



Globally, tree fecundity exceeds productivity gradients

Valentin Journé, Robert Andrus, Marie-Claire Aravena, Davide Ascoli, Roberta Berretti, Daniel Berveiller, Michal Bogdziewicz, Thomas Boivin, Raul Bonal, Thomas Caignard, et al.

► To cite this version:

Valentin Journé, Robert Andrus, Marie-Claire Aravena, Davide Ascoli, Roberta Berretti, et al.. Globally, tree fecundity exceeds productivity gradients. *Ecology Letters*, 2022, 25 (6), pp.1471-1482. 10.1111/ele.14012 . hal-03696000

HAL Id: hal-03696000

<https://hal.inrae.fr/hal-03696000>

Submitted on 18 Sep 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

Valentin Journe,¹ Robert Andrus,² Marie-Claire Aravena,³ Davide Ascoli,⁴ Yves Bergeron,⁵ Roberta Berretti,⁴ Daniel Berveiller,⁶ Michal Bogdziewicz,⁷ Thomas Boivin,⁸ Raul Bonal,⁹ Dale Brockway,¹⁰ Thomas Caignard,¹¹ Rafael Calama,¹² J. Julio Camarero,¹³ Chia-Hao Chang-Yang,¹⁴ Natalie L. Cleavitt,¹⁵ Benoit Courbaud,¹ Francois Courbet,⁸ Thomas Curt,¹⁶ Adrian J. Das,¹⁷ Evangelia Daskalakou,¹⁸ Hendrik Davi,⁸ Nicolas Delpierre,⁶ Sylvain Delzon,¹¹ Michael Dietze,¹⁹ Sergio Donoso Calderon,³ Laurent Dormont,²⁰ Josep Espelta,²¹ Timothy J. Fahey,¹⁵ William Farfan-Rios,²² Catherine A. Gehring,²³ Gregory S. Gilbert,²⁴ Georg Gratzer,²⁵ Cathryn H. Greenberg,²⁶ Qinfeng Guo,²⁷ Andrew Hacket-Pain,²⁸ Arndt Hampe,¹¹ Qingmin Han,²⁹ Janneke Hille Ris Lambers,³⁰ Kazuhiko Hoshizaki,³¹ Ines Ibanez,³² Jill F. Johnstone,³³ Daisuke Kabeya,²⁹ Christopher L. Kilner,³⁴ Thomas Kitzberger,³⁵ Johannes M.H. Knops,³⁶ Richard K. Kobe,³⁷ Georges Kunstler,¹ Jonathan G.A. Lageard,³⁸ Jalene M. LaMontagne,³⁹ Mateusz Ledwon,⁴⁰ Francois Lefevre,⁸ Theodor Leininger,⁴¹ Jean-Marc Limousin,⁴² James A. Lutz,⁴³ Diana Macias,⁴⁴ Eliot J.B. McIntire,⁴⁵ Christopher M. Moore,⁴⁶ Emily Moran,⁴⁷ Renzo Motta,⁴ Jonathan A. Myers,⁴⁸ Thomas A. Nagel,⁴⁹ Kyotaro Noguchi,⁵⁰ Jean-Marc Ourcival,⁴² Robert Parmenter,⁵¹ Ian S. Pearse,⁵² Ignacio M. Perez-Ramos,⁵³ Lukasz Piechnik,⁵⁴ John Poulsen,³⁴ Renata Poulton-Kamakura,³⁴ Tong Qiu,³⁴ Miranda D. Redmond,⁵⁵ Chantal D. Reid,³⁴ Kyle C. Rodman,⁵⁶ Francisco Rodriguez-Sanchez,⁵⁷ Javier D. Sanguinetti,⁵⁸ C. Lane Scher,³⁴ Harald Schmidt Van Marle,³ Barbara Seget,⁵⁴ Shubhi Sharma,³⁴ Miles Silman,⁵⁹ Michael A. Steele,⁶⁰ Nathan L. Stephenson,¹⁷ Jacob N. Straub,⁶¹ I-Fang Sun,⁶² Samantha Sutton,³⁴ Jennifer J. Swenson,³⁴ Margaret Swift,³⁴ Peter A. Thomas,⁶³ Maria Uriarte,⁶⁴ Giorgio Vacchiano,⁶⁵ Thomas T. Veblen,² Amy V. Whipple,²³ Thomas G. Whitham,²³ Andreas P. Wion,⁶⁶ Boyd Wright,⁶⁷ S. Joseph Wright,⁶⁸ Kai Zhu,²⁴ Jess K. Zimmerman,⁶⁹ Roman Zlotin,⁷⁰ Magdalena Zywiec,⁵⁴ James S. Clark,³⁴

¹Universite Grenoble Alpes, Institut National de Recherche pour Agriculture, Alimentation et Environnement (INRAE), Laboratoire EcoSystemes et Societes En Montagne (LESSEM), 38402 St. Martin-d'Herès, France

²Department of Geography, University of Colorado Boulder, Boulder, CO 80309 USA

³Universidad de Chile, Facultad de Ciencias Forestales y de la Conservacion de la Naturaleza (FCFCN), La Pintana, 8820808 Santiago, Chile

⁴Department of Agriculture, Forest and Food Sciences, University of Torino, 10095 Grugliasco, TO, Italy

⁵Forest Research Institute, University of Quebec in Abitibi-Temiscamingue, Rouyn-Noranda, QC J9X 5E4, Canada

⁶Universite Paris-Saclay, Centre national de la recherche scientifique, AgroParisTech, Ecologie Systematique et Evolution, 91405 Orsay, France

⁷Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznan, Poland

⁸Institut National de Recherche pour Agriculture, Alimentation et Environnement (INRAE), Ecologie des Forets Meditteranennes, 84000 Avignon, France

⁹Department of Biodiversity, Ecology and Evolution, Complutense University of Madrid, 28040 Madrid, Spain

¹⁰Southern Research Station, USDA Forest Service, Auburn, AL 36849 USA

¹¹Universite Bordeaux, Institut National de Recherche pour Agriculture, Alimentation et Environnement (INRAE),

Biodiversity, Genes, and Communities (BIOGECO), 33615 Pessac, France

¹²Centro de Investigacion Forestal - Instituto Nacional de Investigacion y Tecnologia Agraria y Alimentaria (INIA-CIFOR), 28040 Madrid, Spain

¹³Instituto Pirenaico de Ecologia, Consejo Superior de Investigaciones Cientificas (IPE-CSIC), 50059 Zaragoza, Spain

¹⁴Department of Biological Sciences, National Sun Yat-sen University, Kaohsiung 80424, Taiwan

¹⁵Natural Resources, Cornell University, Ithaca, NY, 14853 USA

¹⁶Aix Marseille universite, Institut National de Recherche pour Agriculture, Alimentation et Environnement (INRAE), 13182 Aix-en-Provence, France

¹⁷USGS Western Ecological Research Center, Three Rivers, CA, 93271 USA

¹⁸Institute of Mediterranean and Forest Ecosystems, Greece

¹⁹Earth and Environment, Boston University, Boston, MA, 02215 USA

²⁰Centre d'Ecologie Fonctionnelle et Evolutive (CEFE), Centre National de la Recherche Scientifique (CNRS), 34293 Montpellier, France.

²¹Centre de Recerca Ecologica i Aplicacions Forestals (CREAF), Bellaterra, Catalunya 08193, Spain

²²Washington University in Saint Louis, Center for Conservation and Sustainable Development, Missouri Botanical Garden, St. Louis, MO 63110 USA

²³Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011 USA

²⁴Department of Environmental Studies, University of California, Santa Cruz, CA 95064 USA

²⁵Institute of Forest Ecology, Peter-Jordan-Strasse 82, 1190 Wien, Austria

²⁶Bent Creek Experimental Forest, USDA Forest Service, Asheville, NC 28801 USA

²⁷Eastern Forest Environmental Threat Assessment Center, USDA Forest Service, Southern Research Station, Research Triangle Park, NC 27709 USA

²⁸Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom

²⁹Department of Plant Ecology Forestry and Forest Products Research Institute (FFPRI), Tsukuba, Ibaraki, 305-8687 Japan

³⁰Department of Environmental Systems Science, ETH Zurich, Switzerland 8092

³¹Department of Biological Environment, Akita Prefectural University, Akita 010-0195, Japan

³²School for Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109

³³Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99700, USA

³⁴Nicholas School of the Environment, Duke University, Durham, NC 27708 USA

³⁵Department of Ecology, Instituto de Investigaciones en Biodiversidad y Medioambiente (Consejo Nacional de Investigaciones Cientificas y Tecnicas - Universidad Nacional del Comahue), Quintral 1250, 8400 Bariloche, Argentina

³⁶Health and Environmental Sciences Department, Xian Jiaotong-Liverpool University, Suzhou, China, 215123

³⁷Department of Plant Biology, Program in Ecology, Evolutionary Biology, and Behavior, Michigan State University, East Lansing, MI 48824

³⁸Department of Natural Sciences, Manchester Metropolitan University, Manchester M1 5GD, UK

³⁹Department of Biological Sciences, DePaul University, Chicago, IL 60614 USA

⁴⁰Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Slawkowska 17, 31-016 Krakow, Poland

⁴¹USDA, Forest Service, Southern Research Station, PO Box 227, Stoneville, MS 38776

⁴²CEFE, Univ Montpellier, CNRS, EPHE, IRD, 1919 route de Mende, 34293 Montpellier Cedex 5, France

⁴³Department of Wildland Resources, and the Ecology Center, Utah State University, Logan, UT 84322 USA

⁴⁴Department of Biology, University of New Mexico, Albuquerque, NM 87131 USA

⁴⁵Pacific Forestry Centre, Victoria, British Columbia, V8Z 1M5 Canada

⁴⁶Department of Biology, Colby College, Waterville, ME 04901 USA

- ⁴⁷School of Natural Sciences, UC Merced, Merced, CA 95343 USA
- ⁴⁸Department of Biology, Washington University in St. Louis, St. Louis, MO
- ⁴⁹Department of forestry and renewable forest resources, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia
- ⁵⁰Tohoku Research Center, Forestry and Forest Products Research Institute, Morioka, Iwate, 020-0123, Japan
- ⁵¹Valles Caldera National Preserve, National Park Service, Jemez Springs, NM 87025 USA
- ⁵²Fort Collins Science Center, 2150 Centre Avenue, Bldg C, Fort Collins, CO 80526 USA
- ⁵³Inst. de Recursos Naturales y Agrobiología de Sevilla, Consejo Superior de Investigaciones Científicas (IRNAS-CSIC), Seville, Andalucía, Spain
- ⁵⁴W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Krakow, Poland
- ⁵⁵Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO, USA
- ⁵⁶Department of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI 53706 USA
- ⁵⁷Department of Biología Vegetal y Ecología, Universidad de Sevilla, 41012 Sevilla, Spain
- ⁵⁸Bilogo Dpto. Conservacin y Manejo Parque Nacional Lanin Elordi y Perito Moreno 8370, San Marten de los Andes Neuquén Argentina
- ⁵⁹Department of Biology, Wake Forest University, 1834 Wake Forest Rd, Winston-Salem, NC 27106 USA
- ⁶⁰Department of Biology, Wilkes University, 84 West South Street, Wilkes-Barre, PA 18766 USA
- ⁶¹Department of Environmental Science and Ecology, State University of New York-Brockport, Brockport, NY 14420 USA
- ⁶²Center for Interdisciplinary Research on Ecology and Sustainability, College of Environmental Studies, National Dong Hwa University, Hualien, Taiwan
- ⁶³School of Life Sciences, Keele University, Staffordshire ST5 5BG, UK
- ⁶⁴Department of Ecology, Evolution and Environmental Biology, Columbia University, 1113 Schermerhorn Ext., 1200 Amsterdam Ave., New York, NY 10027
- ⁶⁵Department of Agricultural and Environmental Sciences - Production, Territory, Agroenergy (DISAA), University of Milan, 20133 Milano, Italy
- ⁶⁶Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523, USA
- ⁶⁷Botany, School of Environmental and Rural Science, University of New England, Armidale, NSW, 2350, Australia
- ⁶⁸Smithsonian Tropical Research Institute, Apartado 0843n03092, Balboa, Republic of Panama
- ⁶⁹Department of Environmental Sciences, University of Puerto Rico, Rio Piedras, PR 00936 USA
- ⁷⁰Geography Department and Russian and East European Institute, Bloomington, IN 47405 USA

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

Abstract

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

Introduction

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

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

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.

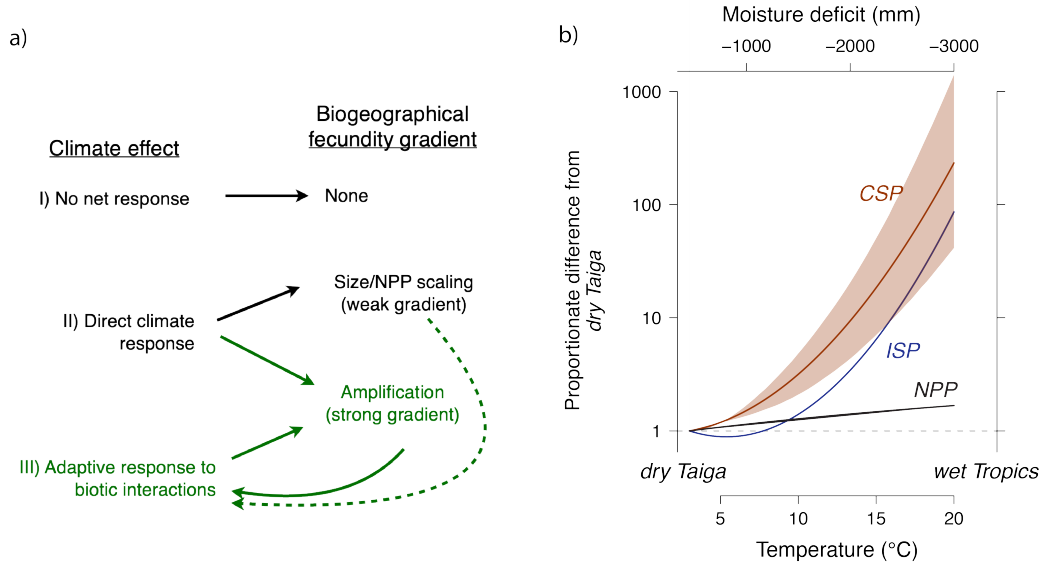


Figure 1: a) Climate effects on fecundity could be I) negligible, in which case there is no latitudinal fecundity gradient (right), or there could be direct (II) or indirect effects through adaptive responses to intense species interactions in tropical climates (III). Both II and III could be amplified 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,

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

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.

While ISP_{ij} quantifies production by individuals, *community seed production*, CSP_j , quantifies 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 ($\text{g ha}^{-1} \text{yr}^{-1}$, 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 of climate on size or NPP, then climate gradients could be a driver of intense biotic interactions in the tropics. There are at least two potential causes for fecundity amplification (Fig. 1a). First, ISP might have flexibility to respond to a longer growing season [34, 35] well in excess of tree growth, which is limited by mechanical and hydraulic constraints on tree size [36, 37]. At the community scale, NPP is further constrained by the compensatory losses in stand biomass as mortality increases to offset increases in growth [22]. Thus, while NPP increases with warm, wet conditions, the lack of structural constraints on producing more seeds might allow for a disproportionate fecundity response, the *amplification* of figure 1a, II.

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

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

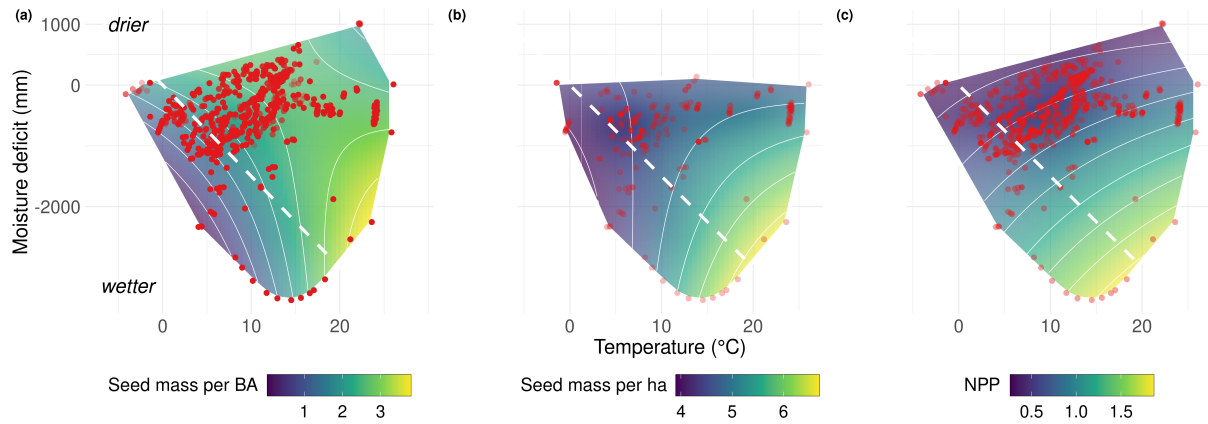


Figure 2: a) Climate responses for (a) ISP (seed mass per tree basal area, $\log_{10} \text{ g m}^{-2} \text{ y}^{-1}$) (b) CSP (seed mass per ha forest floor, $\log_{10} \text{ g ha}^{-1} \text{ y}^{-1}$), and (c) NPP ($\text{kg C m}^{-2} \text{ y}^{-1}$). Dashed lines indicate the transect from dry 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 S4 and Table S2 for NPP.

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

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

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

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

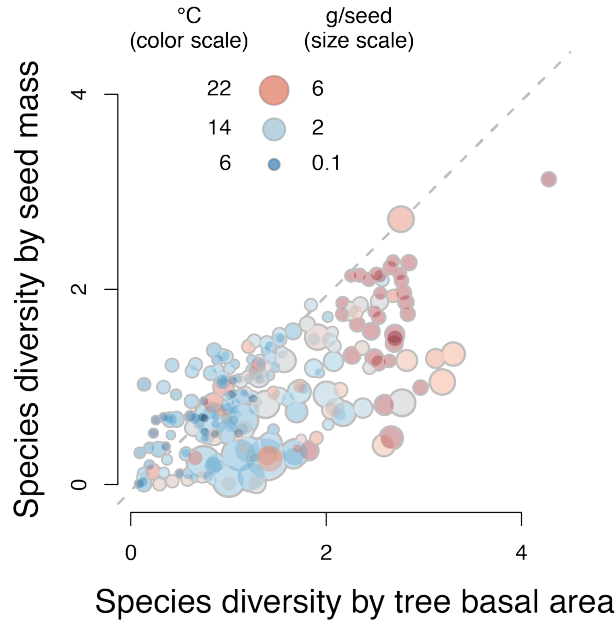


Figure 3: Species diversity in seeds (vertical axis) is lower than expected from species diversity in trees (horizontal axis). In both cases, diversity is evaluated from the Shannon index, $-\sum_s p_s \log p_s$, where p_s is the fraction of species s in basal area (trees) and CSP (seeds). Each point 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 is poorly predicted by the standard inventory of trees. Species diversity of both seed mass and tree basal area is highest in the warm climates where diversity of the seed resource would be overestimated on the basis of tree diversity (Fig. 3). The lower species diversity for seeds in warm climates results from the fact that species having modest differences in tree basal area vary widely in fecundity; tendency for a subset of species to dominate seed production reduces seed diversity below that for trees. In the cool climates where seeds tend to be small (small, blue symbols in Fig. 3), the low diversity that would be estimated on the basis of trees masks an unexpectedly high seed diversity (Fig. 2). Although many studies do not record fecundity for species having the smallest seeds (e.g., Salicaceae), these are also the seeds that are least apparent to vertebrate consumers. Omission of these smallest seeds means that values are overestimates, but still relevant for many consumers. The net effect of reduced seed diversity in warm climates affects frequency-dependent processes [46], such as host-specific seed predation. The concentration of seed mass in a smaller than expected species diversity reduces the apparency of weak producers, while potentially concentrating consumption on species that are not necessarily abundant, but that can dominate seed production.

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

References

- [1] R. H. MacArthur, *Geographical Ecology: Patterns in the Distribution of Species* (1972), princeton edn.
- [2] J. Chave, H. C. Muller-Landau, S. A. Levin, *The American Naturalist* **159**, 1 (2002).
- [3] J. H. Brown, *Journal of Biogeography* **41**, 8 (2014).
- [4] A. L. Hargreaves, *et al.*, *Science Advances* **5**, 1 (2019).
- [5] O. L. Phillips, A. H. Gentry, *Science* **263**, 954 (1994).
- [6] S. L. Lewis, *et al.*, *Journal of Ecology* **92**, 929 (2004).
- [7] N. L. Stephenson, P. J. Van Mantgem, *Ecology Letters* **8**, 524 (2005).
- [8] D. Janzen, *The American Naturalist* **104**, 501 (1970).
- [9] J. Connell, *Herbivores and the Number of Tree Species in Tropical Forests* (Pudoc, Wageningen, 1970), p. 298–312.
- [10] K. Zhu, C. W. Woodall, J. V. Monteiro, J. S. Clark, *Ecology* **96**, 2319 (2015).
- [11] J. Terborgh, *Community aspects of frugivory in tropical forests* (Springer, Dordrecht, 1986), vol. 15 of *Tasks for Vegetation Science*.
- [12] R. T. Corlett, *Biological Conservation* **163**, 13 (2013).
- [13] K. Mokany, S. Prasad, D. A. Westcott, *Nature Communications* **5**, 3971 (2014).
- [14] R. J. Petit, R. Bialozyt, P. Garnier-Géré, A. Hampe, *Forest Ecology and Management* **197**, 117 (2004).
- [15] H. X. Wu, R. Ker, Z. Chen, M. Ivkovic, *Evolutionary Applications* **14**, 834 (2021).
- [16] S. Sitch, *et al.*, *Global Change Biology* **9**, 161 (2003).
- [17] G. Krinner, *et al.*, *Global Biogeochemical Cycles* **19**, 1 (2005).
- [18] R. S. Ostfeld, F. Keesing, *Trends in Ecology and Evolution* **15**, 232 (2000).
- [19] A. E. Rosenblatt, O. J. Schmitz, *Trends in Ecology and Evolution* **31**, 965 (2016).
- [20] R. J. Brien, *et al.*, *Nature Communications* **11**, 1 (2020).
- [21] E. Assmann, *The principles of forest yield study. Studies in the organic production, structure, increment and yield of forest stands.* (1970).
- [22] J. S. Clark, *Journal of Ecology* **78**, 275 (1990).
- [23] N. L. Stephenson, *et al.*, *Ecological Monographs* **81**, 527 (2011).
- [24] R. Bagchi, *et al.*, *Nature* **506**, 85 (2014).
- [25] T. Levi, *et al.*, *Proceedings of the National Academy of Sciences* **116**, 581 (2019).

- [26] R. Dawkins, J. R. Krebs, *Proceedings of the Royal Society of London. Series B, Biological Sciences* **205**, 489 (1979).
- [27] M. Gruntman, D. Groß, M. Májeková, K. Tielbörger, *Nature Communications* **8**, 2235 (2017).
- [28] A. B. Berdanier, J. S. Clark, *Ecosphere* **7**, e01313 (2016).
- [29] J. D. Lauder, E. V. Moran, S. C. Hart, *Tree Physiology* **39**, 1071 (2019).
- [30] M. Westoby, E. Jurado, M. Leishman, *Trends in Ecology and Evolution* **7**, 368 (1992).
- [31] T. Qiu, *et al.*, *Proceedings of the National Academy of Sciences* **118** (2021).
- [32] G. Vacchiano, *et al.*, *Ecological Modelling* **376**, 40 (2018).
- [33] S. Del Grosso, *et al.*, *Ecology* **89**, 2117 (2008).
- [34] S. H. Yeoh, *et al.*, *Molecular Ecology* **26**, 5074 (2017).
- [35] I. Mendoza, *et al.*, *Biotropica* **50**, 431 (2018).
- [36] G. W. Koch, S. C. Sillett, G. M. Jennings, S. D. Davis, *Nature* **428**, 851 (2004).
- [37] D. A. King, S. J. Davies, S. Tan, N. S. Md. Noor, *Functional Ecology* **23**, 284 (2009).
- [38] L. S. Comita, *et al.*, *Journal of Ecology* **102**, 845 (2014).
- [39] J. R. Obeso, *New Phytologist* **155**, 321 (2002).
- [40] J. D. Fridley, *Journal of Ecology* **105**, 95 (2017).
- [41] J. M. LaMontagne, I. S. Pearse, D. F. Greene, W. D. Koenig, *Nature Plants* **6**, 460 (2020).
- [42] I. S. Pearse, J. M. LaMontagne, M. Lordon, A. L. Hipp, W. D. Koenig, *New Phytologist* **227**, 1557 (2020).
- [43] A. T. Moles, I. J. Wright, A. J. Pitman, B. R. Murray, M. Westoby, *Ecography* **32**, 78 (2009).
- [44] S. Tautenhahn, H. Heilmeyer, L. Go, S. Klotz, C. Wirth, *Ecography* **31**, 457 (2008).
- [45] J. S. Clark, *et al.*, *Nature Communications* **12**, 1 (2021).
- [46] P. T. Green, K. E. Harms, J. H. Connell, *Proceedings of the National Academy of Sciences* **111**, 18649 (2014).
- [47] J. S. Clark, D. M. Bell, M. C. Kwit, K. Zhu, *Global Change Biology* **20**, 1979 (2014).
- [48] T. Caignard, *et al.*, *Scientific Reports* **7**, 1 (2017).
- [49] M. Bogdziewicz, M. Fernández-Martínez, J. M. Espelta, R. Ogaya, J. Penuelas, *New Phytologist* **227**, 1073 (2020).
- [50] D. Kelly, *et al.*, *Ecology Letters* **16**, 90 (2013).

- 376 [51] M. Bogdziewicz, M. Pesendorfer, E. E. Crone, C. Pérez-Izquierdo, R. Bonal, *Ecology*
377 *Letters* **23**, 1820 (2020).
- 378 [52] T. G. Whitham, G. J. Allan, H. F. Cooper, S. M. Shuster, *Annual Review of Ecology,*
379 *Evolution, and Systematics* **51**, 587 (2020).
- 380 [53] D. R. Strong, K. T. Frank, *Annual Review of Environment and Resources* **35**, 1 (2010).

Acknowledgements

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

Supplementary Materials

Materials and Methods Supplementary Text

Table S1 – S4

Fig S1 - S5

References (1 – 13)

Supplementary material

Materials and Methods

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

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

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.

Climate variables include annual temperature (°C) from the previous year, and moisture deficit (summed monthly evapotranspiration minus precipitation, mm) from the previous and current years. Because seasonality varies globally (there is no uniform definition of a 'growing season'), we describe climate with annual norms for temperature and moisture-deficit. Moisture 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 the familiar Standardized Precipitation Evapotranspiration Index (SPEI) [58], but omitting here 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], [Terra-](#)

Climate [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].

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

$$\mathbf{u}_j = \begin{cases} u_{j,1} = \sin(s_j) \\ u_{j,2} = \sin(s_j) \sin(a_j) \\ u_{j,3} = \sin(s_j) \cos(a_j) \end{cases} \quad (1)$$

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 ²	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 × cm	
CEC _j (0 - 30cm)	mmolc/kg	soilgrid250m
Slope, aspect (u_{1j}, u_{2j}, u_{3j})	radians	DEM, USGS

Model inference with MASTIF

The MASTIF model used to analyse seed trap/crop count data is detailed in [56]. This (hierarchical) state-space, auto-regressive model accommodates dependence between trees and within trees over years through a joint analysis. For each tree i and year t there is a mean fecundity 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 $\hat{\rho}_{i,t}$. 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 $\mathbf{x}_{i,t}$ 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 that are random across groups g and fixed for year t , and $\epsilon_{i,t}$ is Gaussian error. The group membership for a tree i is $g[i]$, which is defined by species-ecoregions [56]. Conditional log fecundity ψ is censored at zero to allow for the immature state and for failed seed crops in larger individuals,

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

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].

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 large as the smallest measured size in inventory data.

Individual mean fecundity was obtained as

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

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 down-weighting 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

$$CSP_j = \frac{1}{A_j} \frac{\sum_{is} w_{ijs} \hat{f}_{ijs}}{\sum_{is} w_{ijs}} \quad (4)$$

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.

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

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

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

508 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 Region	Species	Sites	Tree-years	Trees	Complete 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.

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

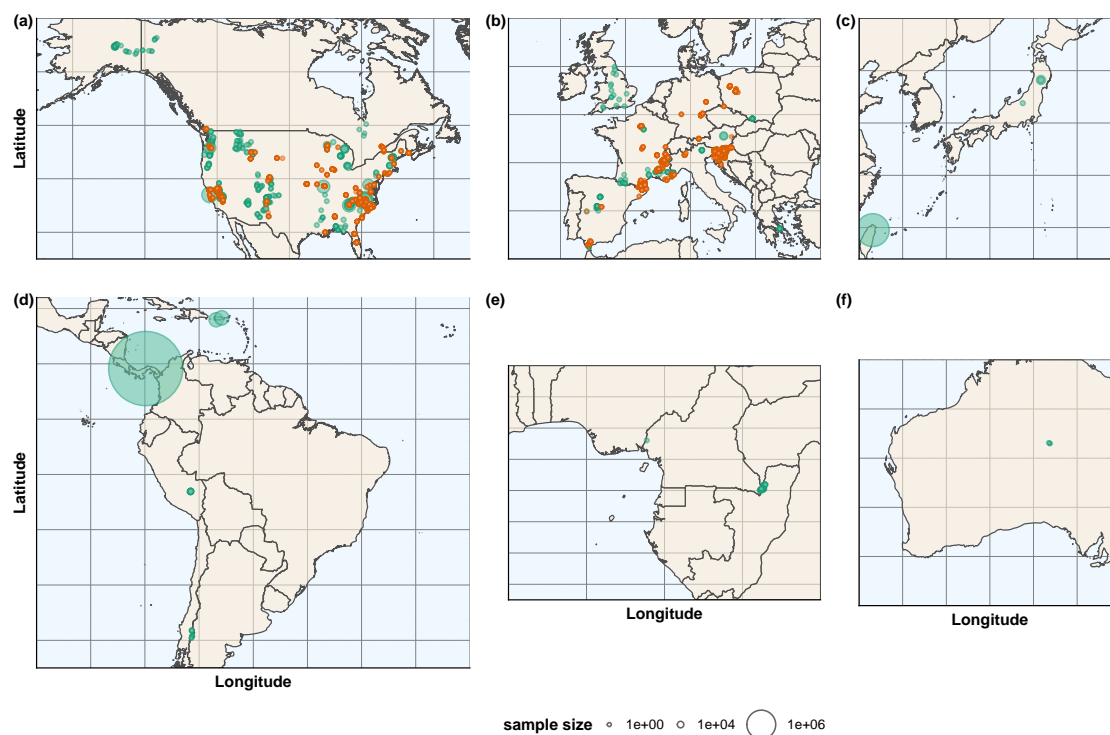


Figure S1: MASTIF network data, including longitudinal (in green) and opportunistic (in orange) observations in North America (a), Europe (b), Asia (c), South and Central America (d), Africa (e) and Oceania (f). Number of observations are reported in Table S3.

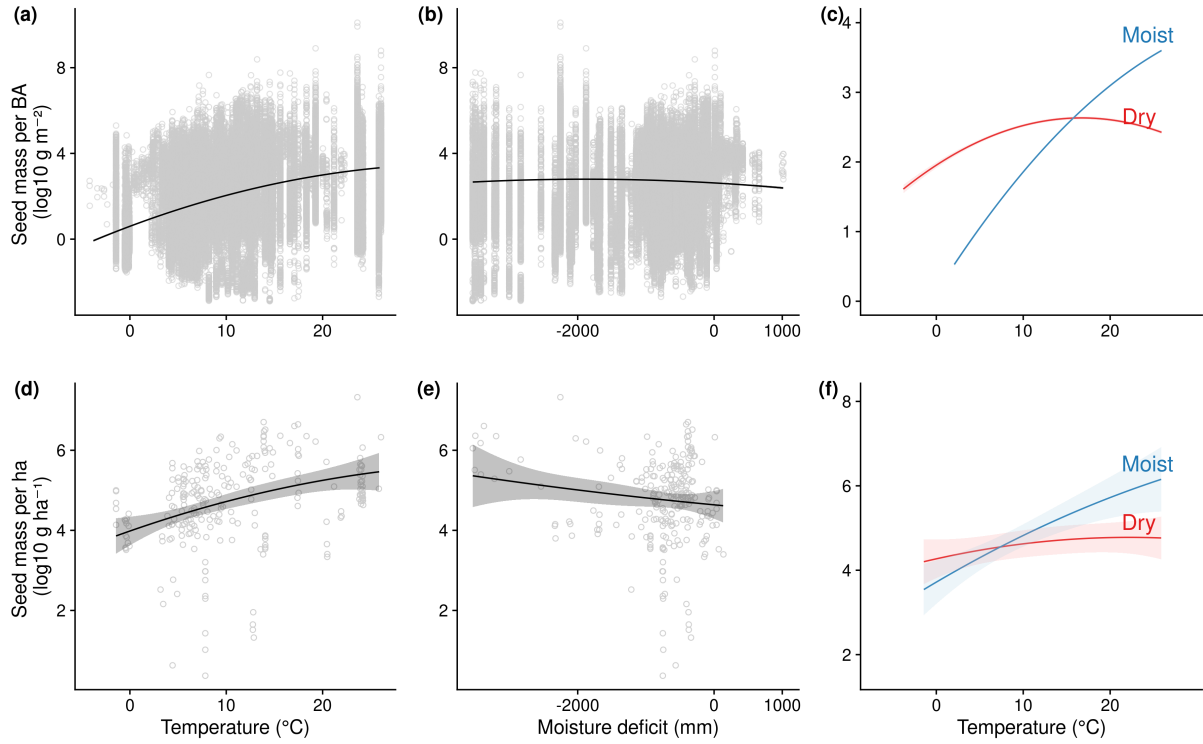


Figure S2: Climate responses for ISP (seed mass per basal area) (a, b, c) and stand-level CSP, as g ha^{-1} (d, e, f) showing marginal responses to temperature (a and d) and moisture deficit (d and e) with observations (dots) and the fitted model, and interactions between temperature and moisture deficit (c and f). Coefficient are reported in Table S4. Low and high values used for conditional plots in (c and f), labelled as Moist ($D = -1500 \text{ mm}$) and Dry ($D = -50 \text{ mm}$). 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.

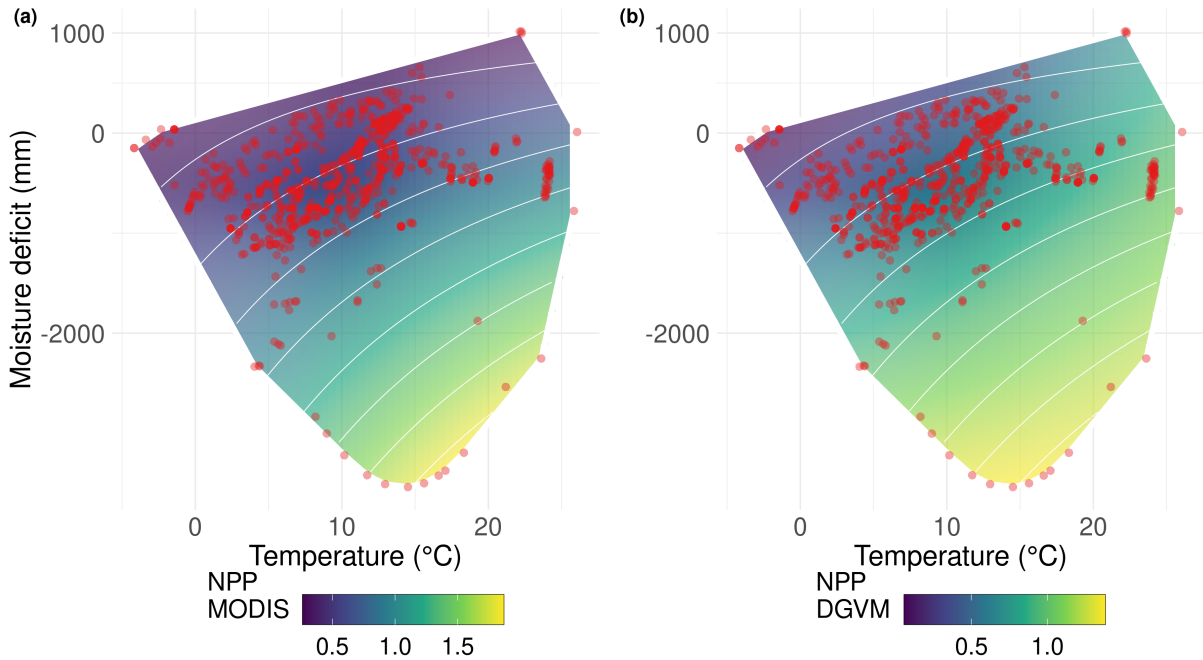


Figure S3: Climate response for NPP from MODIS product (a) and DGVM product from TRENDY DGVM products (b).

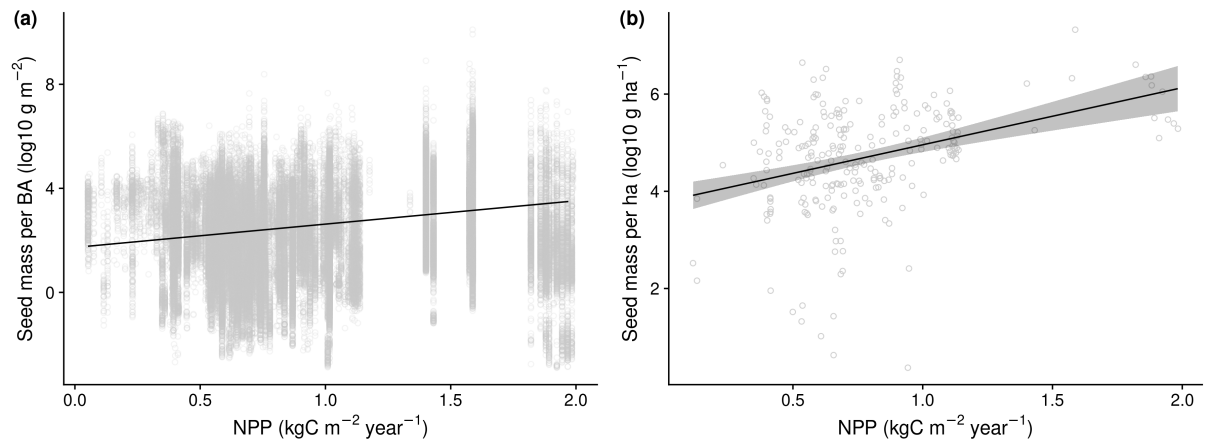


Figure S4: Relationships between NPP from MODIS and individual (standardized) fecundity ISP (a) and stand CSP (b), both positive ($p < 0.00001$) and both accounting for little of the variability ($r^2 = 0.05$ and 0.13 , respectively). Coefficient are reported in Table S4

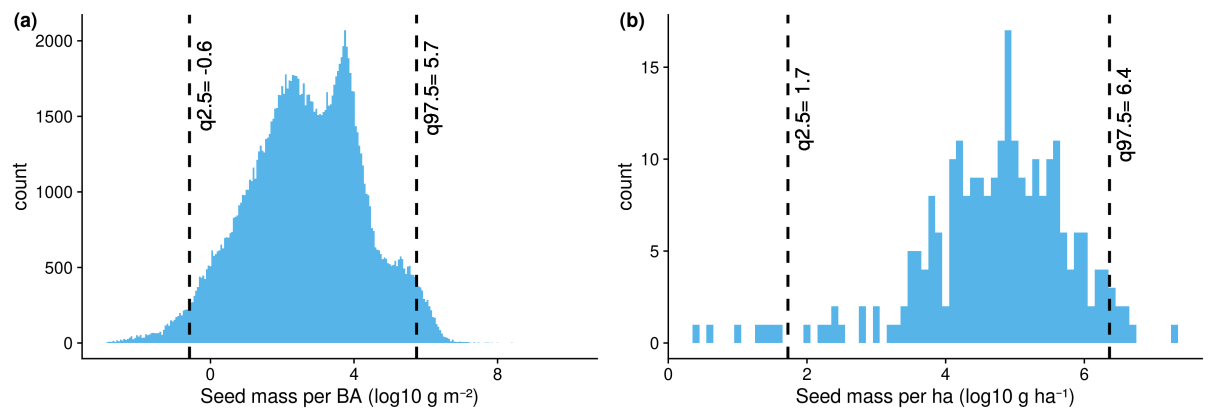


Figure S5: Distribution of (a) ISP (g seed per m² basal area) and (b) CSP (g seed per ha basal area) fecundities. Black dotted lines represent the quantile at 2.5 and 97.5%.

References in Supplementary materials

- [54] J. S. Clark, *et al.*, *Nature Communications* **12**, 1 (2021).
- [55] T. Qiu, *et al.*, *Proceedings of the National Academy of Sciences* **118** (2021).
- [56] J. S. Clark, C. L. Nuñez, B. Tomasek, *Ecological Monographs* **89**, 1 (2019).
- [57] J. Kattge, *et al.*, *Global Change Biology* **26**, 119 (2020).
- [58] S. M. Vicente-Serrano, S. Beguería, J. I. López-Moreno, *Journal of Climate* **23**, 1696 (2010).
- [59] D. N. Karger, *et al.*, *Scientific Data* **4**, 1 (2017).
- [60] J. T. Abatzoglou, S. Z. Dobrowski, S. A. Parks, K. C. Hegewisch, *Scientific Data* **5**, 170191 (2018).
- [61] T. Hengl, *et al.*, *PLoS ONE* **12** (2017).
- [62] T. G. Farr, *et al.*, *Reviews of Geophysics* **45** (2007).
- [63] D. Gesch, *et al.*, *Photogrammetric Engineering and Remote Sensing* (American Society for Photogrammetry and Remote Sensing, 2002), vol. 68, pp. 5–11.
- [64] J. S. Clark, *Ecological Monographs* **60**, 135 (1990).
- [65] R Core Team, *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, Austria, 2020).
- [66] S. W. Running, M. Zhao .
- [67] S. Sitch, *et al.*, *Biogeosciences* **12**, 653 (2015).