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Linking seed size and number to trait syndromes in trees

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

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55 Data availability statement

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

57 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.

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

66 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.

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

keywords: fecundity | functional traits | life history strategies | size syndrome | leaf economics | tree recruitment |

Introduction

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

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

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

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

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

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

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

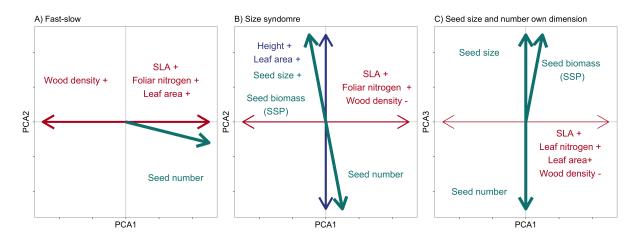


Figure 1: Hypothetical associations between dimensions of plant life strategies represented by functional traits and the seed number, seed size, and species seed productivity (the product of seed number and seed size, SSP developed by Qiu *et al.* (2022)). Seed production can be associated with: A) fast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

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

This large sample size is important for the notoriously noisy seed production in trees (Kelly et al., 2021), where tree-to-tree and year-to-year variation in seed number span several orders of magnitude (Clark et al., 2004; Journé et al., 2022). By combining seed number with seed size into species seed productivity (seed size x seed number, SSP, developed by Qiu et al. (2022)), we show how reproductive traits relate to one another separately and in combination. Combining seed number and seed size into SSP brings more exhaustive information on reproductive investment because species that invest in large seeds are producing more seeds than expected from the 1:1 trade-off (Qiu et al., 2022). For this reason, SSP should be more strongly aligned with seed size than seed number. By standardizing these metrics for the tree size we account for the variation in size distribution within the data and facilitate comparisons. For example, the SSP is the average annual species seed productivity per m2 basal area at average environmental conditions across the species' range in the data (Qiu et al., 2021a, 2022). If large seeds confer an advantage in competitive, shaded understories, while many small seeds allow colonization of distant sites, then SSP provides a direct link to fitness. The hypothesized relationships between seed number, seed size, SSP, and traits are summarized in Figure 1.

Methods

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

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

314 file.

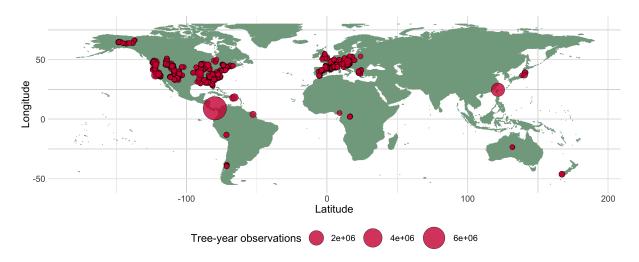


Figure 2: Map of raw data used to estimate the number of seeds produced by trees with the MASTIF model.

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

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

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

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

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

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

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

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

Traits We selected six functional plant traits previously shown to capture plant life strategies well (Díaz *et al.*, 2016; Carmona *et al.*, 2021): plant height (measured in m), leaf area (measured in mm²), specific leaf area (SLA; measured in mm²/mg; the inverse of leaf mass per area), leaf nitrogen concentration (measured in mg/g), wood density (measured in g/m³) and seed size (measured in g). The data was obtained from primary sources and supplemented with publicly available data from the latest version of the TRY Plant Trait Database (Kattge *et al.*, 2020) extracted from the Carmona *et al.* (2021). Missing values for the six traits were filled with genus-level means. Bivariate relationships are summarized in Fig. S4).

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

$$[\mathbf{T}|P,X] = \frac{[\mathbf{T},P,X]}{[P,X]} \tag{3}$$

where the distribution of groups and environments [P, X] is that which occurs in the data set. To determine trait relationships we fit a joint model to the conditional distribution $[\mathbf{T}|P,X]$, which provides estimates of the phylogeny as random groups $\mathbf{g}[s], g = 1, ..., M$ for species s and S as a S and S as a S and S and S are distribution into (conditional) effects of other traits and the environment (Seyednasrollah & Clark, 2020; Qiu S and S are distribution of S and S are distribution S and S are distribution of S are distribution of S and S are

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

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

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

Results

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

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

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

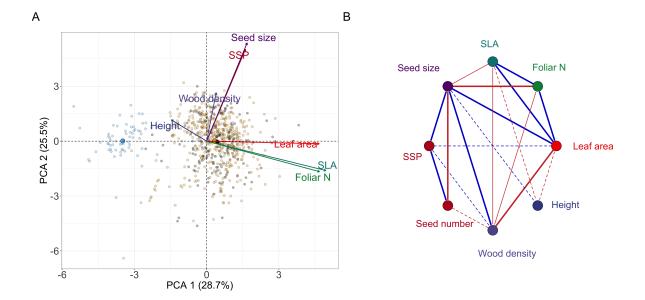


Figure 3: Seed size, seed number, and species seed productivity (SSP) on the spectrum of tree form. A) Biplot; arrow length indicates the loading of each considered trait onto the first two PCA axes. Points represent the position of species, coded blue for the needle, black for broad-deciduous, and yellow for broad evergreen leaf habit. Larger points indicate means for the groups. An extended version of that graph is given in Fig. S1. B) Summary of GJAM coefficients presented in Fig. 4. Significant associations between traits are highlighted by lines, coded red for negative and blue for positive relationships. Dashed lines highlight associations that are significant only in the model without phylogenetical control (see Fig. S3). Extended PCA plots are available in supplement Fig. S2. SSP stands for species seed productivity and is the product of seed size × 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.

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

28 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

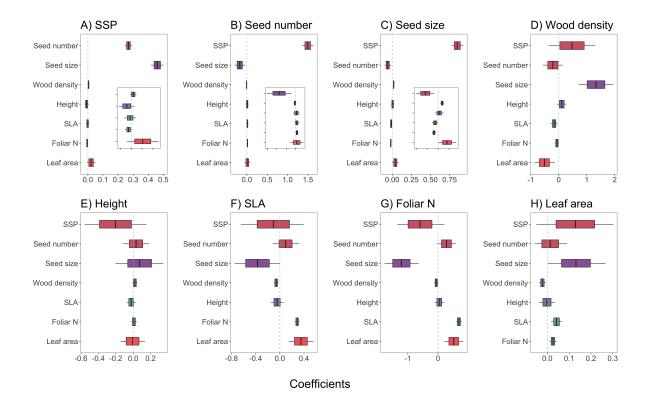


Figure 4: Conditional relationships between traits after accounting for climate and phylogeny. Posterior distributions are shown as boxes that contain median vertical lines and are bounded by 68% credible intervals (CI), with 95% CI whiskers. Coefficients are evaluated on a standardized scale. The inset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

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

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

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

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

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

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

59 Materials and Methods

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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):

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

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

$$SSP_s = \frac{\sum_{ij} w_{ijs} ISP_{ijs}}{\sum_{ij} w_{ijs}}$$
 (3)

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

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

$$[\mathbf{T}_{s}|P,X] = MVN_{M}(\mathbf{T}_{s}|\mathbf{B}'\mathbf{x}_{s} + \mathbf{g}[s],\Sigma)$$

$$\mathbf{g} \sim MVN(\mathbf{0},\Omega)$$
(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

$$\mathbf{B} = \begin{pmatrix} \mathbf{B}_{-m} \\ \mathbf{B}_{m} \end{pmatrix} \tag{5}$$

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

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

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

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

$$\boldsymbol{\mu}_{-m,s} = \mathbf{B}_{-m}\mathbf{x}_s + \mathbf{A}(T_{m,s} - \mathbf{B}_m\mathbf{x}_s)$$

$$= \mathbf{C}\mathbf{x}_s + \mathbf{A}T_{m,s} \tag{8}$$

$$\mathbf{P} = \Sigma_{-m,-m} - \mathbf{A}\Sigma_{m,-m} \tag{9}$$

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

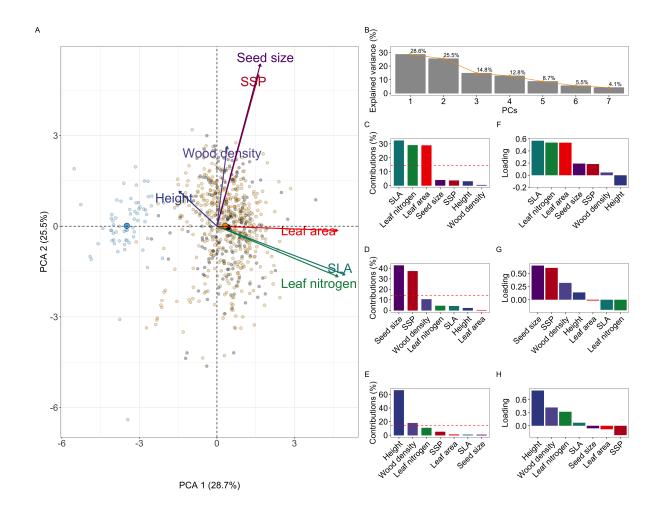


Figure S1: PCA as presented on Fig. 3 extended with contributions and loadings of the three axes that explained the most variance. A) Species seed productivity (SSP) on the global spectrum of tree form. Arrow length indicates the loading of each considered functional trait onto PCA axes. Points represent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

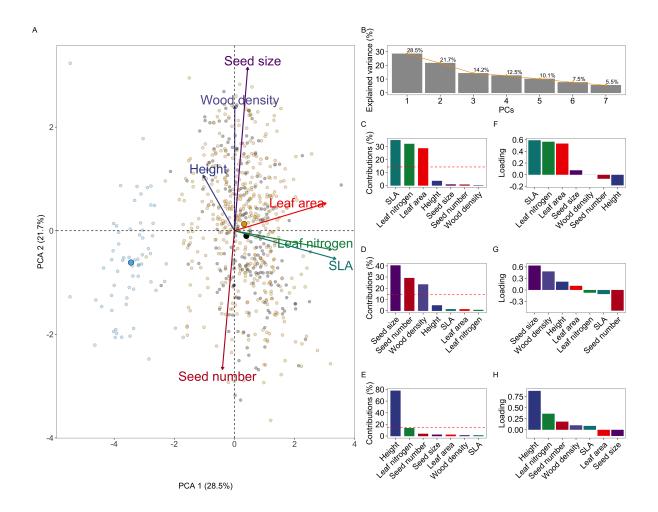


Figure S2: A) Seed number on the spectrum of tree form. Arrow length indicates the loading of each considered functional trait onto PCA axes. Points represent the position of species. B) Explained variance for each principal component. Bar plots present the contribution (C,D,E) and loading (F,G,H) of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

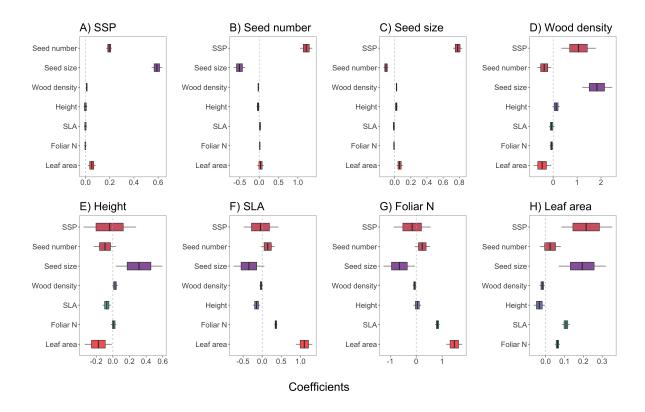


Figure S3: Conditional relationships between traits after accounting for climate but not shared ancestry. Marginal posterior distributions are shown as boxes that contain median vertical lines and are bounded by 68% credible intervals (CI), with 95% CI whiskers. Fig. 3 summarizes the significant relationships.

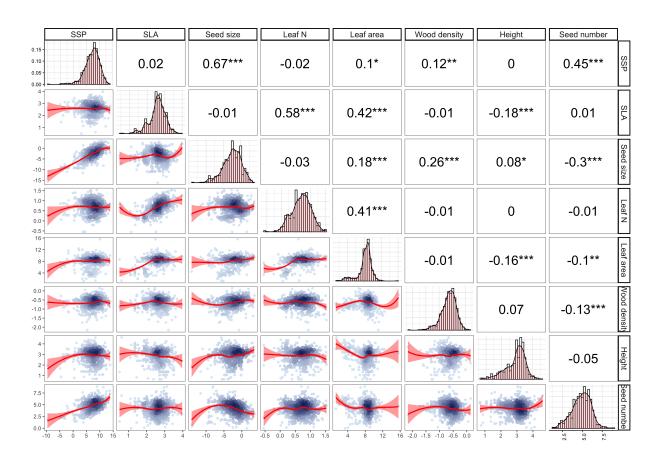


Figure S4: Summary of bivariate relationships between considered traits. Points are species, lines are loess regression and associated 95% CI. Coefficients are Pearson correlations. Traits are log-transformed. Significance levels are * < 0.05; ** < 0.01; *** p < 0.001.