

**Please cite the Published Version**

Bogdziewicz, M, Acuña, MCA, Andrus, R, Ascoli, D, Bergeron, Y, Brveiller, D, Boivin, T, Bonal, R, Caignard, T, Cailleret, M, Calama, R, Calderon, SD, Camarero, JJ, Chang-Yang, CH, Chave, J, Chianucci, F, Cleavitt, NL, Courbaud, B, Cutini, A, Curt, T, Das, A, Davi, H, Delpierre, N, Delzon, S, Dietze, M, Dormont, L, Farfan-Rios, W, Gehring, CA, Gilbert, GS, Gratzer, G, Greenberg, CH, Guignabert, A, Guo, Q, Hackett-Pain, A, Hampe, A, Han, Q, Hoshizaki, K, Ibanez, I, Johnstone, JF, Journé, V, Kitzberger, T, Knops, JMH, Kunstler, G, Kobe, R, Lagueard, JGA , LaMontagne, JM, Ledwon, M, Leininger, T, Limousin, JM, Lutz, JA, Macias, D, Marell, A, McIntire, EJB, Moran, E, Motta, R, Myers, J, Nagel, TA, Naoe, S, Noguchi, M, Oguro, M, Kurokawa, H, Ourcival, JM, Parmenter, R, Perez-Ramos, IM, Piechnik, L, Podgórski, T, Poulsen, J, Qiu, T, Redmond, MD, Reid, CD, Rodman, KC, Šamonil, P, Holik, J, Scher, CL, Van Marle, HS, Seget, B, Shibata, M, Sharma, S, Silman, M, Steele, MA, Straub, JN, Sun, IF, Sutton, S, Swenson, J, Thomas, PA, Uriarte, M, Vacchiano, G, Veblen, TT, Wright, B, Wright, Sam , Whitham, TG, Zhu, K, Zimmerman, JK, Zywiec, M and Clark, JS (2023) Linking seed size and number to trait syndromes in trees. *Global Ecology and Biogeography*, 32 (5). pp. 683-694. ISSN 1466-822X

**DOI:** <https://doi.org/10.1111/geb.13652>

**Publisher:** Wiley

**Version:** Accepted Version

**Downloaded from:** <https://e-space.mmu.ac.uk/631958/>

**Additional Information:** This is an Author Accepted Manuscript of an article published in *Global Ecology and Biogeography*, by Wiley.

**Enquiries:**

If you have questions about this document, contact [openresearch@mmu.ac.uk](mailto:openresearch@mmu.ac.uk). Please include the URL of the record in e-space. If you believe that your, or a third party's rights have been compromised through this document please see our Take Down policy (available from <https://www.mmu.ac.uk/library/using-the-library/policies-and-guidelines>)

1 The global trait syndrome for trees with reproductive  
2 strategies

3 —

## 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.

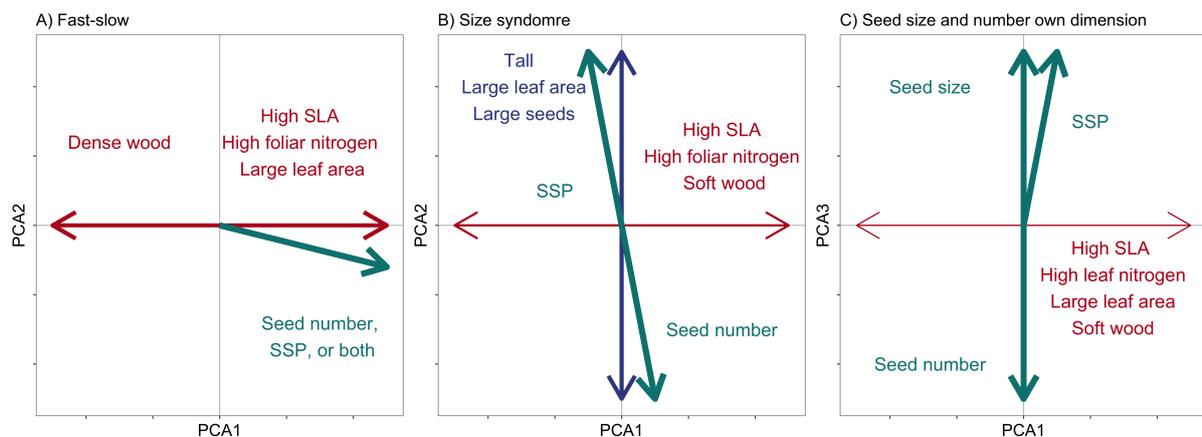
23 —  
24 *keywords:* fecundity | forest recruitment | functional traits | life history strategies | seed size and  
25 number trade-off | size syndrome | leaf economics syndrome

## 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.

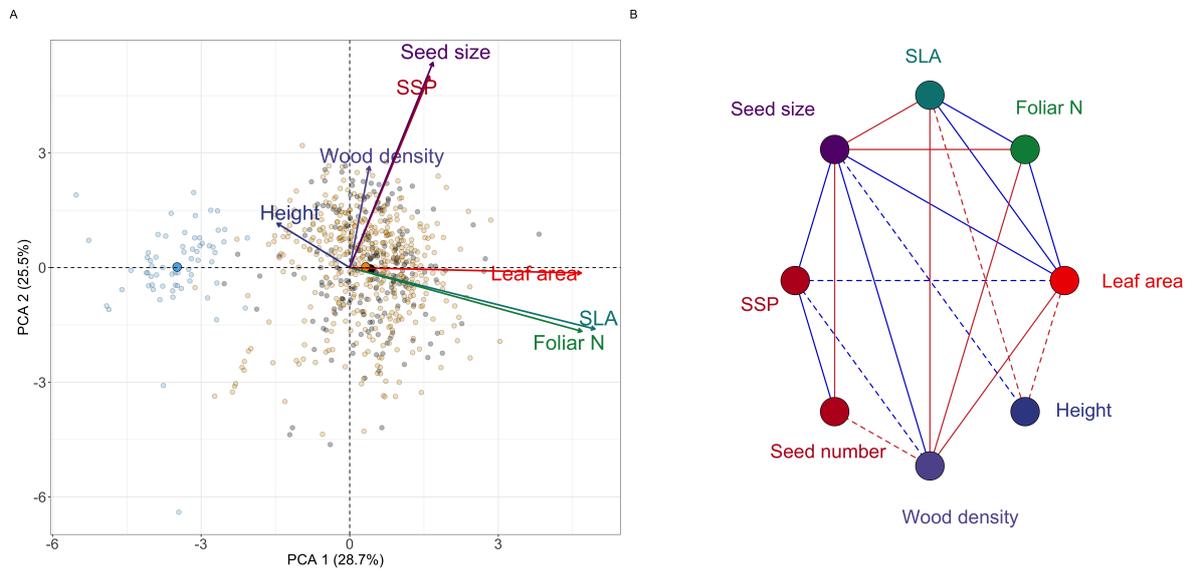
79 A limitation of summaries available from PCA comes from the fact that correlations include  
80 all the indirect ways that traits could be associated. For example, a seed-size/wood-density  
81 correlation could come from a need for high wood density in order to produce large seeds; if  
82 true, 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  $\text{basal area}$ , 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 m<sup>2</sup> 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 m<sup>2</sup> tree basal area,  
 126 rather than seed mass per m<sup>2</sup> 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).

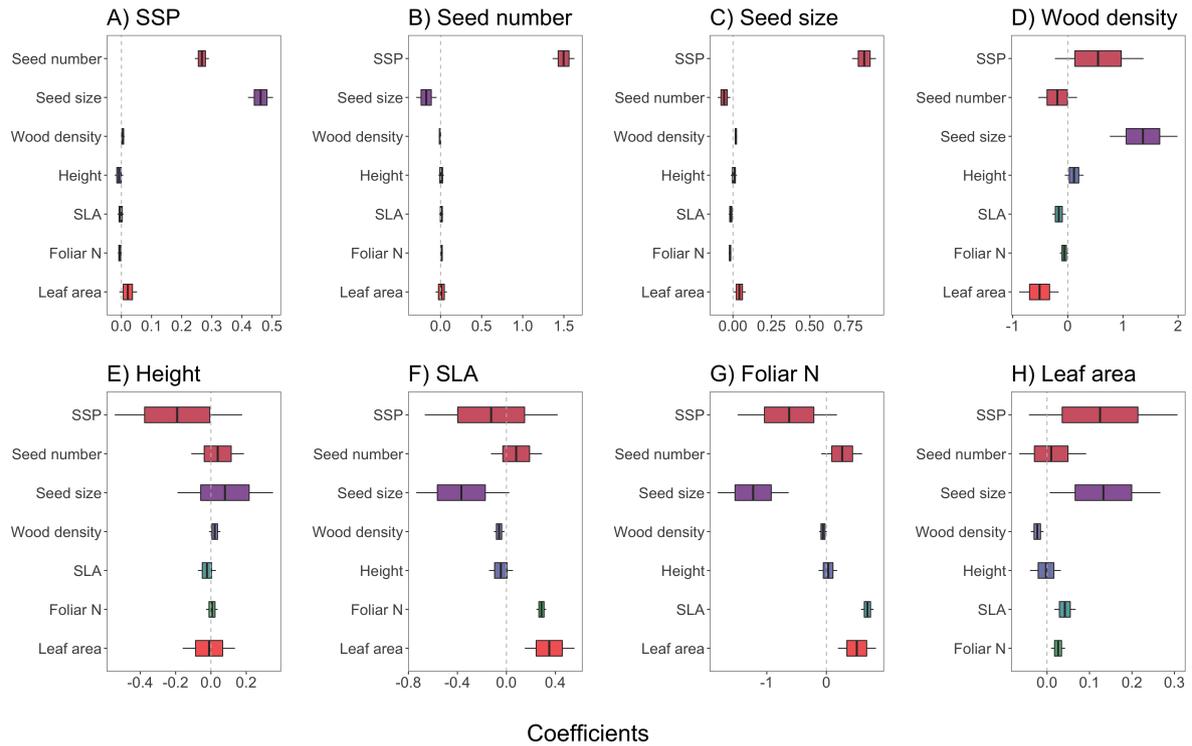


**Figure 2:** Fecundity on the global spectrum of tree form. A) Biplot; arrows length indicates the loading of each considered functional trait onto the first two PCA axes. Points represent the position of species, coded blue for needle, black for broad-deciduous, and yellow for broad evergreen leaf 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 × 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.

## 210 **Acknowledgments**

211 We thank the National Ecological Observatory Network (NEON) for access to sites and veg-  
212 etation structure data, W. Koenig and F. Lefèvre for additional data. The project has been

213 funded by grants to JSC from the National Science Foundation, most recently DEB-1754443,  
 214 and by the Belmont Forum (1854976), NASA (AIST16-0052, AIST18-0063), and the Pro-  
 215 gramme d’Investissement d’Avenir under project FORBIC (18-MPGA-0004) (Make Our Planet  
 216 Great Again). Jerry Franklin’s data remain accessible through NSF LTER DEB-1440409.  
 217 Data from Hubbard Brook (New Hampshire) were funded through NSF-LTER. Puerto Rico  
 218 data were funded by NSF grants, most recently, DEB 0963447 and LTREB 11222325. Data  
 219 from the Andes Biodiversity and Ecosystem Research Group were funded by the Gordon and  
 220 Betty Moore Foundation and NSF 727 LTREB 1754647. MB was supported by grant no.  
 221 2019/35/D/NZ8/00050 from the (Polish) National Science Centre, and Polish National Agency  
 222 for Academic Exchange Bekker programme PPN/BEK/2020/1/00009/U/00001. Research by  
 223 the USDA Forest Service and the USGS was funded by these agencies. Any use of trade, firm,  
 224 or product names does not imply endorsement by the U.S. Government.

## 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,

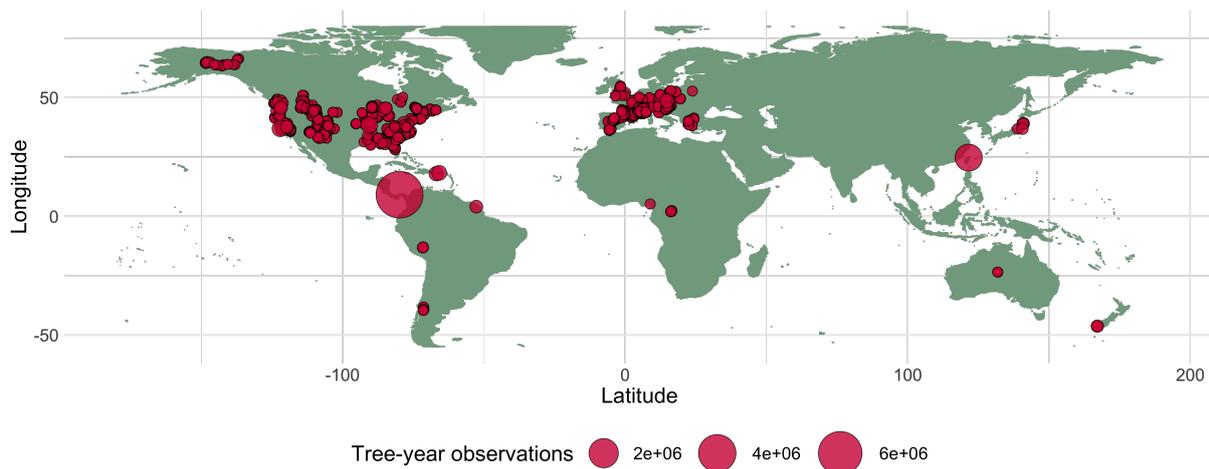
$$E(\mathbf{T}_{-m}|T_m, P, X) = E(\mathbf{T}_{-m}|T_m) + E(\mathbf{T}_{-m}|P, X) \quad (2)$$

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  $\text{yr}^{-1}$  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  $\text{mm}^2$ ), specific leaf area (SLA; measured in  $\text{mm}^2/\text{mg}$ ; the inverse of leaf  
 308 mass per area), leaf nitrogen concentration (measured in  $\text{mg}/\text{g}$ ), wood density (measured in  $\text{g}/\text{m}^3$ )  
 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 <sup>2</sup>
Seed number	seeds/m <sup>2</sup>
Seed size	mg
Height	m
Wood density	g/m <sup>3</sup>
Leaf area	mm <sup>2</sup>
Leaf nitrogen	mg/g
SLA	mm <sup>2</sup> /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  $\Omega$  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.

## References

- 335
- 336 Adier, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache,  
337 C. *et al.* (2014). Functional traits explain variation in plant lifehistory strategies. *Proceedings*  
338 *of the National Academy of Sciences of the United States of America*, 111, 740–745.
- 339 Bazzaz, F.A. (1979). The physiological ecology of plant succession. *Annual Review of Ecology*  
340 *and Systematics*, 10, 351–371.
- 341 Bogdziewicz, M. (2022). How will global change affect plant reproduction? a framework for  
342 mast seeding trends. *New Phytologist*, 234, 14–20.
- 343 Bogdziewicz, M., Hacket-Pain, A., Ascoli, D. & Szymkowiak, J. (2021). Environmental vari-  
344 ation drives continental-scale synchrony of european beech reproduction. *Ecology*, 102,  
345 e03384.
- 346 Carmona, C.P., Bueno, C.G., Toussaint, A., Träger, S., Díaz, S., Moora, M. *et al.* (2021).  
347 Fine-root traits in the global spectrum of plant form and function. *Nature*, 597, 683–687.
- 348 Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009). Towards  
349 a worldwide wood economics spectrum. *Ecology Letters*, 12, 351–366.
- 350 Clark, J.S., Andrus, R., Aubry-Kientz, M., Bergeron, Y., Bogdziewicz, M., Bragg, D.C. *et al.*  
351 (2021). Continent-wide tree fecundity driven by indirect climate effects. *Nature Communi-*  
352 *cations*, 12, 1242.
- 353 Clark, J.S., Iverson, L., Woodall, C.W., Allen, C.D., Bell, D.M., Bragg, D.C. *et al.* (2016). The  
354 impacts of increasing drought on forest dynamics, structure, and biodiversity in the united  
355 states. *Global Change Biology*, 22, 2329–2352.
- 356 Clark, J.S., LaDeau, S. & Ibanez, I. (2004). Fecundity of trees and the colonization–competition  
357 hypothesis. *Ecological Monographs*, 74, 415–442.
- 358 Clark, J.S., Nemergut, D., Seyednasrollah, B., Turner, P.J. & Zhang, S. (2017). Generalized  
359 joint attribute modeling for biodiversity analysis: median-zero, multivariate, multifarious  
360 data. *Ecological Monographs*, 87, 34–56.
- 361 Clark, J.S., Nuñez, C.L. & Tomasek, B. (2019). Foodwebs based on unreliable foundations:  
362 spatiotemporal masting merged with consumer movement, storage, and diet. *Ecological*  
363 *Monographs*, 89, e01381.
- 364 Crone, E.E., McIntire, E.J.B. & Brodie, J. (2011). What defines mast seeding? spatio-temporal  
365 patterns of cone production by whitebark pine. *Journal of Ecology*, 99, 438–444.
- 366 Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S. *et al.* (2016). The global  
367 spectrum of plant form and function. *Nature*, 529, 167–171.
- 368 Falster, D.S. & Westoby, M. (2005). Alternative height strategies among 45 dicot rain forest  
369 species from tropical queensland, australia. *Journal of Ecology*, 93, 521–535.
- 370 Field, C. & Mooney, H. (1986). In T. Givnish (ed) *On the Economy of Plant Form and Function*.

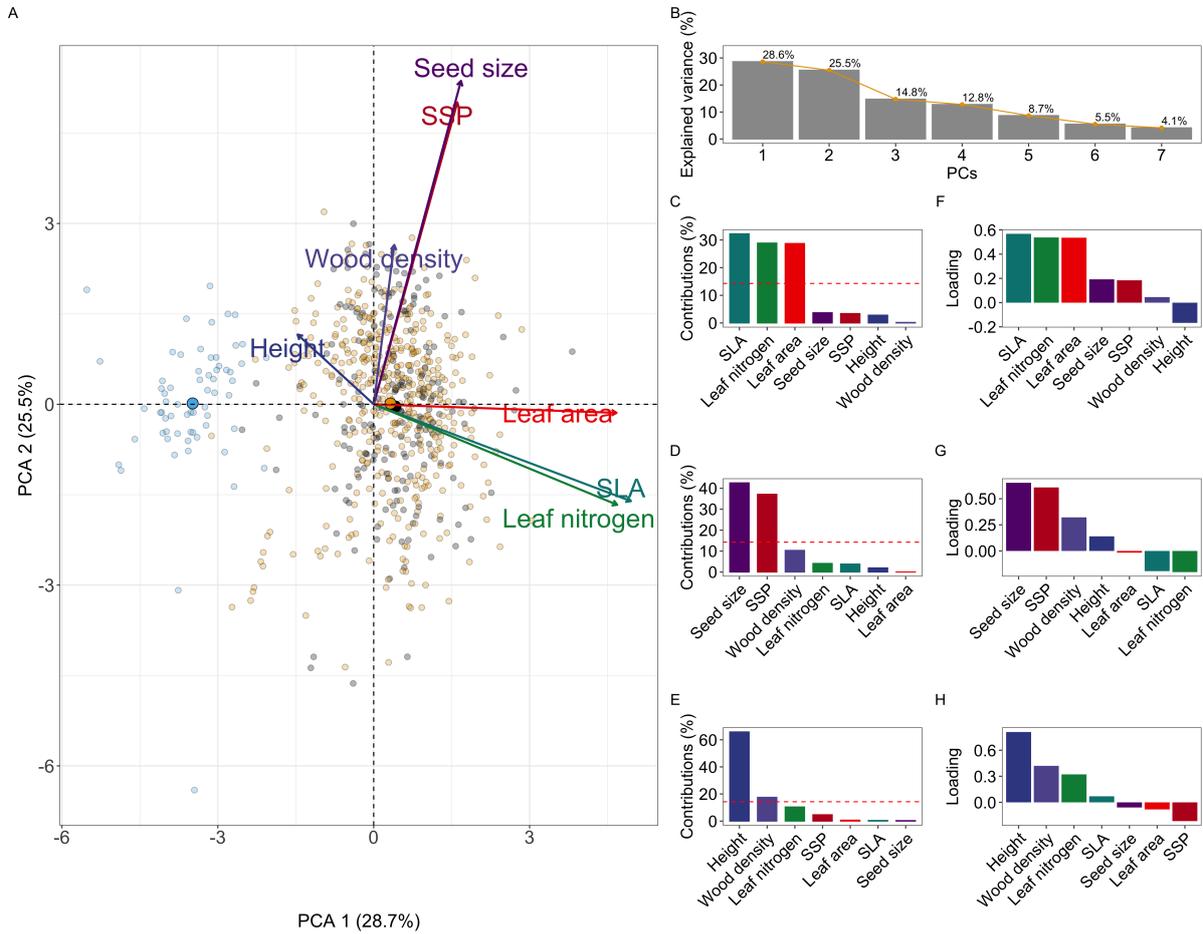
- 371 Fricke, E.C., Tewksbury, J.J. & Rogers, H.S. (2019). Linking intra-specific trait variation  
372 and plant function: seed size mediates performance tradeoffs within species. *Oikos*, 128,  
373 1716–1725.
- 374 Grime, J.P. & Pierce, S. (2012). The evolutionary strategies that shape ecosystems. p. 244.
- 375 Guillemot, J., Martin-StPaul, N.K., Bulascoschi, L., Poorter, L., Morin, X., Pinho, B.X. *et al.*  
376 (2022). Small and slow is safe: On the drought tolerance of tropical tree species. *Global*  
377 *Change Biology*, 28, 2622–2638.
- 378 Hanbury-Brown, A.R., Ward, R.E. & Kueppers, L.M. (2022). Forest regeneration within earth  
379 system models: current process representations and ways forward. *New Phytologist*, n/a,  
380 <https://doi.org/10.1111/nph.18131>.
- 381 Henery, M.L. & Westoby, M. (2001). Seed mass and seed nutrient content as predictors of seed  
382 output variation between species. *Oikos*, 92, 479–490.
- 383 Huston, M. & Smith, T. (1987). Plant succession: Life history and competition.  
384 <https://doi.org/10.1086/284704>, 130, 168–198.
- 385 Journé, V., Andrus, R., Aravena, M.C., Ascoli, D., Berretti, R., Berveiller, D. *et al.*  
386 (2022). Globally, tree fecundity exceeds productivity gradients. *Ecology Letters*, n/a,  
387 <https://doi.org/10.1111/ele.14012>.
- 388 Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P. *et al.* (2020). Try plant  
389 trait database – enhanced coverage and open access. *Global Change Biology*, 26, 119–188.
- 390 Kelly, R., Healy, K., Anand, M., Baudraz, M.E., Bahn, M., Cerabolini, B.E. *et al.* (2021).  
391 Climatic and evolutionary contexts are required to infer plant life history strategies from  
392 functional traits at a global scale. *Ecology Letters*, 24, 970–983.
- 393 Kohyama, T. (1993). Size-structured tree populations in gap-dynamic forest—the forest archite-  
394 cture hypothesis for the stable coexistence of species. *Journal of Ecology*, 81, 131.
- 395 Kohyama, T., Suzuki, E., Partomihardjo, T., Yamada, T. & Kubo, T. (2003). Tree species  
396 differentiation in growth, recruitment and allometry in relation to maximum height in a  
397 bornean mixed dipterocarp forest. *Journal of Ecology*, 91, 797–806.
- 398 Lebrija-Trejos, E., Reich, P.B., Hernández, A. & Wright, S.J. (2016). Species with greater seed  
399 mass are more tolerant of conspecific neighbours: a key driver of early survival and future  
400 abundances in a tropical forest. *Ecology Letters*, 19, 1071–1080.
- 401 McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B.,  
402 Chini, L. *et al.* (2020). Pervasive shifts in forest dynamics in a changing world. *Science*, 368,  
403 eaz9463.
- 404 Moles, A.T. (2018). Being john harper: Using evolutionary ideas to improve understanding of  
405 global patterns in plant traits. *Journal of Ecology*, 106, 1–18.
- 406 Muller-Landau, H.C. (2010). The tolerance-fecundity trade-off and the maintenance of diversity  
407 in seed size. *Proceedings of the National Academy of Sciences of the United States of America*,  
408 107, 4242–4247.

- 409 Muller-Landau, H.C., Wright, S.J., Calderón, O., Condit, R. & Hubbell, S.P. (2008). Interspecific  
410 variation in primary seed dispersal in a tropical forest. *Journal of Ecology*, 96, 653–667.
- 411 Paine, C.E., Amissah, L., Auge, H., Baraloto, C., Baruffol, M., Bourland, N. *et al.* (2015).  
412 Globally, functional traits are weak predictors of juvenile tree growth, and we do not know  
413 why. *Journal of Ecology*, 103, 978–989.
- 414 Pearse, I.S., LaMontagne, J.M., Lordon, M., Hipp, A.L. & Koenig, W.D. (2020). Biogeography  
415 and phylogeny of masting: do global patterns fit functional hypotheses? *New Phytologist*,  
416 227, 1557–1567.
- 417 Pesendorfer, M.B., Ascoli, D., Bogdziewicz, M., Hacket-Pain, A., Pearse, I.S. & Vacchiano,  
418 G. (2021). The ecology and evolution of synchronized reproduction in long-lived plants.  
419 *Philosophical Transactions of the Royal Society B: Biological Sciences*, 376, 20200369.
- 420 Pesendorfer, M.B., Bogdziewicz, M., Szymkowiak, J., Borowski, Z., Kantorowicz, W., Espelta,  
421 J.M. *et al.* (2020). Investigating the relationship between climate, stand age, and temporal  
422 trends in masting behavior of european forest trees. *Global Change Biology*, 26, 1654–1667.
- 423 Pierce, S., Bottinelli, A., Bassani, I., Ceriani, R.M. & Cerabolini, B.E.L. (2014). How well  
424 do seed production traits correlate with leaf traits, whole-plant traits and plant ecological  
425 strategies? *Ecology*, 215, 1351–1359.
- 426 Poorter, L. (2015). Are species adapted to their regeneration niche, adult niche, or both?  
427 <https://doi.org/10.1086/512045>, 169, 433–442.
- 428 Poorter, L., Wright, S.J., Paz, H., Ackerly, D.D., Condit, R., Ibarra-Manríquez, G. *et al.* (2008).  
429 Are functional traits good predictors of demographic rates? evidence from five neotropical  
430 forests. *Ecology*, 89, 1908–1920.
- 431 Poorter, L., Zuidema, P.A., Peña-claros, M. & Boot, R.G.A. (2005). A monocarpic tree species  
432 in a polycarpic world: How can tachigali vasquezii maintain itself so successfully in a tropical  
433 rain forest community? *Journal of Ecology*, 93, 268–278.
- 434 Qiu, T., Andrus, R., Aravena, M.C., Ascoli, D., Bergeron, Y., Berretti, R. *et al.* (2022). Limits to  
435 reproduction and seed size-number trade-offs that shape forest dominance and future recovery.  
436 *Nature Communications*, 13, 1–12.
- 437 Qiu, T., Aravena, M.C., Andrus, R., Ascoli, D., Bergeron, Y., Berretti, R. *et al.* (2021). Is there  
438 tree senescence? the fecundity evidence. *Proceedings of the National Academy of Sciences  
439 of the United States of America*, 118, e2106130118.
- 440 R Core Team (2020). *R: A Language and Environment for Statistical Computing*. R Foundation  
441 for Statistical Computing, Vienna, Austria.
- 442 Reich, P.B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto.  
443 *Journal of Ecology*, 102, 275–301.
- 444 Reich, P.B. & Oleksyn, J. (2004). Global patterns of plant leaf n and p in relation to temperature  
445 and latitude. *PNAS*, 101, 11001–11006.
- 446 Reich, P.B., Walters, M.B., Ellsworth, D.S., Vose, J.M., Volin, J.C., Gresham, C. *et al.* (1998).  
447 Relationships of leaf dark respiration to leaf nitrogen, specific leaf area and leaf life-span: a  
448 test across biomes and functional groups. *Oecologia* 1998 114:4, 114, 471–482.

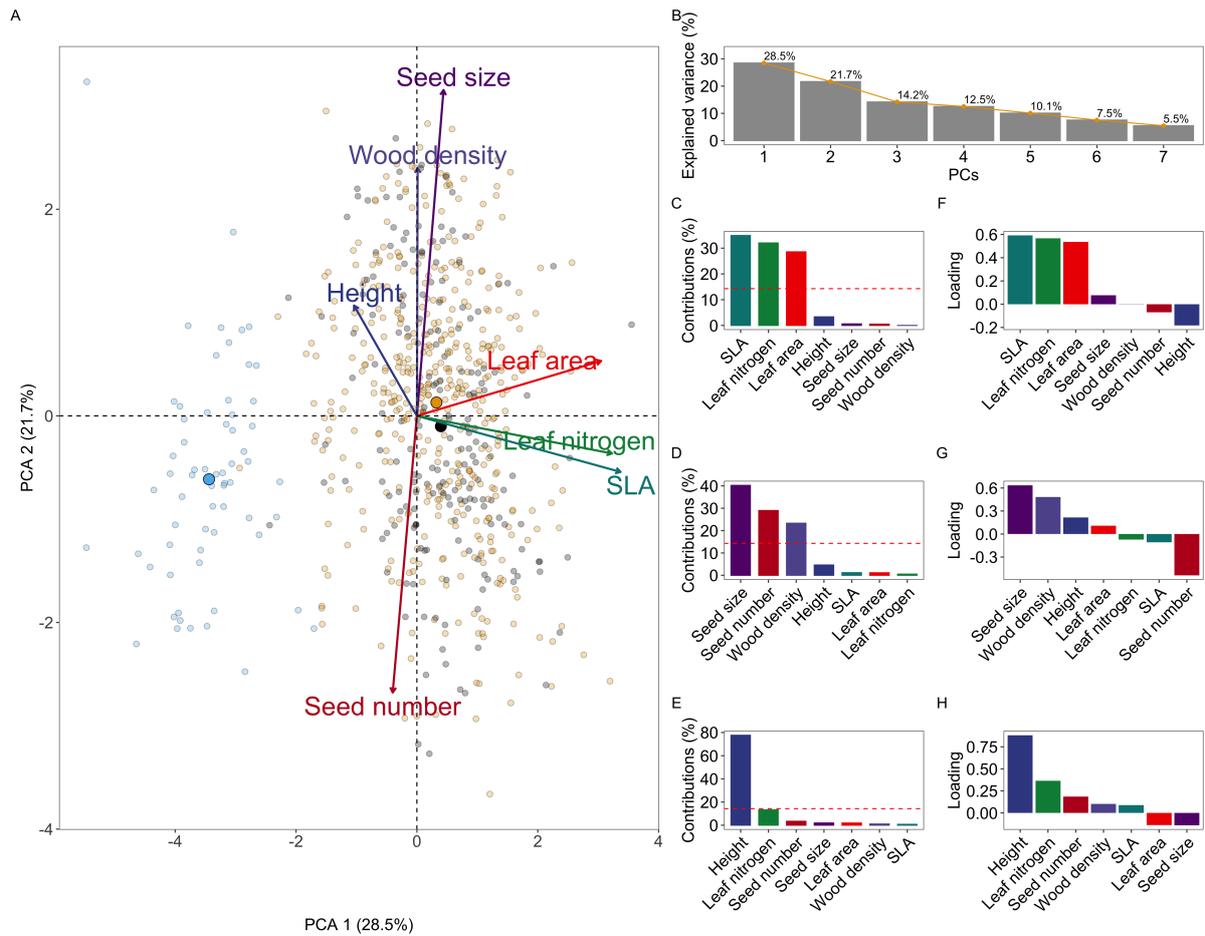
- 449 Rüger, N., Comita, L.S., Condit, R., Purves, D., Rosenbaum, B., Visser, M.D. *et al.* (2018).  
450 Beyond the fast–slow continuum: demographic dimensions structuring a tropical tree com-  
451 munity. *Ecology Letters*, 21, 1075–1084.
- 452 Rüger, N., Condit, R., Dent, D.H., DeWalt, S.J., Hubbell, S.P., Lichstein, J.W. *et al.* (2020).  
453 Demographic trade-offs predict tropical forest dynamics. *Science*, 368, 165–168.
- 454 Scholze, M., Knorr, W., Arnell, N.W. & Prentice, I.C. (2006). A climate-change risk analysis  
455 for world ecosystems. *Proceedings of the National Academy of Sciences of the United States*  
456 *of America*, 103, 13116–13120.
- 457 Seyednasrollah, B. & Clark, J.S. (2020). Where resource-acquisitive species are located: The  
458 role of habitat heterogeneity. *Geophysical Research Letters*, 47, e2020GL087626.
- 459 Sharma, S., Andrus, R., Bergeron, Y., Bogdziewicz, M., Bragg, D.C., Brockway, D. *et al.* (2022).  
460 North american tree migration paced by climate in the west, lagging in the east. *Proceedings*  
461 *of the National Academy of Sciences*, 119, e2116691118.
- 462 Shibata, M., Masaki, T., Yagihashi, T., Shimada, T. & Saitoh, T. (2020). Decadal changes in  
463 masting behaviour of oak trees with rising temperature. *Journal of Ecology*, 108, 1088–1100.
- 464 Shreve, F. (1925). Ecological aspects of the deserts of california. *Ecology*, 6, 93–103.
- 465 Tilman, D. (1994). Competition and biodiversity in spatially structured habitats. *Ecology*, 75,  
466 2–16.
- 467 Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. *et al.* (2007). Let the  
468 concept of trait be functional! *Oikos*, 116, 882–892.
- 469 Westoby, M. (1998). A leaf-height-seed (lhs) plant ecology strategy scheme. *Plant and Soil*,  
470 199, 213–227.
- 471 Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002). Plant ecological  
472 strategies: Some leading dimensions of variation between species. *Annual Review of Ecology*  
473 *and Systematics*, 33, 125–159.
- 474 Wilfahrt, P.A., Collins, B. & White, P.S. (2014). Shifts in functional traits among tree commu-  
475 nities across succession in eastern deciduous forests. *Forest Ecology and Management*, 324,  
476 179–185.
- 477 Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004). The  
478 worldwide leaf economics spectrum. *Nature* 2004 428:6985, 428, 821–827.
- 479 Wright, S.J., Kitajima, K., Kraft, N.J., Reich, P.B., Wright, I.J., Bunker, D.E. *et al.* (2010).  
480 Functional traits and the growth–mortality trade-off in tropical trees. *Ecology*, 91, 3664–  
481 3674.
- 482 Yang, J., Cao, M. & Swenson, N.G. (2018). Why functional traits do not predict tree demographic  
483 rates.

484 **Supplementary material**

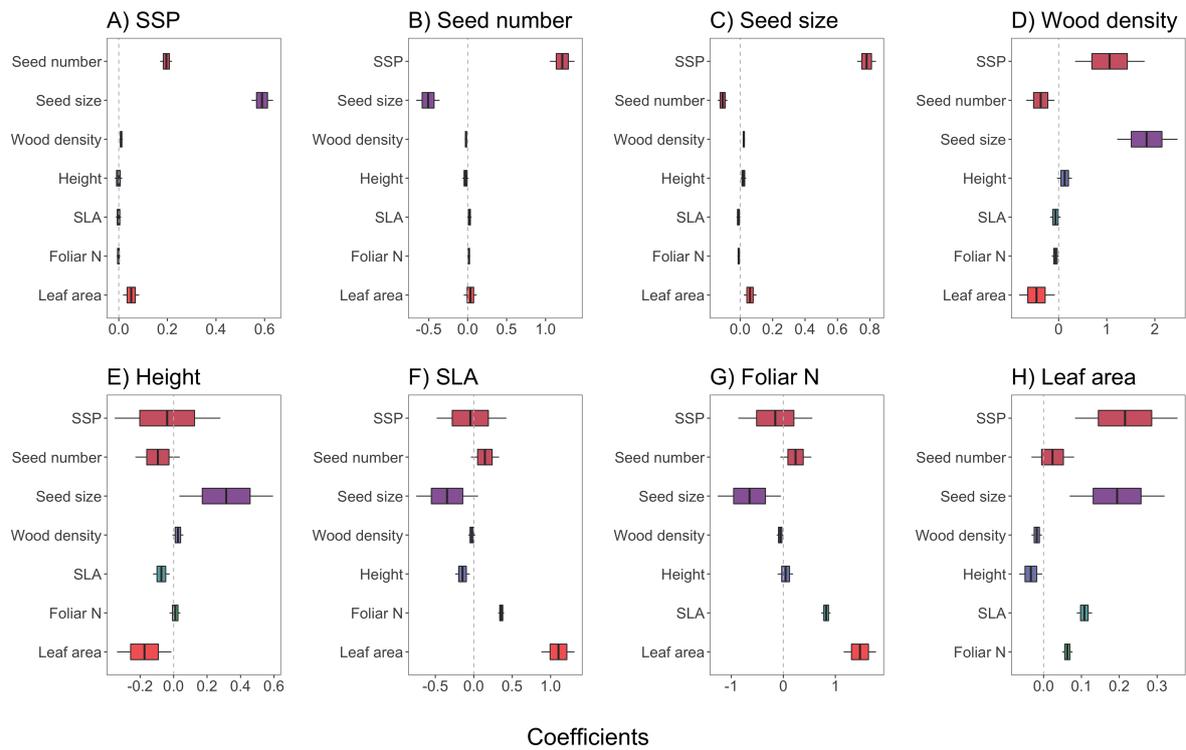
485 This Supplement provides additional data summaries as tables and figures. Full summaries of  
 486 the [MASTIF network](#) are available these links for [sites](#) and [species](#).



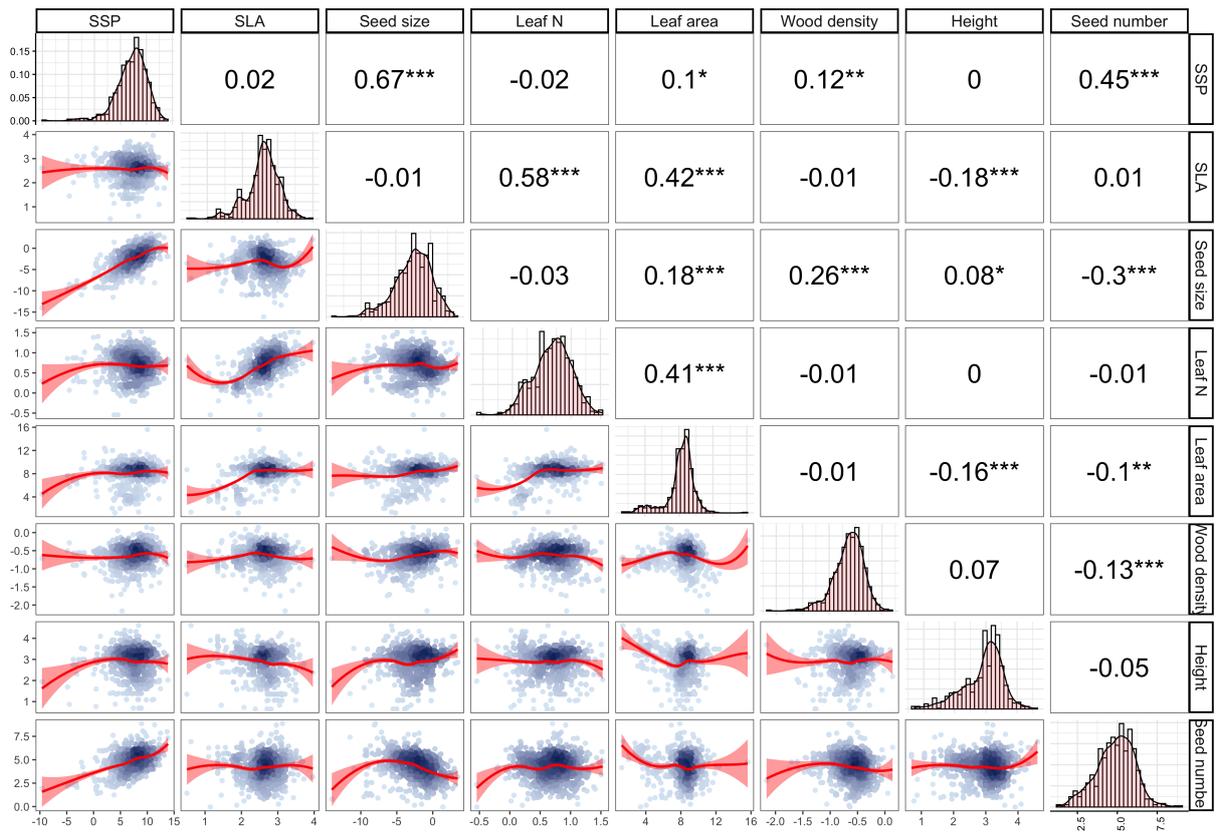
**Figure S1:** PCA as presented on Fig. 2 extended with contributions and loadings of the three axes that explained the most variance. A) Species seed productivity (SSP) on the global spectrum of tree form. Arrow length indicates the loading of each considered functional trait onto PCA axes. Points represent 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.