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1 The global trait syndrome for trees with reproductive
2 strategies

3

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4 **Summary**

5 Understanding trait syndromes can benefit from traits that are closely tied to fitness. In trees,
6 traits are often so weakly tied to fitness that their utility for comparative studies remains uncertain.
7 To address this, we analyze trait syndromes in trees from a perspective that includes fecundity.
8 We gathered 12 million observations of seed production of 775,991 trees in 784 tree species.
9 We tested whether seed production is associated with the leaf economic spectrum, the plant
10 size syndrome, or whether reproduction creates its own, independent dimension related to seed
11 mass and number trade-off. Bringing seed production into trait analysis, while allowing for
12 effect of environment and phylogeny, exposes a number of novel relationships in trees. The most
13 direct connection to fitness, represented by numbers of seeds and production of seed biomass,
14 comes through seed size, which, in turn, associates large seeds with high leaf area, low foliar
15 nitrogen and low SLA, and dense wood. Trees with large leaves, low nutrient demands and low
16 photosynthetic capacity indicated by low foliar nitrogen concentrations and low SLA, that grow
17 slowly to attain dense wood, are being selected for production of large seeds and high investment
18 into seed biomass. Abundant seed shadows are associated with small seeds produced by fast-
19 growing, nutrient-demanding trees with small and cheap leaves. The trait turnover appears to
20 reflect a shift from fast-growing, early successional vegetation with greater dispersal abilities
21 to slower-growing, and stress-tolerant species that recruit in high shade; showing that trees life
22 strategies align along the successional axis globally.

23 —
24 *keywords:* fecundity | forest recruitment | functional traits | life history strategies | seed size and
25 number trade-off | size syndrome | leaf economics syndrome

27 **Introduction**

28 Understanding forest diversity can benefit from knowledge of traits that are closely linked to
29 fitness (Adier *et al.*, 2014; Paine *et al.*, 2015; Yang *et al.*, 2018; Kelly *et al.*, 2021). Adaptive
30 evolution operates on variation that affects survival and reproduction. Leaf traits, wood density,
31 and plant height are clearly important for trees, yet their connections to fitness are indirect
32 (Wright *et al.*, 2004; Violle *et al.*, 2007; Chave *et al.*, 2009; Díaz *et al.*, 2016). Large, thin,
33 short-lived leaves with high nitrogen content confer clear advantages in settings where long-
34 lived, highly lignified leaves do not (Shreve, 1925; Field & Mooney, 1986; Reich, 2014).
35 However, interpreting the fitness implications of many traits can require broad extrapolation,
36 such as ecophysiological measurements describing minute-scale responses of leaves, roots, or
37 xylem elements that are integrated with many other responses to determine survival and/or
38 reproduction over the lifetimes of whole plants. While no trait links directly to fitness in trees,
39 many are so weakly tied to fitness that their utility for comparative studies remains uncertain.
40 Seedling recruitment at one site (Rüger *et al.*, 2018, 2020) provides a more direct link to
41 fitness. Given that recruitment varies for each species at each site, species-level reproductive
42 effort could be a valuable extension to trait understanding. The long-term and geographically
43 extensive measurements of tree seed production needed for species-level synthesis is only
44 recently available (Clark *et al.*, 2021; Journé *et al.*, 2022; Qiu *et al.*, 2022; Sharma *et al.*, 2022).
45 With newly available estimates, we re-examine the hypotheses that describe reproduction as part
46 of an omnibus syndrome that explains all traits (e.g., fast-slow) or, alternatively, as a separate
47 axis of variation. Diverging from both extremes, we find that the global link between seed
48 attributes and wood density is more consistent with an adaptive solution that is different from

49 (even orthogonal to) the leaf-economic spectrum.

50 Principal components analysis (PCA) has been a primary tool for exploring trait variation,
51 contributing to at least three interpretations for forest trees. One view sees reproduction and
52 leaf traits as part of a “fast-slow” continuum of plant strategies (Reich, 2014) (Fig. 1a). That
53 dimension represents the trade-off between resource acquisition and processing, and it could
54 be linked to a growth-survival trade-off (Poorter *et al.*, 2008; Wright *et al.*, 2010; Rüger *et al.*,
55 2018). Leaves that assimilate carbon quickly, together with low wood density, characterize
56 species that are resource-demanding, grow fast, and die young (Westoby *et al.*, 2002; Moles,
57 2018). Abundant seed production may offset mortality losses (Muller-Landau, 2010; Reich,
58 2014). Species with some or all of these traits might dominate early successional stages through
59 effective colonization, and they might not persist under intense competition (Poorter *et al.*, 2008;
60 Wright *et al.*, 2010).

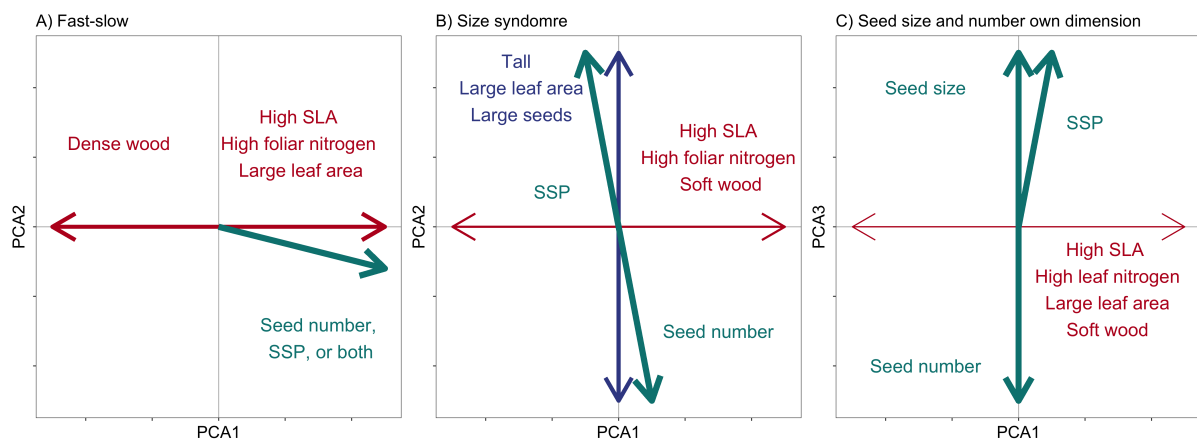


Figure 1: Hypothetical associations between dimensions of plant life strategies represented by functional traits and reproduction. Abundant seed production can be associated with: A) fast life syndrome (slow-fast resource turnover axis); B) plant size syndrome; C) create its own, largely independent axis of seed size-seed number trade-off. Species seed productivity (SSP) is the product of seed number and seed size divided by tree basal area.

61 Alternatively, the size hypothesis suggests that reproduction is part of a stature-recruitment
62 trade-off (Fig. 1b) (Kohyama, 1993; Díaz *et al.*, 2016; Rüger *et al.*, 2018, 2020). According to
63 this hypothesis, large size maximizes canopy performance at the expense of recruitment, and
64 vice versa. The analysis of 282 co-occurring tree species at tropical Barro Colorado Island (BCI)
65 emphasized a leaf-trait axis and a size-recruitment axis (Fig. 1b), with species characterized by
66 small stature, small leaves, and small seeds having high recruitment at the BCI (Rüger *et al.*,
67 2018).

68 Finally, seed abundance and seed size may represent a third, largely independent, dimension
69 of variation (Fig. 1c), as proposed by the twin-filter (TF) hypothesis (Grime & Pierce, 2012).
70 According to the TF, primary strategies such as fast-slow determine persistence for the cli-
71 mate/habitat norms, while traits involved in episodic events, which might include reproduction,
72 affect fitness independently of the primary strategy (Grime & Pierce, 2012; Pierce *et al.*, 2014).
73 The leaf-height-seed (LHS) scheme of Westoby (1998) hypothesizes that seed size plays a role
74 similar to reproduction in the TF model. In both hypotheses, plants can produce either many or
75 few seeds (TF) or small or large seeds (LHS) independent of other plant traits. All three of the
76 foregoing hypotheses imply an important role for fecundity, and they depend on the assumption
77 that all traits having some connection to fitness. The availability of species-level seed production
78 can lend novel insight to trait analysis due to its close connection to tree fitness.

79 A limitation of summaries available from PCA comes from the fact that correlations include
80 all the indirect ways that traits could be associated. For example, a seed-size/wood-density
81 correlation could come from a need for high wood density in order to produce large seeds; if
82 true, this would be a direct relationship. Alternatively, both variables might be driven by climate
83 for reasons that do not depend on one another; this is an indirect relationship. Another indirect
84 relationship is represented by phylogenetic conservatism; some species groups tend to produce
85 larger seeds or denser wood than others, even as environments that might select for one or both
86 traits change. The correlation structure exposed by PCA does not discriminate between direct
87 (conditional) and indirect (marginal) relationships. If relationships are indirect, then conditional
88 estimates offer the most transparent view of their connections (Seyednasrollah & Clark, 2020).

89 The Masting Inference and Forecasting (MASTIF) network includes 12 million tree-year
90 observations of seed production on 775,991 trees from 784 tree species from a broad range of
91 biomes (Journé *et al.*, 2022; Qiu *et al.*, 2022). To control for variation within species and, thus,
92 to sharpen our understanding of species differences, we estimate fecundity with an analytical
93 framework that includes trees condition (species, size, shading), habitat (soils), and climate
94 (temperature and moisture deficit), while accommodating dependence between and within trees
95 across years (Clark *et al.*, 2019). The large sample size is important for the notoriously noisy
96 seed production in trees (Kelly *et al.*, 2021), where tree-to-tree and year-to-year variation spans
97 several orders of magnitude (Clark *et al.*, 2004; Journé *et al.*, 2022). The traditional study of
98 trait syndromes with PCA is supplemented here with conditional (direct) relationships between
99 traits using Generalized Joint Attribute Modeling (GJAM) (Clark *et al.*, 2017). Including
100 environment as fixed effects and phylogenetic groups as random effects, GJAM decomposes
101 trait relationships into direct and indirect relationships. By combining seed production with
102 seed size, we show how reproductive traits relate to one another separately and in combination,
103 including on a size basis: the species seed productivity, $SSP = \text{seed size} \times \text{seed number/tree}$
104 basal area , standardizes for tree size (Qiu *et al.*, 2021). If large seeds confer an advantage in
105 competitive, shaded understories, while many, small seeds allow colonization of distant sites,
106 then species seed productivity (SSP) provides a direct link to reproduction.

107 Results

108 Across the 784 species in this analysis, dominant sources of variation derive from foliar traits and
109 seed/wood density. In the principal components analysis (PCA) of our data that includes mean
110 annual SSP (species seed productivity as seed biomass per m² tree basal area), 54.2% of variation
111 is concentrated in two principal components of equal importance (Fig. 2A). PCA1 is associated
112 with leaf traits. At one end are species with thin, large, acquisitive leaves (large SLA, high area,
113 high foliar nitrogen), including heaven lotus (*Gustavia superba*), Panama tree (*Sterculia apetala*),
114 pawpaw (*Asimina triloba*), and eastern walnut (*Juglans nigra*). At the other end are species
115 with low SLA, low foliar nitrogen, and low leaf area, including evergreen conifers like giant
116 sequoia (*Sequoiadendron giganteum*), California redwood (*Sequoia sempervirens*), monkey
117 puzzle (*Araucaria araucana*), Fraser fir (*Abies fraseri*), and white cedar (*Thuja occidentalis*).
118 PCA2 is dominated by seed size, SSP, and wood density. Large seeds are associated with high
119 SSP, because seed size has a larger effect on SSP than does seed numbers (Qiu *et al.*, 2022).
120 Dense wood is associated with both variables, with examples including African crabwood
121 (*Carapa procera*) and Fagales like chestnuts (*Castanea*) and oaks (*Quercus*). At the opposite
122 end with low-density wood and small seeds are willows (*Salix*), fuchsia (*Fuchsia excorticata*),
123 and trumpet tree (*Cecropia obtusa*). Tree height is weakly associated with foliar attributes:
124 small trees tend to have large, thin leaves.

125 A second PCA in which SSP is replaced with seed number (seeds per m² tree basal area,
 126 rather than seed mass per m² tree basal area) yields similar results (Fig. S2). As with the PCA
 127 using SSP (fig. 2A), the first axis of this second PCA is associated with foliar traits with no
 128 contributions from seed numbers. The second PCA axis separates species according to seed
 129 size, seed number, and wood density. Tree height is again weakly associated foliar attributes but
 130 also with reproduction: small trees tend to produce small seeds in large numbers (Fig. S2).

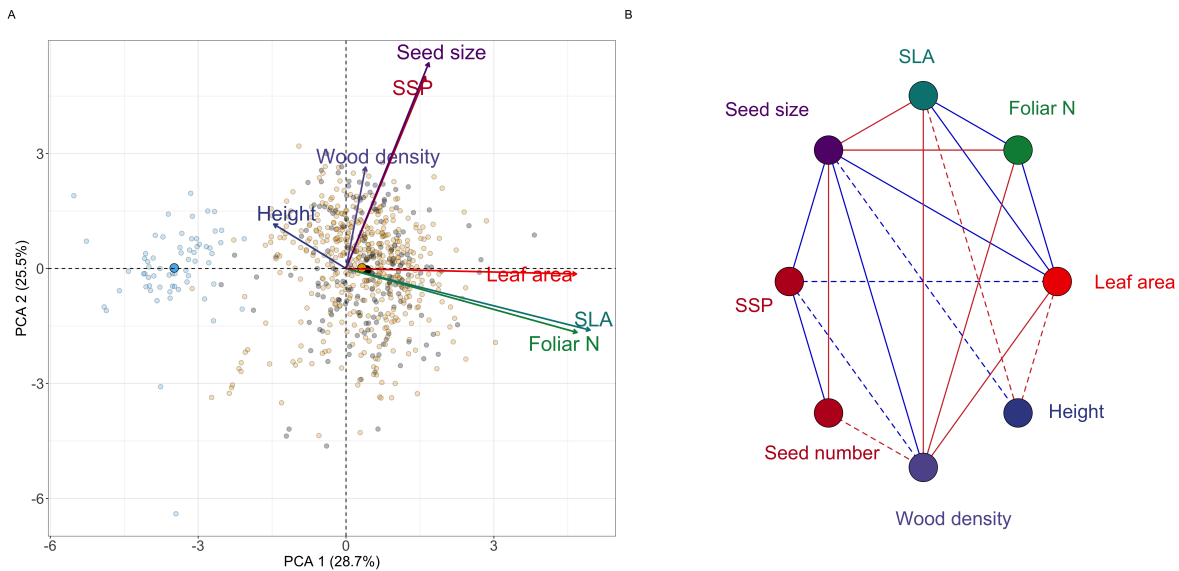


Figure 2: Fecundity on the global spectrum of tree form. A) Biplot; arrows length indicates the loading of each considered functional trait onto the first two PCA axes. Points represent the position of species, coded blue for needle, black for broad-deciduous, and yellow for broad evergreen leaf habit. B) Summary of GJAM coefficients presented at Fig. 3. Significant associations between traits are highlighted by lines, coded red for negative and blue for positive relationship. Dashed lines highlight associations that are significant only in model without phylogenetical control (see Fig. S3). Extended PCA plots are available in supplement Fig. S2. SSP stands for species seed production and is the product of seed size \times seed number. Both SSP and seed number are standardized to a tree basal area. Traits are summarized in Table 1.

131 Conditional associations that allow for the effects of environmental conditions and taxonomic
 132 relatedness show that seed size is positively related to SSP and negatively related to seed number
 133 (Fig. 2B). The solid lines in Fig. 2B are different from zero in Figure 3, whereas dashed
 134 highlight associations that are significant only in model without phylogenetical control. Nutrient-
 135 demanding species with high foliar nitrogen concentrations and high SLA produce small seeds,
 136 a relationship that is not apparent in PCA. Large seeds are produced by trees with dense wood,
 137 low seed number, high leaf area, low foliar N, and low SLA (Fig. 3B-G). Relationships between
 138 high SSP and dense wood and between large seeds and tree height are suggested by PCA (Fig.
 139 2A), but these relationships are not significant after accounting for environment and phylogeny
 140 (Fig. 2B). Although the links between wood density and foliar traits are significant, they are
 141 weaker than the relationships of wood density with seed attributes (Fig. 3D).

142 Discussion

143 Across 784 species in our sample spanning from tropical to boreal environments, the introduction
 144 of tree fecundity brings a direct connection of trait syndromes to fitness. Seed production makes
 145 a dominant contribution to trait syndromes in trees, but one that is not strictly consistent with

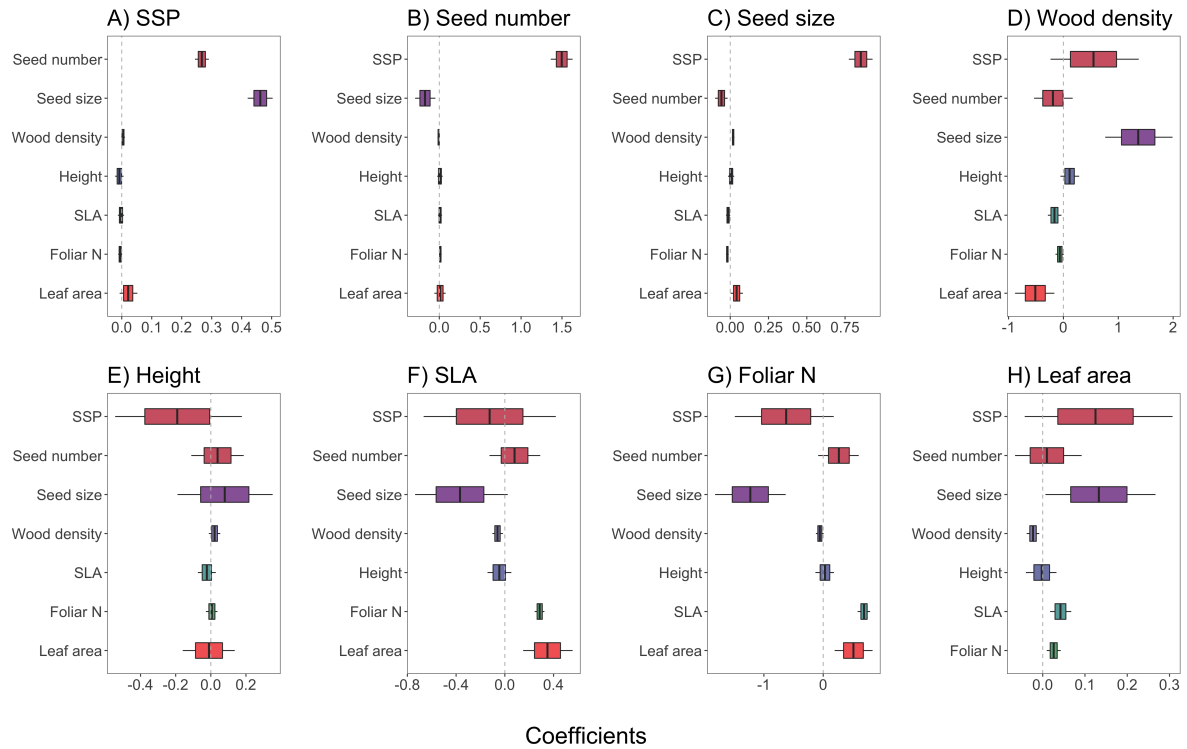


Figure 3: Conditional relationships between traits after accounting for climate and shared ancestry. Marginal posterior distributions are shown as boxes that contain median vertical lines and are bounded by 68% credible intervals (CI), with 95% CI whiskers. Fig. 2 summarizes the significant relationships. See Fig. S3 for conditional relationships derived from GJAM without the phylogenetical control. SSP stands for species seed production and is the product of seed size \times seed number. Both SSP and seed number are standardized to a tree basal area. Traits are summarized in Table 1.

146 fast-slow or stature trade-offs. The traits most directly connected to fitness include numbers of
 147 seeds and SSP (seed mass for a given tree size). Because seed size is weakly associated with
 148 high leaf area, low foliar nitrogen, low SLA, and dense wood, there is a weak, indirect link of
 149 these traits to SSP, but not to seed number. Fast strategies, as captured by leaf traits, were not
 150 coupled with abundant seed production, even though nutrient demanding trees show a tendency
 151 to produce small seeds. Reproduction (seed size and number) was also not associated with
 152 tree height as in the stature-recruitment hypothesis at a tropical BCI (Rüger *et al.*, 2018, 2020).
 153 Across all species and sites in this study, trees with dense wood, large leaves, and low nutrient
 154 demands produce large but few seeds. These species invest heavily in seed biomass, as indicated
 155 by high SSP. In contrast, high seed number is associated with small seeds, most common in
 156 species with low-density wood, low leaf area, high foliar N, and high SLA.

157 Trait syndromes identified here are consistent with traditional trait concepts, including
 158 turnover through succession (Bazzaz, 1979; Falster & Westoby, 2005; Wilfahrt *et al.*, 2014).
 159 Production of abundant, small seeds increases recruitment in distant, disturbed habitats (Muller-
 160 Landau, 2010). The r strategy of the r - K spectrum is associated with fast growth and high
 161 nutrient requirements (Bazzaz, 1979; Huston & Smith, 1987; Henery & Westoby, 2001; Muller-
 162 Landau *et al.*, 2008). By including reproduction, our analysis indicates that the traditional r
 163 strategy, which might include low-density wood that often comes with fast growth (Chave *et al.*,
 164 2009), includes production of small seeds. High foliar nitrogen and cheap leaf construction
 165 (high SLA) agrees with high photosynthetic rates (Reich & Oleksyn, 2004; Reich, 2014; Moles,
 166 2018). On the K side are species with dense wood and slow growth (Westoby, 1998; Poorter

167 *et al.*, 2005). Low foliar nitrogen and low SLA can align with low foliar Rubisco content, low
168 photosynthetic capacity, and, thus, low maintenance respiration in low light (Reich *et al.*, 1998;
169 Poorter, 2015; Moles, 2018). Species with such conservative leaves are also selected for large
170 seeds needed for seedling establishment in shade, at the expense of the many small seeds that
171 would promote colonization of distant sites (Westoby *et al.*, 2002; Muller-Landau, 2010). High
172 SSP further suggests selection for proportionally high reproductive investment per individual to
173 maintain populations in low light conditions (Kohyama *et al.*, 2003; Falster & Westoby, 2005).

174 Estimates of reproductive investment for a given tree size, or SSP, enrich the interpretation of
175 plant reproductive strategies beyond the insights that come from seed size alone (Westoby *et al.*,
176 2002; Muller-Landau, 2010; Lebrija-Trejos *et al.*, 2016). Production of small, copious seeds
177 increases the number of recruitment opportunities at the cost of limited investment per individual
178 seed. Small seeds can mean low tolerance of abiotic stress and limited resources in competitive
179 sites (Westoby *et al.*, 2002; Tilman, 1994; Fricke *et al.*, 2019). Conversely, large seeds come
180 with a cost of producing fewer of them (Henery & Westoby, 2001; Muller-Landau *et al.*, 2008;
181 Fricke *et al.*, 2019). That trade-off means that small-seeded species produce more germinants
182 per unit of reproductive mass, while large-seeded species should produce better performing
183 seedlings in smaller numbers (Fricke *et al.*, 2019; Muller-Landau *et al.*, 2008). However, the
184 size-numbers trade-off is not 1:1 (Qiu *et al.*, 2022). Instead, species that produce large seeds
185 more than compensate (on a mass basis) for fewer of them, resulting in higher SSP (seed mass
186 per tree basal area (Qiu *et al.*, 2022)). The size-numbers trade-off will differ for each species in
187 each setting. Nevertheless, the higher seed biomass investment in high-SSP species means that
188 simultaneous inclusion of seed size and number provides the most accurate link to reproductive
189 potential.

190 The divergent results from this study and those suggesting a stature-recruitment trade-off at
191 a tropical site (Rüger *et al.*, 2018, 2020; Guillemot *et al.*, 2022) are not necessarily in conflict.
192 The within-site covariation in traits, where short trees might be associated with small seeds and
193 leaves in the shaded understory (Rüger *et al.*, 2018), need not predict with among-site, species
194 level difference, which average over environments for a each species at many sites. At the species
195 level, fecundity is largely independent of tree size and more closely aligned wood density and
196 several foliar traits.

197 Anticipating individual and combined effects of global change pressures on future forests
198 requires understanding vulnerability not only of mature trees, but also of fecundity and re-
199 cruitment (McDowell *et al.*, 2020; Sharma *et al.*, 2022; Clark *et al.*, 2021; Bogdziewicz, 2022;
200 Hanbury-Brown *et al.*, 2022). Earth system models currently assume that reproductive alloca-
201 tion is indifferent among plant functional types (Scholze *et al.*, 2006; Hanbury-Brown *et al.*,
202 2022). There is area and promise for improvement as shown by a recent study at the BCI that
203 accurately predicted forest succession by replacing the hyperdiversity of tropical forest with just
204 two trait axes associated with fast-slow and size dimensions (Rüger *et al.*, 2020). Globally,
205 significant links exist between fecundity and trait syndromes that broadly reflect turnover of
206 trees life strategies across successions time. However, many of these trait relationships appear to
207 weak to be useful predictors of fecundity in the Earth system models. Instead, easily measurable
208 seed mass had strong links to SSP and seed number, and can form a first basis of fecundity
209 prediction across global forests.

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225 Methods

226 **Trait relationships** A data set, including one that might be assembled from meta-analysis,
 227 contains species that are characterized by traits and sample locations, each with its own en-
 228 vironmental setting. PCA summarizes correlation in the joint distribution of traits, written in
 229 bracket notation as $[\mathbf{T}] = [T_1, \dots, T_M]$. If the relationship between traits depends on phylogeny,
 230 summarized by phylogenetic groups $P_{g=1\dots G}$ (taxonomic, e.g., genus or family), and on the envi-
 231 ronment X , then there is a joint distribution $[\mathbf{T}, P, X]$. The indirect environment and phylogeny
 232 effects may dominate the relationships between some or many traits. An alternative approach
 233 uses the conditional distribution,

$$[\mathbf{T}|P, X] = \frac{[\mathbf{T}, P, X]}{[P, X]} \quad (1)$$

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

235 To determine trait relationships we fit a joint model to the conditional distribution $[\mathbf{T}|P, X]$,
 236 which provides estimates of the of phylogeny as random groups $\mathbf{g}[s]$, $g = 1, \dots, M$ for species s
 237 and X as a $Q \times M$ matrix of coefficients \mathbf{B} . We then decompose the distribution into (conditional)
 238 effects of other traits and the environment. The effect of trait m on the remaining $-m$ traits is
 239 the conditional distribution $[\mathbf{T}_{-m}|T_m, P, X]$. Using the fitted model in GJAM (see below), we
 240 decompose the conditional effect of m on other traits as,

$$E(\mathbf{T}_{-m}|T_m, P, X) = E(\mathbf{T}_{-m}|T_m) + E(\mathbf{T}_{-m}|P, X) \quad (2)$$

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

242 **Fecundity data and MASTIF model** Seed production in perennial plants suffers from extreme
 243 signal-to-noise problem, created by orders of magnitude variation from year to year and tree
 244 to tree (Pesendorfer *et al.*, 2021; Pearse *et al.*, 2020; Clark *et al.*, 2004) that can bury any
 245 trends (Clark *et al.*, 2021). Autoregression models assume a fixed periodicity, but mast intervals
 246 are not fixed (Shibata *et al.*, 2020; Pesendorfer *et al.*, 2020). There are as many time series as
 247 there are trees that must be modeled together because there is dependence created by among-
 248 trees synchrony in masting variation (Crone *et al.*, 2011; Bogdziewicz *et al.*, 2021). Masting
 249 patterns are further complicated by spatio-temporal variation in habitat and climate (Pesendorfer
 250 *et al.*, 2021; Pearse *et al.*, 2020). The many sources of variation means that estimation of trees
 251 fecundity can only be achieved from broad coverage and large sample sizes, while accounting

252 for individual tree condition, local habitat, and climate (Clark *et al.*, 2021; Qiu *et al.*, 2021;
253 Sharma *et al.*, 2022). This is here achieved with the MASTIF model (Clark *et al.*, 2019).

254 The MASTIF model and data from the Masting Inference and Forecasting (MASTIF) network
255 are summarized here, and extensively described in recent papers (Clark *et al.*, 2019, 2021; Qiu
256 *et al.*, 2021; Sharma *et al.*, 2022). The tree-year observations in the network comes from seed
257 traps and from crop counts. Data include longitudinal (repeated) observations on individual
258 trees (99%) and opportunistic observations that come through the iNaturalist project (Clark
259 *et al.*, 2019). Seed trap data consist of numbers of seeds that accumulate annually in mapped
260 seed traps on forest inventory plots. A fitted dispersal kernel relates seed counts to mapped
261 trees, accounting for uncertainty in seed transport and Poisson seed counts (Clark *et al.*, 2019).
262 Crop counts include counts of reproductive structures with estimates of the fraction of the crop
263 observed, and beta-binomial distribution accounts for uncertainty in the crop-fraction estimates
264 (Clark *et al.*, 2019). This study includes 12,008,722 tree-years from North America, South
265 and Central America, Europe, Africa, Asia, and Oceania, which is gathered over 5,115 plots
266 and 787,444 trees (Fig. 4). Unlike meta-analysis, the MASTIF model jointly estimate trees
267 fecundity based on all the observations; the SN and SSP used in the PCA analysis are calculated
268 based on 297,690 mature individuals and 3,730,381 tree-years. The list of species included in
269 the analysis is given in the Online Supplement as a csv file.

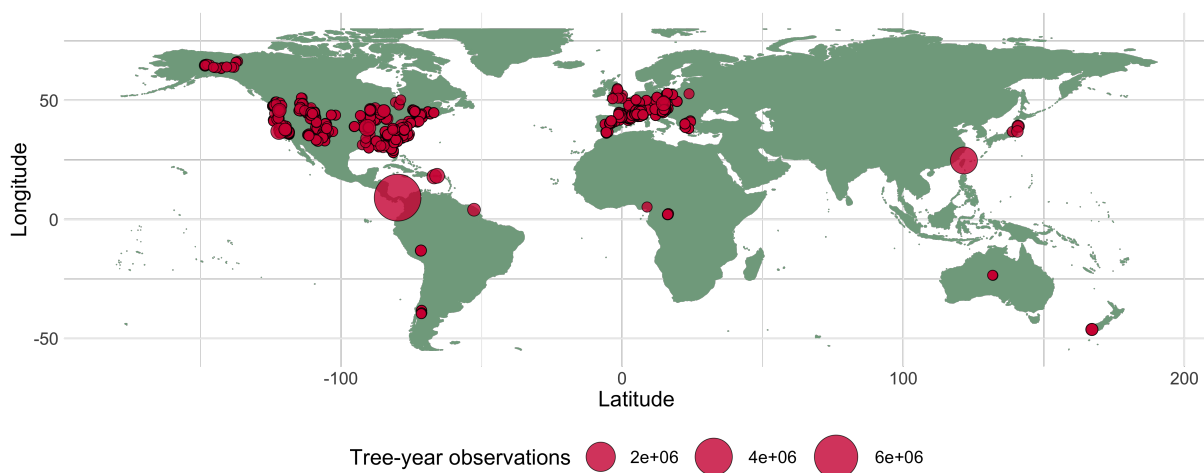


Figure 4: Map of raw data used to estimate trees fecundity with the MASTIF model.

270 The MASTIF model, detailed in Clark *et al.* (2019), is a dynamic biophysical model for
271 year-to-year and tree-to-tree seed production. The MASTIF model is Bayesian hierarchical,
272 state–space model that allows for conditional independence in crop-count and seed-trap data
273 through latent states. The model estimates seed production with conditional fecundity, which
274 depends on a probability that the tree is sexually mature, tree size, shading, local climate, and
275 soil conditions. Random effects on individual and year allow for wide variation between trees
276 and over time that are typical of seed production. The posterior covariance between trees and
277 years can take any form, avoiding assumptions of standard time-series models, important due to
278 the quasiperiodic variation in time and varying levels of synchronicity between individual trees.
279 Model structure and methodology was implemented with R, version 4.0 (R Core Team, 2020)
280 and the R package Mast Inference and Forecasting (MASTIF) (Clark *et al.*, 2019).

281 **Fecundity at the species level** We estimated species investment into seed production using
 282 two metrics, both scaled to the tree basal area: annual seed number (SN), and species seed
 283 productivity (SSP), which can be summarized as annual seed biomass investment (seed number
 284 \times seed mass) (Qiu *et al.*, 2022). Estimation of both SN and SSP starts with the estimation of
 285 individual tree mean seed production that depends on each tree location that accounts for effects
 286 of the environment and includes uncertainty for each year. Individual trees seed production
 287 over a species is then summarized as SN or SSP. Tree-level estimate of seed production, i.e.,
 288 individual seed production (ISP), is the product of mass per seed m_s and seeds per tree basal
 289 area per year. Calculation of ISP combines posterior mean values with their uncertainties, as an
 290 expectation over the variations across years:

$$\text{ISP}_{ijs} = \frac{m_s}{b_{ij}} \times \frac{\sum_t w_{ijs,t} \hat{f}_{ijs,t}}{\sum_t w_{ijs,t}} \quad (3)$$

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

$$w_{ijs,t} = CV_{ijs,t}^{-1} = \hat{f}_{ijs,t} / s_{ijs,t} \quad (4)$$

293 $s_{ijs,t}$ is the standard error of the estimate. The CV^{-1} is used instead of the inverse of variance,
 294 because the mean tends to scale with variance. Low values for $\hat{f}_{ijs,t}$ are noisy and less important
 295 than high values, which are emphasized by the CV . We quantify ISP as the mass of a tree's
 296 seed production relative to its basal area to standardize for tree size (intermediate trees produce
 297 more seeds than smaller ones Qiu *et al.* (2021)). All estimates are time averages across annual
 298 estimates, so we hereafter omit yr^{-1} from dimensions. Therefore, ISP has the units of g/m^2 .

299 Species seed production (SSP) comes from expectation of all ISP for a given species s :

$$\text{SSP}_s = \frac{\sum_{ij} w_{ijs} \text{ISP}_{ijs}}{\sum_{ij} w_{ijs}} \quad (5)$$

300 where w_{ijs} is defined the same way as $w_{ijs,t}$, i.e., root mean predictive variance divided by
 301 the mean ISP for tree ijs . Analyses of SSP are done on the proportionate (log) scale to avoid
 302 dominance of results by the few species that produce the highest seed production. Visualizations
 303 are based on \log_{10} to facilitate interpretation of scales in results. SN is estimated following the
 304 same steps, but the calculations omits seed mass (g).

305 **Functional traits** We selected six functional plant traits previously shown to well capture plant
 306 life strategies (Díaz *et al.*, 2016; Carmona *et al.*, 2021) (Table 1): plant height (measured in m),
 307 leaf area (measured in mm^2), specific leaf area (SLA; measured in mm^2/mg ; the inverse of leaf
 308 mass per area), leaf nitrogen concentration (measured in mg/g), wood density (measured in g/m^3)
 309 and seed mass (measured in mg). The data was obtained from primary sources and supplemented
 310 with publicly available data from the latest version of the TRY Plant Trait Database [TRY Plant](#)
 311 [Trait Database](#) (Kattge *et al.*, 2020) extracted from the Carmona *et al.* (2021). Missing values
 312 for the six traits were filled with genus-level means. Bivariate relationships are summarized at
 313 Fig. S4).

314 **Generalized joint attribute modeling** To incorporate the effects of environment and phy-
 315 logeny on the distribution of traits, we use GJAM to account for the different variable types
 316 represented by each trait (Clark *et al.*, 2016). Trait variable types are given in Table (Ta-
 317 ble 1). Environmental covariates include soil fertility (Cation Exchange Capacity), mean annual

Table 1: Summary of traits used in the analysis.

Trait	Units
Species seed production (SSP)	g/m ²
Seed number	seeds/m ²
Seed size	mg
Height	m
Wood density	g/m ³
Leaf area	mm ²
Leaf nitrogen	mg/g
SLA	mm ² /mg

318 temperature, and annual moisture deficit (difference between potential evapotranspiration and
 319 precipitation) averaged at the species level for the MASTIF data set. GJAM allowed us to
 320 accommodate the dependence between traits and phylogeny as random groups.

321 To partition the expected effects a trait on others (eq. (2)), we start with the joint distribution
 322 of M traits from a species s fitted with GJAM,

$$\begin{aligned} [\mathbf{T}_s | P, X] &= MVN_M(\mathbf{T}_s | \mathbf{B}'\mathbf{x}_s + \mathbf{g}[s], \Sigma) \\ \mathbf{g} &\sim MVN(\mathbf{0}, \Omega) \end{aligned} \quad (6)$$

323 (Clark *et al.*, 2016), where $\mathbf{g}[s]$ is a random vector for the phylogenetic group to which s
 324 belongs, and Ω is the $M \times M$ covariance between traits taken over phylogenetic groups. With
 325 this fitted model, we consider the effects of trait m on all other traits, organized in the vector
 326 $[\mathbf{T}] = [\mathbf{T}_{-m}, T_m]$. We can partition the mean and covariance as

$$\mathbf{B} = \begin{pmatrix} \mathbf{B}_{-m} \\ \mathbf{B}_m \end{pmatrix} \quad (7)$$

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

$$\Sigma = \begin{pmatrix} \Sigma_{-m,-m} & \Sigma_{-m,m} \\ \Sigma_{m,-m} & \Sigma_{m,m} \end{pmatrix} \quad (8)$$

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

$$\tilde{\mathbf{T}}_{-m,s} | T_{m,s} \sim MVN(\boldsymbol{\mu}_{-m,s}, \mathbf{P}) \quad (9)$$

$$\begin{aligned} \boldsymbol{\mu}_{-m,s} &= \mathbf{B}_{-m}\mathbf{x}_s + \mathbf{A}(T_{m,s} - \mathbf{B}_m\mathbf{x}_s) \\ &= \mathbf{C}\mathbf{x}_s + \mathbf{A}T_{m,s} \end{aligned} \quad (10)$$

$$\mathbf{P} = \Sigma_{-m,-m} - \mathbf{A}\Sigma_{m,-m} \quad (11)$$

331 There are now two sets of coefficients, a length $M - 1$ vector for effects of m , $\mathbf{A} = \Sigma_{-m,m}\Sigma_{m,m}^{-1}$,
 332 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
 333 arrows in figure fig. 2. Matrix \mathbf{A} were obtained with the `conditionalParameters` function in
 334 the GJAM package. GJAM fitting is open-access with R package [GJAM](#) on CRAN.

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484 **Supplementary material**

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

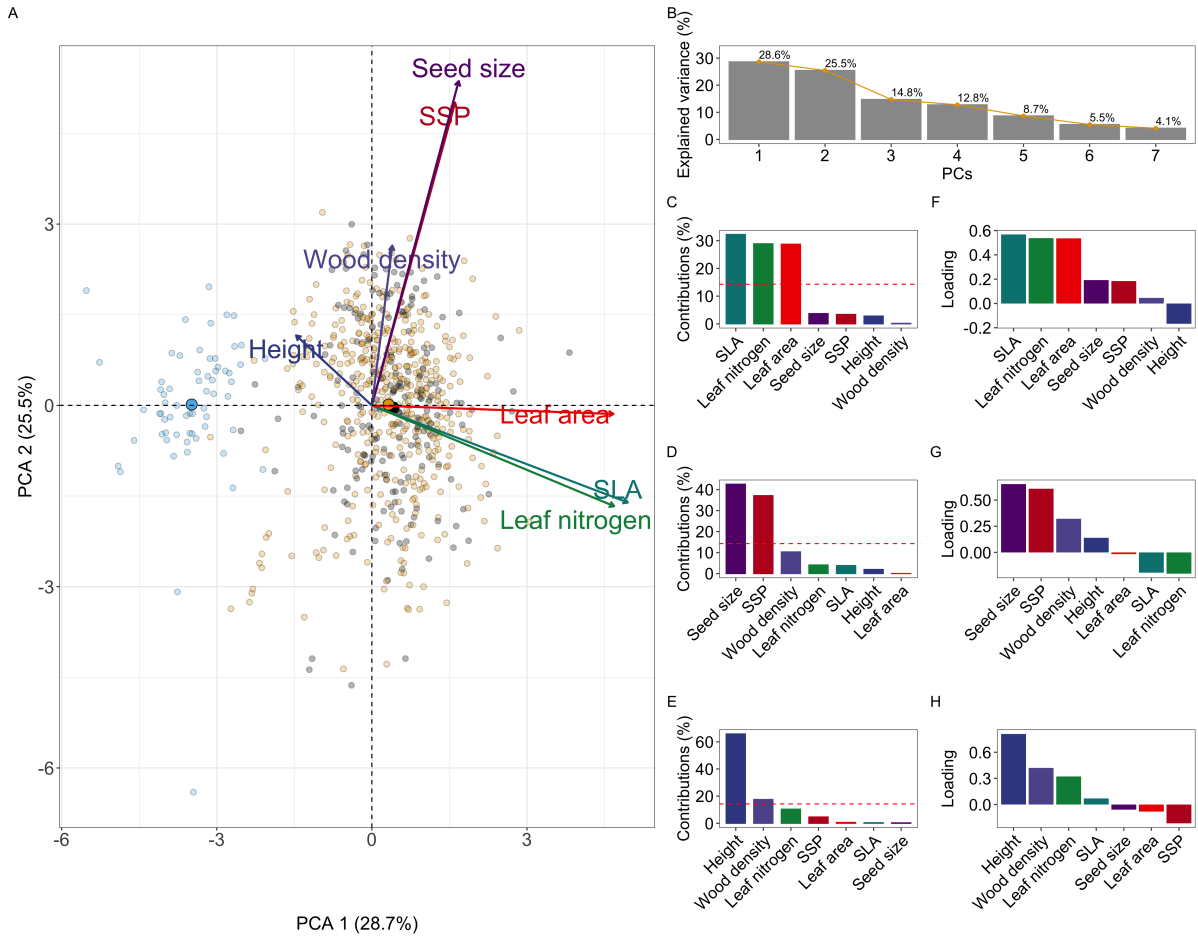


Figure S1: PCA as presented on Fig. 2 extended with contributions and loadings of the three axes that explained the most variance. A) Species seed productivity (SSP) on the global spectrum of tree form. Arrow length indicates the loading of each considered functional trait onto PCA axes. Points represent the position of species. B) Explained variance for each principal component. Bar plots of the contribution (C,D,E) and loading (F,G,H) of each trait to each principal component. Large point shows the mean position for each group .

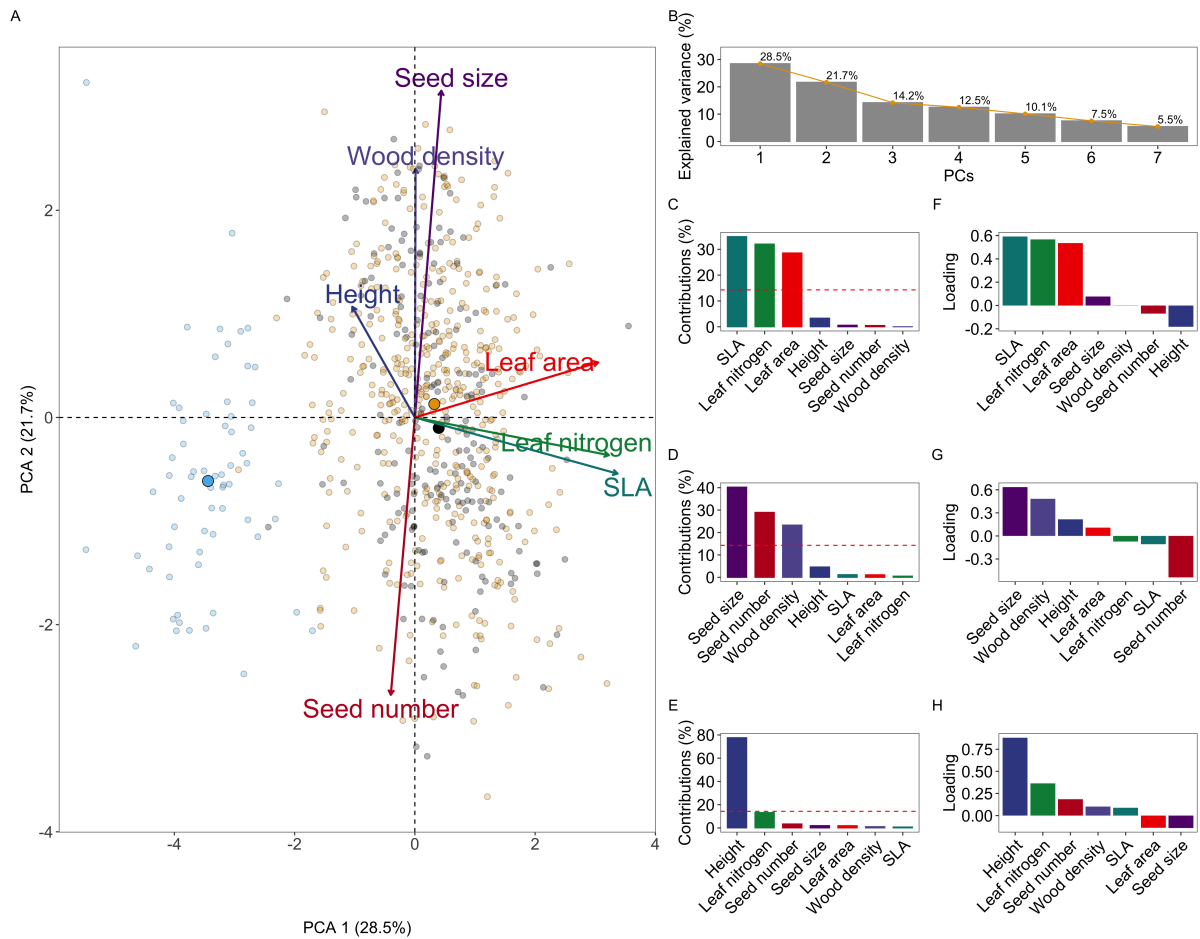


Figure S2: A) Species fecundity (seed number) on the global spectrum of tree form. Arrow length indicates the loading of each considered functional trait onto PCA axes. Points represent the position of species. B) Explained variance for each principal component. Bar plots of the contribution (C,D,E)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

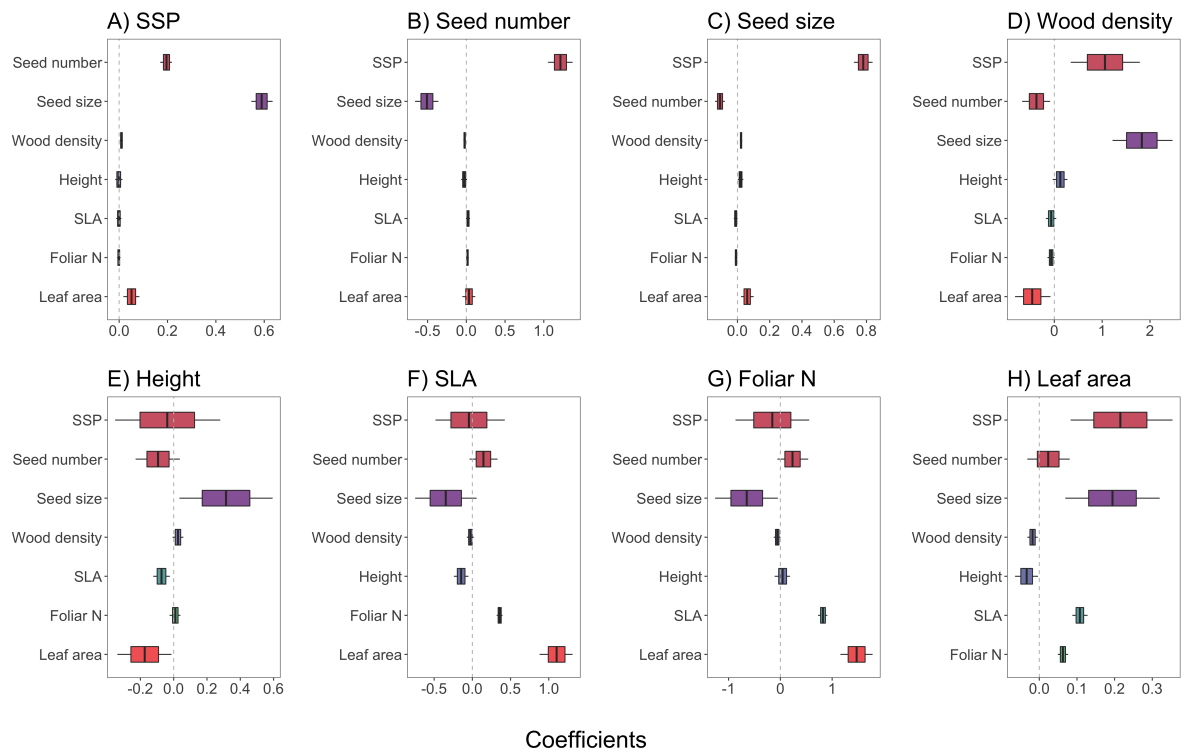


Figure S3: Conditional relationships between traits after accounting for climate but not shared ancestry. Marginal posterior distributions are shown as boxes that contain median vertical lines and are bounded by 68% credible intervals (CI), with 95% CI whiskers. Fig. 2 summarizes the significant relationships.

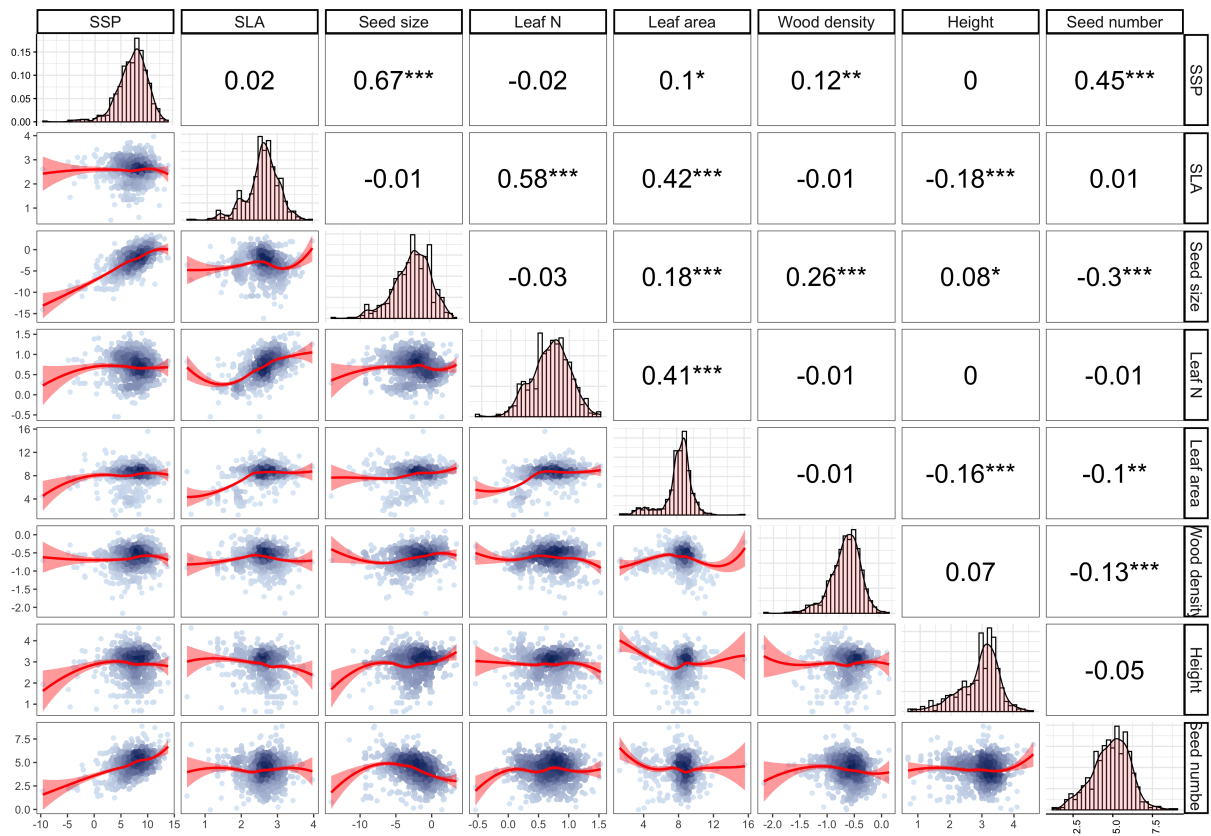


Figure S4: Summary of bivariate relationships between considered traits. Points are species, lines are loess regression and associated 95% CI. Coefficients are Pearson correlations. Traits are log-transformed.