# Global tree-fecundity is linked to the intensity of species interactions

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- *keywords:* climate | competition | forest regeneration | seed consumption | species interactions
- 125 | tree fecundity

## **Abstract**

Increasing evidence points to intense species competition in wet tropical forests that that may 127 be explained by interactions involving seeds, seedlings, and their consumers. Lack of tree 128 fecundity data across temperate to tropical communities precludes analysis of how the seed 129 resource contributes to biotic interactions that can drive biogeographic diversity patterns. A 130 global synthesis of raw seed-production data shows a 2.4 order of magnitude increase in seed 131 abundance from cold, dry to warm, wet climates, driven by a 2.0 order of magnitude increase 132 in seed production for a given tree size. The modest increase in forest productivity across the 133 same climate gradient cannot explain this 100-fold increase in seed production or the 250-fold 134 increase in seed mass per forest area reported here. The increase in seeds per tree can arise from 135 adaptive evolution driven by intense species interactions or from the direct effects of a warm, 136 moist climate on tree fecundity. Either way, the massive differences in seed supply to temperate 137 versus tropical communities ramifies through food webs, affecting community and ecosystem 138 dynamics, including seedling competition, populations of seed consumers and frugivore-seed 139 dispersers, all of which appear to be especially important in the wet tropics. 140

## **Introduction**

Understanding seed production can help resolve the paradox of extreme tree diversity in the 142 warm latitudes where intense competition is expected to limit coexistence [1, 2, 3, 4]. High net 143 primary productivity (NPP) that comes with long growing seasons accelerates growth, increases 144 plant competition, and elevates mortality rates [5, 6, 7]. This coincidence of high diversity with 145 intense competition is increasingly explained by coexistence mechanisms involving interactions 146 between seeds and seedlings through their natural enemies [8, 9, 10]. Tree fecundity determines 147 the density of competing offspring and the diets of consumers and seed dispersers that depend on 148 them [11, 12, 13], and it is clearly subject to adaptive evolution [14, 15]. If there is a latitudinal 149 gradient in seed production, is it a product of greater seed production for a given tree size, or is it 150 the case that tropical trees are simply larger and/or embedded in more productive communities, 151 as assumed in the Dynamic Global Vegetation Models (DGVMs) used to understand effects 152 of climate change [16, 17]? Temperate-tropical fecundity gradients that go beyond what could 153 be explained by differences in tree size or NPP would provide evidence that biogeographic 154 diversity trends depend on this critical demographic variable that is a foundation for many forest 155 food webs [18, 19]. While forest inventory data continue to improve estimates of growth and 156 mortality across climate gradients [7, 20], fecundity evidence has remained unavailable. This 157 synthesis allows us to quantify the fecundity gradient on a global scale and determine that it is 158 amplified in warm/moist climates beyond what can be explained by tree size or NPP. 159

Seed and seedling densities are the starting point not only for competition, but also for 160 consumer-based explanations of coexistence that were first recognized in the tropics [8, 9]. 161 Intense plant competition is an inevitable consequence of long growing seasons and high annual 162 growth [21, 22, 23]. Accumulating evidence indicates that consumer pressure is likewise 163 intense [24, 25, 4]. Selection for high seed production might offset high losses to biotic 164 interactions, while at the same time intensifying them by increasing density- and frequency-165 dependent interactions. By the widely invoked Janzen-Connell mechanism [8, 9], a host tree 166 can escape its specialist consumers where that host is rare, i.e., a density-dependent process. 167 A generalist consumer imposes indirect competition between its multiple hosts, as an increase 168 in one attracts the natural enemies it shares with others, a density- and frequency-dependent 169 process. The seed diversity available to consumers could differ from that of trees, because the 170

abundant species may not produce large seed crops, and vice versa. There is potential for an arms race between species [26, 27] as selective pressures balance the benefits of producing more seed against the costs of diverting resources from growth and defense [28, 29]. Taken together, tree fecundity is a foundation for community interactions that increasingly appear to be most intense in tropical forests.



**Figure 1:** a) Climate effects on fecundity could be I) negligible, in which case there is no latitudinal fecundity gradient (right), or there could be direct (II) or indirect effects through adaptive responses to intense species interactions in tropical climates (III). Both II and III could be amplified beyond what could be explained by gradients in tree size or NPP. Either way, there is potential for positive feedback involving arrows in green. b) Orders of magnitude increases from cold/dry to warm/moist for individual (ISP) and community (CSP) seed production compared with NPP. Curves are sections through surfaces (dashed lines) in Fig. 2, with scales for moisture deficit (above) and temperature (below). Curves are in proportion to minimum values in cold, dry conditions. Confidence intervals (95%) are not visible for ISP and NPP due to the large number of trees. They are wider for CSP due to fewer inventory plots at high temperatures (Fig. 2b).

Fecundity could vary due to climate directly or indirectly, the latter through adaptation to biotic interactions that, in turn, respond to climate (Fig. 1a). Because reproductive effort depends on both seed sizes and numbers [30], and it varies with tree size [31], *individual seed productivity* (ISP) is standardized for tree basal area,

$$ISP_{ij} = \frac{\hat{f}_{ijs} \times g_s}{\text{basal area}_i}$$
(1)  
= g m<sup>-2</sup>yr<sup>-1</sup>

depending on mass of a seed  $g_s$  produced by species *s*, where the estimate of mean seed production  $\hat{f}_{ijs}$  for tree *i* at location *j* accounts for the uncertainty in its seed production each year,  $f_{ijs,t}$  (see Methods). If seed production is determined solely by tree size, as assumed in ecological models (reviewed in [31]), then climate effects could come through its effects on past growth that results in larger trees (Fig. 1a, II), and ISP (standardized for size) will be constant across climate gradients.

<sup>186</sup> While  $ISP_{ij}$  quantifies production by individuals, *community seed production*,  $CSP_j$ , quan-<sup>187</sup> tifies seed density on the forest floor, the starting point for interactions between seeds, seedlings, consumers, and dispersers. [We hereafter omit subscripts to reduce clutter.] Like NPP, CSP is a community property, defined as the seed production summed over all trees on a plot (g ha<sup>-1</sup> yr<sup>-1</sup>, eqn 4). CSP might scale as a fraction of NPP, as suggested by some empirical evidence [32] and assumed in DGVMs [16, 17], predicting high CSP where NPP is highest in warm/moist climates [33]. If ISP is determined as a simple fraction of tree size, or CSP as a fraction of NPP, then it is hard to invoke biotic interactions as an explanation for variation along climate gradients.

Alternatively, if the responses are amplified beyond what could be explained by the effects 195 of climate on size or NPP, then climate gradients could be a driver of intense biotic interactions 196 in the tropics. There are at least two potential causes for fecundity amplification (Fig. 1a). First, 197 ISP might have flexibility to respond to a longer growing season [34, 35] well in excess of tree 198 growth, which is limited by mechanical and hydraulic constraints on tree size [36, 37]. At the 199 community scale, NPP is further constrained by the compensatory losses in stand biomass as 200 mortality increases to offset increases in growth [22]. Thus, while NPP increases with warm, 201 wet conditions, the lack of structural constraints on producing more seeds might allow for a 202 disproportionate fecundity response, the *amplification* of figure 1a, II. 203

Amplification could also be driven by intense species interactions in the wet tropics [4, 38] that increase selection for seed production, mediated by allocation trade-offs between seeds versus growth and defense [39, 40]. Whether amplification occurs as a direct response to climate or as an adaptive response to intense biotic interactions (Fig. 1a, II and III), the densityand frequency-dependent processes involving competition, consumers, and seed dispersers have community-wide implications. A potential arms race follows from the feedback between high seed production and the selection pressures to offset mortality losses (green arrows in Fig. 1a).

Biogeographic variation in fecundity remains largely unknown. Fecundity studies typically 211 report on one to a few species from one to a few sites. Recent compilations of seed numbers 212 recognise the challenges posed by differing methods, some yielding estimates of stand averages 213 and others offering various individual-tree estimates that are difficult to compare [41, 42]. Efforts 214 to synthesize this literature globally report that seed size [43] or variation in seed numbers (e.g., 215 [42]) increase with temperature or with variability in precipitation or temperature. Latitudinal 216 trends in seed size [43, 44] may not translate to trends in fecundity, which depends on the number 217 of seeds  $\times$  seed size. A decline in predicted seed-mass density (per forest floor) with increasing 218 latitude reported from a study that included only forests at low latitudes and mostly heath and 219 grasslands at high latitudes [43] highlights the need to separate variation in tree fecundity from 220 variation in tree abundance. 221

This synthesis extends the Masting Inference and Forecasting (MASTIF) network [45] to determine the climate controls on seed production globally and the extent to which those trends go beyond what can be explained by effects of size and productivity. Climate trends are summarized by mean annual temperature and moisture deficit. We additionally allow for effects of individual condition and local habitat variation by including tree diameter, shade class, and soil cation exchange capacity (Materials and Methods).

## **Results and Discussion**

Community seed production (CSP) increases 2.4 orders of magnitude to a global maximum in the
warm, moist tropics, primarily driven by a two order-of-magnitude increase in seed production
for a given tree size (ISP) (Fig. 1b). These increases align with the geographic trend in NPP
(panels in Fig. 2), but the amplification for seed production in excess of the NPP gradient
provides first evidence that it can play a central role in the species interactions hypothesized to



**Figure 2:** a) Climate responses for (a) ISP (seed mass per tree basal area,  $\log 10 \text{ g m}^{-2} \text{ y}^{-1}$ ) (b) CSP (seed mass per ha forest floor,  $\log 10 \text{ g ha}^{-1} \text{ y}^{-1}$ ), and (c) NPP (kg C m<sup>-2</sup> y<sup>-1</sup>). Dashed lines indicate the transect from dry taiga to wet tropics in Fig. 1b. Note the linear scale for (c) and  $\log_{10}$  scales for (a) and (b). Convex hulls are defined by observations (red), including individual trees (a, c) and inventory plots (b). Surface transparency increases as the inverse of the predictive standard error-faded edges reflect increased uncertainty at data extremes. Coefficients are reported in Table S2 for NPP.

<sup>234</sup> be most intense in warm, moist climates. If individual fecundity scales with tree basal area, then
<sup>235</sup> ISP (seed mass per tree basal area) would be flat in Fig. 1b. If community seed production
<sup>236</sup> scales with NPP, then CSP would increase no faster than NPP on the proportionate scale in Fig.
<sup>237</sup> 1b. The amplification over size and NPP observed here has implications for trophic interactions,
<sup>238</sup> and it provides insights into cause.

A first important benchmark of this study is the exposure of fecundity trends with global 239 climate. The average seed production for 95% of trees of a given size varies over five orders 240 of magnitude, with ISP ranging from 0.000025 to 50 g per  $cm^2$  of basal area (Figure S5a). 241 The increase in ISP to its highest values in warm, moist climates (Fig. 2b) is driven more 242 by temperature than by moisture (Table S4), amplified by moisture where temperatures are 243 high (Figure S2c). The five order-of-magnitude range for individual ISP is matched by that 244 for community seed production, with 95% of CSP values ranging from 50 g to 2500 kg ha<sup>-1</sup> 245 (Figure S5b). The 100-fold increase in ISP across the climate gradient is more than matched by 246 the 250-fold increase in CSP. 247

Forest productivity cannot explain the global fecundity gradient evident at the individual or 248 community levels. Like fecundity trends, NPP shows high values in warm, moist climates (Fig. 249 2c). However, the three-fold range of NPP across this climate space is swamped by the 100-250 and 250-fold ranges for ISP and CSP (Fig. 1b). The amplification of both ISP and CSP means 251 that not only do individual trees produce more seed for a given size in the wet tropics, but also 252 that seed abundance is amplified at the community level (Figure S2f). [Community-level CSP 253 need not necessarily track ISP responses due to heterogeneous size-species structures associated 254 with local site conditions, past disturbance, and competition.] These results extend the previous 255 discovery of a fecundity hotspot in the warm, moist southeastern North America [45] to a global 256 pattern. 257

Fecundity trends that are amplified well beyond what can be explained by size or productivity alone could be driven by direct climate effects, by selective pressures due to high losses to biotic interactions, or both (Fig. 1a). The two order-of-magnitude climatic and latitudinal trend in seed mass per forest-floor area (CSP) has its most direct implications for density-dependent interactions, which include competition within tree species and frequency-dependent consumers. All else being equal, a 100-fold gradient in seed supply requires corresponding mortality losses



Species diversity by tree basal area

**Figure 3:** Species diversity in seeds (vertical axis) is lower than expected from species diversity in trees (horizontal axis). In both cases, diversity is evaluated from the Shannon index,  $-\sum_s p_s \log p_s$ , where  $p_s$  is the fraction of species *s* in basal area (trees) and CSP (seeds). Each point represents an inventory plot. Except at low tree diversity, points lie almost entirely below the 1:1 line (dashed). The legend at top left shows mean annual temperature (symbol color) and mass of the average seed (symbol size).

to yield similar densities of adult trees [21, 22]. Elevated densities of seeds, fruits, and nuts and

their offsetting mortality losses increase selective pressure for the most competitive phenotypes.
 The bottom-up enrichment of food webs that cascades to higher trophic levels [18, 19, 25] must
 inevitably increase consumer and disperser densities that, in turn, impose frequency-dependence

selection on seed and seedling survival [8]. The magnitude of amplification leaves no doubt that
 it intensifies species interactions in the wet tropics.

Frequency-dependent consumer pressures depend on diversity of the seed resource, which 270 is poorly predicted by the standard inventory of trees. Species diversity of both seed mass and 271 tree basal area is highest in the warm climates where diversity of the seed resource would be 272 overestimated on the basis of tree diversity (Fig. 3). The lower species diversity for seeds in 273 warm climates results from the fact that species having modest differences in tree basal area 274 vary widely in fecundity; tendency for a subset of species to dominate seed production reduces 275 seed diversity below that for trees. In the cool climates where seeds tend to be small (small, 276 blue symbols in Fig. 3), the low diversity that would be estimated on the basis of trees masks 277 an unexpectedly high seed diversity (Fig. 2). Although many studies do not record fecundity 278 for species having the smallest seeds (e.g., Salicaceae), these are also the seeds that are least 279 apparent to vertebrate consumers. Omission of these smallest seeds means that values are over-280 estimates, but still relevant for many consumers. The net effect of reduced seed diversity in warm 281 climates affects frequency-dependent processes [46], such as host-specific seed predation. The 282 concentration of seed mass in a smaller than expected species diversity reduces the apparency of 283 weak producers, while potentially concentrating consumption on species that are not necessarily 284 abundant, but that can dominate seed production. 285

The biogeographic variation between trees (ISP) and communities (CSP) is distinct from the large masting literature focused on variation in the magnitude of reproduction over time within trees or stands. Temporal variation in climate [47, 48, 49] that interacts with variable storage and pollen supply [50, 51] is of great interest for understanding allocation shifts within individuals, but it fundamentally differs from geographic variation in populations subjected to divergent selection histories [47]. The 100-fold trend in expected ISP and CSP (Fig. 2a) is still modest relative to the within-tree (over time) and between-tree variation that motivates local-scale studies (Figure S2). The fact that the massive geographic trend in Fig. 2a can be readily masked by other sources of variation emphasizes the importance of large data sets that span broad coverage in individual condition, habitat, and climate.

Whether or not the amplified fecundity response in warm, moist climates represents a legacy 296 of adaptive evolution to intense species interactions, its 100-fold biogeographic gradient adds a 297 new dimension to the understanding of trophic processes that may control latitudinal diversity 298 gradients. The fact that both individual fecundity and community-level CSP overwhelm climate 299 responses in NPP (Fig. 2a) means that fecundity of many species can contribute to the selection 300 pressures on others and on their consumers [52]. If host-specific consumers regulate diversity 301 through density- and frequency-dependent attack, then their strongest impacts are occurring 302 where seed supply can support their highest numbers. The dramatic biogeographic trend sets 303 up the potential for an evolutionary arms race to increase fecundity in the warm, moist tropics. 304 Regardless of whether this arms race has occurred, the trends in stand-level seed rain imply 305 profound implications for food web dynamics. A positive feedback on selection pressure in 306 diverse tropical forests could ensue where species from every major angiosperm clade enrich 307 functional space and niche overlap. Declines in biodiversity that result from climate change, 308 habitat degradation, and human exploitation in the tropical regions where interaction strength 309 is intense is expected to ramify through food webs to a degree that is not expected where 310 interactions are loose and generally weak [53]. The temperate-tropical gradient can motivate 31 research on its contribution to consumer and disperser guilds [4] and the broader implications 312 for diversity. 313

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## **Acknowledgements**

We thank the National Ecological Observatory Network (NEON) for access to sites and veg-382 etation structure data, W. Koening for useful data on crop production and S. Sitch for access 383 to TRENDY products. The project has been funded since 1992 by grants to JSC from the Na-384 tional Science Foundation, most recently DEB-1754443, and by the Belmont Forum (1854976), 385 NASA (AIST16-0052, AIST18-0063), and the Programme d'Investissement d'Avenir under 386 project FORBIC (18-MPGA-0004) (Make Our Planet Great Again). Jerry Franklin's data re-387 main accessible through NSF LTER DEB-1440409. Puerto Rico data were funded by NSF 388 grants, most recently, DEB 0963447 and LTREB 11222325. Data from the Andes Biodiversity 389 and Ecosystem Research Group were funded by the Gordon and Betty Moore Foundation and 390 NSF LTREB 1754647. MB was supported by grant no. 2019/35/D/NZ8/00050 from (Polish) 391 National Science Centre, and Polish National Agency for Academic Exchange Bekker pro-392 gramme PPN/BEK/2020/1/00009/U/00001. Research by the USDA Forest Service and the the 393 USGS was funded by these agencies. Any use of trade, firm, or product names does not imply 394 endorsement by the U.S. Government. 395 396

- <sup>397</sup> Supplementary Materials
- <sup>398</sup> Materials and Methods Supplementary Text
- <sup>399</sup> Table S1 S4
- 400 Fig S1 S5
- 401 References (1 13)

## **402** Supplementary material

#### **403** Materials and Methods

#### 404 Fecundity data

Comprehensive data were needed to estimate climate effects due to the large variation in seed production. Masting, where large crop years exceed intervening years by orders of magnitude, is further complicated by spatio-temporal variation in habitat and climate. The many sources of variation means that biogeographic trends of interest can only be identified from broad coverage and large sample sizes, while accounting for individual tree condition, local habitat, and climate [45, 31].

The study uses crop-count and seed-trap data from the Masting Inference and Forecasting 411 (MASTIF) project, including opportunistic data through the iNaturalist project MASTIF [56]. 412 Observations include 12,053,732 tree-year observation from 748 species and 146,744 mature 413 individuals. For crop-count data, an observation consists of tree species, diameter, crown shade 414 class, the number of seeds/fruits or cones counted, and an estimate of the fraction of the total 415 crop represented by the count. For seed-trap data, an observation consists of a count for a seed 416 trap, trap location from an inventory plot where trees are measured and mapped, and trap area. 417 Data models for the two data types in the MASTIF model include a beta-binomial distribution 418 for crop counts (uncertainty in the count and in the crop-fraction estimate) and a redistribution 419 model for seed counts (uncertainty in seed transport and in the count) [56]. Seed mass is taken 420 as an average for the species, obtained from collections in our labs, supplemented with the TRY 421 Plant Trait Database [57]. 422

All observations provide estimates of ISP, including those on isolated trees. Because it 423 requires seed production from a known area, only inventory plots offer estimates of CSP (Table 424 S3). Together, ISP and CSP allow us to test how size-standardized seed production by individuals 425 (ISP) and stand-level density of seed (CSP) vary with climate. As in all observational studies, 426 geographic coverage is not uniform. The majority of sites are temperate (98%), while most 427 observations (tree-years, 80%) and species (74%) are tropical. Sample sizes are included in 428 Table S3 and their locations are shown in Figure S1. To clarify coverage, the distribution of data 429 is displayed in each figure and detailed in the Supplement (Table S3, Figure S1). 430

#### 431 Environmental and individual covariates

Predictors of fecundity for a given tree include diameter, crown class, climate, and soil and terrain covariates (Table S1). We included both linear and quadratic terms for diameter to allow changes of fecundity with tree size [31]. Crown class ranges from 1 (full sun) to 5 (full shade), following the protocol used in the National Ecological Observation Network (NEON) and the USDA Forest Inventory and Analysis (FIA) program.

<sup>437</sup> Climate variables include annual temperature (°C) from the previous year, and moisture <sup>438</sup> deficit (summed monthly evapotranspiration minus precipitation, mm) from the previous and <sup>439</sup> current years. Because seasonality varies globally (there is no uniform definition of a 'growing <sup>440</sup> season'), we describe climate with annual norms for temperature and moisture-deficit. Moisture <sup>441</sup> deficit is defined as  $(D_j = \sum_{k=1}^{12} PET_{jk} - P_{jk}$  for location *j* and month *k*), which is the basis for <sup>442</sup> the familiar Standardized Precipitation Evapotranspiration Index (SPEI) [58], but omitting here <sup>443</sup> the standardization, which allows for comparisons between sites.

To allow for changes in moisture access with tree size we included the interaction between moisture deficit and tree diameter. Climate variables were derived from CHELSA [59], TerraClimate [60], and local climate monitoring data where available. TerraClimate provides monthly
 but spatially coarse resolution [60] through 2020. CHELSA provides high spatial resolution (1
 km) but it is not available after 2016. We used regression to project CHELSA climate forward
 based on Terraclimate, followed by calibration to local weather data where available. Details
 are available in [45].

<sup>451</sup> Cation exchange capacity (CEC), used as an indicator of soil fertility, was obtained from <sup>452</sup> soilGrid250 [61] as weighted mean from three soil depths: 0-5, 5-15 and 15-30 cm, weights are <sup>453</sup> reported uncertainty. Slope and aspect were obtained from the global digital elevation model <sup>454</sup> from the NASA shuttle radar topography mission [62] and, for latitudes above 61°, from USGS <sup>455</sup> National Elevation Dataset [63] with a resolution at 30 meters for both products. The covariates <sup>456</sup> for slope and aspect ( $u_1$ ,  $u_2$ ,  $u_3$ ) constitute a length-3 vector,

$$\mathbf{u}_{j} = \begin{cases} u_{j,1} = \sin(s_{j}) \\ u_{j,2} = \sin(s_{j}) \sin(a_{j}) \\ u_{j,3} = \sin(s_{j}) \cos(a_{j}) \end{cases}$$
(1)

<sup>457</sup> for slope *s*, where aspect *a* is taken in radians [64].

**Table S1:** Covariates used to fit the MASTIF model and data sources. Subscripts are tree i, site j, and year t.

Covariate	Units	Data source	
Diameter $(G_{ij,t}, G_{ij,t}^2)$	cm, cm <sup>2</sup>	MASTIF	
Crown class $(C_{ij,t})$	ordinal (class 1-5)	MASTIF	
Moisture deficit $(D_j)$	mm	terraClimate, CHELSA	
Deficit anomaly $(D_{j,t})$	mm	terraClimate, CHELSA	
Temperature $(T_j)$	°C	terraClimate, CHELSA	
Temperature anomaly $(T_{j,t})$	°C	terraClimate, CHELSA	
$D_j \times G_{ij,t}$	$mm \times cm$		
$CEC_{j}$ (0 - 30cm)	mmolc/kg	soilgrid250m	
Slope, aspect $(u_{1j}, u_{2j}, u_{3j})$	radians	DEM, USGS	

#### 458 Model inference with MASTIF

The MASTIF model used to analyse seed trap/crop count data is detailed in [56]. This (hierar-459 chical) state-space, auto-regressive model accommodates dependence between trees and within 460 trees over years through a joint analysis. For each tree i and year t there is a mean fecundity 461 estimate  $\hat{f}_{i,t} = \hat{\rho}_{i,t}\hat{\psi}_{i,t}$  that is the product of conditional fecundity  $\hat{\psi}$  and maturation probability 462  $\hat{\rho}_{i,t}$ . The model for conditional fecundity is given by  $\log \psi_{it} = \mathbf{x}'_{i,t} \boldsymbol{\beta}^{(x)} + \beta_i^{(w)} + \gamma_{g[i],t} + \epsilon_{i,t}$ , where  $\mathbf{x}_{it}$  is a design vector holding climate, soils, local crowding, and individual attributes (sTable S1),  $\boldsymbol{\beta}^{(x)}$  are fixed-effects coefficients,  $\beta_i^{(w)}$  is the random effect for tree *i*,  $\gamma_{g[i],t}$  are year effects 463 464 465 that are random across groups g and fixed for year t, and  $\epsilon_{i,t}$  is Gaussian error. The group 466 membership for a tree *i* is g[i], which is defined by species-ecoregions [56]. Conditional log 467 fecundity  $\psi$  is censored at zero to allow for the immature state and for failed seed crops in larger 468 individuals, 469

$$E[f] = \begin{cases} 0 \quad \psi \le 1\\ \psi \quad \psi > 1 \end{cases}$$
(2)

This censoring means that seed production requires the potential to produce at least one seed and follows the same approach as a Tobit model for the linear scale, which is censored at zero rather than one. Fecundity can be calculated as mass of seeds, and it can be standardized for tree basal area as in eqn 1.

The posterior distribution includes parameters and latent variables for maturation state and tree-year seed production. Posterior simulation uses direct sampling and Metropolis and Hamiltonian Markov Chain (HMC) updates within Gibbs. Model structure and methodology was implemented with R (version 4.0, [65]) and the R package Mast Inference and Forecasting (MASTIF), detailed in [56].

#### 479 Uncertainty in fecundity estimates

We evaluated weighted mean fecundity at the individual and plot scales (CSP), where weights accommodate year-to-year uncertainty for an individual tree and tree-to-tree uncertainty for a stand. For individual and stand-level CSP we included only trees > 7 cm in diameter, i.e., at least as larges as the smallest measured size in inventory data.

<sup>484</sup> Individual mean fecundity was obtained as

$$\hat{f}_{ijs} = \frac{\sum_{t} w_{ijs,t} \hat{f}_{ijs,t}}{\sum_{t} w_{ijs,t}}$$
(3)

where the weight  $w_{ijs,t}$  is the inverse of the predictive coefficient of variation for the estimate,  $w_{ijs,t} = CV_{ijs,t}^{-1}$ . This is used rather than the predictive variance, because the mean tends to scale with the variance such that a variance weight would have the undesirable property of downweighting the important large values while up-weighting the low values, which are dominated by noise. Community seed production (CSP) was evaluated from the individual means

$$CSP_{j} = \frac{1}{A_{j}} \frac{\sum_{is} w_{ijs} \hat{f}_{ijs}}{\sum_{is} w_{ijs}}$$
(4)

where  $A_j$  is plot area, and  $w_{ijs}$  is the inverse of the coefficient of variation evaluated as the root mean predictive variance for tree *ijs* divided by the the mean prediction for that individual. Because CSP requires a plot area, only trees on inventory plots are included in the CSP analysis.

#### **493** Net Primary Production

We extracted Net Primary Production (NPP) from the Moderate Resolution Imaging Spectroradiometer (MODIS) product MOD17 at 500 m resolution (MOD17A3HGFv006, [66]). For 2000 to 2020, we merged yearly CSP estimates with NPP from matching site years, which are available from 2000 to 2020. Because seed production data span the interval 1959 to 2020, we used the location-specific mean NPP values for the limited number of earlier years.

Because MODIS NPP can depend on uneven cloud coverage, we compared MODIS with 499 NPP predictions from DGVMs in the TRENDY project [67], using the S3 experiment. For each 500 site we averaged NPP from 11 models (CABLE-POP, CLASSIC, CLM5.0, ISAM, JSBACH, 501 JULES, LPJ-GUESS, LPX, OCN, ORCHIDEE, ORCHIDEE-CNP) for all sites and fitted them 502 to the same climate variables (temperature, moisture deficit) used for ISP and CSP (Table 503 S2). The two NPP products show similar main effects, but differ in temperature  $\times$  moisture 504 interaction, which is negative for MODIS and positive for the aggregated DGVM. Despite this 505 difference in the interaction term, the main effects dominated such that surfaces show the same 506 trends (Figure S3). Thus, we included only MODIS results in S4. 507

Variable	Parameter	Estimate	SE	P-value
Climate effects on NPP (MODIS)				
Intercept	-	3.52e-01	2.46e-02	< 2e-16
Т	$\beta_{N,T}$	1.54e-02	1.92e-03	4.99e-15
D	$\beta_{N,D}$	-1.81e-04	3.35e-05	8.41e-08
$T \times D$	$\beta_{N,DT}$	-1.11e-05	2.65e-06	2.99e-05
Climate effects on NPP (DGVMs TRENDY)				
Intercept	-	1.455e-01	2.2e-02	7.71e-11
Т	$\beta_{N,T}$	3.19e-02	1.72e-03	< 2e-16
D	$\beta_{N,D}$	-3.25e-04	3.01e-05	< 2e-16
$T \times D$	$\beta_{N,DT}$	7.36e-06	2.38e-06	0.00205
NPP effect (MODIS) on log <sub>e</sub> ISP				
Intercept	-	3.98	0.027	<2e-16
NPP	$eta_{fN}$	2.06	0.024	<2e-16
NPP effect (DGVMs TRENDY) on log <sub>e</sub> ISP				
Intercept	-	4.88	0.037	<2e-16
NPP	$eta_{fN}$	1.64	0.047	<2e-16
NPP effect (MODIS) on log <sub>e</sub> CSP				
Intercept	-	8.70	0.38	<2e-16
NPP	$eta_{fN}$	2.70	0.44	3.31e-09
NPP effect (DGVMs TRENDY) on log <sub>e</sub> CSP				
Intercept	-	9.26	0.44	<2e-16
NPP	$eta_{fN}$	2.21	0.58	1.77e-4

**Table S2:** Coefficients for climate on NPP MODIS and NPP DGVM products.  $r^2$  for NPP MODIS = 0.48, NPP DGVM = 0.52.

## **Supplementary Tables**

**Table S3:** Numbers of species, stands, trees, and tree-years for ISP analysis and complete inventories for CSP analysis by tropical and temperate regions. Complete inventories include all trees within a mapped plot and are needed to determine seeds per area in CSP. Because not all inventory plots use the same minimum diameter, the latter is based on trees > 7 cm.

Floristic					Complete
Region	Species	Sites	<b>Tree-years</b>	Trees	inventories
Tropical	559	64	9,723,438	85,261	47
Temperate	194	3506	2,330,294	61,461	204

**Table S4:** Coefficients for climate effect on individual (ISP), community fecundity (CSP). ISP and CSP fecundity are fitted on a natural log scale.  $r^2$  for ISP = 0.2, CSP = 0.15.

Variable	Parameter	Estimate	SE	P-value
Climate effects on log <sub>e</sub> ISI	P			
Intercept	-	4.64e+00	4.93e-02	<2e-16
Т	$\beta_{f,T}$	1.78e-01	6.01e-03	<2e-16
$T^2$	$\beta_{f,T^2}$	-5.60e-03	1.770e-04	<2e-16
D	$\hat{\beta}_{f,D}$	2.72e-03	4.80e-05	<2e-16
$D^2$	$\beta_{f,D^2}$	-1.12e-07	1.14e-08	<2e-16
$T \times D$	$\beta_{f,DT}$	-1.84e-04	1.73e-06	<2e-16
Climate effects on log <sub>e</sub> CS	P			
Intercept	-	9.88e+00	5.61e-01	<2e-16
Т	$\beta_{f,T}$	9.96e-02	7.88e-02	0.21
$T^2$	$\beta_{f,T^2}$	-2.38e-03	2.82e-03	0.40
D	$\beta_{f,D}$	9.21e-04	7.16e-04	0.20
$D^2$	$\beta_{f,D^2}$	2.87e-08	2.20e-07	0.90
$T \times D$	$\beta_{f,DT}$	-1.19e-04	4.05e-05	3.60e-3

## 509 Supplementary Figures



**Figure S1:** MASTIF network data, including longitudinal (in green) and opportunistic (in orange) observations in North America (a), Europe (b), Asia (c), South and Central America (d), Africa (e) and Oceania (f). Number of observations are reported in Table S3.



**Figure S2:** Climate responses for ISP (seed mass per basal area) (a, b, c) and stand-level CSP, as g ha<sup>-1</sup> (d, e, f) showing marginal responses to temperature (a and d) and moisture deficit (d and e) with observations (dots) and the fitted model, and interactions between temperature and moisture deficit (c and f). Coefficient are reported in Table S4. Low and high values used for conditional plots in (c and f), labelled as Moist (D = -1500 mm) and Dry (D = -50 mm). Due to large sample size, confidence intervals around lines in (a, b, c) are not distinct from the predictive mean. Temperature and moisture deficit correspond here to a mean annual value for each sites.



Figure S3: Climate response for NPP from MODIS product (a) and DGVM product from TRENDY DGVM products



**Figure S4:** Relationships between NPP from MODIS and individual (standardized) fecundity ISP (a) and stand CSP (b), both positive (p < 0.00001) and both accounting for little of the variability ( $r^2 = 0.05$  and 0.13, respectively). Coefficient are reported in Table S4



**Figure S5:** Distribution of (a) ISP (g seed per  $m^2$  basal area) and (b) CSP (g seed per ha basal area) fecundities. Black dotted lines represent the quantile at 2.5 and 97.5%.

## **References in Supplementary materials**

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