

Linking seed size and number to trait syndromes in trees

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Data availability statement

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

Summary

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

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

Time period : 1960-2022.

Major taxa studied : Trees.

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

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

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

34 —
35 *keywords:* fecundity | functional traits | life history strategies | size syndrome | leaf economics
36 | tree recruitment |

38 Introduction

39 Understanding the mechanisms that promote and maintain forest tree diversity under a warming
40 climate can benefit from the knowledge of traits that are closely linked to fitness (Adler *et al.*,
41 2014; Paine *et al.*, 2015; Yang *et al.*, 2018; Kelly *et al.*, 2021). Adaptive evolution operates on
42 the variation that affects survival and reproduction. Leaf traits, wood density, and plant height
43 are clearly important for trees, yet their connections to fitness are indirect (Wright *et al.*, 2004;
44 Violle *et al.*, 2007; Chave *et al.*, 2009; Díaz *et al.*, 2016). For example, large, thin, short-lived
45 leaves with high nitrogen content confer clear benefits in high-resource environments where
46 long-lived, highly lignified leaves are less advantageous (Shreve, 1925; Field & Mooney, 1986;
47 Reich, 2014). Fitness is the quantitative representation of individual reproductive success, an
48 organism's ability to pass its genetic material to its offspring. Thus, interpreting the fitness
49 implications of traits often requires broad extrapolation, such as ecophysiological measurements
50 describing minute-scale responses of leaves, roots, or xylem elements that are integrated with
51 many other responses to determine survival and/or reproduction over the lifetimes of whole
52 plants. While no trait links directly to fitness in trees, many are so weakly tied to fitness
53 that their utility for comparative studies remains uncertain. In that light, seedling recruitment
54 at tropical Barro Colorado Island provides a more direct link to fitness (Rüger *et al.*, 2018,
55 2020). Nonetheless, given that recruitment varies for each species at each site, the species-level
56 reproductive effort could be a valuable extension for trait understanding. Only recently have
57 long-term and geographically extensive measurements of the number of seeds produced by trees
58 needed for species-level synthesis become available (Clark *et al.*, 2021; Journé *et al.*, 2022; Qiu
59 *et al.*, 2022; Sharma *et al.*, 2022). Here, we re-examine the hypotheses that describe the seed
60 number and size as part of an omnibus syndrome that explains all traits (e.g., fast-slow plant
61 economics spectrum) or, alternatively, as a separate axis of variation.

62 Principal components analysis (PCA) has been a primary tool for exploring combined trait
63 variation, contributing to at least three interpretations for forest trees. One view sees the number
64 of seeds produced and their size together with leaf traits as part of a “fast-slow” continuum
65 of plant strategies (Reich, 2014). That dimension represents the trade-off between resource
66 acquisition and processing, and it could be linked to a growth-survival trade-off (Poorter *et al.*,
67 2008; Wright *et al.*, 2010; Rüger *et al.*, 2018). Cheaply constructed leaves that assimilate carbon
68 quickly, together with low wood density, characterize species that are resource-demanding, grow
69 fast, and die young (Westoby *et al.*, 2002; Moles, 2018). In such species, the production of a
70 large number of seeds may offset mortality losses (Muller-Landau, 2010; Reich, 2014). Species
71 with some or all of these traits might dominate early successional stages through effective
72 colonization, and they might not persist under intense competition (Poorter *et al.*, 2008; Wright
73 *et al.*, 2010).

74 Alternatively, the size hypothesis suggests that the seed number and seed size is part of
75 a stature-recruitment trade-off (Kohyama, 1993; Díaz *et al.*, 2016; Rüger *et al.*, 2018, 2020).

76 According to this hypothesis, large plant size maximizes canopy performance at the expense
77 of recruitment, and vice versa. The analysis of 282 co-occurring tree species at tropical Barro
78 Colorado Island (BCI) emphasized a leaf-trait axis and a size-recruitment axis, with species
79 characterized by small stature, small leaves, and small seeds having high recruitment (Rüger
80 *et al.*, 2018). Follow-up studies indicated that stature-recruitment trade-off extends to tropical
81 forests more generally Kambach *et al.* (2022).

82 Finally, seed number and seed size may represent a third, largely independent, dimension of
83 variation, as proposed by the twin-filter (TF) hypothesis (Grime & Pierce, 2012). According
84 to the TF, primary strategies such as fast-slow determine persistence for the climate/habitat
85 norms, while traits involved in episodic events, which might include reproduction, affect fitness
86 independent of other traits (Grime & Pierce, 2012; Pierce *et al.*, 2014). The leaf-height-seed
87 (LHS) scheme of Westoby (1998) hypothesizes that seed size plays a role similar to reproduction
88 in the TF model. In both hypotheses, plants can produce either many or few seeds (TF) or small
89 or large seeds (LHS), largely independent of other plant traits. All three of the foregoing
90 hypotheses imply an important role of seed number and seed size, and they assume that all traits
91 have some connection to fitness. The availability of species-level seed numbers can lend novel
92 insight to trait analysis due to its close connection to recruitment, a major demographic and
93 fitness indicator.

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

110 In this study, we analyze trait syndromes in trees from a perspective that includes the number
111 of seeds produced and seed size. The Masting Inference and Forecasting (MASTIF) network
112 includes 12 million tree-year observations of the number of seeds produced by 775,991 trees
113 from 784 species from a broad range of biomes (Journé *et al.*, 2022; Qiu *et al.*, 2022). To control
114 for variation within species and, thus, to sharpen our understanding of interspecific differences,
115 we estimate seed numbers produced by trees with an analytical framework that includes trees'
116 condition (species, size, shading), habitat (soils), and climate (temperature and moisture deficit),
117 while accommodating dependence between and within trees across years (Clark *et al.*, 2019).
118 This large sample size is important for the notoriously noisy seed production in trees (Kelly
119 *et al.*, 2021), where tree-to-tree and year-to-year variation in seed number span several orders of
120 magnitude (Clark *et al.*, 2004; Journé *et al.*, 2022). By combining seed number with seed size into
121 species seed productivity (seed size x seed number, SSP, developed by Qiu *et al.* (2022)), we show
122 how reproductive traits relate to one another separately and in combination. Combining seed
123 number and seed size into SSP brings more exhaustive information on reproductive investment

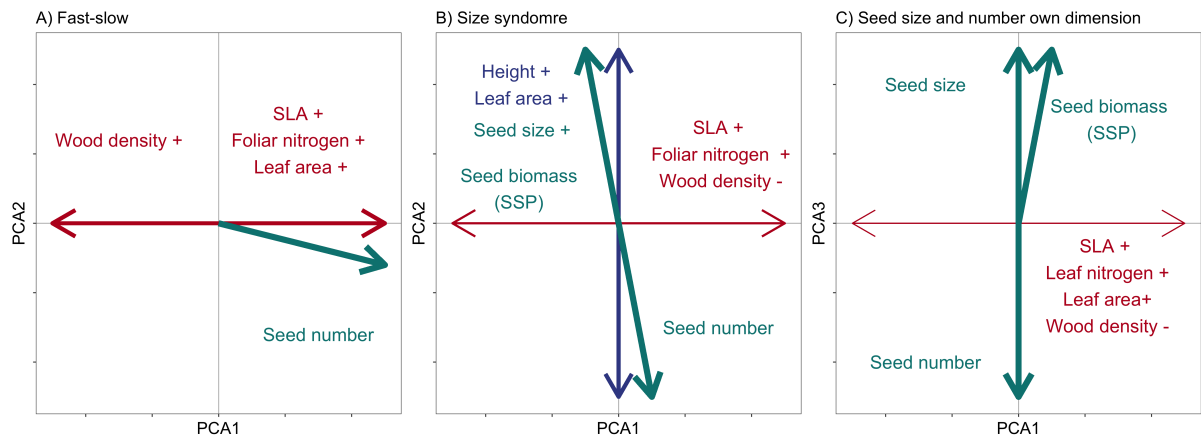


Figure 1: Hypothetical associations between dimensions of plant life strategies represented by functional traits and the seed number, seed size, and species seed productivity (the product of seed number and seed size, SSP developed by Qiu *et al.* (2022)). Seed production can be associated with: A) fast 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.

124 because species that invest in large seeds are producing more seeds than expected from the 1:1
 125 trade-off (Qiu *et al.*, 2022). For this reason, SSP should be more strongly aligned with seed size
 126 than seed number. By standardizing these metrics for the tree size we account for the variation in
 127 size distribution within the data and facilitate comparisons. For example, the SSP is the average
 128 annual species seed productivity per m² basal area at average environmental conditions across
 129 the species' range in the data (Qiu *et al.*, 2021a, 2022). If large seeds confer an advantage in
 130 competitive, shaded understories, while many small seeds allow colonization of distant sites,
 131 then SSP provides a direct link to fitness. The hypothesized relationships between seed number,
 132 seed size, SSP, and traits are summarized in Figure 1.

133 Methods

134 **Seed number, species seed productivity (SSP) and MASTIF model** Estimating the number
 135 of seeds produced in perennial plants suffers from extreme signal-to-noise problem, created
 136 by orders of magnitude variation from year to year and tree to tree (Pesendorfer *et al.*, 2021;
 137 Pearse *et al.*, 2020; Clark *et al.*, 2004) that can bury any trend (Clark *et al.*, 2021). There are as
 138 many time series as there are trees that must be modeled together because there is dependence
 139 created by among-trees synchrony in masting variation (Crone *et al.*, 2011; Bogdziewicz *et al.*,
 140 2021). Masting patterns are further complicated by the spatio-temporal variation in habitat and
 141 climate (Pesendorfer *et al.*, 2021; Pearse *et al.*, 2020). The many sources of variation mean that
 142 estimation of a seed number produced by trees can only be achieved from broad coverage and
 143 large sample sizes while accounting for individual trees' condition, local habitat, and climate
 144 (Clark *et al.*, 2021; Qiu *et al.*, 2021a; Sharma *et al.*, 2022). This is here achieved with the
 145 MASTIF model (Clark *et al.*, 2019).

146 The MASTIF model and data from the MASTIF network are summarized here, and exten-
 147 sively described in recent papers (Clark *et al.*, 2019, 2021; Qiu *et al.*, 2021a; Sharma *et al.*,
 148 2022; Journé *et al.*, 2022). The tree-year observations of seed numbers in the network come
 149 from seed traps and from crop counts. Data include longitudinal (repeated) observations on
 150 individual trees (99%) and opportunistic observations that come through the iNaturalist project

151 (Clark *et al.*, 2019). Seed trap data consists of numbers of seeds that accumulate annually in
152 mapped seed traps on forest inventory plots. A fitted dispersal kernel relates seed counts to
153 mapped trees, accounting for uncertainty in seed transport and Poisson seed counts (Clark *et al.*,
154 2019). Crop counts include counts of reproductive structures with estimates of the fraction of
155 the crop observed, and beta-binomial distribution accounts for uncertainty in the crop-fraction
156 estimates (Clark *et al.*, 2019). This study includes 12,008,722 tree-years from North America,
157 South and Central America, Europe, Africa, Asia, and Oceania, which is gathered over 5,115
158 sites and 787,444 trees (Fig. 2). The MASTIF model jointly estimates the number of seeds
159 produced based on all the observations. The seed number (SN) and species seed productivity
160 (SSP) (Qiu *et al.*, 2022) used in the analysis are calculated based on 297,690 mature individuals
161 and 3,730,381 tree-years. The MASTIF model uses the whole dataset to estimate seed numbers
162 produced annually, but the SN and SSP are calculated based on a mature tree subset of these
163 estimates. The list of species included in the analysis is given in the Online Supplement as a csv
164 file.

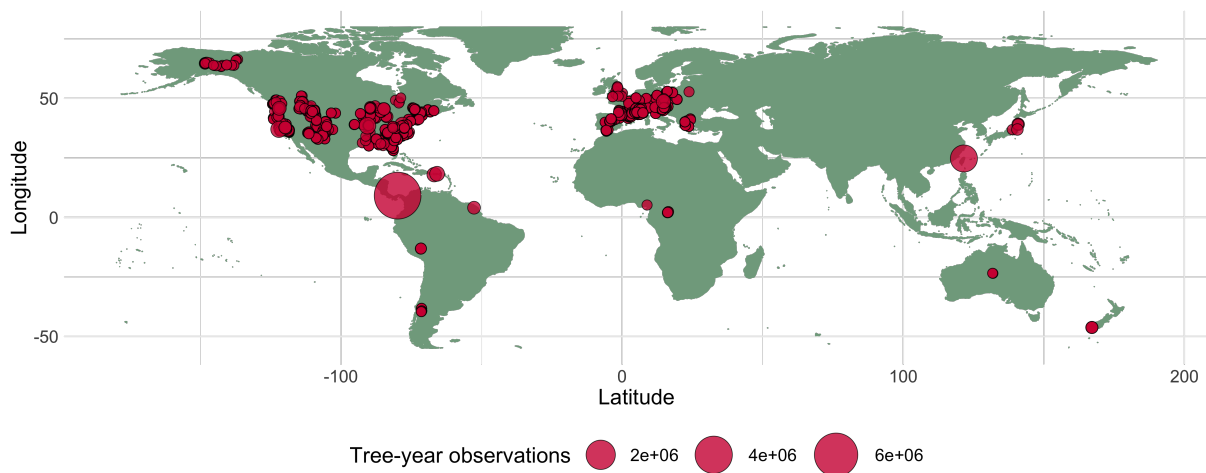


Figure 2: Map of raw data used to estimate the number of seeds produced by trees with the MASTIF model.

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

177 **Seed number and species seed productivity (SSP) at the tree and the species level** The
178 MASTIF model incorporates the effects of tree attributes with the environment on maturation
179 and conditional fecundity. To allow for an uncertain identification of seeds from trees of the
180 same genus and for dependence within trees over time and between trees, all three-years of a

181 genus are modeled jointly (Clark *et al.*, 2019, 2021). For each tree i of species s at stand j
 182 in year t , the expected seed number is the product of maturation probability $\hat{\rho}$ and conditional
 183 fecundity $\hat{\psi}$,

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

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

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

185 where \mathbf{x}_{it} is a matrix holding individual attributes and environmental conditions (see *Gener-*
 186 *alized joint attribute modeling* below), and $\boldsymbol{\beta}^{(x)}$ are fixed-effects coefficients. $\beta_{ijs}^{(w)}$ is the random
 187 effect for tree i of species s at stand j . $\gamma_{g[ij]s,t}$ are year effects that are random across groups g
 188 and fixed for the year t to account for interannual variation that is not fully captured by climate
 189 anomalies. Group membership for year effects ($g[ij]s$) is defined by species-ecoRegion (Clark
 190 *et al.*, 2019). There is a noise term $\epsilon_{ijs,t}$. Maturation probability $\hat{\rho}_{ijs,t}$ accounts for the immature
 191 state (for small trees) and failed crop in larger trees. The model implementation is open-access
 192 with R package MASTIF, with algorithm details provided in Clark *et al.* (2019).

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

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

218 **Trait relationships** PCA summarizes correlation in the joint distribution of traits, written in
 219 bracket notation as $[\mathbf{T}] = [T_1, \dots, T_M]$. If the relationship between traits depends on phylogeny,
 220 summarized by phylogenetic groups $P_{g=1\dots G}$ (taxonomic, e.g., genus or family), and on the
 221 environment X , then there is a joint distribution $[\mathbf{T}, P, X]$. The indirect environment and

222 phylogeny effects may dominate the relationships between some or many traits. An alternative
223 approach uses conditional distribution,

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

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

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

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

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

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

241 Results

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

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

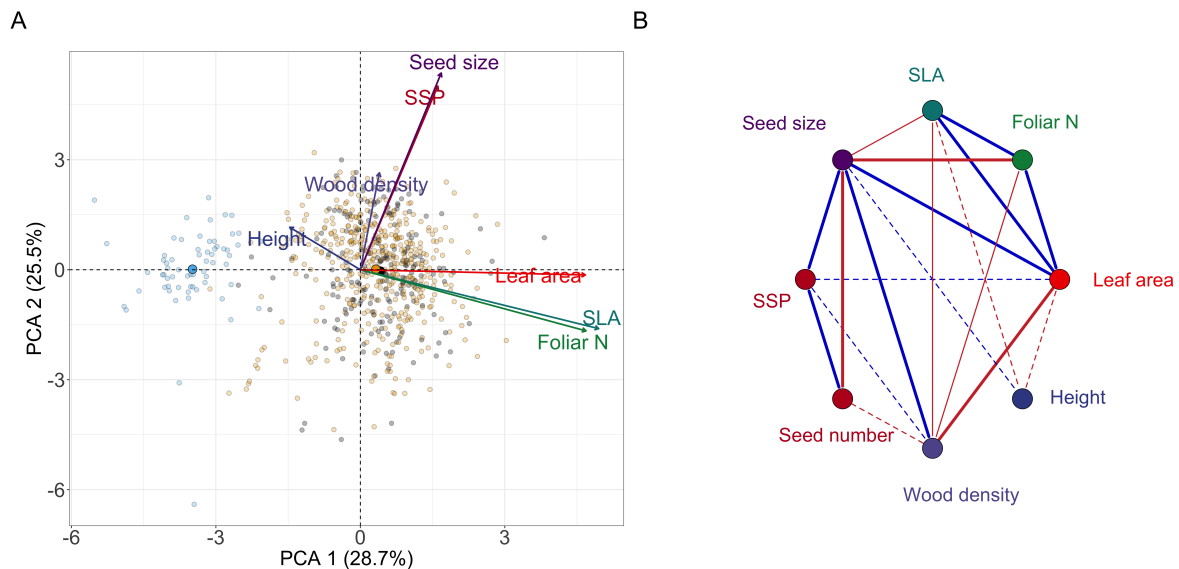


Figure 3: Seed size, seed number, and species seed productivity (SSP) on the spectrum of tree form. A) Biplot; arrow length indicates the loading of each considered trait onto the first two PCA axes. Points represent the position of species, coded blue for the needle, black for broad-deciduous, and yellow 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.

266 Using conditional prediction to control for the environment and taxonomic relatedness
 267 shows that seed size is positively related to SSP and negatively related to seed number (Fig. 3B).
 268 Conditional prediction allows for uncertainty and the effects of the environment on all traits,
 269 but then isolates their direct (conditional) relationships to one another (see Methods). Nutrient-
 270 demanding species with high foliar nitrogen concentrations, high SLA, and low-density wood,
 271 produce small seeds in high numbers, a relationship that is not apparent in PCA. Large seeds
 272 are produced by trees with dense wood, few seeds, high leaf area, low foliar N, and low SLA
 273 (Fig. 4B-G). The relationship between high SSP and dense wood is suggested by PCA (Fig.
 274 3A), but that relationship is not significant after accounting for environment and phylogeny (Fig.
 275 3B). Rather, the PCA can be driven by indirect links between traits. Although the links between
 276 wood density and foliar traits are significant, they are weaker than the relationship between wood
 277 density and seed size (Fig. 4D).

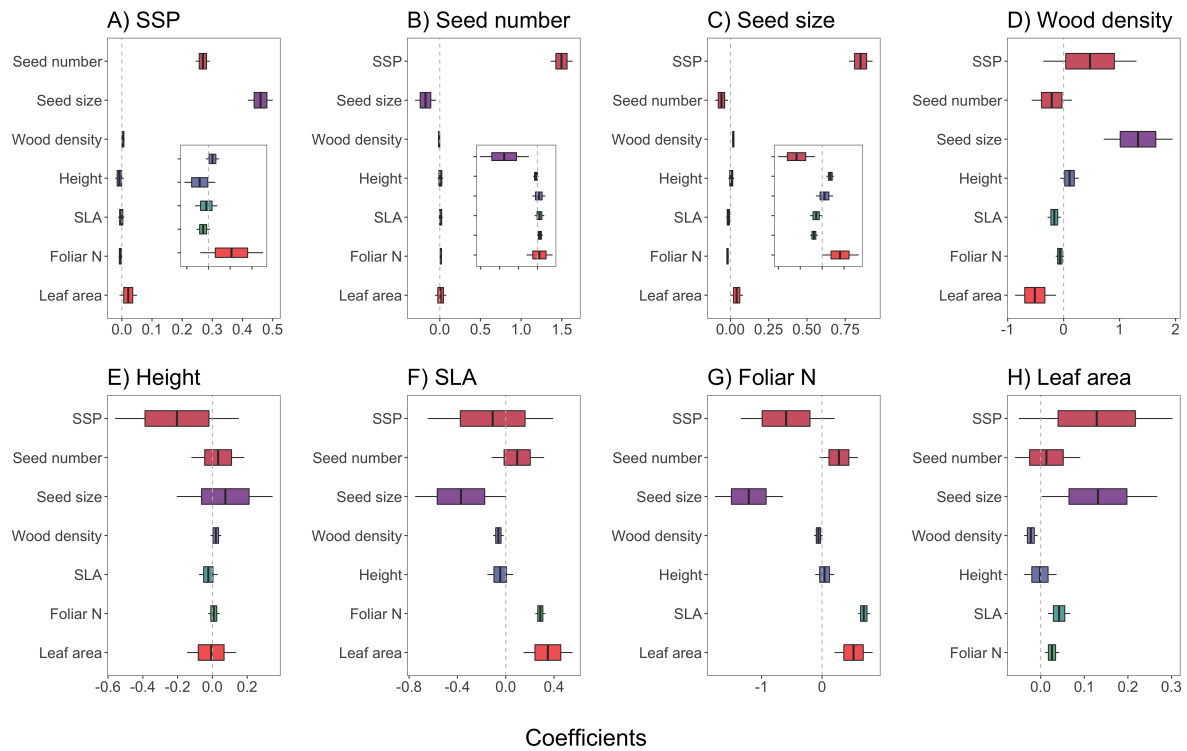


Figure 4: Conditional relationships between traits after accounting for climate and phylogeny. Posterior distributions are shown as boxes that contain median vertical lines and are bounded by 68% credible intervals (CI), with 95% CI whiskers. Coefficients are evaluated on a standardized scale. The inset 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.

Discussion

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

Trait relationships identified here are consistent with some traditional trait concepts, including change of traits associated with species turnover through succession (Bazzaz, 1979;

296 Falster & Westoby, 2005; Wilfahrt *et al.*, 2014). Production of a large number of small seeds
297 increases recruitment in distant, disturbed habitats (Muller-Landau, 2010). The r strategy of
298 the r - K spectrum is associated with fast growth and high nutrient requirements (Bazzaz, 1979;
299 Huston & Smith, 1987; Henery & Westoby, 2001; Muller-Landau *et al.*, 2008). By including
300 seed size and number, our analysis indicates that the traditional r strategy, which might include
301 low-density wood that often comes with fast growth (Chave *et al.*, 2009), also includes the
302 production of small seeds. High foliar nitrogen and cheap leaf construction (high SLA) align
303 with high photosynthetic rates (Reich & Oleksyn, 2004; Reich, 2014; Moles, 2018). On the
304 K side are species with dense wood and slow growth (Westoby, 1998; Poorter *et al.*, 2005).
305 Low foliar nitrogen and low SLA can align with low foliar Rubisco content, low photosynthetic
306 capacity, and, thus, low maintenance respiration in low light (Reich *et al.*, 1998; Poorter, 2015;
307 Moles, 2018). Species with such conservative leaves are also selected for large seeds needed
308 for seedling establishment in shade, at the expense of the many small seeds that would promote
309 colonization of distant sites (Westoby *et al.*, 2002; Muller-Landau, 2010).

310 Species seed productivity (SSP) is more strongly driven by seed size than seed number, which
311 follows from the observation that the size-numbers trade-off in trees is not 1:1 (Qiu *et al.*, 2022).
312 Instead, species that produce large seeds more than compensate (on a mass basis) for fewer of
313 them, resulting in higher species seed productivity (Qiu *et al.*, 2022). Therefore, the estimates
314 of SSP for a given tree size, enrich the interpretation of plant reproductive strategies beyond the
315 insights that come from seed size alone (Westoby *et al.*, 2002; Muller-Landau, 2010; Lebrija-
316 Trejos *et al.*, 2016). On one hand, the production of small, copious seeds increases recruitment
317 opportunities at the cost of limited investment per individual seed. Small seeds can mean low
318 abiotic stress tolerance in competitive sites (Westoby *et al.*, 2002; Tilman, 1994; Fricke *et al.*,
319 2019). On the other hand, large seeds come with a cost of producing fewer of them (Henery &
320 Westoby, 2001; Muller-Landau *et al.*, 2008; Fricke *et al.*, 2019), each with a greater investment
321 in seedling survival (Fricke *et al.*, 2019; Muller-Landau *et al.*, 2008). However, the high SSP
322 in species that produce large seeds means that such species are selected for proportionally high
323 total seed biomass investment per individual to maintain populations in low light conditions
324 (Kohyama *et al.*, 2003; Falster & Westoby, 2005). In other words, the production of a large
325 number of seeds appears to generate a generally higher cost of reproduction. Testing whether
326 SSP is a better indicator of reproductive success than seed number or size alone appears a fruitful
327 avenue for future research.

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

341 Anticipating individual and combined effects of global change requires understanding the
342 vulnerability not only of mature trees but also of seed number and recruitment (Clark *et al.*,
343 2021; Sharma *et al.*, 2022; Qiu *et al.*, 2021b; Bogdziewicz, 2022; Hanbury-Brown *et al.*, 2022).

344 One major challenge, that exists in ecology more generally (Nuñez *et al.*, 2021), is to increase
345 the data coverage to underrepresented regions such as Africa or Southeast Asia in our case.
346 Earth system models currently assume that reproductive allocation does not differ among plant
347 functional types (Scholze *et al.*, 2006; Hanbury-Brown *et al.*, 2022). There is area and promise
348 for improvement using functional trait data. A recent study at the BCI predicted forest succession
349 by replacing the hyper-diversity of tropical forests with just two trait axes associated with fast-
350 slow and size dimensions (Rüger *et al.*, 2020). While the size of our seed production dataset
351 is unprecedented, seed number is much more difficult to measure due to its variable nature, as
352 compared to e.g. seed size. This could explain why we found stronger links between traits with
353 seed size. The good news is that the easily measurable seed size is a strong predictor of species
354 seed productivity (SSP) and seed number. The connection of SSP with the functional traits can
355 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,

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

(Clark *et al.*, 2016), where MVN is the multivariate normal distribution, $\mathbf{g}[s]$ is a random vector for the phylogenetic group to which s belongs, and Ω 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

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

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

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

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

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

535 There are now two sets of coefficients, a length $M - 1$ vector for effects of m , $\mathbf{A} = \Sigma_{-m,m}\Sigma_{m,m}^{-1}$,
 536 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
 537 arrows in figure fig. 3. Matrix \mathbf{A} were obtained with the `conditionalParameters` function in
 538 the GJAM package (Qiu *et al.*, 2021b).

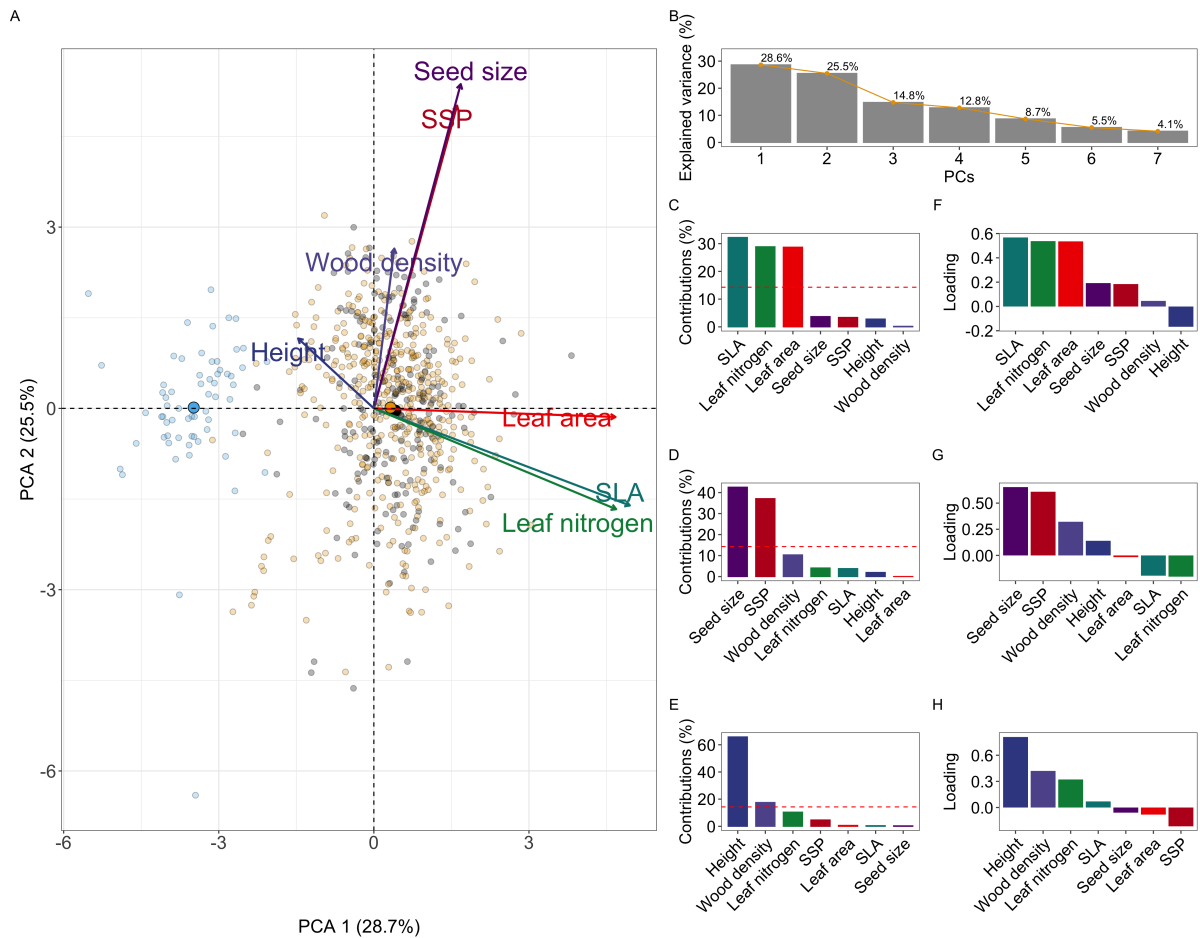


Figure S1: PCA as presented on Fig. 3 extended with contributions and loadings of the three axes that explained the most variance. A) Species seed productivity (SSP) on the global spectrum of tree form. Arrow length indicates the loading of each considered functional trait onto PCA axes. Points represent 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.

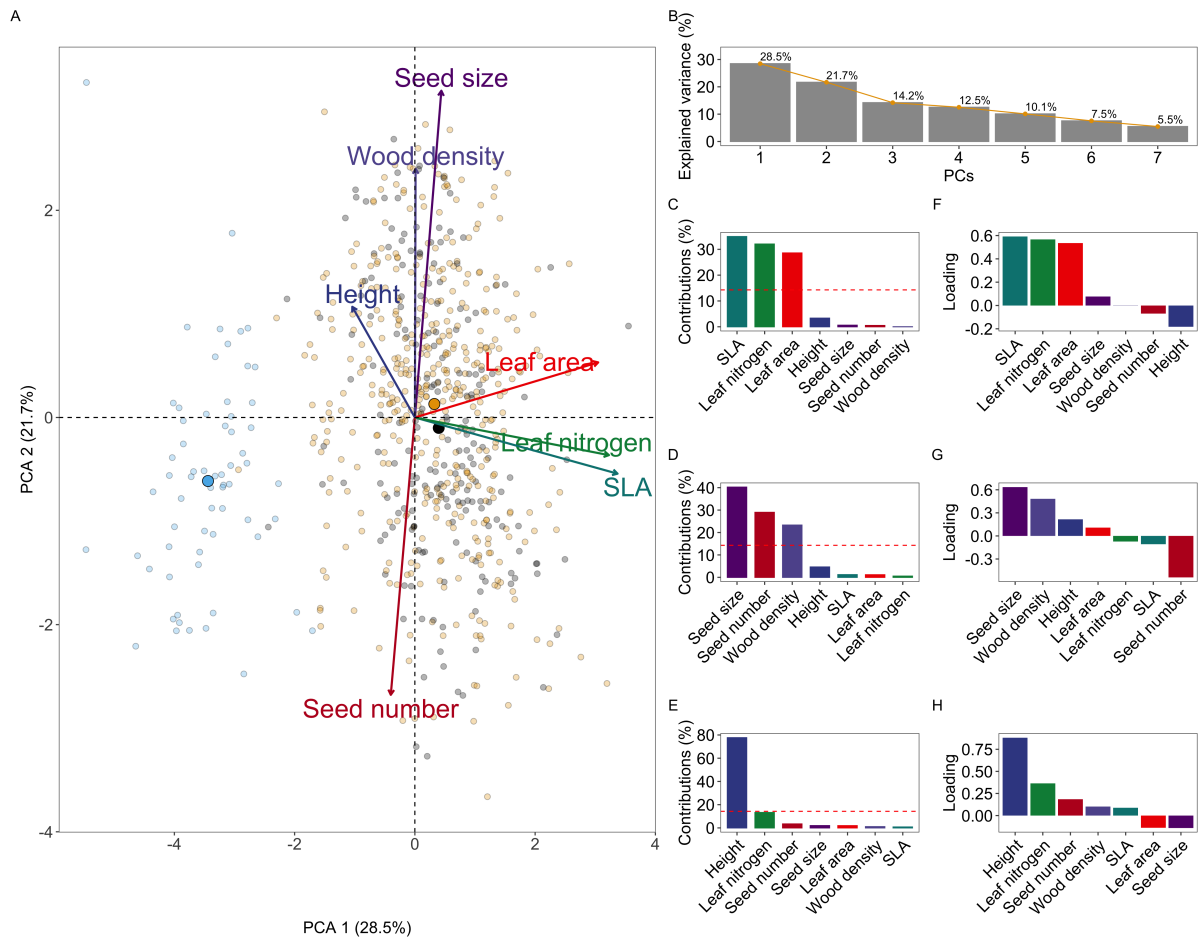


Figure S2: A) Seed number on the spectrum of tree form. Arrow length indicates the loading of each considered functional trait onto PCA axes. Points represent the position of species. B) Explained variance for each principal component. Bar plots present the contribution (C,D,E) and loading (F,G,H) of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

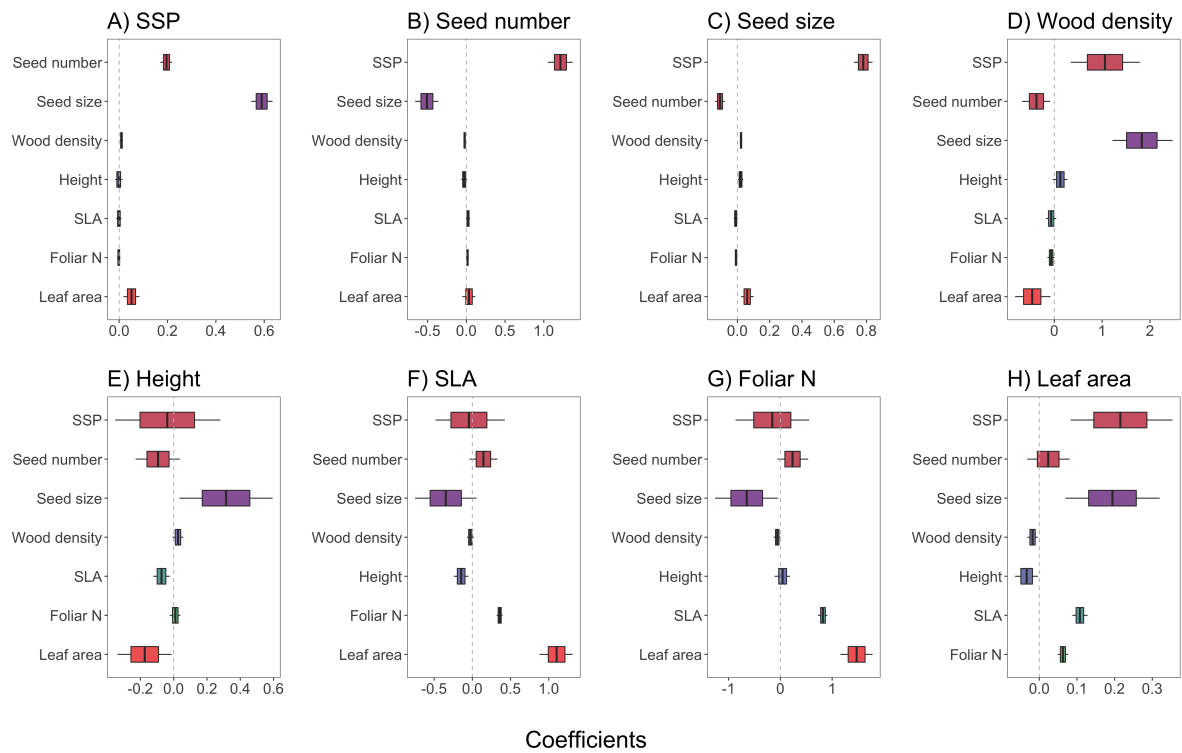


Figure S3: Conditional relationships between traits after accounting for climate but not shared ancestry. Marginal posterior distributions are shown as boxes that contain median vertical lines and are bounded by 68% credible intervals (CI), with 95% CI whiskers. Fig. 3 summarizes the significant relationships.

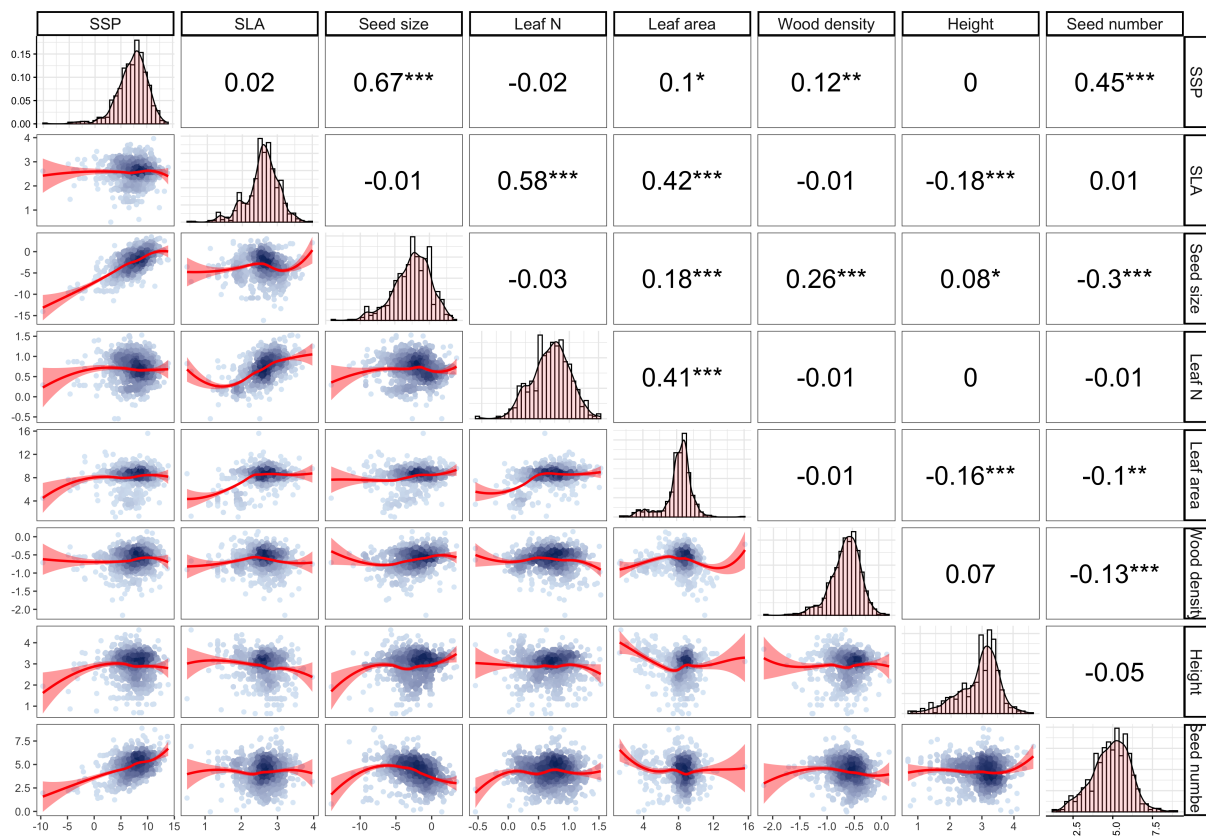


Figure S4: Summary of bivariate relationships between considered traits. Points are species, lines are loess regression and associated 95% CI. Coefficients are Pearson correlations. Traits are log-transformed. Significance levels are * < 0.05; ** < 0.01; *** p < 0.001.