

Masting is uncommon in trees that depend on mutualist dispersers in the context of global climate and fertility gradients

Tong Qiu¹, Marie-Claire Aravena², Davide Ascoli³, Yves Bergeron⁴, Michal Bogdziewicz⁵, Thomas Boivin⁶, Raul Bonal⁷, Thomas Caignard⁸, Maxime Cailleret⁹, Rafael Calama¹⁰, Sergio Donoso Calderon², J. Julio Camarero¹¹, Chia-Hao Chang-Yang¹², Jerome Chave¹³, Francesco Chianucci¹⁴, Benoit Courbaud¹⁵, Andrea Cutini¹⁶, Adrian J. Das¹⁷, Nicolas Delpierre¹⁸, Sylvain Delzon⁸, Michael Dietze¹⁹, Laurent Dormont²⁰, Josep Maria Espelta²¹, Timothy J. Fahey²², William Farfan-Rios²³, Jerry F. Franklin²⁴, Catherine A. Gehring²⁵, Gregory S. Gilbert²⁶, Georg Gratzer²⁷, Cathryn H. Greenberg²⁸, Arthur Guignabert²⁹, Qinfeng Guo³⁰, Andrew Hacket-Pain³¹, Arndt Hampe⁸, Qingmin Han³², Jan Holik³³, Kazuhiko Hoshizaki³⁴, Ines Ibanez³⁵, Jill F. Johnstone³⁶, Valentin Journe¹⁵, Thomas Kitzberger³⁷, Johannes M.H. Knops³⁸, Georges Kunstler¹⁵, Hiroko Kurokawa³⁹, Jonathan G.A. Lageard⁴⁰, Jalene M. LaMontagne⁴¹, Francois Lefevre⁶, Theodor Leininger⁴², Jean-Marc Limousin⁴³, James A. Lutz⁴⁴, Diana Macias⁴⁵, Anders Marell⁴⁶, Eliot J.B. McIntire⁴⁷, Christopher M. Moore⁴⁸, Emily Moran⁴⁹, Renzo Motta³, Jonathan A. Myers⁵⁰, Thomas A. Nagel⁵¹, Shoji Naoe⁵², Mahoko Noguchi⁵², Michio Oguro⁵³, Robert Parmenter⁵⁴, Ian S. Pearse⁵⁵, Ignacio M. Perez-Ramos⁵⁶, Lukasz Piechnik⁵⁷, Tomasz Podgorski⁵⁸, John Poulsen⁵⁹, Miranda D. Redmond⁶⁰, Chantal D. Reid⁵⁹, Kyle C. Rodman⁶¹, Francisco Rodriguez-Sanchez⁶², Pavel Samonil³³, Javier D. Sanguinetti⁶³, C. Lane Scher⁵⁹, Barbara Seget⁵⁷, Shubhi Sharma⁵⁹, Mitsue Shibata⁵³, Miles Silman⁶⁴, Michael A. Steele⁶⁵, Nathan L. Stephenson¹⁷, Jacob N. Straub⁶⁶, Samantha Sutton⁵⁹, Jennifer J. Swenson⁵⁹, Margaret Swift⁵⁹, Peter A. Thomas⁶⁷, Maria Uriarte⁶⁸, Giorgio Vacchiano⁶⁹, Amy V. Whipple⁷⁰, Thomas G. Whitham⁷⁰, Andreas P. Wion⁷¹, S. Joseph Wright⁷², Kai Zhu³⁵, Jess K. Zimmerman⁷³, Magdalena Zywiec⁵⁷, James S. Clark^{15,59}

¹Department of Ecosystem Science and Management, Pennsylvania State University, University Park, PA 16802 USA.

²Universidad de Chile, Facultad de Ciencias Forestales y de la Conservacion de la Naturaleza (FCFCN), La Pintana, 8820808 Santiago, Chile.

³Department of Agriculture, Forest and Food Sciences, University of Torino, 10095 Grugliasco, TO, Italy.

⁴Forest Research Institute, University of Quebec in Abitibi-Temiscamingue, Rouyn-Noranda, QC J9X 5E4, Canada.

⁵Department of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, Umultowska 89, 61-614 Poznan, Poland.

⁶Institut National de Recherche pour Agriculture, Alimentation et Environnement (INRAE), Ecologie des Forets Mediteranennes, 84000 Avignon, France.

⁷Department of Biodiversity, Ecology and Evolution, Complutense University of Madrid, 28040 Madrid, Spain.

⁸Universite Bordeaux, Institut National de Recherche pour Agriculture, Alimentation et Environnement (INRAE), Biodiversity, Genes, and Communities (BIOGECO), 33615 Pessac, France.

⁹INRAE, Aix-Marseille University, UMR RECOVER, 3275 Route de Cezanne, CS 40061, Aix-en-Provence Cedex 5, France.

¹⁰Centro de Investigacion Forestal (INIA-CSIC), 28040 Madrid, Spain .

¹¹Instituto Pirenaico de Ecologia, Consejo Superior de Investigaciones Cientificas (IPE-CSIC), 50059 Zaragoza, Spain.

¹²Department of Biological Sciences, National Sun Yat-sen University, Kaohsiung 80424, Taiwan.

¹³Laboratoire Evolution et Diversite Biologique, UMR 5174 (CNRS/IRD/UPS), 31062 Toulouse Cedex 9, France.

¹⁴CREA - Research Centre for Forestry and Wood, Viale S. Margherita 80, 52100 Arezzo, Italy.

¹⁵Universite 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.

¹⁶Research Centre for Forestry and Wood, Arezzo, Italy.

¹⁷U.S. Geological Survey Western Ecological Research Center, Three Rivers, CA, 93271 USA.

¹⁸Universite Paris-Saclay, Centre national de la recherche scientifique, AgroParisTech, Ecologie Systematique et Evolution, 91405 Orsay, France.

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.

²²Natural Resources, Cornell University, Ithaca, NY, 14853 USA.

- ²³Washington University in Saint Louis, Center for Conservation and Sustainable Development, Missouri Botanical Garden, St. Louis, MO 63110 USA.
- ²⁴Forest Resources, University of Washington, Seattle, WA 98195 USA.
- ²⁵Department of Biological Sciences and Center for Adaptive Western Landscapes.
- ²⁶Department of Environmental Studies, University of California, Santa Cruz, CA 95064 USA.
- ²⁷Institute of Forest Ecology, Peter-Jordan-Strasse 82, 1190 Wien, Austria.
- ²⁸Bent Creek Experimental Forest, USDA Forest Service, Asheville, NC 28801 USA.
- ²⁹INRAE, Bordeaux Sciences Agro, UMR 1391 ISPA, Villenave d'Ornon, France.
- ³⁰Eastern Forest Environmental Threat Assessment Center, USDA Forest Service, Southern Research Station, Research Triangle Park, NC 27709 USA.
- ³¹Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, United Kingdom.
- ³²Department of Plant Ecology Forestry and Forest Products Research Institute (FFPRI), Tsukuba, Ibaraki, 305-8687 Japan.
- ³³Department of Forest Ecology, Silva Tarouca Research Institute, 60200 Brno, Czech Republic.
- ³⁴Department of Biological Environment, Akita Prefectural University, Akita 010-0195, Japan.
- ³⁵School for Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109.
- ³⁶Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99700, USA.
- ³⁷Department of Ecology, Instituto de Investigaciones en Biodiversidad y Medioambiente (Consejo Nacional de Investigaciones Científicas y Técnicas - Universidad Nacional del Comahue), Quintral 1250, 8400 Bariloche, Argentina.
- ³⁸Health and Environmental Sciences Department, Xian Jiaotong-Liverpool University, Suzhou, China, 215123.
- ³⁹address Kurokawa.
- ⁴⁰Department of Natural Sciences, Manchester Metropolitan University, Manchester M1 5GD, UK.
- ⁴¹Department of Biological Sciences, DePaul University, Chicago, IL 60614 USA.
- ⁴²USDA, Forest Service, Southern Research Station, PO Box 227, Stoneville, MS 38776.
- ⁴³CEFE, Univ Montpellier, CNRS, EPHE, IRD, 1919 route de Mende, 34293 Montpellier Cedex 5, France.
- ⁴⁴Department of Wildland Resources, and the Ecology Center, Utah State University, Logan, UT 84322 USA.
- ⁴⁵Department of Biology, University of New Mexico, Albuquerque, NM 87131 USA.
- ⁴⁶INRAE, UR EFNO, FR-45290 Nogent-sur-Vernisson, France.
- ⁴⁷Pacific Forestry Centre, Victoria, British Columbia, V8Z 1M5 Canada.
- ⁴⁸Department of Biology, Colby College, Waterville, ME 04901 USA.
- ⁴⁹School of Natural Sciences, UC Merced, Merced, CA 95343 USA.
- ⁵⁰Department of Biology, Washington University in St. Louis, St. Louis, MO.
- ⁵¹Department of forestry and renewable forest resources, Biotechnical Faculty, University of Ljubljana, Ljubljana, Slovenia.
- ⁵²Tohoku Research Center, Forestry and Forest Products Research Institute, Morioka, Iwate, 020-0123, Japan.
- ⁵³Department of Forest vegetation, Forestry and Forest Products Research Institute, Tsukuba, Ibaraki, 305-8687, Japan.
- ⁵⁴Valles Caldera National Preserve, National Park Service, Jemez Springs, NM 87025 USA.
- ⁵⁵U.S. Geological Survey Fort Collins Science Center, 2150 Centre Avenue, Bldg C, Fort Collins, CO 80526 USA.
- ⁵⁶Inst. de Recursos Naturales y Agrobiología de Sevilla, Consejo Superior de Investigaciones Científicas (IRNAS-CSIC), Seville, Andalucía, Spain.
- ⁵⁷W. Szafer Institute of Botany, Polish Academy of Sciences, Lubicz 46, 31-512 Krakow, Poland.
- ⁵⁸Mammal Research Institute, Polish Academy of Sciences, Ul. Stoczek 1, 17-230, Bialowieza, Poland, Mammal Research Institute, Polish Academy of Sciences, Bialowieza, Poland.
- ⁵⁹Nicholas School of the Environment, Duke University, Durham, NC 27708 USA.
- ⁶⁰Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO, USA.
- ⁶¹Ecological Restoration Institute, Northern Arizona University, Flagstaff AZ 86011, USA.
- ⁶²Department of Biología Vegetal y Ecología, Universidad de Sevilla, 41012 Sevilla, Spain.
- ⁶³Bilogo Dpto. Conservacin y Manejo Parque Nacional Lanin Elordi y Perito Moreno 8370, San Marten de los Andes Neuquén Argentina.
- ⁶⁴Department of Biology, Wake Forest University, 1834 Wake Forest Rd, Winston-Salem, NC 27106 USA.
- ⁶⁵Department of Biology, Wilkes University, 84 West South Street, Wilkes-Barre, PA 18766 USA.
- ⁶⁶Department of Environmental Science and Ecology, State University of New York-Brockport, Brockport, NY 14420 USA.
- ⁶⁷School of Life Sciences, Keele University, Staffordshire ST5 5BG, UK.
- ⁶⁸Department of Ecology, Evolution and Environmental Biology, Columbia University, 1113 Schermerhorn Ext., 1200 Amsterdam Ave., New York, NY 10027.
- ⁶⁹Department of Agricultural and Environmental Sciences - Production, Territory, Agroenergy (DISAA), University of Milan, 20133 Milano, Italy.
- ⁷⁰Department of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011 USA.

⁷¹Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523, USA.

⁷²Smithsonian Tropical Research Institute, Apartado 0843n03092, Balboa, Republic of Panama.

⁷³Department of Environmental Sciences, University of Puerto Rico, Rio Piedras, PR 00936 USA

Abstract

The benefits of masting (volatile, quasi-synchronous seed production at lagged intervals) include satiation of seed predators, but these benefits come with the cost to mutualist pollen and seed dispersers. If the evolution of masting represents a balance between these benefits and costs, we expect mast avoidance in the species that are heavily reliant on mutualist dispersers. These effects play out in the context of variable climate and site fertility among species that vary widely in nutrient demand. Meta-analyses of published data have focused on variation at the population scale, thus omitting periodicity within trees and synchronicity between trees. From raw data on 12 million tree-years worldwide, we quantified three components of masting that have not previously been analyzed together: 1) volatility (frequency-weighted year-to-year variation); 2) periodicity (lag between high-seed years); and 3) synchronicity (tree-to-tree correlation). Results show that mast avoidance (low volatility, low synchronicity) by species dependent on mutualist dispersers explains more variation than any other effect. Nutrient-demanding species, species that are most common on nutrient-rich and warm/wet sites, have low volatility and short periods. The prevalence of masting in cold/dry sites coincides with the climatic conditions where dependence on vertebrate dispersers is less common compared to the wet tropics. Mutualist dispersers neutralize the benefits of masting for predator satiation, further balancing the effects of climate, fertility, and nutrient demands.

Keywords: *masting, periodicity, pollination, synchronicity, seed production, seed dispersal, traits, volatility*

1 Introduction

2 Unpredictable reproduction in trees (“masting”) could be an evolved response to thwart seed con-
3 sumers^(1,2,3), but then there is a conundrum: the volatility that limits seed predators could be just as
4 deleterious to mutualist pollen and seed dispersers^(4,2,5,6), while also concentrating competition within
5 offspring^(7,8). For natural enemies and mutualists alike, masting effects depend on three elements (fig. 1),
6 i) year-to-year *volatility*, or the time-dependent magnitude of variation, ii) *quasi-periodicity*, the lag be-
7 tween high seed-production years, and iii) *quasi-synchronicity*, the tendency for individuals to produce
8 large seed crops in the same years⁽⁹⁾. Explanations for forest diversity invoke combinations of these
9 three elements^(10,11,12), but they operate together: the costs and benefits of masting depend on the
10 interactions between them and the foraging ranges of consumers and dispersers^(13,9). Meta-analyses
11 provide important insights at the aggregate population or species scale⁽¹⁴⁾ but miss the volatility within
12 and synchronicity between trees^(15,16,17). Efforts to generalize species- and site-specific results confront
13 a diversity of methods, measurements, and scales used in each study. In this paper we integrate raw
14 data at the individual tree-scale from all vegetated continents to allow formal inference on the joint
15 distribution of masting components. We show that variation of masting components across the diversity
16 of tree species depends on how seeds and pollen are dispersed, indicating that mutualists may be just as
17 important as consumers for the evolution of masting. Results show mediation of these effects by climate,
18 soil fertility, and nutrient demand.

19 We introduce specific definitions for volatility and periodicity that emphasize the contributions of low-
20 frequency (long-period) variation. The masting phenomenon is remarkable (and important), because
21 it does not simply reoccur each year; it is frequency-dependent, with low-frequency variation being
22 especially important for its effects on animal dispersers and consumers. We define frequency-dependent
23 variation as *volatility*, to avoid confusion with the term *variance* (and its derivatives, *variation* and
24 *variability*), which does not depend on time. Volatility emphasizes the contribution of variance that
25 is concentrated at low frequency (long time lags). In the context of our analysis, *periodicity* likewise
26 emphasizes variance that is concentrated at low frequency. In both cases, variance is determined as a
27 function of frequency, followed by transformation to frequency-weighted volatility and periodicity (see
28 Methods).

29 The adaptive foundation for masting may involve escape from natural enemies that are satiated by
30 large, quasi-synchronized crops and limited by intervening lean years^(18,19), but this same variation can
31 likewise negatively impact mutualists (fig. 2a). Scatter-hoarding birds and rodents can be both seed
32 predators and mutualists, consuming the entire seed crop in some years, while also aiding reproduc-
33 tion through seed burial⁽²⁰⁾. Predator satiation is most likely with high reproductive volatility, long
34 periods between high-yield years, and synchronicity between trees; this synchronicity reduces a con-
35 sumer’s capacity to simply average over inter-annual variation in one host tree by accessing others^(13,9)
36 (fig. 2a). For example, erratic seed production by individual trees (volatile and quasi-periodic) may
37 not deter natural enemies if high-production years are asynchronous between trees⁽⁹⁾. Any negative
38 effects of quasi-periodic variation on a tree’s consumers would be amplified by high year-to-year varia-
39 tion, especially when concentrated at long lags^(2,21), again, defined here as *volatility*. Weighing against
40 the benefits of unreliable fruiting for its deleterious effects on enemies are the negative effects on mu-
41 tualist dispersers^(4,2,22); the predator satiation hypothesis might not benefit species that are reliant on
42 specialized pollinators and seed dispersers.

43 While volatility amplifies the effects of periodicity and synchronicity on enemies and benefactors
44 alike, this same volatility could be mediated by resource availability and climate^(21,23) (fig. 2a). Limited
45 resources might promote reproductive variation in trees^(24,25,26) or not⁽²⁷⁾. The mast interval could be
46 prolonged where large crops deplete reserves that require years to replenish^(28,29,21,30) or not^(14,27). In
47 this global analysis, we use cation exchange capacity (CEC), a widely used index of soil fertility^(31,32),
48 and foliar nitrogen (N) and phosphorous (P) concentrations⁽²⁷⁾ to quantify the association between
49 masting and resource supply (CEC) and resource demand: nutrient demanding species tend to have high
50 foliar N and P⁽³³⁾.

51 In addition to site differences in resources and climate norms, weather anomalies might contribute
52 to large seed crops (e.g. Kelly et al⁽³⁴⁾), especially for species with limited dependence on stored re-
53 serves^(1,23) (fig. 2a). An *anomaly* is defined here as the difference between a climate variable in a given
54 year from the average of that variable for that site (the site *norm*). At least for a few species at one or
55 a few sites, warm and wet years may be associated with low seed production^(35,36,37,38,39) and increased
56 reproductive synchronicity^(40,41) (fig. 2a).

57 Because the distribution of species across environments is uneven, species differences cannot be fully

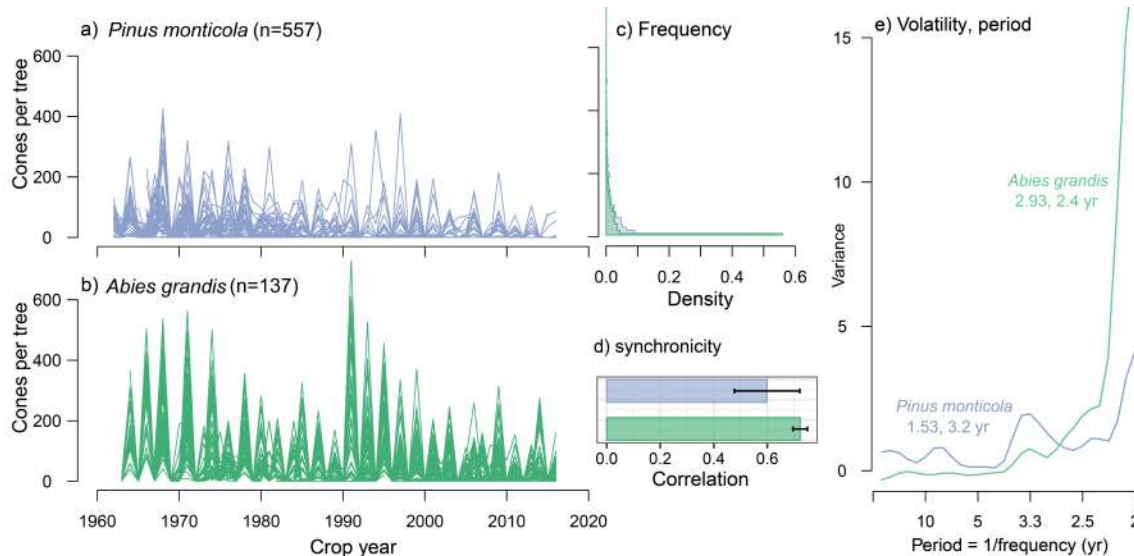


Fig. 1: **Illustration of three masting components** for *Pinus monticola* and *Abies grandis* from the central Cascades, U.S.A. Crop counts for these species (a, b) vary between individual trees, and they drift over time. The frequency of counts (c) in both species shows that zeros dominate, and there is no threshold that could be used to define masting events. *A. grandis* shows higher synchronicity between individuals (mean pairwise correlations between trees and their standard deviations are shown in d) and higher volatility, especially concentrated at the 2-yr period (e). *P. monticola* also shows variance concentrated at 2-yr, with a secondary peak at 3.4 yr. The (volatility, period) for this example are shown beneath species names in (e).

58 assessed from observational data, which dominate the masting literature. Climate anomalies in specific
 59 seasons are clearly important for many temperate species^(42,38,41,40), but our analysis evaluates vari-
 60 ation globally, spanning seasonal and a-seasonal environments. The effect of a climate anomaly such
 61 as temperature or moisture must depend on the climate norm at each site, including seasonality. For
 62 example, the estimated effect of an spring-time temperature anomaly of 1°C is not comparable between
 63 highly seasonal taiga and a-seasonal wet tropics, where the notion of spring is not relevant. Including an
 64 interaction between anomalies and norms in data models cannot clarify their respective contributions,
 65 because species are not observed across the same combinations of norms and anomalies in the data. For
 66 this reason, environmental anomalies are limited here to annual variation in temperature and moisture
 67 deficit, and comparisons between species in fig. 2a include the caveat that we are not observing all of
 68 them in all of the same settings.

69 The three components of masting have not been analyzed together, in part, because a joint anal-
 70 ysis requires substantial data at the individual (tree-year) scale. Unless individuals are perfectly syn-
 71 chronized, periodicity at the population scale underestimates periodicity at the individual scale; in
 72 fact, asynchronicity can entirely mask periodic reproduction where observed with population-scale data.
 73 Studies that examine both individual and population variation show that fecundity is typically quasi-
 74 synchronous at best^(15,43,9,17,44). Understanding spatial scales⁽⁴⁵⁾, allocation tradeoffs^(46,47), responses
 75 to climate^(48,42,49,39,50), and effects on consumers^(51,9) and dispersers^(4,2) all require joint analysis of
 76 reproductive variance within and between individuals.

77 Synthesis is challenged not just by the incompatible reference used in literature studies (Supplemen-
 78 tary information), but also by a need for measures of volatile, periodic, synchronous variability. All
 79 three elements vary between species and regions. The commonly used coefficient of variation (CV) omits
 80 time and frequency, one of the defining features of masting, and applications of CV to log values cannot
 81 properly incorporate zeros. This is important, because zero is the most frequent observation in many
 82 data sets (e.g., fig. 1c) (Supplementary information). Estimating periodicity requires a definition for
 83 what constitutes a mast year^(30,52,53,54), which is challenging because there is no identifiable threshold
 84 (e.g., fig. 1c) despite detectable indicators on trees (e.g., twigs hanging from seed weights) and peaked
 85 seed numbers in fig. 1a,b. The interval between mast years that would come from imposing an artificial
 86 threshold can range widely, in part due to variation within and between trees^(55,56). Using methods
 87 developed in this study, *P. monticola* (fig. 1a) and *A. grandis* (fig. 1b) share biennial variation but differ
 88 in the secondary concentration of variance at 3 to 4 yr in *P. monticola*. The period-weighted variance
 89 spectrum (to emphasize low-frequency) gives estimates of 2.4 and 3.2 yr in *P. monticola* and *A. grandis*,

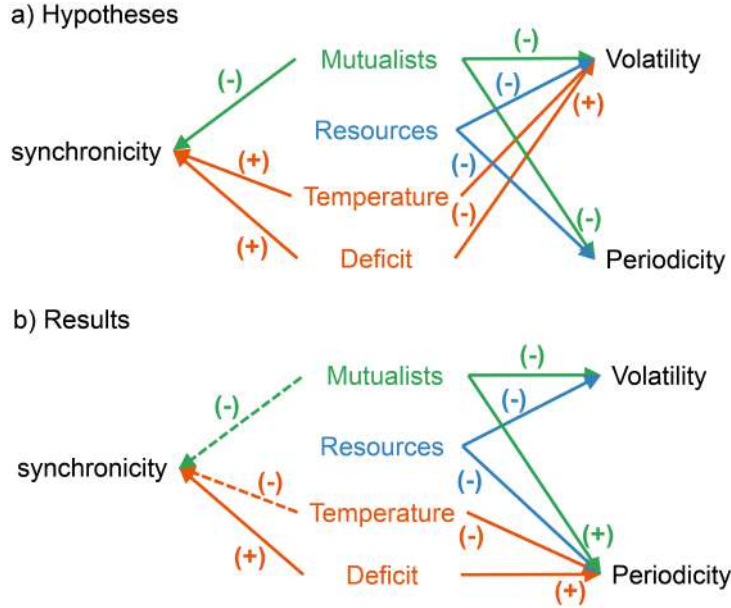


Fig. 2: **Hypothesized effects (a) and summary of results (b)** of mutualists (green), resources (blue), and climate (red) on the three masting components. Arrows with + and – represent positive and negative effects, respectively. We expect tree species with low volatility, short periodicity, and low synchronicity benefit most from their mutualist pollinators and dispersers (a). Resources reduce volatility and periodicity (a). High temperature decreases volatility while promoting synchronicity (a). Dry sites (deficit) have higher volatility and synchronicity than wet sites (a). The summary of results in (b) comes from the joint model in fig. 3. Dashed lines indicate that 90% credible intervals contain zero.

90 respectively (fig. 1e). Not only are both species strongly biennial, they are also quasi-synchronous, with
 91 mean pairwise individual correlations being especially high for *A. grandis* (0.72 ± 0.12 compared with
 92 0.60 ± 0.27 in *P. monticola*) (fig. 1d). Quasi-synchronicity between trees within a species can extend over
 93 regions^(40,41,45), but it is not global. In our case, regional variation is defined at the eco-region scale,
 94 and synchronicity is evaluated at the 1-km scale (Methods).

95 Our approach that leads to the summaries in fig. 1 takes the perspective of each tree as a time
 96 series, with dependence between individuals from the same species, using a state-space representation
 97 for maturation and fecundity status^(16,42). A model that allows for dependent observations is especially
 98 important for masting, where synchronicity means that a single individual may offer almost the same
 99 information as an entire population. In our approach, dependent observations are taken up by the
 100 correlation structure contained in the posterior distribution of latent states, one for each tree-year. The
 101 approach can allow for either year effects or autoregressive [AR(p) with lag p] terms as alternative ways
 102 to incorporate variation over time. Zeros are accommodated by a hidden Markov process for maturation
 103 status and allowance for failed crops with censoring (see Methods). Year effects that are random by
 104 ecoregion have the advantage that they do not assume a fixed AR structure over time⁽⁹⁾.

105 In three steps, we evaluate masting across species with contrasting reliance on mutualist dispersers at
 106 the global scale, and how the relationship between masting and mutualists varies with resources, climate,
 107 and phylogeny. We hypothesized that mutualist pollinators and dispersers select for low volatility, short
 108 periods, and low synchronicity^(4,2,9) (fig. 2a). We expected that nutrient-demanding species and species
 109 that commonly occur on fertile sites tend toward low volatility, rapid replenishment times following large
 110 crops and, thus, short periods^(29,23) (fig. 2a). We further hypothesized that warm climates favor low
 111 volatility and high synchronicity^(2,14,40), while dry climates (high moisture deficit) favor high volatility
 112 and synchronicity^(45,41) (fig. 2a). To test those hypotheses, we begin by extracting the three compo-
 113 nents of masting (fig. 1) from inter-annual and inter-tree variation⁽⁹⁾ using methods that derive from
 114 signal-processing for the time-series aspect of data and tree-to-tree correlation. Second, individual time
 115 series were aggregated by ecoregion-species, weighted by fecundity to emphasize large producers^(57,58)
 116 (Methods). Finally, we evaluated the effects of pollen and seed dispersal modes, resources, and climate
 117 on the joint response of masting components, both including and controlling for phylogeny.

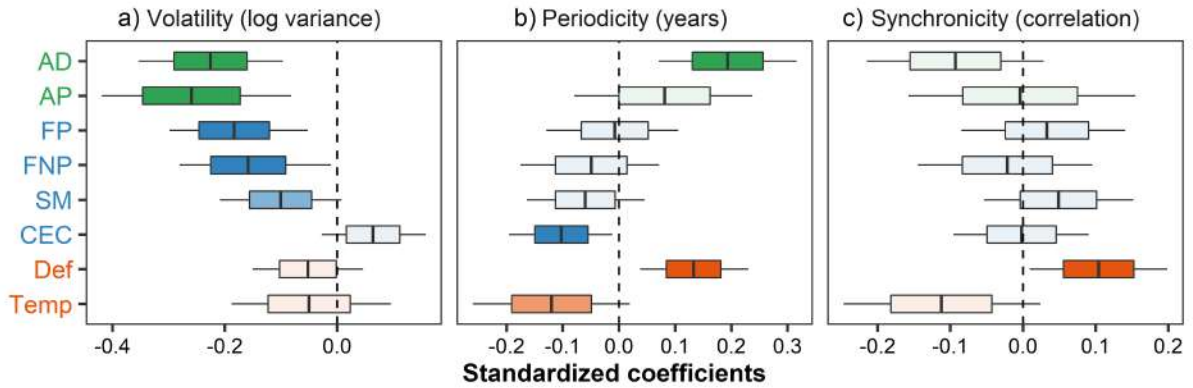


Fig. 3: **Variables that contribute to the joint response of masting components** including volatility (a), periodicity (b), and synchronicity (c) at ecoregion-species scales. Predictors include vertebrate dispersers (animal seed dispersal (AD), animal pollination (AP)), resources (soil cation exchange capacity (CEC), foliar P (FP), and foliar N:P ratio (FNP)), seed mass (SM), and climate (accumulated moisture deficit (Def, ranging from wet to dry) and mean annual temperature (Temp, ranging from cold to warm)). Dispersal and pollination syndromes are included as two-level factors, so the negative coefficients for animal seed dispersal (AD) and pollination (AP) have as mirror images the (positive) effects of wind dispersal and pollination. The analysis accounts for phylogeny as a random effect (Methods). Marginal posterior distributions are shown as boxes that contain median vertical lines and are bounded by 68% credible intervals (CI), with 95% CI whiskers. Colors highlight different variable types, with opacity increasing from 90% to 95% of the distribution outside of zero. Variables included in the model were based on the lowest Deviance Information Criterion (DIC). Coefficients are on the standard deviation scale for predictors and the correlation scale for responses (Methods). Results are summarized in fig. 2b to compare with hypotheses.

Results

Across all species in the study, dependence on mutualist dispersers is linked to low masting volatility (fig. 3a). Volatility for species that depend on animals for seed and/or pollen dispersal is substantially lower than that for wind-pollinated flowers and wind-dispersed seeds. The link between volatility and dispersal syndrome is mediated by resources and climate (fig. 3a). In addition to wind dispersal (the positive mirror images of negative AD and AP in fig. 3a), high volatility is associated with low nutrient demand (low foliar P and N:P) and with fertile soils (cation exchange capacity, CEC in fig. 3a). Of course, there is within-species variation in response to fertility⁽⁵⁸⁾, which is distinct from the mean CEC on which species are located, as used in this study. There is a weak tendency for low volatility in cold, moist climates (credible intervals include zero for Temp and Def in fig. 3a). High volatility is further associated with small seeds (SM < 0).

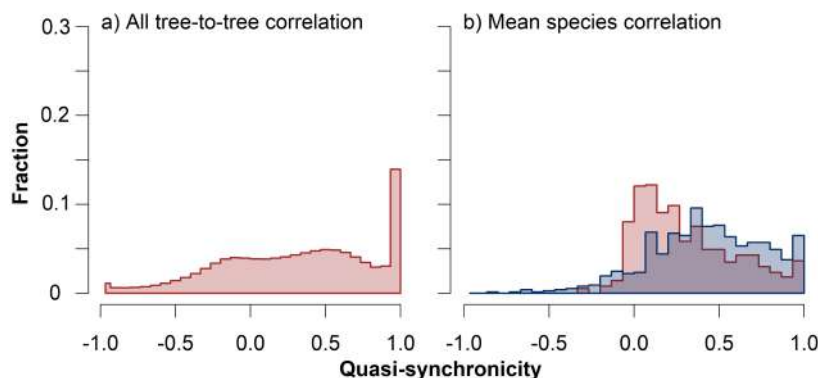


Fig. 4: **Quasi-synchronicity at individual and species level** a) Correlations between every pair of trees of the same species within 1 km show a mode near one, but a broad range. b) Species average correlations are concentrated near zero (red), but fecundity-weighted correlations are substantially higher (blue) (Methods).

The volatility relationships are not isolated from the two other components of masting. High peri-

130 odicity values in [fig. 3b](#) mean that there are long periods between high-yield years. High synchronicity
 131 values in [fig. 3c](#) mean that individuals produce large crops in the same years, and vice versa. Because
 132 period and synchronicity are important only for trees with non-negligible seed production, both are
 133 weighted here by individual fecundity (see Methods). In the case of synchronicity, the distribution of
 134 pairwise correlations for trees of the same species within 1 km of one another (see Methods) has the
 135 mode near +1, but is broadly distributed over negative and positive values ([fig. 4a](#)). When aggregated
 136 to the species level (averaged over pairwise correlations for the species), the distribution shifts to pre-
 137 dominantly positive values ([fig. 4b](#), red). When weighted by fecundity, these averages increases further
 138 ([fig. 4b](#), blue), due to the fact that large producers have the highest levels of synchronicity.

139 The long periods associated with animal seed dispersal ([fig. 3b](#)) may not have meaningful effects on
 140 consumers or mutualist, because these species are weakly synchronized ([fig. 3c](#)). For consumers that
 141 can move between host trees, weak synchronicity means that there will be individuals producing seed
 142 in many years. Short periods are associated with warm, wet, fertile sites (negative Temp and CEC,
 143 positive Def in [fig. 3b](#)). The quasi-synchronicity that is strongest for wind dispersal is amplified in cold,
 144 dry climates (negative AD and Temp, positive Def in [fig. 3c](#)).

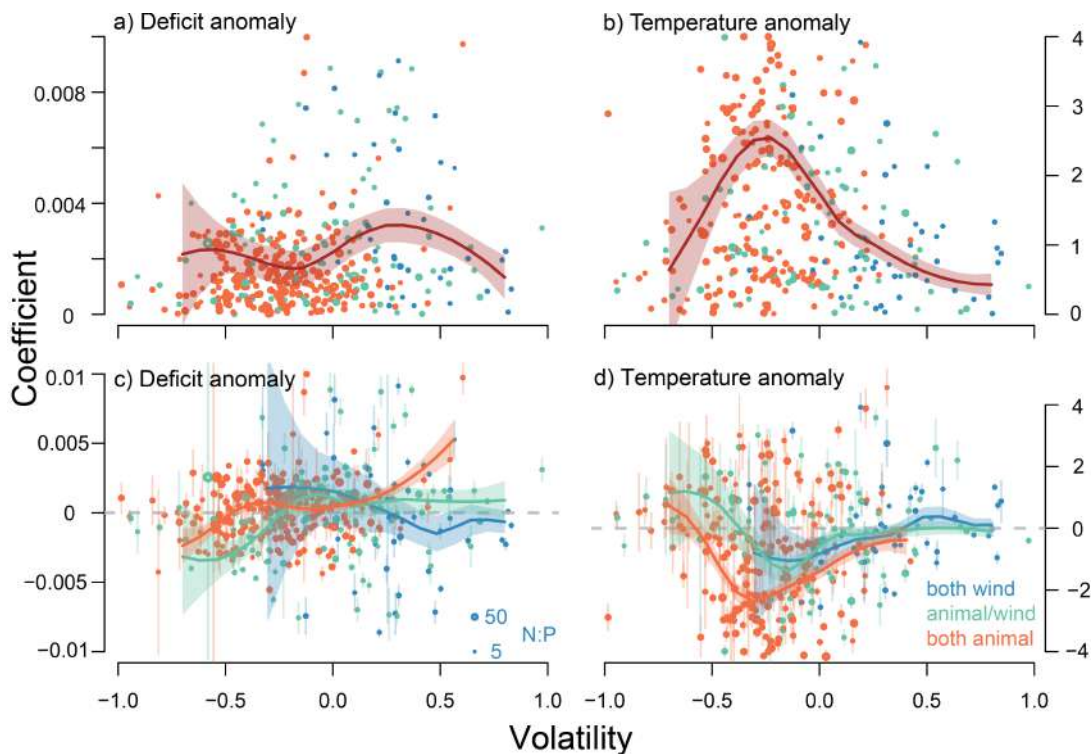


Fig. 5: **Volatility, dispersal mode, climate anomalies, and foliar N:P.** Each point locates species volatility (variability between years on log scales) with its coefficients to climatic anomalies in moisture deficit (panel a and c) and temperature (panel b and d). Coefficients were obtained from the fitted model (see methods). Overall sensitivity with no grouping by dispersal/pollination syndromes is shown as absolute values in the above panel (a, b); and with their signs in the below panel (c, d). The mean temperature from the previous year and accumulated moisture deficit from both the previous and current year were used to calculate anomalies. Symbol size scales with foliar N:P ratio. “Both animal” species (orange) have both pollen and seeds dispersed by animals. “Animal/wind” species (green) have either pollen or seeds dispersed by animals. High volatility is associated with positive responses to moisture deficit (c) and temperature (d) in animal-dispersed species, but generally declining absolute sensitivity to both variables (a and b). Loess regressions on parameter estimates (dots), weighted by the standard errors of the estimate (error bars), summarize trends with their confidence intervals (the colored shades) in absolute sensitivity (a, b) and for the three dispersal groups (c, d).

145 The most volatile species are not those having the highest sensitivity to climate anomalies. It is
 146 important to first note that climate anomalies make large contributions to variation in many species,
 147 both positive and negative (large coefficients in [fig. 5c, d](#)). The absolute values of anomaly responses
 148 ([fig. 5a](#)) summarize both positive and negative sensitivity to moisture deficit and temperature anomalies
 149 ([fig. 5a, b](#)). The coefficients are less meaningful for low volatility species, because there is less total
 150 variation that could be driven by climate or intrinsic factors. Thus, the positive log volatility values

151 in fig. 5 are most telling, and, at log volatility above zero, absolute sensitivity declines on average for
152 both climate variables (fig. 5a, b). Because few animal-dispersed species are highly volatile, the trends
153 in these high values are driven more by wind-dispersed species (blue symbols) with low foliar N:P (small
154 symbols). For animal dispersed species, moisture-deficit sensitivities shift from negative to positive with
155 increasing volatility (fig. 5c, orange, green). For both dispersal modes (wind versus animals), temperature
156 sensitivities trend from negative to near-zero with increasing volatility (fig. 5d).

157 All elements of the three-part syndrome have phylogenetic dependence, especially strong for volatility
158 and periodicity and less so for synchronicity (fig. 6). Volatility is highest in the temperate clades Pinales,
159 Fagales, and Sapindaceae (prominent exceptions include the shrub maples *Acer pensylvanicum* and *A.*
160 *spicatum*). The wind pollinated and (primarily) wind seed-dispersed genera *Abies* and *Betula* are near
161 the highest volatility and the shortest period. Other volatile, wind-dispersed temperate groups include
162 the Ulmaceae (*Ulmus*, *Zelkova*). Volatile animal-dispersed groups include the genera *Ficus*, *Swida*, and
163 *Nyssa*. Synchronicity is especially high in many of the Pinales and Fagales. Low volatility is common in
164 the tropical groups Fabales, Malpighiales, and Gentianales. For groups with mixed tropical/temperate
165 affinities, volatility tends to be low in Magnoliids, Ericales, and Cornales. Periodicity and synchronicity
166 of most tropical species are not included in fig. 6b, c, because their low volatility values fall below the
167 range where period and synchrony become meaningful (Methods).

168 Taken over all ecoregion-species combinations, volatile seed production is most common for species
169 with short periods between productive years (correlation = -0.28, 95% CI = (-0.36,-0.21), fig. S2). This
170 negative relationship between volatility and period holds within phylogenetic groups, where there are
171 more negative than positive correlations between volatility and period (fig. S2). High volatility aligns
172 with short periods in most temperate groups (in *Abies*, *Quercus*, *Fagus*, residual Fagaceae, Pinaceae,
173 and Magnoliaceae), some tropical species (in Meliaceae, Melastomataceae), and some with mixed tropi-
174 cal/temperate affinities (residual Sapindaceae). Correlations in other large temperate groups (in *Pinus*,
175 *Acer*, Cupressaceae, Betulaceae, and Oleaceae), as well as in mixed tropical/temperate groups (in An-
176 nonaceae, Araliaceae, Moraceae, Symplocaceae, Lauraceae), are negative but not significantly less than
177 zero. Conversely, positive relationships are dominated by one mostly temperate group (Aquifoliaceae),
178 others being non-significant, but predominantly tropical.

179 Across species, the relationship between volatility and synchronicity is weak (correlation = -0.039,
180 95% CI = (-0.12, 0.043)), but strong correlations emerge within many phylogenetic groups (fig. S3).
181 Volatile species have low synchronicity in many families of mixed temperate/tropical affinity (blue in
182 fig. S3). High volatility combines with high synchronicity in the temperate genera *Fagus* and *Abies*, but
183 only weakly in *Quercus* (brown in fig. S3). For the majority of species groups, high synchronicity is
184 associated with low volatility.

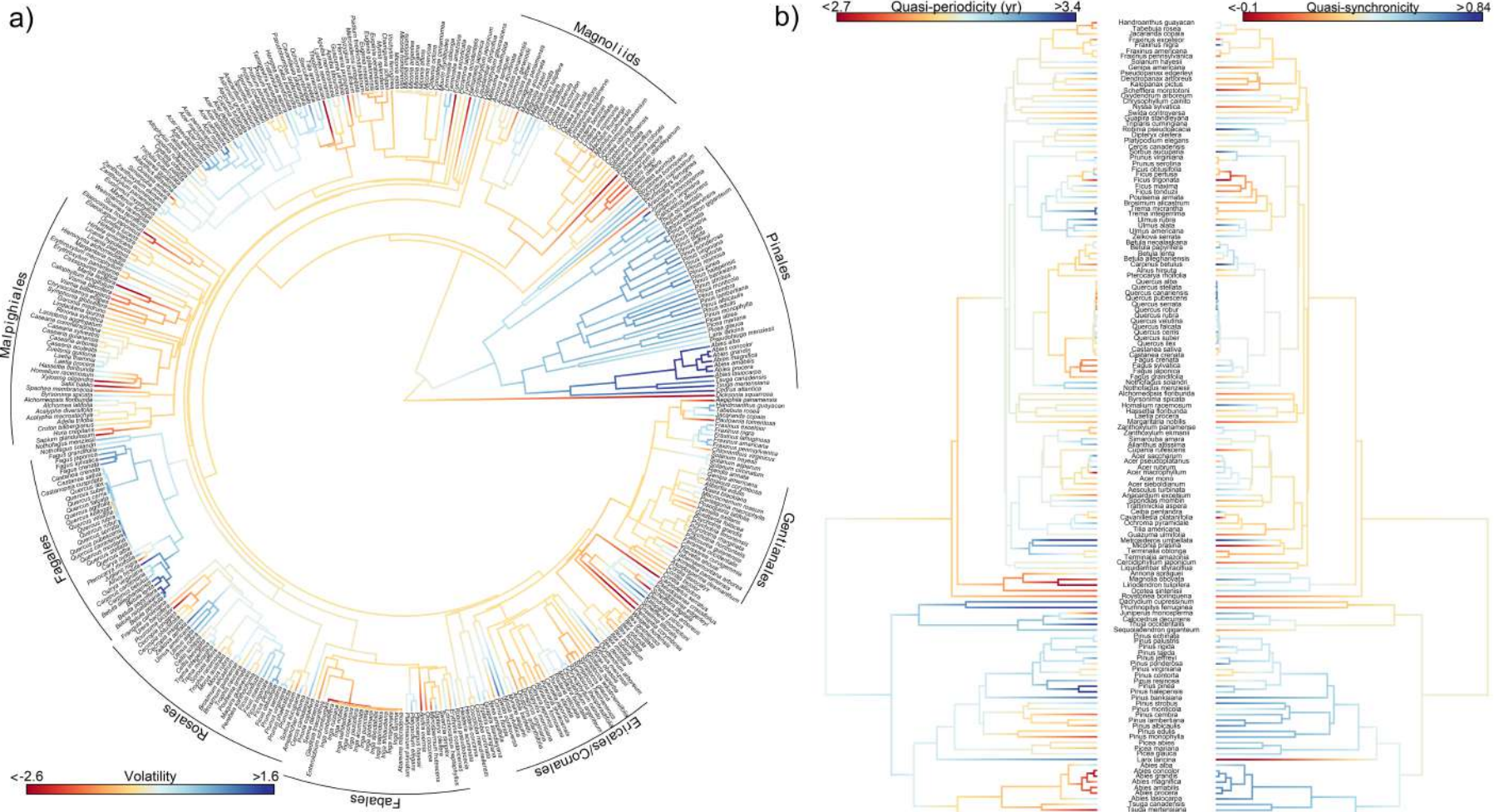


Fig. 6: **Phylogenetic coherence in the three masting components.** (a) Volatility (on log scale) has a phylogeny component (*Pagel's* $\lambda = 0.83$, $p < 10^{-9}$, $n = 394$). (b) Quasi-periodicity (left) exhibits a weaker phylogenetic coherence compared to volatility (*Pagel's* $\lambda = 0.52$, $p = 0.0023$, $n = 142$). Quasi-synchronicity (right) shows the weakest signal (*Pagel's* $\lambda = 0.21$, $p = 0.0064$, $n = 142$). Species with volatility of at least 0.94 (62.5% quantile) are shown in (b) because periodicity becomes noisy and less meaningful at low level of volatility.

185 Discussion

186 Seed and pollen dispersal syndromes emerge as the dominant trait associated with volatile seed pro-
187 duction in trees; reliance on mutualist pollen and seed dispersal is among the strongest predictors of
188 masting avoidance (fig. 3a). The selective forces that have shaped associations between masting and
189 animal-dispersal include costs to mutualist dispersers and the benefits of reduced predation^(4,2,14). These
190 selective forces are further complicated by the fact that at least some animal dispersers are also seed
191 predators (e.g., in *Quercus* and other species that are dispersed by scatter-hoarding vertebrates). While
192 animal-dispersed species are overall less volatile (fig. 3a), there are notable exceptions. For example, the
193 volatile Fagaceae (fig. 6a) have primarily wind-dispersed pollen, but depend on scatter-hoarding seed
194 dispersers–mutualists that suffer in low-yield years and disperse and satiate in high-yield years^(59,60).
195 Perhaps as an exception that supports the rule, within Fagaceae the lowest volatility is estimated for
196 *Castanea* with primarily insect-dispersed pollen⁽⁶¹⁾. The strong connection between mast volatility and
197 wind dispersal (fig. 3a) supports the hypothesis that animal pollination may suffer from volatile mast-
198 ing^(4,2,23,6,62).

199 Insights from this study could not have come from a traditional treatment of variation. Traditional
200 comparisons based on the coefficient of variation and its derivatives omit the basic attribute of frequency
201 (fig. 1). Extracting mean intervals between events becomes highly subjective, because there is no thresh-
202 old value that distinguishes an event from background (fig. 1c). All three components of mast variation
203 require individual-scale data. Analysis of raw data, with dependence between individuals and over time,
204 allowed quantification of the contributions of volatility, quasi-periodicity, and quasi-synchronicity.

205 Volatile species have low reliance on animal dispersal, low nutrient demands, and generally low sensi-
206 tivity to climate anomalies (fig. 5a, b). The classic masting response–volatile, synchronized reproduction
207 at lagged intervals—is associated with species traits and conditions that lead to low seed production.
208 Cold, dry climates at high latitudes, where reproductive output is two orders of magnitude lower than
209 in the wet tropics⁽⁶³⁾, are dominated by small seeds, wind dispersed pollen and seeds, and volatile re-
210 production (fig. 3a). Synchronized reproduction at long periods is a feature of dry climates (fig. 3b, c)
211 where pollination efficiency is expected to be high⁽⁴⁵⁾. Even the increased volatility with soil fertility
212 fits this negative relationship between fecundity and volatility: mean fecundity declines with foliar P⁽⁵⁸⁾
213 as volatility increases (foliar nutrients and soil CEC in fig. 3a). Despite the limitations of comparing
214 environmental responses across species that differ in their distribution of exposures to the environment,
215 results are not consistent with the expectation that volatility at the species level increases with higher
216 variations in climate anomalies⁽³⁴⁾.

217 Synchronicity has the tendency to be associated with wind dispersal (fig. 3c), consistent with costs
218 to mutualist dispersers that include not only satiated frugivores, but also competition for animal polli-
219 nators⁽⁶⁴⁾. Synchronized flowering may increase pollinator visitation rates^(65,66); however, if unreliable
220 flowering limits specialized pollen dispersers, then benefits of synchronicity could be mixed (fig. 3c).
221 A tendency for long intervals between mast years in mast-avoiding tree species has a muted effect on
222 their animal seed dispersers, because it is associated with low volatility and asynchronicity (fig. 3b,
223 c). The association of wind pollination with high volatility but not with long periods agrees with the
224 largely untested notion that quasi-synchronous flowering effort increases pollination efficiency while long
225 intervals between mast years have no additional benefits⁽¹⁾.

226 The synchronicity that is typically emphasized for masting populations belies the overall weak tree-to-
227 tree correlation. The distribution of inter-tree correlations weighted by fecundity (fig. 4b) could resolve
228 the paradox of low synchronicity in species traditionally identified as iconic mast producers^(15,16,17).
229 Low and even negative correlations characterize populations on the whole (fig. 4a), but strong producers
230 are dominated by positive correlations (fig. 4b). The production of some non-synchronized offspring
231 is an expected bet-hedging maternal strategy even where quasi-synchronicity is generally beneficial.
232 The advantages of predator satiation have to balance the potential costs of concentrated intraspecific
233 competition between sibling seedlings and of satiating mutualist pollinators and dispersers. Indeed,
234 heterogeneous volatility-synchronicity relationships between lineages (Fig. S2) suggests the potential for
235 region/species-scale adaptation in response to variable predation pressure^(67,22).

236 The finding that volatile species tend to have short periods (fig. 6), including within multiple phy-
237 logenetic groups (fig. S2), is not consistent with the view that resource depletion followed by delayed
238 replenishment is a dominant source of variation between species. This lack of association *between* species
239 does not preclude a need for extended replenishment following high-yields *within individuals* in ways that
240 differ between species. Although less studied, it is also important to understand how local adaptation
241 (i.e., genetic differences among populations⁽⁶⁸⁾) and gene \times environment interactions that affect seed

242 enemies and dispersers^(69,5) may contribute to the evolution of volatility, periodicity and synchronicity.

243 If consistently high nutrient concentrations obviate the need for prolonged nutrient recovery, then we
244 expect the observed negative association between foliar nutrients and volatility (fig. 3a). By allowing
245 for the effects of both foliar nutrient concentrations and site fertility, our results diverge from previous
246 studies suggesting low volatility on fertile sites. However, comparisons have to consider that previous
247 studies include few species^(24,25,26). The effects of nutrient demand versus supply can be confounded by
248 the fact that nutrient-demanding species are most abundant on fertile sites. By including differences in
249 foliar nutrients as a species-level trait with the CEC where trees occur, this global analysis finds that
250 low volatility is associated with nutrient-demanding species, not low-fertility sites. The association of
251 high volatility and short periods with nutrient-rich habitats (CEC in fig. 3) could result from accelerated
252 nutrient replenishment on fertile soils. However, as noted above, volatile species are not those with short
253 periods in general. Not only do nutrient-demanding species (as reflected in foliar nutrient content) have
254 lower species seed production (SSP, defined as seed number \times seed size)⁽⁵⁸⁾; they also are less volatile
255 (fig. 3a). Limited effects of resources on synchronicity can be related to the weak effects of soil CEC on
256 seed production⁽⁵⁸⁾ and intense competition on nutrient-rich sites⁽⁴²⁾.

257 The expectation that large seeds might demand long recovery intervals was not supported by compar-
258 isons between species. Using data from Schopmeyer et al⁽⁷⁰⁾, Sork et al⁽³⁰⁾ found a positive relationship
259 between acorn size and mast period for 18 temperate *Quercus* species. We find a negative relationship
260 at the global scale: species with large seeds are less volatile and have short periods in fig. 3a, b. In
261 the limited dataset⁽⁷⁰⁾, the negative correlation is driven by a longer interval for *Quercus alba* than *Q.*
262 *falcata*. In general, we find that red oaks (*Q. falcata*, *Q. rubra*, *Q. velutina*, *Q. coccinea*) have longer
263 periods than white oaks (*Q. alba*, *Q. montana*, *Q. pubescens*, *Q. robur*, *Q. stellata*, *Q. serrata*), Cerris
264 oaks (*Q. cerris*, *Q. ilex*, *Q. suber*) and *Fagus* (fig. 6b), perhaps related to the two-yr development time
265 for red oak seeds.

266 The wide variation in seed production^(57,58) emphasizes the importance of large data sets to estimate
267 effects, represented here by 12 million tree-years at a global scale. As is common in observational studies,
268 the geographic coverage of raw observations is not uniform across different regions (Fig. S1). Expanding
269 the MASTIF network with additional sites in South America and Africa would contribute to a more
270 balanced global coverage.

271 The negative association between masting intensity and fecundity suggests the view of masting as
272 desperation: an evolutionary option most common in species and settings where seed production is
273 limited primarily by climate and habitat and where animal dispersal is less common. There is no
274 question that predator satiation occurs, and seedling escape can result^(71,72,73). Despite the fact that
275 it is not uncommon for a given tree species to have multiple pollinators and seed dispersers⁽⁷⁴⁾, the
276 diet breadth of seed consumers (e.g., specialist and generalist) clearly affects masting⁽⁹⁾. Quantifying
277 different degrees of specialization between seed predators, pollinators and dispersers is an important
278 future research avenue. Still, at the global scale, species differences in masting depend on their reliance
279 on animal dispersers.

280 The emergence of dispersal syndrome as a dominant link to species differences in masting intensity
281 (fig. 3) supports the view that mutualist relationships could be just as important as predator satiation–
282 the cold, dry settings where masting is intense coincides with the low reliance on mutualist dispersers.
283 The conundrum faced by species that depend on animal dispersal while also suffering from seed predation
284 makes for conflicting selection pressures that are evident when viewed across the diversity of tree species.

285 Methods

286 MASTIF summary

287 The MASTIF model allows us to jointly model individual trees, with their dependence on one another
288 and over time. This hierarchical, state-space model and the Gibbs sampling used for posterior simulation
289 are detailed in Clark et al.⁽⁹⁾, with only key elements that relate to mast syndromes summarized here.
290 Model fitting includes approximately 12 million tree-years from 898 species (fig. S1). MASTIF model is
291 open-access with R package MASTIF on CRAN.

292 The core quantity of interest is the tree-year fecundity $f_{ijr,t}$ for tree i on stand j , in ecoregion-
293 species r , and year t . Fecundity varies individually with tree size and crowding, locally with interannual
294 climate anomalies, geographically with climate norms, soil and drainage, and regionally through shared
295 year effects. The shared variation between trees in year effects are random between ecoregion-species
296 combinations, allowing for covariation that is broader than local climate but still regionally variable.

297 Because the model includes interannual anomalies at the local scale, year effects quantify shared variation
 298 beyond that explained by climate anomalies and at a coarse (ecoregion) scale.

299 The MASTIF model incorporates two data types including crop counts and seed traps. Crop counts
 300 $c_{ijr,t}$ are conditionally beta-binomial, which allows for the uncertainty in fraction of the crop that is
 301 observed,

$$\text{betaBinom}(c_{ijr,t}|f_{ijr,t}, a_{ijr,t}, b_{ijr,t}) = \int_0^1 \text{binom}(c_{ijr,t}|f_{ijr,t}, q_{ijr,t})\text{beta}(q_{ijr,t}|a_{ijr,t}, b_{ijr,t})dq_{ijr,t} \quad (1)$$

302 where $q_{ijr,t}$ is an estimate of the fraction of the crop observed, and $(a_{ijr,t}, b_{ijr,t})$ are parameters selected
 303 have mean fraction $q_{ijr,t}$ (i.e., the fraction reported), but error that increases with small $q_{ijr,t}$. This
 304 approach allows for the fact that the lower the reported crop fraction, the less certain it is.

305 Seed trap counts are conditionally Poisson,

$$\text{Poi}(\mathbf{y}_{jr,t}|A_{j,t}\mathbf{S}\mathbf{f}_{jr,t}) \quad (2)$$

306 where trap area $A_{j,t}$ can vary by study and year t , $\mathbf{y}_{jr,t}$ is a vector of seed counts for S_j traps, \mathbf{S} is the
 307 $S_j \times n_j$ kernel matrix that determines dispersal from each of $i = 1, \dots, n_j$ trees to S_j traps, depending
 308 tree-to-trap distances, and $\mathbf{f}_{jr,t}$ is the length- n_j vector of tree fecundities. The dispersal kernel follows⁽⁷⁵⁾.

309 Fecundity is the product of latent states for maturation status and conditional fecundity, $f_{ijr,t} =$
 310 $\psi_{ij,t}\rho_{ijr,t}$ having the joint distribution $[\psi_{ijr,t}, \rho_{ijr,t}] = [\psi_{ijr,t}|\rho_{ijr,t}][\rho_{ijr,t}]$. (We use bracket notation $[x]$
 311 to indicate a distribution or density of x). Maturation is a one-way process, modelled as a probit hidden-
 312 Markov model. The maturation status $\rho_{ijr,t} \in \{0, 1\}$ is known to be 1 (i.e., mature) for trees that have
 313 been observed to produce seed in the past, i.e., $[\rho_{ijr,t} = 1|\rho_{ij,t-1} = 1] = 1$, and 0 if known to be immature
 314 subsequently $[\rho_{ijr,t} = 1|\rho_{ij,t+1} = 0] = 0$. For tree-years of unobserved maturation status, the probability
 315 of being mature in year t , given past and future status is the probit,

$$\begin{aligned} \rho_{ijr,t}|\rho_{ijr,t-1}, \rho_{ijr,t+1} &\sim \text{Bernoulli}(p_{ijr,t}) \\ p_{ijr,t} &= \rho_{ijr,t-1} + (1 - \rho_{ijr,t-1})\rho_{ijr,t+1}\Phi(\mathbf{v}'_{ijr,t}\boldsymbol{\beta}^v) \end{aligned} \quad (3)$$

316 where $\Phi(\cdot)$ is the standard cumulative normal distribution, $\mathbf{v}_{ijr,t}$ are predictors, and $\boldsymbol{\beta}^v$ are fitted coeffi-
 317 cients. All unknown statuses must be imputed, so that ρ coefficients in eq. (3) are the currently imputed
 318 values in Gibbs sampling.

319 The process model for fecundity is log-normal and dynamic,

$$\log \psi_{ijr,t}|\rho_{ij,t} \sim N(\mathbf{x}'_{ij,t-1}\boldsymbol{\beta} + \alpha_{ij} + \gamma_{r,t}, \sigma^2)I(\psi_{ij,t} \leq 1)^{1-\rho_{ijr,t}}I(\psi_{ij,t} > 1)^{\rho_{ijr,t}} \quad (4)$$

320 where $\mathbf{x}_{ij,t}$ are predictors in the model with coefficients $\boldsymbol{\beta}$, α_{ij} is the random effect for tree ij , $\gamma_{r,t}$ is the
 321 year effect for ecoregion-species r , and σ^2 is the residual variance. The factors containing the indicator
 322 function specify that mature individuals have latent conditional fecundity sufficient to generate at least
 323 one seed. Importantly, the approach allows for observed zero fecundity for both seed traps and crop
 324 counts while latent fecundity remains finite. This approach follows the approach used in Tobit models
 325 for discrete zeros in otherwise continuous data^(76,77). Predictors in the design vector $\mathbf{x}_{ijr,t}$ include known
 326 climate and habitat variables combined with variable selection by DIC.

327 Masting syndromes

328 The analysis of masting components at individual level is based on the estimate of the fecundity, $f_{ijr,t}$,
 329 on the log (proportionate) scale. The mast syndrome consists of three elements $M = (M_v, M_p, M_c)$, the
 330 volatility M_v having units of variance in $\log f$, period M_p in years, and the dimensionless synchronicity
 331 M_c . The first two elements emerge from the spectral density $S_f(\omega)$, evaluated in the frequency ω domain.
 332 Technically, $S_f(\omega)$ is obtained by transforming the auto-covariance function $C(t)$ from the time domain
 333 to the frequency domain or, alternatively, by taking the Fourier transform of the autocorrelation function
 334 $C(t)/C(0)$. There is an associated spectral *variance*, obtained by integrating the spectral density over
 335 frequency

$$\text{Var}_\omega(f) = \frac{1}{\pi} \sum_{k=0}^{\omega^*} S_f(\omega_k) \quad (5)$$

336 where ω^* is the last frequency term. Period (years) is the reciprocal of frequency, ω^{-1} . To capture the
 337 defining feature of masting, that of variance concentrated at low frequency, we define *volatility* as the
 338 period-weighted spectral variance,

$$E_{\omega}(M_v) = \frac{1}{\pi T} \sum_{k=0}^{T-1} \omega_k^{-1} S_f(\omega_k) \quad (6)$$

339 where T is the number of terms included in the summation. The subscripts of tree i , stand j , and
 340 ecoregion-species r are omitted to reduce clutter. Because short time series could be dominated by
 341 noise, we focused on mature individuals that include at least 10-year of observations (139,785 trees and
 342 2,841,238 tree-years from 468 species). Detailed data distribution can be found in the supplementary
 343 csv file. We set T to be half of the threshold, i.e., $T = 5$ yr. Likewise, *periodicity* emphasizes variance at
 344 low frequency,

$$E_{\omega}(M_p) = \frac{1}{\pi Var_{\omega}[f]} \sum_{k=0}^{T-1} \omega_k^{-1} S_f(\omega_k) \quad (7)$$

345 with variance

$$Var_{\omega}(M_p) = \frac{1}{\pi Var_{\omega}(f)} \sum_{k=0}^{T-1} \omega_k^{-2} S_f(\omega_k) - E_{\omega}^2(M_p) \quad (8)$$

346 The span of variance captures the quasi-periodic nature of masting, being broad where period is unpre-
 347 dictable (fig. 1d). We obtained the spectral density $S_f(\omega_k)$ for each tree ($\log f_{ijr}$) using the R package
 348 `spectrum`. Volatility and periodicity complement currently-used metrics for masting. Volatility measures
 349 variance in the frequency domain, capturing the out-sized importance of variation at the multi-year scale,
 350 moving beyond lag-0 (CV) or lag-1 approaches. Periodicity side-steps the need to define a threshold
 351 productivity for mast years or the fact that a simple mean interval may not represent quasi-periodic
 352 variation.

The ecoregion-species masting syndromes, $M_r = (M_{v,r}, M_{p,r}, M_{c,r})$, are the expectations of individual
 level estimates M_{ijr} . Because individual volatility $M_{v,ijr}$ and quasi-periodicity $M_{p,ijr}$ could be dominated
 by large numbers of small and thus low fecundity trees, we evaluated the $M_{v,r}$ and $M_{p,r}$ in a weighted
 way to increase signal-to-noise ratio and to emphasize the large seed producers:

$$M_{v,r} = \frac{\sum_{ij} ISP_{ij} M_{v,ijr}}{\sum_{ij} ISP_{ij}} \quad (9)$$

$$M_{p,r} = \frac{\sum_{ij} ISP_{ij} M_{p,ijr}}{\sum_{ij} ISP_{ij}} \quad (10)$$

353 where ISP is individual standardized productivity^(58,63). It is defined as seeds per tree times mass per
 354 seed and divided by tree basal area and averaged across multiple years.

355 We evaluated the weighted synchronicity at ecoregion-species level following a similar procedure as
 356 that of volatility and periodicity. Tree-to-tree correlation coefficients were calculated between all con-
 357 specific individuals within 1 km of one another. We included correlations $M_{c,k}$ over years for which both
 358 trees of a pair k that are estimated to be in the mature state (3,539,315 tree-years and 274,024 trees
 359 from 468 species). For the tree-to-tree correlations, both the correlation and the product of fecundity
 360 were calculated for each pair, the latter having large values for trees with high production. A weighted
 361 synchronicity over all trees of a species within 1 km was evaluated as

$$M_{c,r} = \frac{\sum_k M_{c,kr} C_k}{\sum_k C_k} \quad (11)$$

362 for all pairwise correlations $M_{c,kr}$ at ecoregion-species r , with weight C_k being the absolute value of the
 363 pairwise covariance, i.e., the product of fecundities for each pair of trees k .

364 Analyses at ecoregion-species level

365 We evaluated variations in the $M_r = (M_{v,r}, M_{p,r}, M_{c,r})$ jointly at ecoregion-species level ($n = 583$)
 366 through incorporating phylogeny, species traits, soil, and climate covariates in a generalized joint at-
 367 tribute model (GJAM). Our analyses were implemented at ecoregion-species level because 15% of the

368 total species ($n = 468$) have within-species variations across ecoregions (supplementary csv file). The
 369 remaining (85%) species that are sampled at one ecoregion are primarily tropical species. As of now,
 370 MASTIF coverage could be improved with the addition of more sites in South America, Africa, and
 371 Asia. One of the masting families, Dipterocarpaceae, is not included in the network. But the MASTIF
 372 network is continuously expanding to achieve a more balanced global coverage. Ecoregions in this study
 373 follow the same definition as World Wildlife Fund (WWF) terrestrial ecoregions⁽⁷⁸⁾.

374 Phylogeny

375 We quantified the phylogenetic signal in volatility and quasi-periodicity using *Pagel's* λ . Species dif-
 376 ferences in masting syndromes were averaged across ecoregion-species combinations. Phylogeny was
 377 obtained for 394 species (84% of the total 468 species) from⁽⁷⁹⁾. We used the continuous character
 378 mapping method from the R package `phytools`⁽⁸⁰⁾ to visualize the phylogenetic coherence in volatility,
 379 periodicity, and synchronicity.

380 To account for phylogeny in the joint model of three masting syndromes, we depart from traditional
 381 assumptions concerning residual covariance, turning instead to direct inference on the effects of phylo-
 382 genetic groups. The aim to control for phylogenetic association in comparative studies^(81,82) suggests a
 383 capacity to take up variation that might be linked to relatedness in a general sense. Instead, current
 384 methods impose a highly specific assumption that residual variance between species traits results from
 385 a random walk that proceeds at a fixed rate across species pairs. However, natural selection would not
 386 operate in this way, not for a given species pair and certainly not across a large number of species.
 387 Residual variance constitutes all sources of variation that are not taken up by the mean structure of
 388 the model. Just as there could be massive phylogenetically constrained traits between specific species
 389 pairs that have diverged under differing intensities of selection, there could be minimally constrained
 390 pairs within the same comparative study where others are strong. The important modeling concern for
 391 valid inference on coefficients is a covariance matrix that can take up relationships that remain after
 392 accounting for the mean, regardless of their source, and without imposing specific assumptions about
 393 rates of divergence.

394 Our joint analyses of masting syndromes explored phylogenetic contributions with species groups
 395 treated as random effects and covariance that is unconstrained by assumptions on divergence rates.
 396 Rather than assume a fixed relationship between residual covariances, our approach provides a transpar-
 397 ent estimate for differences between species groups, allowing that they need not be anchored to pairwise
 398 divergence times. For genera having at least 10 species in the MASTIF data, species were grouped at
 399 the genus level. All remaining species in families having at least 5 species were grouped at the family
 400 level. Remaining species were aggregated into an 'other' group for purposes of model fitting, but they are
 401 displayed separately in the correlation plots (e.g., Fig. S3). Relationships between masting syndromes
 402 within each phylogenetic group were evaluated using Pearson's correlation coefficient.

403 Joint modeling of masting syndromes

404 To evaluate masting as a syndrome and the variables associated with it, we conducted joint analyses
 405 of mast attributes against predictors that include species traits, environment, and phylogeny. Species
 406 traits included dispersal mode (anemochory vs zoochory), pollination mode (animal vs wind pollinated
 407 syndromes), mean foliar N and P (percentage of dry mass), and seed size (gm per seed). Traits infor-
 408 mation are obtained from collections in our labs and supplemented with the TRY database⁽⁸³⁾. Genus-
 409 or family-level means were used where seed size and foliar nutrients were missing at the species level.
 410 Similarly, genus- or family- modes were used for dispersal and pollination syndromes. Foliar N:P were
 411 calculated as the ratio between the two nutrients. Foliar N:P measures the nutrient limitations⁽³³⁾ and
 412 could affect the masting syndrome⁽²⁹⁾. Environmental covariates include soil fertility (Cation Exchange
 413 Capacity, CEC), mean annual temperature, and accumulated annual moisture deficit (differences between
 414 potential evapotranspiration and precipitation) averaged at ecoregion-species level. We used generalized
 415 joint attribute modeling (GJAM)⁽⁷⁷⁾ to allow for the dependence between mast components and the fact
 416 that masting components are non-negative (they are non-Gaussian),

$$\mathbf{w}_r \sim MVN(\mathbf{x}'_r \boldsymbol{\beta}, \Sigma) \times \prod_{l=1}^S I(w_{r,l} \leq 0)^{I(M_{r,l}=0)} I(w_{r,l} > 0)^{I(M_{r,l}=w_{r,l})} \quad (12)$$

417 where \mathbf{w}_r is the length- S vector holding the latent (and uncensored) mast response for ecoregion-species
 418 r and \mathbf{M}_r is the length- S observation vector ($S = 3$ for the three components). Covariates occupy the

length- Q vector \mathbf{x}'_r , including species traits and environmental conditions. Responses to covariates are included in the $Q \times S$ matrix of coefficients β . The latent variable has the mean vector $\mathbf{x}'_r\beta$ and $S \times S$ covariance matrix Σ . The product including indicator functions $I(\cdot)$ allows for negative values on the latent scale, essentially a multivariate Tobit⁽⁷⁷⁾.

Model fitting with GJAM included phylogeny as random groups (previous section). Variable selection was done using Deviance Information Criterion (DIC) as the criterion for additional predictors in the model. Volatility (response) and seed mass (covariates) were modeled on the log (proportionate) scale. Dispersal and pollination modes were included as factors. Standardized coefficients β was summarized using the posterior median, 90%, and 95% credible intervals from the MCMC chains. GJAM fitting is open-access with R package GJAM on CRAN.

Data availability

Seed production data are available at the Duke Data Repository <https://doi.org/10.7924/r4348ph5t>. Species traits are downloaded from TRY Plant Trait database at <https://www.try-db.org/TryWeb/Home.php>. Cation exchange capacity data are obtained at <https://soilgrids.org/>. Climate data are extracted from Terraclimate at <http://www.climatologylab.org/> and CHELSA at <https://chelsa-climate.org/>.

Code availability

R statistical software v4.0.2 was used in this work. All analyses used published R packages, with details stated in the section Methods. MASTIF includes code in R and C++, which is published on CRAN at <https://cran.r-project.org/web/packages/mastif/index.html>.

Acknowledgements

For access to sites and logistical support we thank the National Ecological Observatory Network (NEON). The project has been funded continuously since 1992 by National Science Foundation grants to J.S.C, 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*). T.Q. acknowledges the support from the start-up funds provided by Pennsylvania State University. Puerto Rico data were funded by NSF grants to M.U., 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 to M.S. Additional funding to M.Z. came from the W. Szafer Institute of Botany of the Polish Academy of Sciences and the Polish National Science Foundation (2019/33/B/NZ8/0134). M.B. was supported by Polish National Agency for Academic Exchange Bekker programme PPN/BEK/2020/1/00009/U/00001. FRS was supported by FEDER 2014-2020 and Consejería de Economía, Conocimiento, Empresas y Universidad of Junta de Andalucía (grant US-1381388). Jerry Franklin's data remain accessible through NSF LTER DEB-1440409. USDA Forest Service and USGS research was funded by those agencies. Any use of trade, firm, or product names does not imply endorsement by the U.S. Government.

Author contributions statement

J.S.C and T.Q. designed the study, performed analyses, and wrote the paper. J.S.C. compiled the MASTIF data and wrote the MASTIF model and software. M.B, B.C., V.J, and G.K. co-wrote the paper. T.Q, M.A, D.A, Y.B, M.B, T.B, R.B, T.C, M.C, R.C, S.C, J.J.C, C.C, J.C, F.C, B.C, A.C, A.J.D, N.D, S.D, M.D, L.D, J.E, T.J.F, W.F, J.F.F, C.A.G, G.S.G, G.G, C.H.G, A.G, Q.G, A.H, A.H, Q.H, J.H, K.H, I.I, J.F.J, V.J, T.K, J.M.K, G.K, H.K, J.G.L, J.M.L, F.L, T.L, J.L, J.A.L, D.M, A.M, E.J.M, C.M.M, E.M, R.M, J.A.M, T.A.N, S.N, M.N, M.O, R.P, I.S.P, I.M.P, L.P, T.P, J.P, M.D.R, C.D.R, K.C.R, F.R, P.S, J.D.S, C.L.S, B.S, S.S, M.S, M.S, M.A.S, N.L.S, J.N.S, S.S, J.J.S, M.S, P.A.T, M.U, G.V, A.V.W, T.G.W, A.P.W, S.J.W, K.Z, J.K.Z, M.Z, J.S.C contributed data and revised the paper.

465 Competing interests statement

466 The authors declare no competing interests.

467 Figure caption

468 **Fig. 1: Illustration of three masting components** for *Pinus monticola* and *Abies grandis* from the
469 central Cascades, U.S.A. Crop counts for these species (a, b) vary between individual trees, and they
470 drift over time. The frequency of counts (c) in both species shows that zeros dominate, and there is no
471 threshold that could be used to define masting events. *A. grandis* shows higher synchronicity between
472 individuals (mean pairwise correlations between trees and their standard deviations are shown in d)
473 and higher volatility, especially concentrated at the 2-yr period (e). *P. monticola* also shows variance
474 concentrated at 2-yr, with a secondary peak at 3.4 yr. The (volatility, period) for this example are shown
475 beneath species names in (e).

476 **Fig. 2: Hypothesized effects (a) and summary of results (b)** of mutualists (green), resources
477 (blue), and climate (red) on the three masting components. Arrows with + and - represent positive
478 and negative effects, respectively. We expect tree species with low volatility, short periodicity, and low
479 synchronicity benefit most from their mutualist pollinators and dispersers (a). Resources reduce volatil-
480 ity and periodicity (a). High temperature decreases volatility while promoting synchronicity (a). Dry
481 sites (deficit) have higher volatility and synchronicity than wet sites (a). The summary of results in (b)
482 comes from the joint model in [fig. 3](#). Dashed lines indicate that 90% credible intervals contain zero.

483 **Fig. 3: Variables that contribute to the joint response of masting components** including
484 volatility (a), periodicity (b), and synchronicity (c) at ecoregion-species scales. Predictors include verte-
485 brate dispersers (animal seed dispersal (AD), animal pollination (AP)), resources (soil cation exchange
486 capacity (CEC), foliar P (FP), and foliar N:P ratio (FNP)), seed mass (SM), and climate (accumulated
487 moisture deficit (Def, ranging from wet to dry) and mean annual temperature (Temp, ranging from cold
488 to warm)). Dispersal and pollination syndromes are included as two-level factors, so the negative coeffi-
489 cients for animal seed dispersal (AD) and pollination (AP) have as mirror images the (positive) effects
490 of wind dispersal and pollination. The analysis accounts for phylogeny as a random effect (Methods).
491 Marginal posterior distributions are shown as boxes that contain median vertical lines and are bounded
492 by 68% credible intervals (CI), with 95% CI whiskers. Colors highlight different variable types, with
493 opacity increasing from 90% to 95% of the distribution outside of zero. Variables included in the model
494 were based on the lowest Deviance Information Criterion (DIC). Coefficients are on the standard deviation
495 scale for predictors and the correlation scale for responses (Methods). Results are summarized in
496 [fig. 2b](#) to compare with hypotheses.

497 **Fig. 4: Quasi-synchronicity at individual and species level** a) Correlations between every pair
498 of trees of the same species within 1 km show a mode near one, but a broad range. b) Species average
499 correlations are concentrated near zero (red), but fecundity-weighted correlations are substantially higher
500 (blue) (Methods).

501 **Fig. 5: Volatility, dispersal mode, climate anomalies, and foliar N:P.** Each point locates species
502 volatility (variability between years on log scales) with its coefficients to climatic anomalies in moisture
503 deficit (panel a and c) and temperature (panel b and d). Coefficients were obtained from the fitted
504 model (see methods). Overall sensitivity with no grouping by dispersal/pollination syndromes is shown
505 as absolute values in the above panel (a, b); and with their signs in the below panel (c, d). The mean
506 temperature from the previous year and accumulated moisture deficit from both the previous and current
507 year were used to calculate anomalies. Symbol size scales with foliar N:P ratio. “Both animal” species
508 (orange) have both pollen and seeds dispersed by animals. “Animal/wind” species (green) have either
509 pollen or seeds dispersed by animals. High volatility is associated with positive responses to moisture
510 deficit (c) and temperature (d) in animal-dispersed species, but generally declining absolute sensitivity
511 to both variables (a and b). Loess regressions on parameter estimates (dots), weighted by the standard
512 errors of the estimate (error bars), summarize trends with their confidence intervals (the colored shades)
513 in absolute sensitivity (a, b) and for the three dispersal groups (c, d).

514 **Fig. 6: Phylogenetic coherence in the three masting components.** (a) Volatility (on log scale)
515 has a phylogeny component (*Pagel's* $\lambda = 0.83$, $p < 10^{-9}$, $n = 394$). (b) Quasi-periodicity (left) exhibits
516 a weaker phylogenetic coherence compared to volatility (*Pagel's* $\lambda = 0.52$, $p = 0.0023$, $n = 142$). Quasi-
517 synchronicity (right) shows the weakest signal (*Pagel's* $\lambda = 0.21$, $p = 0.0064$, $n = 142$). Species with
518 volatility of at least 0.94 (62.5% quantile) are shown in (b) because periodicity becomes noisy and less
519 meaningful at low level of volatility.

References

- [1] D. H. Janzen, “Seed predation by animals,” *Annual Review of Ecology and Systematics*, vol. 2, no. 1, pp. 465–492, 1971.
- [2] D. Kelly and V. L. Sork, “Mast seeding in perennial plants: Why, how, where?,” *Annual Review of Ecology and Systematics*, vol. 33, no. 1, pp. 427–447, 2002.
- [3] P. A. Jansen, F. Bongers, and L. Hemerik, “Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent,” *Ecological Monographs*, vol. 74, no. 4, pp. 569–589, 2004.
- [4] C. M. Herrera, P. Jordano, J. Guitian, and A. Traveset, “Annual variability in seed production by woody plants and the masting concept: Reassessment of principles and relationship to pollination and seed dispersal,” *American Naturalist*, vol. 152, no. 4, pp. 576–594, 1998.
- [5] A. M. Siepielski and C. W. Benkman, “Conflicting selection from an antagonist and a mutualist enhances phenotypic variation in a plant,” *Evolution*, vol. 64, no. 4, pp. 1120–1128, 2010.
- [6] Y. Y. Wang, J. Zhang, J. M. LaMontagne, F. Lin, B. H. Li, J. Ye, Z. Q. Yuan, X. G. Wang, and Z. Q. Hao, “Variation and synchrony of tree species mast seeding in an old-growth temperate forest,” *Journal of Vegetation Science*, vol. 28, no. 2, pp. 413–423, 2017.
- [7] L. Huang, C. Jin, L. Zhou, K. Song, S. Qian, D. Lin, L. Zhao, B. Chen, E. Yan, R. Michalet, and Y. Yang, “Benefit versus cost trade-offs of masting across seed-to-seedling transition for a dominant subtropical forest species,” *Journal of Ecology*, vol. 109, no. 8, pp. 3087–3098, 2021.
- [8] B. Seget, M. Bogdziewicz, J. Holeksa, M. Ledwon, F. Milne-Rostkowska, L. Piechnik, A. Rzepczak, and M. Zywiec, “Costs and benefits of masting: economies of scale are not reduced by negative density-dependence in seedling survival in sorbus aucuparia,” *New Phytologist*, vol. 233, no. 4, pp. 1931–1938, 2022.
- [9] J. S. Clark, C. Nunez, and B. Tomasek, “Foodwebs based on unreliable foundations: spatiotemporal masting merged with consumer movement, storage, and diet,” *Ecological Monographs*, vol. 89, no. 4, p. e01381, 2019.
- [10] D. Janzen, “Herbivores and the number of tree species in tropical forests,” *The American Naturalist*, vol. 104, no. 940, pp. 501–528, 1970.
- [11] E. D. Clotfelter, A. B. Pedersen, J. A. Cranford, N. Ram, E. A. Snajdr, V. Nolan, and E. D. Ketterson, “Acorn mast drives long-term dynamics of rodent and songbird populations,” *Oecologia*, vol. 154, no. 3, pp. 493–503, 2007.
- [12] W. Chen, J. Zhong, W. P. Carson, Z. Tang, Z. Xie, S. Sun, and Y. Zhou, “Proximity to roads disrupts rodents’ contributions to seed dispersal services and subsequent recruitment dynamics,” *Journal of Ecology*, vol. 107, no. 6, pp. 2623–2634, 2019.
- [13] L. M. Curran and M. Leighton, “Vertebrate responses to spatiotemporal variation in seed production of mast-fruited dipterocarpaceae,” *Ecological Monographs*, vol. 70, no. 1, pp. 101–128, 2000.
- [14] I. S. Pearse, J. M. LaMontagne, M. Lordon, A. L. Hipp, and W. D. Koenig, “Biogeography and phylogeny of masting: do global patterns fit functional hypotheses?,” *New Phytologist*, vol. 227, no. 5, pp. 1557–1567, 2020.
- [15] C. H. Greenberg, “Individual variation in acorn production by five species of southern appalachian oaks,” *Forest Ecology and Management*, vol. 132, no. 2, pp. 199–210, 2000.
- [16] J. S. Clark, S. LaDeau, and I. Ibanez, “Fecundity of trees and the colonization-competition hypothesis,” *Ecological Monographs*, vol. 74, no. 3, pp. 415–442, 2004.
- [17] X. Chen, D. G. Brockway, and Q. Guo, “Characterizing the dynamics of cone production for longleaf pine forests in the southeastern united states,” *Forest Ecology and Management*, vol. 429, pp. 1–6, 2018.

- 565 [18] Z. Pucek, W. Jedrzejewski, B. Jedrzejewska, and M. Pucek, “Rodent population-dynamics in a
566 primeval deciduous forest (bialowieza-national-park) in relation to weather, seed crop, and preda-
567 tion,” *Acta Theriologica*, vol. 38, no. 2, pp. 199–232, 1993.
- 568 [19] M. Bogdziewicz, R. Zwolak, and E. E. Crone, “How do vertebrates respond to mast seeding?,”
569 *Oikos*, vol. 125, no. 3, pp. 300–307, 2016.
- 570 [20] K. M. Christensen and T. G. Whitham, “Impact of insect herbivores on competition between birds
571 and mammals for pinyon pine seeds,” *Ecology*, vol. 74, no. 8, pp. 2270–2278, 1993.
- 572 [21] E. E. Crone and J. M. Rapp, “Resource depletion, pollen coupling, and the ecology of mast seeding,”
573 *Year in Ecology and Conservation Biology*, vol. 1322, pp. 21–34, 2014.
- 574 [22] M. A. Steele and X. Yi, “Squirrel-seed interactions: The evolutionary strategies and impact of
575 squirrels as both seed predators and seed dispersers,” *Frontiers in Ecology and Evolution*, vol. 8,
576 no. 259, 2020.
- 577 [23] I. S. Pearse, W. D. Koenig, and D. Kelly, “Mechanisms of mast seeding: resources, weather, cues,
578 and selection,” *New Phytologist*, vol. 212, no. 3, pp. 546–562, 2016.
- 579 [24] D. H. Janzen, “Tropical blackwater rivers, animals, and mast fruiting by the dipterocarpaceae,”
580 *Biotropica*, pp. 69–103, 1974.
- 581 [25] S. J. Smaill, P. W. Clinton, R. B. Allen, and M. R. Davis, “Climate cues and resources interact to
582 determine seed production by a masting species,” *Journal of Ecology*, vol. 99, no. 3, pp. 870–877,
583 2011.
- 584 [26] A. J. Tanentzap, W. G. Lee, and D. A. Coomes, “Soil nutrient supply modulates temperature-
585 induction cues in mast-seeding grasses,” *Ecology*, vol. 93, no. 3, pp. 462–469, 2012.
- 586 [27] M. Fernández-Martínez, I. Pearse, J. Sardans, F. Sayol, W. D. Koenig, J. M. LaMontagne,
587 M. Bogdziewicz, A. Collalti, A. Hacket-Pain, G. Vacchiano, J. M. Espelta, J. Peñuelas, and I. A.
588 Janssens, “Nutrient scarcity as a selective pressure for mast seeding,” *Nature Plants*, vol. 5, no. 12,
589 pp. 1222–1228, 2019.
- 590 [28] R. C. Rosecrance, S. A. Weinbaum, and P. H. Brown, “Alternate bearing affects nitrogen, phospho-
591 rus, potassium and starch storage pools in mature pistachio trees,” *Annals of Botany*, vol. 82, no. 4,
592 pp. 463–470, 1998.
- 593 [29] A. Sala, K. Hopping, E. J. B. McIntire, S. Delzon, and E. E. Crone, “Masting in whitebark pine
594 (*Pinus albicaulis*) depletes stored nutrients,” *New Phytologist*, vol. 196, no. 1, pp. 189–199, 2012.
- 595 [30] V. L. Sork, “Evolutionary ecology of mast-seeding in temperate and tropical oaks (*Quercus* spp.),”
596 *Vegetatio*, vol. 107, no. 1, pp. 133–147, 1993.
- 597 [31] A. Sharma, D. C. Weindorf, D. D. Wang, and S. Chakraborty, “Characterizing soils via portable x-
598 ray fluorescence spectrometer: 4. cation exchange capacity (cec),” *Geoderma*, vol. 239, pp. 130–134,
599 2015.
- 600 [32] P. Hazelton and B. Murphy, *Interpreting soil test results: What do all the numbers mean?* CSIRO
601 publishing, 2016.
- 602 [33] J. J. Elser, K. Acharya, M. Kyle, J. Cotner, W. Makino, T. Markow, T. Watts, S. Hobbie, W. Fagan,
603 J. Schade, J. Hood, and R. W. Sterner, “Growth rate–stoichiometry couplings in diverse biota,”
604 *Ecology Letters*, vol. 6, no. 10, pp. 936–943, 2003.
- 605 [34] D. Kelly, A. Geldenhuis, A. James, E. Penelope Holland, M. J. Plank, R. E. Brockie, P. E. Cowan,
606 G. A. Harper, W. G. Lee, M. J. Maitland, A. F. Mark, J. A. Mills, P. R. Wilson, and A. E. Byrom,
607 “Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change,”
608 *Ecology Letters*, vol. 16, no. 1, pp. 90–98, 2013.
- 609 [35] E. M. Schaubert, D. Kelly, P. Turchin, C. Simon, W. G. Lee, R. B. Allen, I. J. Payton, P. R. Wilson,
610 P. E. Cowan, and R. E. Brockie, “Masting by eighteen new Zealand plant species: The role of
611 temperature as a synchronizing cue,” *Ecology*, vol. 83, no. 5, pp. 1214–1225, 2002.

- 612 [36] J. M. Espelta, P. Cortés, R. Molowny-Horas, B. Sánchez-Humanes, and J. Retana, “Masting mediated by summer drought reduces acorn predation in mediterranean oak forests,” *Ecology*, vol. 89, 613 no. 3, pp. 805–817, 2008.
- 615 [37] I. M. Pérez-Ramos, J. M. Ourcival, J. M. Limousin, and S. Rambal, “Mast seeding under increasing 616 drought: results from a long-term data set and from a rainfall exclusion experiment,” *Ecology*, 617 vol. 91, no. 10, pp. 3057–3068, 2010.
- 618 [38] W. D. Koenig, J. M. H. Knops, W. J. Carmen, and I. S. Pearse, “What drives masting? the 619 phenological synchrony hypothesis,” *Ecology*, vol. 96, no. 1, pp. 184–192, 2015.
- 620 [39] A. P. Wion, P. J. Weisberg, I. S. Pearse, and M. D. Redmond, “Aridity drives spatiotemporal 621 patterns of masting across the latitudinal range of a dryland conifer,” *Ecography*, vol. 43, no. 4, 622 pp. 569–580, 2020.
- 623 [40] J. M. LaMontagne, I. S. Pearse, D. F. Greene, and W. D. Koenig, “Mast seeding patterns are 624 asynchronous at a continental scale,” *Nature Plants*, vol. 6, no. 5, pp. 460–465, 2020.
- 625 [41] G. Vacchiano, A. Hacket-Pain, M. Turco, R. Motta, J. Maringer, M. Conedera, I. Drobyshev, and 626 D. Ascoli, “Spatial patterns and broad-scale weather cues of beech mast seeding in europe,” *New 627 Phytologist*, vol. 215, no. 2, pp. 595–608, 2017.
- 628 [42] J. S. Clark, D. M. Bell, M. C. Kwit, and K. Zhu, “Competition-interaction landscapes for the joint 629 response of forests to climate change,” *Glob Chang Biol*, vol. 20, no. 6, pp. 1979–91, 2014.
- 630 [43] J. M. Lamontagne and S. Boutin, “Local-scale synchrony and variability in mast seed production 631 patterns of picea glauca,” *Journal of Ecology*, vol. 95, no. 5, pp. 991–1000, 2007.
- 632 [44] J. N. Straub, A. G. Leach, R. M. Kaminski, A. W. Ezell, and T. D. Leininger, “Red oak acorn 633 yields in green-tree reservoirs and non-impounded forests in mississippi,” *Wildlife Society Bulletin*, 634 vol. 43, no. 3, pp. 491–499, 2019.
- 635 [45] D. Ascoli, G. Vacchiano, M. Turco, M. Conedera, I. Drobyshev, J. Maringer, R. Motta, and 636 A. Hacket-Pain, “Inter-annual and decadal changes in teleconnections drive continental-scale syn- 637 chronization of tree reproduction,” *Nature Communications*, vol. 8, 2017.
- 638 [46] A. J. Hacket-Pain, A. D. Friend, J. G. Lagueard, and P. A. Thomas, “The influence of masting 639 phenomenon on growth–climate relationships in trees: explaining the influence of previous summers’ 640 climate on ring width,” *Tree Physiology*, vol. 35, no. 3, pp. 319–330, 2015.
- 641 [47] A. B. Berdanier and J. S. Clark, “Divergent reproductive allocation trade-offs with canopy exposure 642 across tree species in temperate forests,” *Ecosphere*, vol. 7, no. 6, pp. e01313–n/a, 2016.
- 643 [48] M. D. Redmond, F. Forcella, and N. N. Barger, “Declines in pinyon pine cone production associated 644 with regional warming,” *Ecosphere*, vol. 3, no. 12, p. art120, 2012.
- 645 [49] A. V. Whipple, N. S. Cobb, C. A. Gehring, S. Mopper, L. Flores-Rentería, and T. G. Whitham, 646 “Long-term studies reveal differential responses to climate change for trees under soil- or herbivore- 647 related stress,” *Frontiers in Plant Science*, vol. 10, no. 132, 2019.
- 648 [50] M. Bogdziewicz, D. Kelly, P. A. Thomas, J. G. A. Lagueard, and A. Hacket-Pain, “Climate warming 649 disrupts mast seeding and its fitness benefits in european beech,” *Nature Plants*, vol. 6, no. 2, 650 pp. 88–94, 2020.
- 651 [51] J. M. Espelta, R. Bonal, and B. Sanchez-Humanes, “Pre-dispersal acorn predation in mixed oak 652 forests: interspecific differences are driven by the interplay among seed phenology, seed size and 653 predator size,” *Journal of Ecology*, vol. 97, no. 6, pp. 1416–1423, 2009.
- 654 [52] A. Yamauchi, “Theory of mast reproduction in plants: Storage-size dependent strategy,” *Evolution*, 655 vol. 50, no. 5, pp. 1795–1807, 1996.
- 656 [53] W. D. Koenig and J. M. H. Knops, “The mystery of masting in trees: Some trees reproduce 657 synchronously over large areas, with widespread ecological effects, but how and why?,” *American 658 Scientist*, vol. 93, no. 4, pp. 340–347, 2005.

- 659 [54] J. M. LaMontagne and S. Boutin, “Quantitative methods for defining mast-seeding years across
660 species and studies,” *Journal of Vegetation Science*, vol. 20, no. 4, pp. 745–753, 2009.
- 661 [55] J. S. Clark, “Individuals and the variation needed for high species diversity in forest trees,” *Science*,
662 vol. 327, no. 5969, pp. 1129–1132, 2010.
- 663 [56] M. Shibata, T. Masaki, T. Yagihashi, T. Shimada, and T. Saitoh, “Decadal changes in masting
664 behaviour of oak trees with rising temperature,” *Journal of Ecology*, vol. 108, no. 3, pp. 1088–1100,
665 2020.
- 666 [57] J. S. Clark, R. Andrus, M. Aubry-Kientz, Y. Bergeron, M. Bogdziewicz, D. C. Bragg, D. Brockway,
667 N. L. Cleavitt, S. Cohen, B. Courbaud, R. Daley, A. J. Das, M. Dietze, T. J. Fahey, I. Fer, J. F.
668 Franklin, C. A. Gehring, G. S. Gilbert, C. H. Greenberg, Q. Guo, J. HilleRisLambers, I. Ibanez,
669 J. Johnstone, C. L. Kilner, J. Knops, W. D. Koenig, G. Kunstler, J. M. LaMontagne, K. L. Legg,
670 J. Luongo, J. A. Lutz, D. Macias, E. J. B. McIntire, Y. Messaoud, C. M. Moore, E. Moran, J. A. My-
671 ers, O. B. Myers, C. Nunez, R. Parmenter, S. Pearse, S. Pearson, R. Poulton-Kamakura, E. Ready,
672 M. D. Redmond, C. D. Reid, K. C. Rodman, C. L. Scher, W. H. Schlesinger, A. M. Schwantes,
673 E. Shanahan, S. Sharma, M. A. Steele, N. L. Stephenson, S. Sutton, J. J. Swenson, M. Swift, T. T.
674 Veblen, A. V. Whipple, T. G. Whitham, A. P. Wion, K. Zhu, and R. Zlotin, “Continent-wide tree
675 fecundity driven by indirect climate effects,” *Nature Communications*, vol. 12, no. 1, p. 1242, 2021.
- 676 [58] T. Qiu, R. Andrus, M.-C. Aravena, D. Ascoli, Y. Bergeron, R. Berretti, D. Berveiller,
677 M. Bogdziewicz, T. Boivin, R. Bonal, D. C. Bragg, T. Caignard, R. Calama, J. J. Camarero,
678 C.-H. Chang-Yang, N. L. Cleavitt, B. Courbaud, F. Courbet, T. Curt, A. J. Das, E. Daskalakou,
679 H. Davi, N. Delpierre, S. Delzon, M. Dietze, S. D. Calderon, L. Dormont, J. Espelta, T. J. Fahey,
680 W. Farfan-Rios, C. A. Gehring, G. S. Gilbert, G. Gratzer, C. H. Greenberg, Q. Guo, A. Hacket-
681 Pain, A. Hampe, Q. Han, J. Hille Ris Lambers, K. Hoshizaki, I. Ibanez, J. F. Johnstone, V. Journé,
682 D. Kabeya, C. L. Kilner, T. Kitzberger, J. M. H. Knops, R. K. Kobe, G. Kunstler, J. G. A. Lageard,
683 J. M. LaMontagne, M. Ledwon, F. Lefevre, T. Leininger, J.-M. Limousin, J. A. Lutz, D. Macias,
684 E. J. B. McIntire, C. M. Moore, E. Moran, R. Motta, J. A. Myers, T. A. Nagel, K. Noguchi,
685 J.-M. Ourcival, R. Parmenter, I. S. Pearse, I. M. Perez-Ramos, L. Piechnik, J. Poulsen, R. Poulton-
686 Kamakura, M. D. Redmond, C. D. Reid, K. C. Rodman, F. Rodriguez-Sanchez, J. D. Sanguinetti,
687 C. L. Scher, W. H. Schlesinger, H. Schmidt Van Marle, B. Seget, S. Sharma, M. Silman, M. A.
688 Steele, N. L. Stephenson, J. N. Straub, I. F. Sun, S. Sutton, J. J. Swenson, M. Swift, P. A. Thomas,
689 M. Uriarte, G. Vacchiano, T. T. Veblen, A. V. Whipple, T. G. Whitham, A. P. Wion, B. Wright, S. J.
690 Wright, K. Zhu, J. K. Zimmerman, *et al.*, “Limits to reproduction and seed size-number trade-offs
691 that shape forest dominance and future recovery,” *Nature Communications*, vol. 13, no. 1, p. 2381,
692 2022.
- 693 [59] S. B. Vander Wall, “How plants manipulate the scatter-hoarding behaviour of seed-dispersing an-
694 imals,” *Philosophical Transactions of the Royal Society B: Biological Sciences*, vol. 365, no. 1542,
695 pp. 989–997, 2010.
- 696 [60] R. Zwolak, M. Bogdziewicz, A. Wrobel, and E. E. Crone, “Advantages of masting in european
697 beech: timing of granivore satiation and benefits of seed caching support the predator dispersal
698 hypothesis,” *Oecologia*, vol. 180, no. 3, pp. 749–758, 2016.
- 699 [61] C. Larue, E. Austruy, G. Basset, and R. J. Petit, “Revisiting pollination mode in chestnut (*castanea*
700 spp.): an integrated approach,” *Botany Letters*, vol. 168, no. 3, pp. 348–372, 2021.
- 701 [62] G. Garcia, B. Re, C. Orians, and E. Crone, “By wind or wing: pollination syndromes and alter-
702 nate bearing in horticultural systems,” *Philosophical Transactions of the Royal Society B*, vol. 376,
703 no. 1839, p. 20200371, 2021.
- 704 [63] V. Journe, R. Andrus, M.-C. Aravena, D. Ascoli, R. Berretti, D. Berveiller, M. Bogdziewicz,
705 T. Boivin, R. Bonal, T. Caignard, R. Calama, J. J. Camarero, C.-H. Chang-Yang, B. Courbaud,
706 F. Courbet, T. Curt, A. J. Das, E. Daskalakou, H. Davi, N. Delpierre, S. Delzon, M. Dietze,
707 S. Donoso Calderon, L. Dormont, J. Maria Espelta, T. J. Fahey, W. Farfan-Rios, C. A. Gehring,
708 G. S. Gilbert, G. Gratzer, C. H. Greenberg, Q. Guo, A. Hacket-Pain, A. Hampe, Q. Han, J. H. R.
709 Lambers, K. Hoshizaki, I. Ibanez, J. F. Johnstone, D. Kabeya, R. Kays, T. Kitzberger, J. M. H.
710 Knops, R. K. Kobe, G. Kunstler, J. G. A. Lageard, J. M. LaMontagne, T. Leininger, J.-M. Limousin,

- 711 J. A. Lutz, D. Macias, E. J. B. McIntire, C. M. Moore, E. Moran, R. Motta, J. A. Myers, T. A. Nagel,
712 K. Noguchi, J.-M. Ourcival, R. Parmenter, I. S. Pearse, I. M. Perez-Ramos, L. Piechnik, J. Poulsen,
713 R. Poulton-Kamakura, T. Qiu, M. D. Redmond, C. D. Reid, K. C. Rodman, F. Rodriguez-Sanchez,
714 J. D. Sanguinetti, C. L. Scher, H. S. V. Marle, B. Seget, S. Sharma, M. Silman, M. A. Steele,
715 N. L. Stephenson, J. N. Straub, J. J. Swenson, M. Swift, P. A. Thomas, M. Uriarte, G. Vacchiano,
716 T. T. Veblen, A. V. Whipple, T. G. Whitham, B. Wright, S. J. Wright, K. Zhu, J. K. Zimmerman,
717 R. Zlotin, M. Zywiec, and J. S. Clark, “Globally, tree fecundity exceeds productivity gradients,”
718 *Ecology Letters*, vol. n/a, no. n/a, 2022.
- 719 [64] C. C. Smith, J. L. Hamrick, and C. L. Kramer, “The advantage of mast years for wind pollination,”
720 *The American Naturalist*, vol. 136, no. 2, pp. 154–166, 1990.
- 721 [65] C. K. Augspurger, “Reproductive synchrony of a tropical shrub: Experimental studies on effects
722 of pollinators and seed predators in *hybanthus prunifolius* (violaceae),” *Ecology*, vol. 62, no. 3,
723 pp. 775–788, 1981.
- 724 [66] E. E. Crone, “Responses of social and solitary bees to pulsed floral resources,” *The American*
725 *Naturalist*, vol. 182, no. 4, pp. 465–473, 2013.
- 726 [67] W. D. Koenig, D. Kelly, V. L. Sork, R. P. Duncan, J. S. Elkinton, M. S. Peltonen, and R. D.
727 Westfall, “Dissecting components of population-level variation in seed production and the evolution
728 of masting behavior,” *Oikos*, vol. 102, no. 3, pp. 581–591, 2003.
- 729 [68] A. Satake and D. Kelly, “Studying the genetic basis of masting,” *Philosophical Transactions of the*
730 *Royal Society B*, vol. 376, no. 1839, p. 20210116, 2021.
- 731 [69] R. C. Mueller, B. D. Wade, C. A. Gehring, and T. G. Whitham, “Chronic herbivory negatively
732 impacts cone and seed production, seed quality and seedling growth of susceptible pinyon pines,”
733 *Oecologia*, vol. 143, no. 4, pp. 558–565, 2005.
- 734 [70] C. S. Schopmeyer *et al.*, “Seeds of woody plants in the united states.,” *Seeds of woody plants in the*
735 *United States.*, no. 450, 1974.
- 736 [71] M. J. Crawley and C. R. Long, “Alternate bearing, predator satiation and seedling recruitment in
737 *quercus robur* l.,” *Journal of Ecology*, vol. 83, no. 4, pp. 683–696, 1995.
- 738 [72] R. H. Manson, R. S. Ostfeld, and C. D. Canham, “The effects of tree seed and seedling density on
739 predation rates by rodents in old fields,” *Écoscience*, vol. 5, no. 2, pp. 183–190, 1998.
- 740 [73] R. Zwolak, P. Celebias, and M. Bogdziewicz, “Global patterns in the predator satiation effect of
741 masting: A meta-analysis,” *Proceedings of the National Academy of Sciences*, vol. 119, no. 11,
742 p. e2105655119, 2022.
- 743 [74] J. Bascompte, “Mutualistic networks,” *Frontiers in Ecology and the Environment*, vol. 7, no. 8,
744 pp. 429–436, 2009.
- 745 [75] J. S. Clark, M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers, “Seed dispersal near and far:
746 Patterns across temperate and tropical forests,” *Ecology*, vol. 80, no. 5, pp. 1475–1494, 1999.
- 747 [76] J. Tobin, “Estimation of relationships for limited dependent variables,” *Econometrica*, vol. 26, no. 1,
748 pp. 24–36, 1958.
- 749 [77] J. S. Clark, D. Nemergut, B. Seyednasrollah, P. J. Turner, and S. Zhang, “Generalized joint at-
750 tribute modeling for biodiversity analysis: median-zero, multivariate, multifarious data,” *Ecological*
751 *Monographs*, vol. 87, no. 1, pp. 34–56, 2017.
- 752 [78] D. M. Olson, E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. Powell, E. C. Underwood,
753 J. A. D’amico, I. Itoua, H. E. Strand, J. C. Morrison, *et al.*, “Terrestrial ecoregions of the world: A
754 new map of life on earth a new global map of terrestrial ecoregions provides an innovative tool for
755 conserving biodiversity,” *BioScience*, vol. 51, no. 11, pp. 933–938, 2001.

- 756 [79] A. E. Zanne, D. C. Tank, W. K. Cornwell, J. M. Eastman, S. A. Smith, R. G. FitzJohn, D. J.
757 McGlinn, B. C. O'Meara, A. T. Moles, P. B. Reich, D. L. Royer, D. E. Soltis, P. F. Stevens,
758 M. Westoby, I. J. Wright, L. Aarssen, R. I. Bertin, A. Calaminus, R. Govaerts, F. Hemmings, M. R.
759 Leishman, J. Oleksyn, P. S. Soltis, N. G. Swenson, L. Warman, and J. M. Beaulieu, "Three keys
760 to the radiation of angiosperms into freezing environments," *Nature*, vol. 506, no. 7486, pp. 89–92,
761 2014.
- 762 [80] L. J. Revell, "phytools: an r package for phylogenetic comparative biology (and other things),"
763 *Methods in Ecology and Evolution*, vol. 3, no. 2, pp. 217–223, 2012.
- 764 [81] R. Freckleton, P. P. Harvey, H. and M. Pagel, "Phylogenetic analysis and comparative data: A test
765 and review of evidence," *The American Naturalist*, vol. 160, no. 6, pp. 712–726, 2002.
- 766 [82] J. D. Hadfield and S. Nakagawa, "General quantitative genetic methods for comparative biology:
767 phylogenies, taxonomies and multi-trait models for continuous and categorical characters," *Journal*
768 *of Evolutionary Biology*, vol. 23, no. 3, pp. 494–508, 2010.
- 769 [83] J. Kattge, G. Boenisch, S. Diaz, S. Lavorel, I. C. Prentice, P. Leadley, S. Tautenhahn, G. D. A.
770 Werner, T. Aakala, M. Abedi, A. T. R. Acosta, G. C. Adamidis, K. Adamson, M. Aiba, C. H.
771 Albert, J. M. Alcantara, C. C. Alcazar, I. Aleixo, H. Ali, B. Amiaud, C. Ammer, M. M. Amoroso,
772 M. Anand, C. Anderson, N. Anten, J. Antos, D. M. G. Apgaua, T.-L. Ashman, D. H. Asmara, G. P.
773 Asner, M. Aspinwall, O. Atkin, I. Aubin, L. Baastrup-Spohr, K. Bahalkeh, M. Bahn, T. Baker,
774 W. J. Baker, J. P. Bakker, D. Baldocchi, J. Baltzer, A. Banerjee, A. Baranger, J. Barlow, D. R.
775 Barneche, Z. Baruch, D. Bastianelli, J. Battles, W. Bauerle, M. Bauters, E. Bazzato, M. Beck-
776 mann, H. Beeckman, C. Beierkuhnlein, R. Bekker, G. Belfry, M. Belluau, M. Beloiu, R. Bena-
777 vides, L. Benomar, M. L. Berdugo-Lattke, E. Berenguer, R. Bergamin, J. Bergmann, M. B. Car-
778 lucci, L. Berner, M. Bernhardt-Roemermann, C. Bigler, A. D. Bjorkman, C. Blackman, C. Blanco,
779 B. Blonder, D. Blumenthal, K. T. Bocanegra-Gonzalez, P. Boeckx, S. Bohlman, K. Boehning-Gaese,
780 L. Boisvert-Marsh, W. Bond, B. Bond-Lamberty, A. Boom, C. C. F. Boonman, K. Bordin, E. H.
781 Boughton, V. Boukili, D. M. J. S. Bowman, S. Bravo, M. R. Brendel, M. R. Broadley, K. A. Brown,
782 H. Bruelheide, F. Brunnich, H. H. Bruun, D. Bruy, S. W. Buchanan, S. F. Bucher, N. Buchmann,
783 R. Buitenwerf, D. E. Bunker, J. Buerger, S. Burrascano, D. F. R. P. Burslem, B. J. Butterfield,
784 C. Byun, M. Marques, M. C. Scalon, M. Caccianiga, M. Cadotte, M. Cailleret, J. Camac, J. Julio Ca-
785 marero, C. Company, G. Campetella, J. A. Campos, L. Cano-Arboleda, R. Canullo, M. Carbognani,
786 F. Carvalho, F. Casanoves, B. Castagneyrol, J. A. Catford, J. Cavender-Bares, B. E. L. Cerabolini,
787 M. Cervellini, E. Chacon-Madrigal, K. Chapin, F. S. Chapin, S. Chelli, S.-C. Chen, A. Chen,
788 P. Cherubini, F. Chianucci, B. Choat, K.-S. Chung, M. Chytry, D. Ciccarelli, L. Coll, C. G. Collins,
789 L. Conti, D. Coomes, J. H. C. Cornelissen, W. K. Cornwell, P. Corona, M. Coyea, J. Craine,
790 D. Craven, J. P. G. M. Croomsigt, A. Csecserits, K. Cufar, M. Cuntz, A. C. da Silva, K. M. Dahlin,
791 M. Dainese, I. Dalke, M. Dalle Fratte, A. T. Dang-Le, J. Danihelka, M. Dannoura, S. Dawson, A. J.
792 de Beer, A. De Frutos, J. R. De Long, B. Dechant, S. Delagrangue, N. Delpierre, G. Derroire, A. S.
793 Dias, M. H. Diaz-Toribio, P. G. Dimitrakopoulos, M. Dobrowolski, D. Doktor, P. Drevojan, N. Dong,
794 J. Dransfield, S. Dressler, L. Duarte, E. Ducouret, S. Dullinger, W. Durka, R. Duursma, O. Dy-
795 mova, A. E-Vojtko, R. L. Eckstein, H. Ejtehadi, J. Elser, T. Emilio, K. Engemann, M. B. Erfanian,
796 A. Erfmeier, A. Esquivel-Muelbert, G. Esser, M. Estiarte, T. F. Domingues, W. F. Fagan, J. Fagun-
797 dez, D. S. Falster, Y. Fan, J. Fang, E. Farris, F. Fazlioglu, Y. Feng, F. Fernandez-Mendez, C. Ferrara,
798 J. Ferreira, A. Fidelis, B. Finegan, J. Firn, T. J. Flowers, D. F. B. Flynn, V. Fontana, E. Forey,
799 C. Forgiarini, L. Francois, M. Frangipani, D. Frank, C. Frenette-Dussault, G. T. Freschet, E. L. Fry,
800 N. M. Fyllas, G. G. Mazzochini, S. Gachet, R. Gallagher, G. Ganade, F. Ganga, P. Garcia-Palacios,
801 V. Gargaglione, E. Garnier, J. Luis Garrido, A. Luis de Gasper, G. Gea-Izquierdo, D. Gibson,
802 A. N. Gillison, A. Giroldo, M.-C. Glasenhardt, S. Gleason, M. Gliesch, E. Goldberg, B. Goedel,
803 E. Gonzalez-Akre, J. L. Gonzalez-Andujar, A. Gonzalez-Melo, A. Gonzalez-Robles, B. J. Graae,
804 E. Granda, S. Graves, W. A. Green, T. Gregor, N. Gross, G. R. Guerin, A. Guenther, A. G. Gutier-
805 rez, L. Haddock, A. Haines, J. Hall, A. Hambuckers, W. Han, S. P. Harrison, W. Hattingh, J. E.
806 Hawes, T. He, P. He, J. M. Heberling, A. Helm, S. Hempel, J. Hentschel, B. Herault, A.-M. Heres,
807 K. Herz, M. Heuertz, T. Hickler, P. Hietz, P. Higuchi, A. L. Hipp, A. Hirons, M. Hock, J. A. Hogan,
808 K. Holl, O. Honnay, D. Hornstein, E. Hou, N. Hough-Snee, K. A. Hovstad, T. Ichie, B. Igic, E. Illa,
809 M. Isaac, M. Ishihara, L. Ivanov, L. Ivanova, C. M. Iversen, J. Izquierdo, R. B. Jackson, B. Jackson,
810 H. Jactel, A. M. Jagodzinski, U. Jandt, S. Jansen, T. Jenkins, A. Jentsch, J. R. P. Jespersen, G.-F.
811 Jiang, J. L. Johansen, D. Johnson, E. J. Jokela, C. A. Joly, G. J. Jordan, G. S. Joseph, D. Junaedi,

812 R. R. Junker, E. Justes, R. Kabzems, J. Kane, Z. Kaplan, T. Kattenborn, L. Kavelenova, E. Kearsley,
813 A. Kempel, T. Kenzo, A. Kerkhoff, M. I. Khalil, N. L. Kinlock, W. D. Kissling, K. Kitajima,
814 T. Kitzberger, R. Kjoller, T. Klein, M. Kleyer, J. Klimesova, J. Klipel, B. Kloeppe, S. Klotz,
815 J. M. H. Knops, T. Kohyama, F. Koike, J. Kollmann, B. Komac, K. Komatsu, C. Koenig, N. J. B.
816 Kraft, K. Kramer, H. Kreft, I. Kuehn, D. Kumarathunge, J. Kuppler, H. Kurokawa, Y. Kurosawa,
817 S. Kuyah, J.-P. Laclau, B. Lafleur, E. Lallai, E. Lamb, A. Lamprecht, D. J. Larkin, D. Laughlin,
818 Y. Le Bagousse-Pinguet, G. le Maire, P. C. le Roux, E. le Roux, T. Lee, F. Lens, S. L. Lewis, B. Lhot-
819 sky, Y. Li, X. Li, J. W. Lichstein, M. Liebergesell, J. Y. Lim, Y.-S. Lin, J. C. Linares, C. Liu, D. Liu,
820 U. Liu, S. Livingstone, J. Llusia, M. Lohbeck, A. Lopez-Garcia, G. Lopez-Gonzalez, Z. Lososova,
821 F. Louault, B. A. Lukacs, P. Lukes, Y. Luo, M. Lussu, S. Ma, C. M. R. Pereira, M. Mack, V. Maire,
822 A. Makela, H. Makinen, A. C. Mendes Malhado, A. Mallik, P. Manning, S. Manzoni, Z. Marchetti,
823 L. Marchino, V. Marcilio-Silva, E. Marcon, M. Marignani, L. Markesteijn, A. Martin, C. Martinez-
824 Garza, J. Martinez-Vilalta, T. Maskova, K. Mason, N. Mason, T. J. Massad, J. Masse, I. Mayrose,
825 J. McCarthy, M. L. McCormack, K. McCulloh, I. R. McFadden, B. J. McGill, M. Y. McPart-
826 land, J. S. Medeiros, B. Medlyn, P. Meerts, Z. Mehrabi, P. Meir, F. P. L. Melo, M. Mencuccini,
827 C. Meredieu, J. Messier, I. Meszaros, J. Metsaranta, S. T. Michaletz, C. Michelaki, S. Migalina,
828 R. Milla, J. E. D. Miller, V. Minden, R. Ming, K. Mokany, A. T. Moles, A. Molnar, V. J. Molofsky,
829 M. Molz, R. A. Montgomery, A. Monty, L. Moravcova, A. Moreno-Martinez, M. Moretti, A. S.
830 Mori, S. Mori, D. Morris, J. Morrison, L. Mucina, S. Mueller, C. D. Muir, S. C. Mueller, F. Munoz,
831 I. H. Myers-Smith, R. W. Myster, M. Nagano, S. Naidu, A. Narayanan, B. Natesan, L. Negoita,
832 A. S. Nelson, E. L. Neuschulz, J. Ni, G. Niedrist, J. Nieto, U. Niinemets, R. Nolan, H. Nottebrock,
833 Y. Nouvellon, A. Novakovskiy, K. O. Nystuen, A. O’Grady, K. O’Hara, A. O’Reilly-Nugent, S. Oak-
834 ley, W. Oberhuber, T. Ohtsuka, R. Oliveira, K. Ollerer, M. E. Olson, V. Onipchenko, Y. Onoda,
835 R. E. Onstein, J. C. Ordonez, N. Osada, I. Ostonen, G. Ottaviani, S. Otto, G. E. Overbeck, W. A.
836 Ozinga, A. T. Pahl, C. E. T. Paine, R. J. Pakeman, A. C. Papageorgiou, E. Parfionova, M. Paertel,
837 M. Patacca, S. Paula, J. Paule, H. Pauli, J. G. Pausas, B. Peco, J. Penuelas, A. Perea, P. Luis Peri,
838 A. C. Petisco-Souza, A. Petraglia, A. M. Petritan, O. L. Phillips, S. Pierce, V. D. Pillar, J. Pisek,
839 A. Pomogaybin, H. Poorter, A. Portsmouth, P. Poschlod, C. Potvin, D. Pounds, A. S. Powell, S. A.
840 Power, A. Prinzing, G. Puglielli, P. Pysek, V. Raevel, A. Rammig, J. Ransijn, C. A. Ray, P. B. Re-
841 ich, M. Reichstein, D. E. B. Reid, M. Rejou-Mechain, V. Resco de Dios, S. Ribeiro, S. Richardson,
842 K. Riibak, M. C. Rillig, F. Riviera, E. M. R. Robert, S. Roberts, B. Robroek, A. Roddy, A. V. Ro-
843 drigues, A. Rogers, E. Rollinson, V. Rolo, C. Roemermann, D. Ronzhina, C. Roscher, J. A. Rosell,
844 M. F. Rosenfield, C. Rossi, D. B. Roy, S. Royer-Tardif, N. Rueger, R. Ruiz-Peinado, S. B. Rumpf,
845 G. M. Rusch, M. Ryo, L. Sack, A. Saldana, B. Salgado-Negret, R. Salguero-Gomez, I. Santa-Regina,
846 A. Carolina Santacruz-Garcia, J. Santos, J. Sardans, B. Schamp, M. Scherer-Lorenzen, M. Schleun-
847 ing, B. Schmid, M. Schmidt, S. Schmitt, J. V. Schneider, S. D. Schowanek, J. Schrader, F. Schrodt,
848 B. Schuldt, F. Schurr, G. Selaya Garvizu, M. Semchenko, C. Seymour, J. C. Sfair, J. M. Sharpe,
849 C. S. Sheppard, S. Sheremetiev, S. Shiodera, B. Shipley, T. A. Shovon, A. Siebenkaes, S. Carlos,
850 V. Silva, M. Silva, T. Sitzia, H. Sjoman, M. Slot, N. G. Smith, D. Sodhi, P. Soltis, D. Soltis,
851 B. Somers, G. Sonnier, M. V. Sorensen, E. E. Sosinski, Jr., N. A. Soudzilovskaia, A. F. Souza,
852 M. Spasojevic, M. G. Sperandii, A. B. Stan, J. Stegen, K. Steinbauer, J. G. Stephan, F. Sterck,
853 D. B. Stojanovic, T. Strydom, M. Laura Suarez, J.-C. Svenning, I. Svitkova, M. Svitok, M. Svo-
854 boda, E. Swaine, N. Swenson, M. Tabarelli, K. Takagi, U. Tappeiner, R. Tarifa, S. Tauougourdeau,
855 C. Tavsanoğlu, M. te Beest, L. Tedersoo, N. Thiffault, D. Thom, E. Thomas, K. Thompson, P. E.
856 Thornton, W. Thuiller, L. Tichy, D. Tissue, M. G. Tjoelker, D. Y. P. Tng, J. Tobias, P. Torok,
857 T. Tarin, J. M. Torres-Ruiz, B. Tothmeresz, M. Treurnicht, V. Trivellone, F. Trolliet, V. Trotsiuk,
858 J. L. Tsakalos, I. Tsiripidis, N. Tysklind, T. Umehara, V. Usoltsev, M. Vadeboncoeur, J. Vaezi,
859 F. Valladares, J. Vamosi, P. M. van Bodegom, M. van Breugel, E. Van Cleemput, M. van de Weg,
860 S. van der Merwe, F. van der Plas, M. T. van der Sande, M. van Kleunen, K. Van Meerbeek,
861 M. Vanderwel, K. A. Vanselow, A. Varhammar, L. Varone, M. Y. Vasquez Valderrama, K. Vassilev,
862 M. Vellend, E. J. Veneklaas, H. Verbeeck, K. Verheyen, A. Vibrans, I. Vieira, J. Villacis, C. Violle,
863 P. Vivek, K. Wagner, M. Waldram, A. Waldron, A. P. Walker, M. Waller, G. Walther, H. Wang,
864 F. Wang, W. Wang, H. Watkins, J. Watkins, U. Weber, J. T. Weedon, L. Wei, P. Weigelt, E. Wei-
865 her, A. W. Wells, C. Wellstein, E. Wenk, M. Westoby, A. Westwood, P. J. White, M. Whitten,
866 M. Williams, D. E. Winkler, K. Winter, C. Womack, I. J. Wright, S. J. Wright, J. Wright, B. X.
867 Pinho, F. Ximenes, T. Yamada, K. Yamaji, R. Yanai, N. Yankov, B. Yguel, K. J. Zanini, A. E.
868 Zanne, D. Zeleny, Y.-P. Zhao, J. Zheng, J. Zheng, K. Zieminska, C. R. Zirbel, G. Zizka, I. C. Zo-
869 Bi, G. Zotz, C. Wirth, and N. Network, “Try plant trait database – enhanced coverage and open

