size-numbers trade-off in trees is not 1:1 (Qiu *et al.*, 2022).  
462 Instead, species that produce large seeds more than compensate (on a mass basis) for fewer of  
463 them, resulting in higher species seed productivity (Qiu *et al.*, 2022)). Therefore, the estimates  
464 of SSP for a given tree size, enrich the interpretation of plant reproductive strategies beyond the  
465 insights that come from seed size alone (Westoby *et al.*, 2002; Muller-Landau, 2010; Lebrija-  
466 Trejos *et al.*, 2016). On one hand, the production of small, copious seeds increases recruitment  
467 opportunities at the cost of limited investment per individual seed. Small seeds can mean low  
468 abiotic stress tolerance in competitive sites (Westoby *et al.*, 2002; Tilman, 1994; Fricke *et al.*,  
469 2019). On the other hand, large seeds come with a cost of producing fewer of them (Henery &  
470 Westoby, 2001; Muller-Landau *et al.*, 2008; Fricke *et al.*, 2019), each with a greater investment  
471 in seedling survival (Fricke *et al.*, 2019; Muller-Landau *et al.*, 2008). However, the high SSP  
472 in species that produce large seeds means that such species are selected for proportionally high  
473 total seed biomass investment per individual to maintain populations in low light conditions  
474 (Kohyama *et al.*, 2003; Falster & Westoby, 2005). In other words, the production of a large  
475 number of seeds appears to generate a generally higher cost of reproduction. Testing whether  
476 SSP is a better indicator of reproductive success than seed number or size alone appears a fruitful  
477 avenue for future research.

478 The divergent results from this study and those suggesting a stature-recruitment trade-off  
479 at tropical forests (Rüger *et al.*, 2018, 2020; Guillemot *et al.*, 2022; Kambach *et al.*, 2022) are  
480 not necessarily in conflict. The within-site covariation in traits, where short trees might be  
481 associated with small seeds and leaves in the shaded understory (Rüger *et al.*, 2018), does not  
482 need to align with an among-site, species-level difference, which integrates over environments  
483 for each species at many sites. Moreover, Rüger *et al.* (2018) measured the recruitment of  
484 saplings, whereas our analysis includes seed numbers. In turn, the lack of relationship between  
485 seed size and plant height reported by past studies (Díaz *et al.*, 2016) may follow from the fact  
486 that the GJAM models control for phylogeny, whereas PCA does not. This is supported by the  
487 fact that both PCA and GJAM models that do not include shared ancestry indicate a positive  
488 relationship between seed size and tree height. This, and other trait relationships, that are present  
489 only in phylogenetically-controlled GJAM indicate that conditional prediction to control for the  
490 environment and taxonomic relatedness may be a step forward for the subdiscipline.

491 Anticipating individual and combined effects of global change requires understanding the  
492 vulnerability not only of mature trees but also of seed number and recruitment (Clark *et al.*,  
493 2021; Sharma *et al.*, 2022; Qiu *et al.*, 2021b; Bogdziewicz, 2022; Hanbury-Brown *et al.*, 2022).  
494 One major challenge, that exists in ecology more generally (Nuñez *et al.*, 2021), is to increase  
495 the data coverage to underrepresented regions such as Africa or Southeast Asia in our case.  
496 Earth system models currently assume that reproductive allocation does not differ among plant  
497 functional types (Scholze *et al.*, 2006; Hanbury-Brown *et al.*, 2022). There is area and promise  
498 for improvement using functional trait data. A recent study at the BCI predicted forest succession  
499 by replacing the hyper-diversity of tropical forests with just two trait axes associated with fast-  
500 slow and size dimensions (Rüger *et al.*, 2020). While the size of our seed production dataset  
501 is unprecedented, seed number is much more difficult to measure due to its variable nature, as  
502 compared to e.g. seed size. This could explain why we found stronger links between traits with  
503 seed size. The good news is that the easily measurable seed size is a strong predictor of species  
504 seed productivity (SSP) and seed number. The connection of SSP with the functional traits can  
505 form the first basis of improved fecundity prediction across global forests.

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## Supplementary material

This Supplement provides additional Methods descriptions and additional data summaries as tables and figures. Full summaries of the [MASTIF network](#) are available at these links for [sites](#) and [species](#).

### Materials and Methods

**Individual seed productivity (ISP) and species seed productivity (SSP)** Calculation of ISP combines posterior mean values with their uncertainties, as an expectation over the variations across years (tree  $i$  of species  $s$  at stand  $j$  in year  $t$ ):

$$\text{ISP}_{ijs} = \frac{m_s}{b_{ij}} \times \frac{\sum_t w_{ijs,t} \hat{f}_{ijs,t}}{\sum_t w_{ijs,t}} \quad (1)$$

where  $m_s$  is seed size (g),  $b_{ij}$  is basal area ( $m^2$ ), and weight  $w_{ijs,t}$  is the inverse of the coefficient of variation (CV),

$$w_{ijs,t} = CV_{ijs,t}^{-1} = \hat{f}_{ijs,t} / s_{ijs,t} \quad (2)$$

$s_{ijs,t}$  is the standard error of the estimate. The  $CV^{-1}$  is used instead of the inverse of variance, because the mean tends to scale with variance. Low values for  $\hat{f}_{ijs,t}$  are noisy and less important than high values, which are emphasized by the CV.

Following Qiu *et al.* (2022), species seed productivity (SSP) comes from the expectation of all ISP for a given species  $s$ :

$$\text{SSP}_s = \frac{\sum_{ij} w_{ijs} \text{ISP}_{ijs}}{\sum_{ij} w_{ijs}} \quad (3)$$

where  $w_{ijs}$  is defined the same way as  $w_{ijs,t}$ , i.e., root mean predictive variance divided by the mean ISP for tree  $ijs$ .

**Generalized joint attribute modeling (GJAM)** To partition the expected effects that one trait can have on the observations of other traits (eq. (4)), we start with the joint distribution of  $M$  traits from a species  $s$  fitted with GJAM, all the traits were log-transformed before entering the model,

$$[\mathbf{T}_s | P, X] = \text{MVN}_M(\mathbf{T}_s | \mathbf{B}'\mathbf{x}_s + \mathbf{g}[s], \Sigma) \\ \mathbf{g} \sim \text{MVN}(\mathbf{0}, \Omega) \quad (4)$$

(Clark *et al.*, 2016), where  $\text{MVN}$  is the multivariate normal distribution,  $\mathbf{g}[s]$  is a random vector for the phylogenetic group to which  $s$  belongs, and  $\Omega$  is the  $M \times M$  covariance between traits taken over phylogenetic groups. With this fitted model, we consider the effects of trait  $m$  on all other traits, organized in the vector  $[\mathbf{T}] = [\mathbf{T}_{-m}, T_m]$ . Following Qiu *et al.* (2021b), we can partition the mean and covariance as

$$\mathbf{B} = \begin{pmatrix} \mathbf{B}_{-m} \\ \mathbf{B}_m \end{pmatrix} \quad (5)$$

where  $\mathbf{B}_m$  holds column  $m$  and  $\mathbf{B}_{-m}$  holds the other  $M - 1$  columns of  $\mathbf{B}$ . The covariance matrix is also partitioned as

$$\Sigma = \begin{pmatrix} \Sigma_{-m,-m} & \Sigma_{-m,m} \\ \Sigma_{m,-m} & \Sigma_{m,m} \end{pmatrix} \quad (6)$$

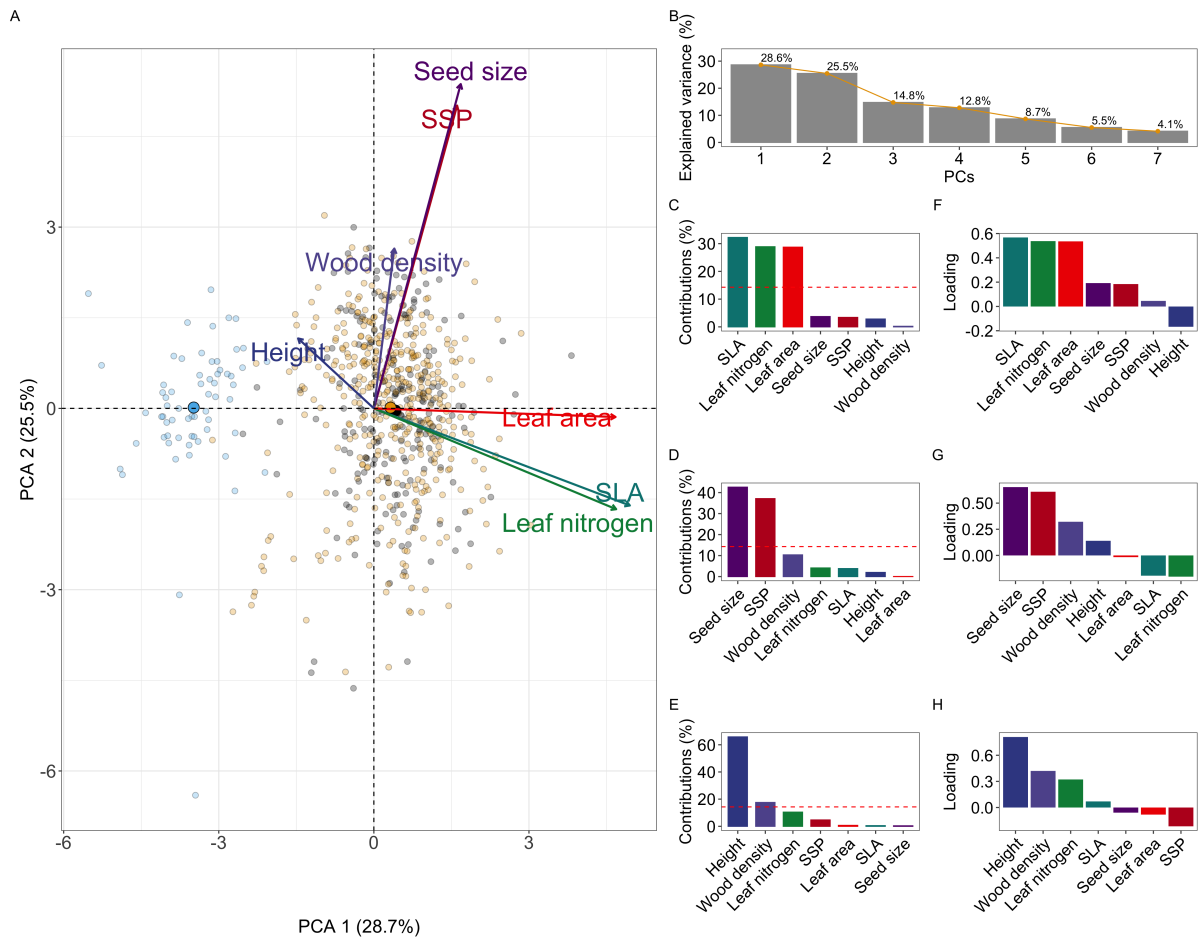
683 This joint distribution allows us to isolate the contributions of trait  $m$  as a conditional distribution.  
 684 Subtracting the random effect for species  $s$  gives the trait vector  $\tilde{\mathbf{T}}_s = \mathbf{T}_s - \mathbf{g}[s]$ . Then

$$\tilde{\mathbf{T}}_{-m,s}|T_{m,s} \sim MVN(\boldsymbol{\mu}_{-m,s}, \mathbf{P}) \quad (7)$$

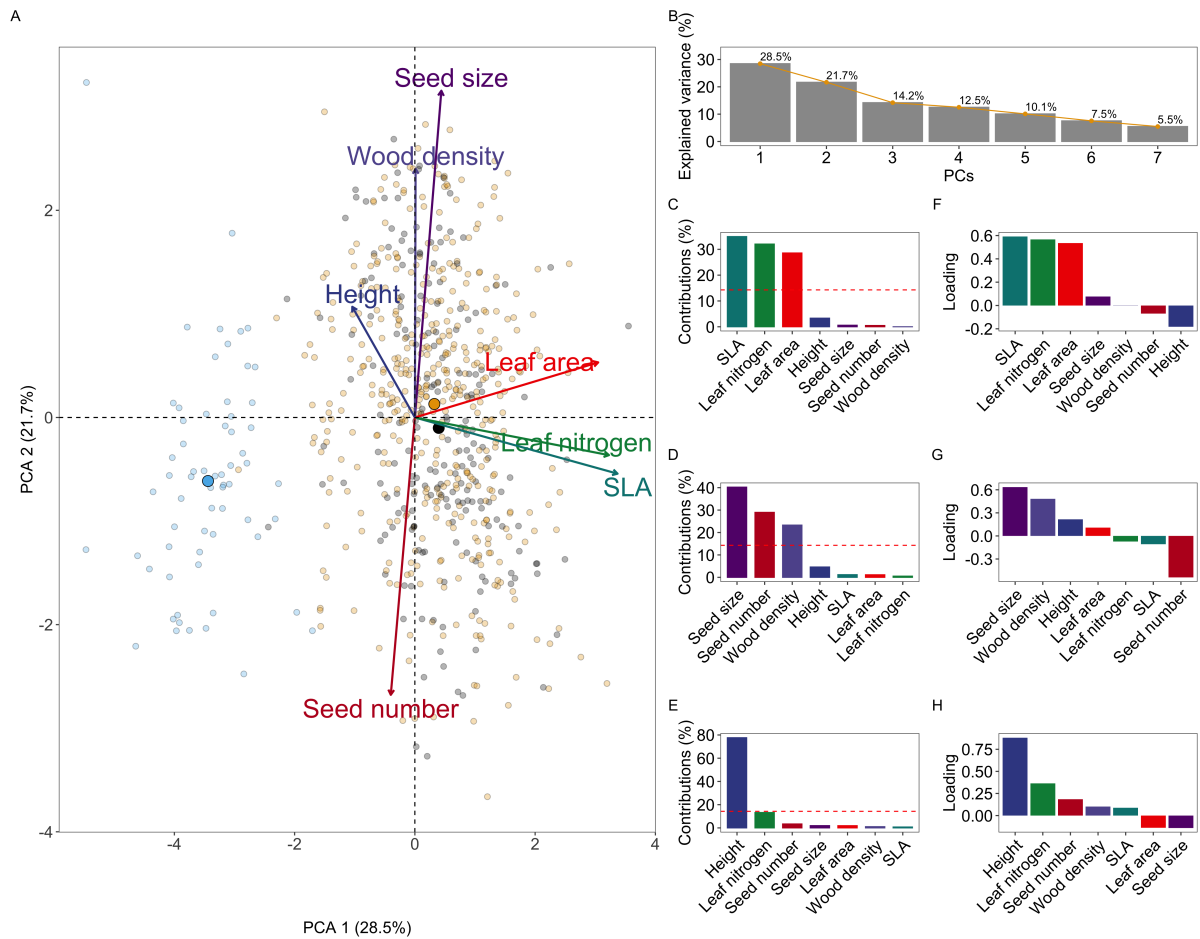
$$\begin{aligned} \boldsymbol{\mu}_{-m,s} &= \mathbf{B}_{-m}\mathbf{x}_s + \mathbf{A}(T_{m,s} - \mathbf{B}_m\mathbf{x}_s) \\ &= \mathbf{C}\mathbf{x}_s + \mathbf{A}T_{m,s} \end{aligned} \quad (8)$$

$$\mathbf{P} = \Sigma_{-m,-m} - \mathbf{A}\Sigma_{m,-m} \quad (9)$$

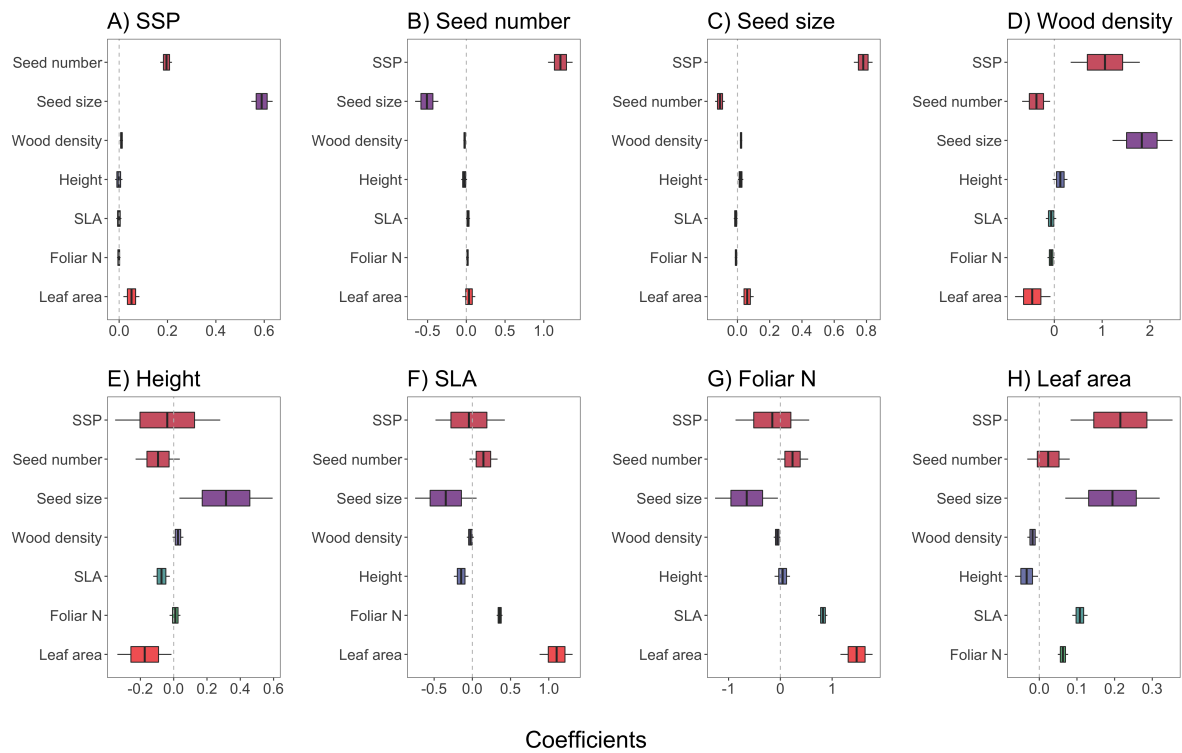
685 There are now two sets of coefficients, a length  $M - 1$  vector for effects of  $m$ ,  $\mathbf{A} = \Sigma_{-m,m}\Sigma_{m,m}^{-1}$ ,  
 686 and another  $M - 1 \times Q$  matrix for effects of  $\mathbf{x}$ ,  $\mathbf{C} = \mathbf{B}_{-m} - \mathbf{A}\mathbf{B}_m$ . The elements of matrix  $\mathbf{A}$  are  
 687 arrows in figure fig. 3. Matrix  $\mathbf{A}$  were obtained with the `conditionalParameters` function in  
 688 the GJAM package (Qiu *et al.*, 2021b).



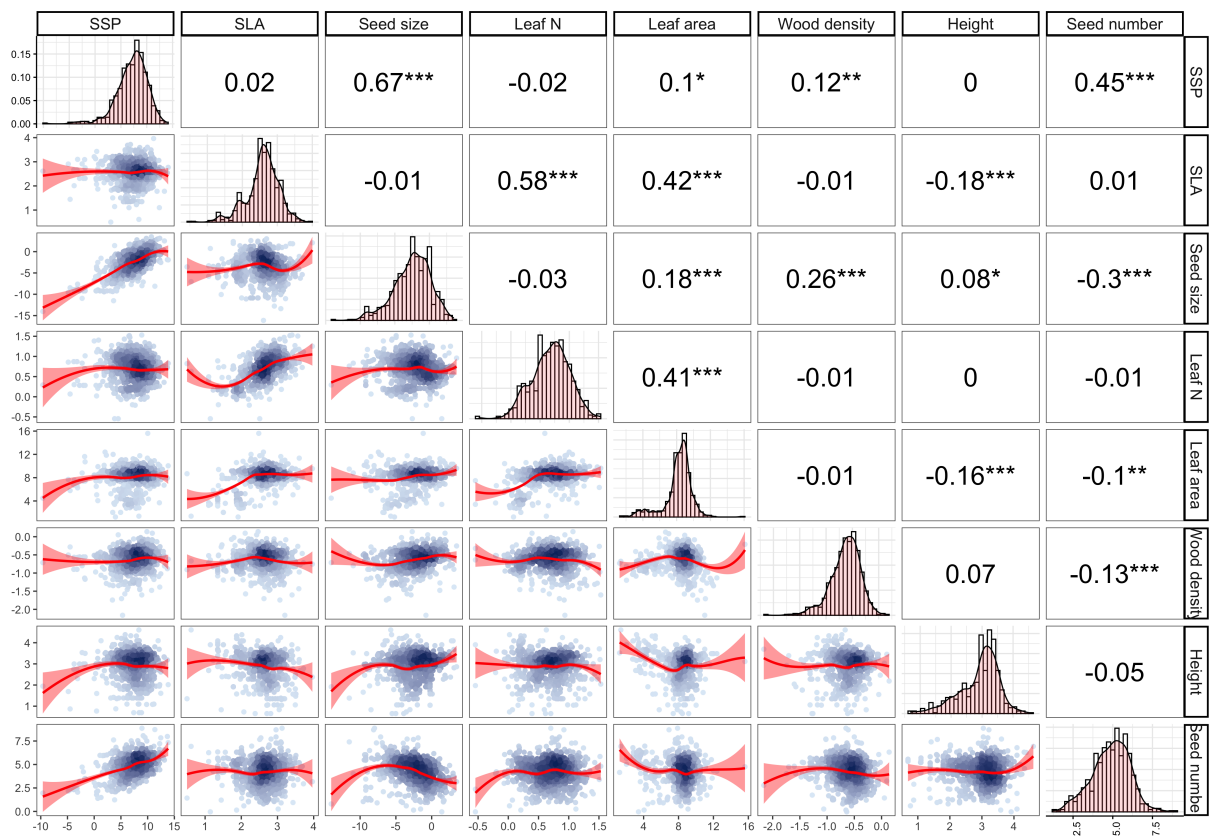
**Figure S1:** PCA as presented on Fig. 3 extended with contributions and loadings of the three axes that explained the most variance. A) Species seed productivity (SSP) on the global spectrum of tree form. Arrow length indicates the loading of each considered functional trait onto PCA axes. Points represent the position of species. B) Explained variance for each principal component. Bar plots present the contribution (C,D,E) and loading (F,G,H) of each trait to each principal component. The large point shows the mean position for each group.



**Figure S2:** A) Seed number on the spectrum of tree form. Arrow length indicates the loading of each considered functional trait onto PCA axes. Points represent the position of species. B) Explained variance for each principal component. Bar plots present the contribution (C,D,E) and loading (F,G,H) of each trait to each principal component. The large point shows the mean position for each group.



**Figure S3:** Conditional relationships between traits after accounting for climate but not shared ancestry. Marginal posterior distributions are shown as boxes that contain median vertical lines and are bounded by 68% credible intervals (CI), with 95% CI whiskers. Fig. 3 summarizes the significant relationships.



**Figure S4:** Summary of bivariate relationships between considered traits. Points are species, lines are loess regression and associated 95% CI. Coefficients are Pearson correlations. Traits are log-transformed. Significance levels are \* < 0.05; \*\* < 0.01; \*\*\* p < 0.001.