

UC Santa Cruz

UC Santa Cruz Previously Published Works

Title

Is there tree senescence? The fecundity evidence

Permalink

<https://escholarship.org/uc/item/7qz7v0jj>

Journal

Proceedings of the National Academy of Sciences of the United States of America,
118(34)

ISSN

0027-8424

Authors

Qiu, Tong
Aravena, Marie-Claire
Andrus, Robert
et al.

Publication Date

2021-08-24

DOI

10.1073/pnas.2106130118

Peer reviewed

Is there tree senescence? The fecundity evidence

Tong Qiu^a, Marie-Claire Aravena^b, Robert Andrus^c, Davide Ascoli^d, Yves Bergeron^{e,f}, Roberta Berretti^d, Michal Bogdziewicz^g, Thomas Boivin^h, Raul Bonalⁱ, Thomas Caignard^j, Rafael Calama^k, J. Julio Camarero^l, Connie J. Clark^a, Benoit Courbaud^m, Sylvain Delzonⁱ, Sergio Donoso Calderon^b, William Farfan-Riosⁿ, Catherine A. Gehring^o, Gregory S. Gilbert^p, Cathryn H. Greenberg^q, Qinfeng Guo^r, Janneke Hille Ris Lambers^s, Kazuhiko Hoshizaki^t, Ines Ibanez^u, Valentin Journé^m, Christopher L. Kilner^a, Richard K. Kobe^{v,w}, Walter D. Koenig^x, Georges Kunstler^m, Jalene M. LaMontagne^y, Mateusz Ledwon^z, James A. Lutz^{aa,bb}, Renzo Motta^d, Jonathan A. Myers^{cc}, Thomas A. Nagel^{dd}, Chase L. Nuñez^{ee}, Ian S. Pearse^{ff}, Łukasz Piechnik^{gg}, John R. Poulsen^a, Renata Poulton-Kamakura^a, Miranda D. Redmond^{hh}, Chantal D. Reid^a, Kyle C. Rodmanⁱⁱ, C. Lane Scher^a, Harald Schmidt Van Marle^b, Barbara Seget^{gg}, Shubhi Sharma^a, Miles Silman^{jj}, Jennifer J. Swenson^a, Margaret Swift^a, Maria Uriarte^{kk}, Giorgio Vacchiano^{ll}, Thomas T. Veblen^c, Amy V. Whipple^o, Thomas G. Whitham^o, Andreas P. Wion^{hh}, S. Joseph Wright^{mmm}, Kai Zhu^p, Jess K. Zimmermanⁿⁿ, Magdalena Żywiec^{gg}, and James S. Clark^{a,m,1}

^aNicholas School of the Environment, Duke University, Durham, NC 27708; ^bUniversidad de Chile, Facultad de Ciencias Forestales y de la Conservación de la Naturaleza (FCFCN), La Pintana, 8820808 Santiago, Chile; ^cDepartment of Geography, University of Colorado, Boulder, CO 80309; ^dDepartment of Agriculture, Forest and Food Sciences, University of Torino, 10095 Grugliasco, TO, Italy; ^eForest Research Institute, University of Quebec in Abitibi-Temiscamingue, Rouyn-Noranda, QC J9X 5E4, Canada; ^fDepartment of Biological Sciences, University of Quebec in Abitibi-Temiscamingue, Rouyn-Noranda, QC H2L 2C4, Canada; ^gDepartment of Systematic Zoology, Faculty of Biology, Adam Mickiewicz University, 61-614 Poznań, Poland; ^hInstitut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement (INRAE), Ecologie des Forêts Méditerranéennes, 84000 Avignon, France; ⁱDepartment of Biodiversity, Ecology and Evolution, Complutense University of Madrid, 28040 Madrid, Spain; ^jUniversité Bordeaux, l'Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement (INRAE), Biodiversity, Genes, and Communities (BIOGECO), 33615 Pessac, France; ^kCentro de Investigación Forestal - Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA-CIFOR), 28040 Madrid, Spain; ^lInstituto Pirenaico de Ecología, Consejo Superior de Investigaciones Científicas (IPE-CSIC), 50059 Zaragoza, Spain; ^mUniversité Grenoble Alpes, l'Institut National de Recherche pour l'Agriculture, l'Alimentation et l'Environnement (INRAE), Laboratoire EcoSystèmes et Sociétés En Montagne (LESSEM), 38402 St.-Martin-d'Hères, France; ⁿCenter for Conservation and Sustainable Development, Missouri Botanical Garden, Washington University in Saint Louis, St. Louis, MO 63110; ^oDepartment of Biological Sciences, Northern Arizona University, Flagstaff, AZ 86011; ^pDepartment of Environmental Studies, University of California, Santa Cruz, CA 95064; ^qBent Creek Experimental Forest, US Department of Agriculture Forest Service, Asheville, NC 28801; ^rEastern Forest Environmental Threat Assessment Center, US Department of Agriculture Forest Service, Research Triangle Park, NC 27709; ^sDepartment of Environmental Systems Science, Eidgenössische Technische Hochschule Zurich, 8092 Zurich, Switzerland; ^tDepartment of Biological Environment, Akita Prefectural University, Akita 010-0195, Japan; ^uSchool for Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109; ^vDepartment of Plant Biology, Program in Ecology, Evolutionary Biology, and Behavior, Michigan State University, East Lansing, MI 48824; ^wDepartment of Forestry, Michigan State University, East Lansing, MI 48824; ^xHastings Reservation, University of California Berkeley, Carmel Valley, CA 93924; ^yDepartment of Biological Sciences, DePaul University, Chicago, IL 60614; ^zInstitute of Systematics and Evolution of Animals, Polish Academy of Sciences, 31-016 Krakow, Poland; ^{aa}Department of Wildland Resources, Utah State University, Logan, UT 84322; ^{bb}Ecology Center, Utah State University, Logan, UT 84322; ^{cc}Department of Biology, Washington University in St. Louis, St. Louis, MO 63130; ^{dd}Department of Forestry and Renewable Forest Resources, Biotechnical Faculty, University of Ljubljana, 1000 Ljubljana, Slovenia; ^{ee}Department for the Ecology of Animal Societies, Max Planck Institute of Animal Behavior, 78457 Konstanz, Germany; ^{ff}US Geological Survey, Fort Collins Science Center, Fort Collins, CO 80526; ^{gg}W. Szafer Institute of Botany, Polish Academy of Sciences, 31-512 Krakow, Poland; ^{hh}Department of Forest and Rangeland Stewardship, Colorado State University, Fort Collins, CO 80523; ⁱⁱDepartment of Forest and Wildlife Ecology, University of Wisconsin-Madison, Madison, WI 53706; ^{jj}Department of Biology, Wake Forest University, Winston-Salem, NC 27106; ^{kk}Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY 10027; ^{ll}Department of Agricultural and Environmental Sciences - Production, Territory, Agroenergy (DISAA), University of Milan, 20133 Milano, Italy; ^{mmm}Smithsonian Tropical Research Institute, Apartado 0843-03092, Balboa, Republic of Panama; and ⁿⁿDepartment of Environmental Sciences, University of Puerto Rico, Rio Piedras, Puerto Rico, United States 00936

This contribution is part of the special series of Inaugural Articles by members of the National Academy of Sciences elected in 2020.

Contributed by James S. Clark, June 16, 2021 (sent for review April 5, 2021; reviewed by Jerome Chave, Malcolm Iltter, and Stephen C. Sillett)

Despite its importance for forest regeneration, food webs, and human economies, changes in tree fecundity with tree size and age remain largely unknown. The allometric increase with tree diameter assumed in ecological models would substantially overestimate seed contributions from large trees if fecundity eventually declines with size. Current estimates are dominated by overrepresentation of small trees in regression models. We combined global fecundity data, including a substantial representation of large trees. We compared size–fecundity relationships against traditional allometric scaling with diameter and two models based on crown architecture. All allometric models fail to describe the declining rate of increase in fecundity with diameter found for 80% of 597 species in our analysis. The strong evidence of declining fecundity, beyond what can be explained by crown architectural change, is consistent with physiological decline. A downward revision of projected fecundity of large trees can improve the next generation of forest dynamic models.

tree fecundity | tree senescence | tree life history | allometric scaling | crown architecture

“Belgium, Luxembourg, and The Netherlands are characterized by “young” apple orchards, where over 60% of the trees are under 10 y old. In comparison, Estonia and the Czech Republic have relatively “old” orchard[s] with almost 60% and 43% over 25 y old” (1).

“The useful lives for fruit and nut trees range from 16 years (peach trees) to 37 years (almond trees). . . . The Depreciation Analysis Division believes that 61 years is the best estimate of the class life of fruit and nut trees based on the information available” (2).

When mandated by the 1986 Tax Reform Act to depreciate aging orchards, the Office of the US Treasury found so

Author contributions: J.S.C. designed research; T.Q. analyzed crown and phylogeny data; J.S.C. compiled the MASTIF data and wrote the MASTIF model and software; T.Q., B.C., V.J., G.K., and J.S.C. wrote the paper; and M.-C.A., R.A., D.A., Y.B., R. Berretti, M.B., T.B., R. Bonal, T.C., R.C., J.J.C., C.J.C., B.C., S.D., S.D.C., W.F.-R., C.A.G., G.S.G., C.H.G., Q.G., J.H.R.L., K.H., I.I., V.J., C.L.K., R.K.K., W.D.K., G.K., J.M.L., M.L., J.A.L., R.M., J.A.M., T.A.N., C.L.N., I.S.P., L.P., J.R.P., R.P.-K., M.D.R., C.D.R., K.C.R., C.L.S., H.S.V.M., B.S., S.S., M. Silman, J.J.S., M. Swift, M.U., G.V., T.T.V., A.V.W., T.G.W., A.P.W., S.J.W., K.Z., J.K.Z., and M.Z. contributed data and provided comments on the paper.

Reviewers: J.C., Centre National de la Recherche Scientifique; M.I., University of Massachusetts Amherst; and S.C.S., Humboldt State University.

Competing interest statement: C.J.C. and J.C. are coauthors on a 2020 article; S.J.W. and J.C. are coauthors on a 2019 article; J.R.P. and J.C. are coauthors on a 2020 article; M.U., J.K.Z., and J.C. are coauthors on two 2019 articles; and M. Silman, W.F.R., and J.C. are coauthors on 2018, 2019, and 2020 articles.

Published under the [PNAS license](#).

¹To whom correspondence may be addressed. Email: jimclark@duke.edu.

This article contains supporting information online at <https://www.pnas.org/lookup/suppl/doi:10.1073/pnas.2106130118/-DCSupplemental>.

Published August 16, 2021.

Significance

Physiological decline in large, old trees could involve diminished reproductive effort, but evidence is lacking. A global analysis finds that fecundity decline in large trees is pervasive, consistent with physiological decline, thus providing new evidence for tree senescence. For the 20% of species not showing fecundity declines, this lack of evidence was linked not to specific species groups, but rather to lack of large trees in the data. Large trees remain important for their structural attributes, but results highlight the critical role of intermediate trees for their contribution to reproduction.

little information that they ultimately resorted to interviews with individual growers (2). One thing is clear from the age distributions of fruit and nut orchards throughout the world (1, 3, 4): Standard practice often replaces trees long before most ecologists would view them to be in physiological decline, despite the interruption of profits borne by growers as transplants establish and mature. Although seed establishment represents the dominant mode for forest regeneration globally, and the seeds, nuts, and fruits of woody plants make up to 3% of the human diet (5, 6), change in fecundity with tree size and age is still poorly understood. We examine here the relationship between tree fecundity and diameter, which is related to tree age in the sense that trees do not shrink in diameter (cambial layers typically add a new increment annually), but growth rates can range widely. Still, it is important not to ignore the evidence that declines with size may also be caused by aging. Although most analyses do not separate effects of size from age (because age is often unknown and confounded with size), both may contribute to size–fecundity relationships (7). Grafting experiments designed to isolate extrinsic influences (size and/or environment) from age-related gene expression suggest that size alone can sometimes explain declines in growth rate and physiological performance (8–10), consistent with pruning/coppicing practice to extend the reproductive life of commercial fruit trees. Hydraulic limitation can affect physiological function, including reduced photosynthetic gain that might contribute to loss of apical dominance, or “flattening” of the crown with increasing height (11–16). The slowing of height growth relative to diameter growth in large trees is observed in many species (12, 17). At least one study suggests that age by itself may not lead to decline in fecundity of open-grown, generally small-statured bristlecone pine (*Pinus longaeva*) (18). By contrast, some studies provide evidence of tree senescence, including age-related genetic changes in meristems of grafted scions that cause declines in physiological function (19–22). Koenig et al. (23) found that fecundity declined in the 5 y preceding death in eight *Quercus* species, although cause of death here, as in most cases, is hard to identify. Fielding (24) found that cone size of *Pinus radiata* declines with tree age and smaller cones produce fewer seeds (25). Some studies support age-related fecundity declines in herbaceous species (26–28). Thus, there is evidence to suggest the fecundity schedules might show declines with size, age, or both.

The reproductive potential of trees as they grow and age is of special concern to ecologists because, despite being relatively rare, large trees can contribute disproportionately to forest biomass due to the allometric scaling that amplifies linear growth in diameter to a volume increase that is more closely related to biomass (29, 30). Understanding the role of large trees can also benefit management in recovering forests (31). If allometric scaling applies to fecundity, then these large individuals might determine the species and genetic composition of seeds that compete for dominance in future forests.

Unfortunately, underrepresentation of big trees in forests frustrates efforts to infer how fecundity changes with size. Simple allometric relationships between seed production and tree diameter can offer useful predictions for the small- to intermediate-size trees that dominate observational data, so it is not surprising that modeling began with the assumption of allometric scaling (32–36). Extrapolation from these models would predict that seed production by the small trees from which most observations come may be overwhelmed by big trees. Despite the increase with tree size assumed by ecologists (37), evidence for declining reproduction in large trees has continued to accumulate from horticultural practice (3, 4, 38, 39) and at least some ecological (40–45) and forestry literature (46, 47). However, we are unaware of studies that evaluate changes in fecundity that include substantial numbers of large trees.

Understanding the role of size and age is further complicated by the fact that tree fecundity ranges over orders of magnitude from tree to tree of the same species and within the same tree from year to year—a phenomenon known as “masting.” The variation in seed-production data requires large sample sizes not only to infer the effects of size, but also to account for local habitat and interannual climate variation. For example, a one-time destructive harvest to count seeds in felled trees (48, 49) misses the fact that the same trees would offer a different picture had they been harvested in a different year. An oak that produces 100 acorns this year may produce 10,000 next year. A pine that produces 500 cones this year can produce zero next year. Few datasets offer the sample sizes of trees and tree years needed to estimate effects of size and habitat conditions in the face of this high intertree and interyear variability (43).

We begin this analysis by extending allometric scaling to better reflect the geometry of fecundity with tree size. We then reexamine the size–fecundity relationship using data from the Masting Inference and Forecasting (MASTIF) project (50), which includes substantial representation of large trees, and a modeling framework that allows for the possibility that fecundity plateaus or even declines in large trees. Unlike previous studies, we account for the nonallometric influences that come through competition and climate. We demonstrate that fecundity–diameter relationships depart substantially from allometric scaling in ways that are consistent with physiological senescence.

Continuous increase with size has been assumed in most models of tree fecundity, supported in part by allometric regressions against diameter, typically of the form

$$\log M_f = \beta_0 + \beta_D \log D \quad [1]$$

for fecundity mass $M_f = m \times f$ (48, 51), where D is tree diameter, m is mass per seed, and fecundity f is seeds per tree per year. Of course, this model cannot be used to determine whether or how fecundity changes with tree diameter unless expanded to include additional quadratic or higher-order terms (52).

The assumption of continual increase in fecundity was interpreted from early seed-trap studies, which initially assumed that $\beta_D = 2$, i.e., fecundity proportional to stem basal area (33–34, 51). Models subsequently became more flexible, first with β_D values fitted, rather than fixed, yielding estimates in the range (0.3, 0.9) in one study (ref. 52, 18 species) and (0, 4.1) in another (ref. 56, 4 species). However, underrepresentation of large trees in typical datasets means that model fitting is dominated by the abundant small size classes.

To understand why data and models could fail to accurately represent change in fecundity with size, consider that allometric scaling in Eq. 1 can be maintained dynamically only if change in both adheres to a strict proportionality

$$\frac{1}{f} \frac{df}{dt} \propto \frac{1}{D} \frac{dD}{dt} \quad [2]$$

(57). For allometric scaling, any variable that affects diameter growth has to simultaneously affect change in fecundity and in the same, proportionate way. In other words, allometric scaling cannot hold if there are selective forces on fecundity that do not operate through diameter growth and vice versa.

On top of this awkward constraint that demands proportionate responses of growth and fecundity, consider further that standard arguments for allometric scaling are not directly relevant for tree fecundity. Allometry is invoked for traits that maintain relationships between body parts as an organism changes size (29). For example, a diameter increment translates to an increase in volume throughout the tree (58, 59). Because the cambial layer essentially blankets the tree, a volume increment cannot depart much from a simple allometric relationship with diameter. However, the same cannot be said for all plant parts, many of which clearly do not allometrically scale; for example, seed size does not scale with leaf size (60), presumably because structural constraints are not the dominant forces that relate them (61).

To highlight why selective forces might not generate strict allometric scaling for reproduction, consider that a tree allocates a small fraction of potential buds to reproduction in a given year (62, 63). Still, if the number of buds on a tree bears some direct relationship to crown dimensions and, thus, diameter, there might be allometric scaling. However, the fraction of buds allocated to reproduction and their subsequent development to seed is affected by interannual weather and other selective forces (e.g., bud abortion, pollen limitation) in ways that diameter growth is not (64–66). In fact, weather might have opposing effects on growth and reproduction (67). Furthermore, resources can change the relationship between diameter and fecundity, including light levels (52, 68–70) and atmospheric CO₂ (71).

Some arguments based on carbon balance anticipate a decline in fecundity with tree size (72). Increased stomatal limitation (11) and reduced leaf turgor pressure (14, 73) from increasing hydraulic path length could reduce carbon gains in large trees. Assimilation rates on a leaf area basis can decline with tree size (74), while respiration rate per leaf area can increase [*Sequoia sempervirens* (75), *Liquidambar styraciflua* (76), and *Pinus sylvestris* (77)], consistent with the notion that whole-plant respiration rate may roughly scale with biomass (78). Maintenance respiration costs scale with diameter in some tropical species (79) but perhaps not in *Pinus contorta* and *Picea engelmannii* (80). Self-pruning of lower branches can reduce maintenance costs (81), but the ratio of carbon gain to respiration cost can still decline with size, especially where leaf area plateaus and per-area assimilation rates of leaves decline in large trees.

The question of size–fecundity relationships is related indirectly to the large literature on interannual variation in growth–fecundity allocation (3, 4, 43, 67, 82–87). The frequency and timing of mast years and species differences in the volatility of seed production can be related to short-term changes in physiological state and pollen limitation that might not predict the long-term relationships between size and reproductive effort. The interannual covariance in diameter growth and reproductive effort can range from strong in some species to weak in others (70, 87, 88). Understanding the relationships between short-term allocation and size–fecundity differences will be an important focus of future research.

Estimating effects of size on fecundity depends on the distribution of diameter data, $[D]$, where the bracket notation indicates a distribution or density. For some early-successional species, the size distribution changes from dominance by small trees in young stands to absence of small trees in old stands. If our goal was to describe the population represented by a forest inventory plot, we would typically think about the joint distribution of fecundity and diameter values, $[f, D] = [f|D][D]$, that is represented by the sample. The size–fecundity relationship estimated

for a stand at different successional stages would diverge simply due to the distribution of diameters, i.e., differences in $[D]$. For example, application of Eq. 1 to harvested trees selected to balance size classes (uniform $[D]$) (48) overpredicts fecundity for large trees (49), but the relevance of such regressions for natural stands, where large trees are often rare, is unclear. Studies that expand Eq. 1 to allow for changing relationships with tree size now provide increasing evidence for a departure from allometric scaling in large trees (43, 70), despite dominance by small-to intermediate-size trees in these datasets. Here our goal is to understand the size–fecundity relationship $[f|D]$ as an attribute of a species, i.e., not tied to a specific distribution of size classes observed in a particular stand.

The well-known weak relationship between tree size and age that comes from variable growth histories makes it important to clarify the implications of any finding of fecundity that declines with tree size: Can it happen if there are not also fecundity declines with tree age? The only argument for continuing increase in fecundity with age in the face of observed decreases with size would have to assume that the biggest trees are also the youngest trees. Of course, a large individual can be younger than a small individual. However, at the species level, integrating over populations sampled widely, mean diameter increases with age; at the species level, declines with size also imply declines with age. Estimating accurate species-level size effects requires distributed data and large sample sizes. The analysis here fits species-level parameters, with 585,670 trees and 10,542,239 tree years across 597 species.

Phylogenetic analysis might provide insight into the pervasiveness of fecundity declines with size. Inferring change in fecundity with size necessarily requires more information than is needed to fit a single slope parameter β_D in the simple allometric model. The noisier the data, the more difficult it becomes to estimate the additional parameters that are needed to describe changes in the fecundity relationship with size. We thus expect that noise alone will preclude finding size-related change in some species, depending on sample size and non-size-related variation. If the vagaries of noisy data and the distribution of diameters preclude estimation of declines in some species, then we do not expect that phylogeny will explain which species do and do not show these declines. Rather than phylogeny, this explanation would instead be tied to sample size and the distribution of diameter data. Conversely, phylogenetic conservatism, i.e., a tendency for declines to be clustered in related species, could suggest that fecundity declines are real.

To understand how seed production changes with tree size, our approach combines theory and data to evaluate allometric scaling and the alternative that fecundity may decline in large trees, consistent with physiological decline and senescence. We exploit two advances that are needed to determine how fecundity scales with tree size. First, datasets are needed with large trees, because studies in the literature often include few or none (85, 89, 90). Second, methods are introduced that are flexible to the possibility that fecundity continues to increase with size or not. We begin with a reformulation of allometric scaling, recognizing that change in fecundity could be regulated by size, without taking the form of Eq. 1 (*Materials and Methods* and *SI Appendix, section S2*). In other words, there could be allometric scaling with diameter, but it is not the relationship that has been used for structural quantities like biomass. We then analyze the relationships in data using a model that not only allows for potential changes in fecundity with size, but at the same time accounts for self-shading and shading by neighbors and for environmental variables that can affect fecundity and growth (*Materials and Methods* and *SI Appendix, section S3*). The fitted model is compared with our expanded allometric model to identify potential agreement. Finally, we examined phylogenetic trends in the species that do and do not show declines.

Results

Sixty-three percent of the 597 species in this study show eventual declines in fecundity with increasing diameter (type A in *Materials and Methods*) (Fig. 1 and Table 1). Seventeen percent showed diminishing rates of increase (type B), indicating that fecundity might eventually plateau or even decrease. Only 20% show the continuous increase in fecundity (type C) that would be consistent with traditional allometric scaling.

The inflection in the fecundity–diameter relationship at D_{opt} is species specific and exhibits phylogenetic coherence ($\lambda = 0.77$, $p < 10^{-25}$, $n = 281$) (Fig. 2). For the species with fecundity declines, D_{opt} (the diameter where maximum fecundity occurs) averaged 41 ± 35 cm. We also compared D_{opt}/D_{max} between species and it shows trends across phylogeny similar to those of D_{opt} (SI Appendix, Fig. S5). Whereas phylogeny contributes to species differences in D_{opt} , the question of whether or not an optimum could be identified was not related to phylogeny (SI Appendix, Fig. S3; $\lambda < 10^{-13}$, $p \approx 1$, $n = 398$). Nor did we find a consistent pattern in the relationship between D_{max} and the three types of fecundity change with diameter across genera from the temperate regions of North America, Europe, and Asia (SI Appendix, Fig. S4). For example, fecundity eventually declines in some *Pinus* species having large D_{max} (e.g., *Pinus monticola*, *Pinus lambertiana*, and *Pinus ponderosa*), while declines could not be identified in *Pinus jeffreyi*.

Whether or not a decline can be detected was related not to phylogeny, but rather to the fraction of large trees in the data. We found that species estimated to have continuous increases

in fecundity tend to have smaller proportions of large trees (SI Appendix, Fig. S6). In addition, the credible intervals were generally wider (higher transparencies in the lines of Fig. 1) in large size classes for species with fewer observations, as expected given the requirement that estimating declines at large size requires more diameter information (two parameters to estimate rather than one). A lack of large individuals can increase the uncertainties in our fecundity estimates, especially at large size.

Neither allometric model we examined (*Materials and Methods*) could explain the slowing and eventual decline in fecundity with tree size. Recall that we are not attempting to find a “best” model for tree allometry, but rather to determine whether alternative assumptions about crown surface could produce declines with tree size. Under assumptions of allometric scaling, crown surface area (C_{SA}) of open-grown trees tends to increase at an increasing rate with diameter; dots representing six species in Fig. 3A show no hint of eventual declining rates, despite flattening crowns (Fig. 4). Similar patterns were found under simulated shading conditions (SI Appendix, Fig. S2). Nor did we observe declines for 110 species in the ideal tree distribution (ITD) model (*Materials and Methods*) in Fig. 3B, which does not admit crown flattening, but does attempt to include idealized shading from neighbors.

Discussion

The fact that 80% of the 597 species tested here show declining rates of increase in fecundity with diameter (types A and B in *Materials and Methods*), and 63% of the total actually decrease

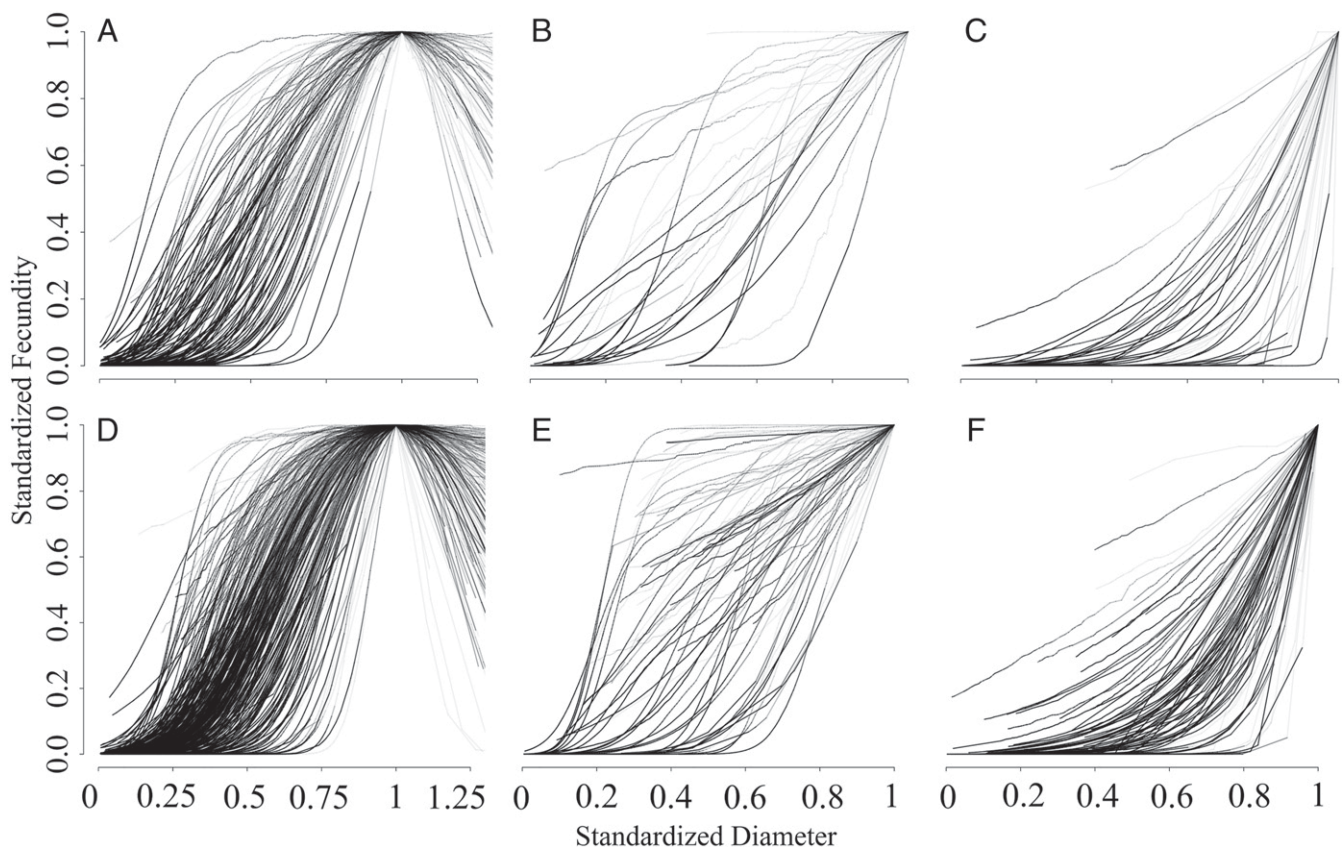


Fig. 1. The relationship between fecundity and diameter for species in temperate (A–C) and tropical (D–F) regions, where diameter and fecundity are scaled as D/D_{opt} and $f(D)/f(D_{opt})$, respectively. A and D exhibit type A species (fecundity eventually declines); B and E show type B species (sigmoid increase in fecundity); C and F represent type C species (continuous increase in fecundity). Line transparency is proportional to the 90% credible interval width across the diameter ranges, such that confident predictions are opaque, and vice versa. The percentages of species for each type of fecundity–diameter relationship are summarized in Table 1. D_{opt} is the diameter when maximum fecundity occurs.

Table 1. Percentage of species in three fecundity–diameter response classes (*Materials and Methods*) by temperate and tropical regions

Region (no. species)	Sample size (tree years)	% of species		
		Type A: Eventual decline	Type B: Sigmoid increase	Type C: Continuous increase
Temperate (169)	2,483,125	61.5	15.4	23.1
Tropical (428)	8,059,114	64.0	17.1	18.9

(type A), provides empirical evidence for declining fecundity with size (Fig. 1). Declining fecundity does not fit the standard allometric model based on stem diameter of Eq. 1. Nor can it be

explained by allometric relationships with crown area (Fig. 4), by either of two models (Fig. 3). In other words, size-related fecundity declines do not align with architectural changes related to flattening crowns.

If declining fecundity is a defining feature of big trees, then why did we not identify it in all species? The parsimonious explanation is that the combination of overrepresentation of small trees and the added information requirement raises the bar for finding declines in large trees. Finding eventual declines in fecundity requires more information than is needed to estimate a single parameter for a rate of increase; the capacity to identify declines with size is expected to be greatest for species represented by a high proportion of large trees (*SI Appendix, Fig. S6*). If continuously increasing fecundity were associated with specific families or genera, then there would be cause for speculation on

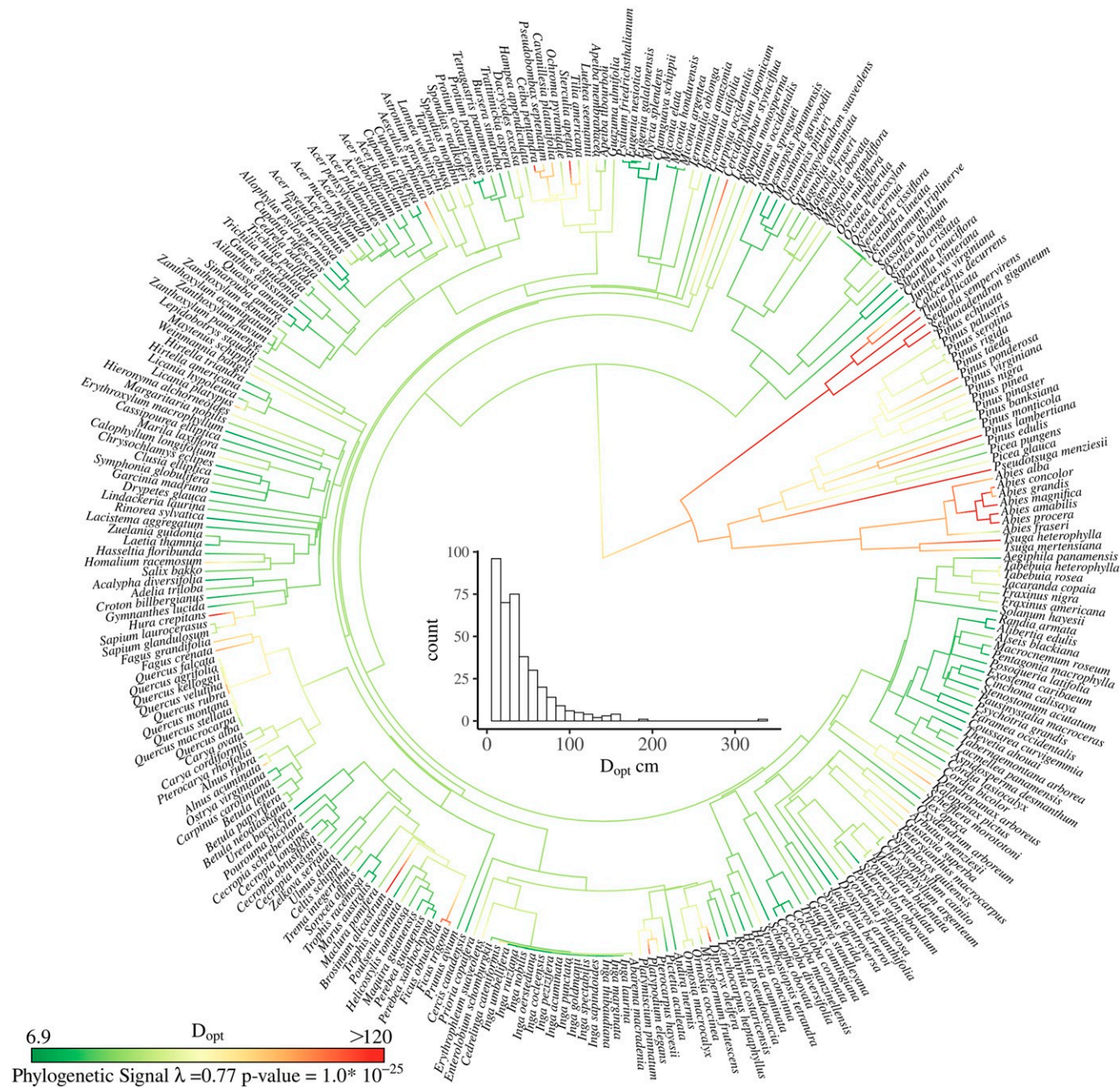


Fig. 2. Reconstructed evolution history of D_{opt} (the diameter when maximum fecundity occurs) using continuous character mapping. Note that the histogram is based on D_{opt} from all type A species (378 species in total) in Fig. 1 while 281 (~ 74.3%) of them have phylogenetic trees. Phylogenetic signal was estimated using Pagel's λ .

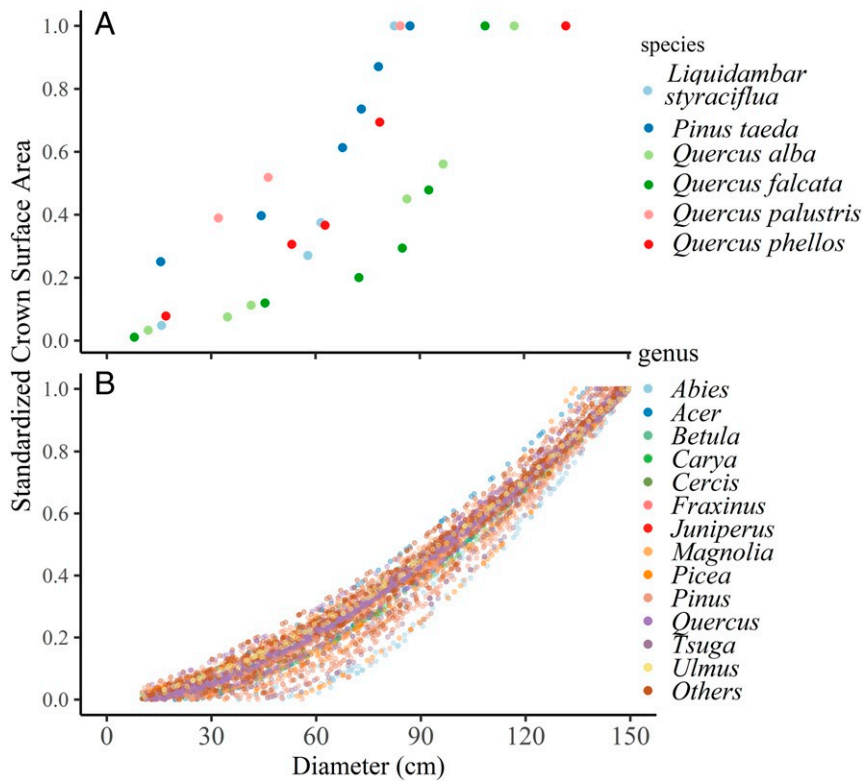


Fig. 3. Neither allometric model can generate fecundity decline with size for realistic parameter ranges. (A) Crown surface area evaluated from images of six species (SI Appendix, Fig. S1). (B) Crown surface area evaluated from 110 species in North America using the ideal tree distribution (ITD) model (91). Colors indicate genera (ordered alphabetically for 13 main genera). Crown surface area C_{SA} continues to increase with diameter from observed and simulated data with C_{SA} for each species displayed as a proportion of the maximum C_{SA} value.

the genetic differences that lead to declines in some species, but not others. Absence of a phylogenetic pattern to explain which species do and do not decrease might be explained by the fact that only some species suffer physiological decline with size and age and that this immunity to aging has arisen multiple times in unrelated species. Alternatively, it is also consistent with the knowledge that accurate estimates depend importantly on the distribution of diameter data, and this relationship to the availability of large trees is shown here. We cannot offer a specific rule for identifying fecundity decline, because that depends on all sources of uncertainty in the data and model. Lack of a phylogenetic signal in whether or not we can estimate a decline, combined with few large trees for nondeclining species, suggests that fecundity decline may be more pervasive than estimated here.

Our results indicate that trees produce proportionately fewer seeds per diameter and per crown area as they increase in size at the species level, consistent with age-related decline. This support for horticultural evidence (3, 4, 38) is also consistent with studies suggesting plateaus and/or declines in fecundity for species of *Quercus* (46, 47, 92), *P. sylvestris* (93), and *Avicennia marina* (92). It confirms increasing reports of fecundity declines in large and old trees in tropical (42) and temperate regions (23, 40, 43, 44, 46, 47). It may agree with a carbon-balance perspective (94) and with a recent meta-analysis reporting that more than half of 20 woody perennial species exhibited age-related declines in reproduction, with only one species suggesting an increase with age (95).

The fact that allometric scaling with diameter fails for fecundity means that fecundity also does not scale with other

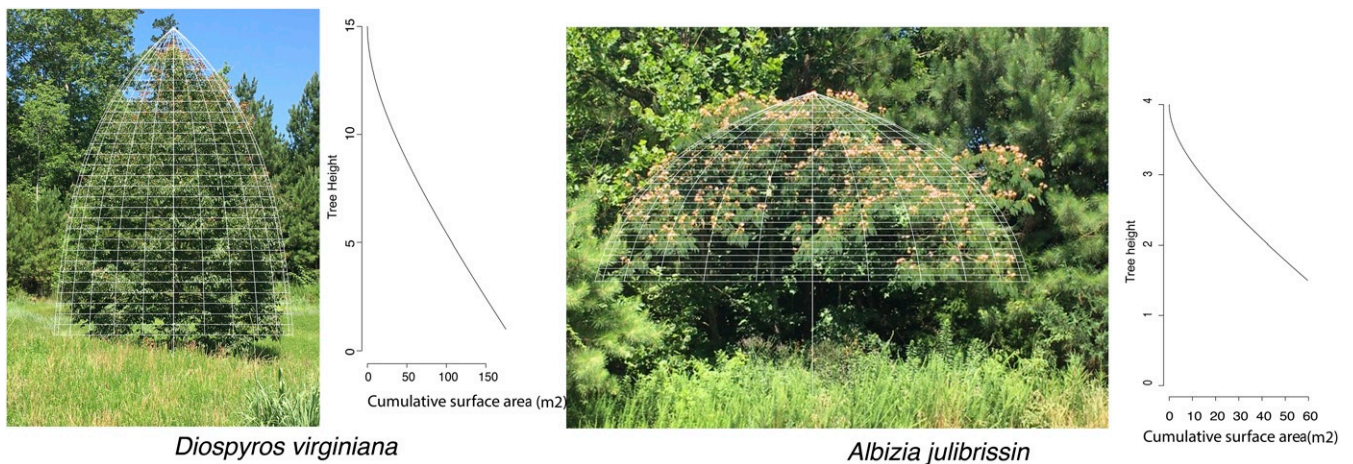


Fig. 4. In open-grown trees CSA describes the allometric relationship between diameter and the crown exposed to high sunlight where reproductive effort is often concentrated. The CSA model combines crown architecture with shading from neighbors to evaluate the cumulative exposure with depth into the crown, as shown with two examples here (details in SI Appendix, section S2). Photo credits: James S. Clark.

dimensional properties that scale with diameter, including basal area, biomass, or wood volume. For example, basal area B scales with diameter $B \propto D^2$, as does biomass $M \propto D^c$, where coefficient c varies by species. Because B and M both scale with diameter, they also scale with each other as a simple ratio of coefficients $M \propto B^{c/2}$. The converse is also true: Because fecundity does not scale with diameter, it cannot scale with basal area or biomass. Our results indicate that fecundity might only roughly be evaluated as a proportionality with stand basal area or biomass.

Our results do not separate the effects of age and size, but they add an additional dimension to existing evidence for aging, that of declining reproductive effort (Fig. 1). Age-related reductions in maximum photosynthetic capacity (72, 96), xylem growth rate (97), specific leaf area (21), and reproductive development (22) may combine with fecundity decline as part of an aging syndrome. Size alone may explain some of these changes if hydraulic limitation develops in tall trees (8, 11, 98, 99). Grafting experiments can help to separate effects of size and age, at least some of which already provide evidence of senescence (7).

The finding that fecundity declines with size means that proportionate allocation to reproduction must also decline. Again, continuing increase in biomass increment is consistent with expanding cambial tissue, as evident from empirical data (58). Unlike biomass, fecundity is not structurally related to size, as bigger trees need not produce bigger seeds or even more of them. Foregoing current for future reproduction can pay when future benefits offset mortality risks (100–102). The exposure to selection on genes that confer high reproductive effort late in life can be essentially zero; this decline in the efficacy of selection for traits that could sufficiently boost later reproductive success would have to offset not only declining survival (103), but also the effects of accumulated deleterious mutations (104) and antagonistic pleiotropy (105, 106). Revised fecundity schedules available here can be combined with survival scenarios to update estimates of tree fitness.

The value of broad representation of species and size classes, combined with a methodology that reduces the dependence on the distribution of size classes, provides an additional perspective on basic dimensional relationships with fecundity. The massive numbers of observations in MASTIF distributed across climate and habitat space allowed us to estimate change in the diameter–fecundity relationship across the diameter range, while accounting for habitat variation. The capacity to combine the evidence from seed-trap studies with crop counts in the MASTIF model (44) played an important role, because seed-trap studies may not include large trees, whereas crop counts can selectively represent the important range of tree attributes. Conversely, small-seeded species that are poorly represented in crop-count studies are those for which fecundity estimates are most accurate in seed-trap studies (50).

The importance of fruit, seed, and nut production for human and animal consumption makes these results relevant to issues from food security to ecological food webs. The generality of fecundity declines with size reported here squares with patterns long recognized in orchard management and suggests the value of stronger connections between basic and applied research. The fact that fecundity is optimal or plateaus at intermediate size is not just important for human fruit consumption, but also has implications for forest food webs. The large numbers of mast consumers in forests are affected by seed supply, especially as a winter food source (107, 108).

Despite the fact that fecundity directly modulates forest demographic processes (52, 109) and range shifts (110), insights here can improve on the assumed constant seed pool in Earth System models (111) and allometric scaling in stand simulators (112) that are used to examine effects of climate change (113).

Materials and Methods

Fecundity Data. Fecundity data were obtained from the MASTIF project (50) on 585,670 trees and 10,542,239 tree years from 597 species in five continents, including North America, South and Central America, Europe, Africa, and Asia (SI Appendix, Table S2). MASTIF data are restricted to seed traps and crop counts, both of which are referenced to fecundity in individual tree years (SI Appendix, section S1), supplemented by observations of maturation status in some datasets (52, 114). Crop counts refer to the current season's production; we do not use counts of accumulated reproductive effort from species where cones might reside on trees for multiple years (e.g., ref. 115). Data from crop counts, seeds traps, and maturation statuses are detailed in previous publications (43, 44).

To gauge whether there might be insufficient numbers of large trees, we compared the distribution of diameters in MASTIF with the largest trees observed in tree inventory data, which were available for North America, Europe, and Asia (SI Appendix, Table S3). We evaluated a “near-maximum” diameter for each species D_{\max} to be the fifth largest tree in forest inventories. We used this order statistic, because, unlike quantiles, it does not depend on the distribution of small trees in the data. We did not use the extreme value due to the potential for error in a single value (as opposed to five values). Due to limited inventory data relative to the numbers of species in South America and Africa, we converted maximum tree heights from Liu et al. (116) to diameter using allometric equations (117) (SI Appendix, Table S3). Approximately 11, 7, and 3% of species had no trees larger than 40% of the D_{\max} in eastern North America, western North America, and Asia, respectively. For South and Central America, ~7% of species were less than 30% of the D_{\max} . They were removed from further analysis. Five species that belong to the family *Arecaceae* were also excluded because diameter growth was irrelevant to fecundity for those palm species. There were 585,670 individual trees and 10,542,239 tree years in the remaining 597 species.

Crown Allometry. We cannot reject allometric scaling solely on the basis of poor fit to Eq. 1, because fecundity might scale with diameter in a different way. To fully evaluate allometric explanations, including whether or not alternative assumptions could explain declines with size, we examined scaling with crown surface area and crown depth, due to their connection to light availability (Fig. 4). Based on thousands of observations on hundreds of species (<https://www.inaturalist.org/projects/mastif>) we found that, for most species, seed production is concentrated in the upper crown that receives high sunlight. (We find exceptions to this, including in some of the genus *Quercus* and for predominantly tropical taxa that bear fruits directly on the stem.) Consistent with the fact that well-lighted trees produce more seeds than shaded individuals (43, 52, 62, 70), and light addition can increase branch reproductive effort (69), we further observed that edge trees concentrate reproductive effort on the side of the crown that is exposed to sunlight, and reproductive effort often decreases from the exposed outer crown to the shaded interior. This strong light dependence is consistent with the observation that many reproductive structures are photosynthetic (e.g., cones of the genus *Pinus*). The crown-surface area (CSA) model was evaluated as an alternative allometric model to Eq. 1 (SI Appendix, section S2).

Crown changes with diameter were evaluated from images obtained in open environments, supplemented with model analysis for effects of shading (SI Appendix, section S2). Tree height H and base of the live crown H_b provide estimates of the reproductive height $H_r = H - H_b$. A crown shape parameter describes how crown surface area C_{SA} accumulates with height from the top of the tree (Fig. 4), a relationship that can change as crowns flatten with tree height. Because crown shape was not fully visible for crowded trees, we evaluated how declining reproductive height H_r with shading from neighbors affected C_{SA} in SI Appendix, section S2.

For completeness we implemented an alternative model, termed the ITD (91). This model uses size and crowding information from inventory data to define an individual's crown status relative to neighbors. A principle difference from the CSA model is an assumption in ITD that crown shape is fixed; i.e., there is no flattening of the crown with tree size. We used the algorithm and parameter values from ref. 91 to evaluate tree height, crown shape, crown radius, and exposed crown depth. As with our model, C_{SA} was obtained by integrating arc-wise and vertically overexposed crown depth (SI Appendix, section S2).

Fecundity Analysis. The analysis allows for increases in fecundity as trees mature and then increase in diameter, followed by change in the diameter–fecundity relationship as trees continue to grow. We estimated the number

of seeds produced by a tree f , which is proportional to reproductive mass through a constant (g per seed) $M_f = m \times f$ and, thus, affects only the intercept coefficient in Eq. 1. We use the MASTIF model for inference, a dynamic biophysical model for year-to-year and tree-to-tree seed production (44). This hierarchical Bayesian (state-space) model allows for conditional independence in crop-count and seed-trap data through latent states. A tree i is mature in year t , z_{it} , with probability ρ_{it} . Given that a tree is mature, $z_{it} = 1$, it produces seed with conditional fecundity ψ_{it} , which depends on tree size, shading, and climate. A mature tree remains mature [$\rho_{it}(z_{i,t-1} = 1) = 1$ and $\rho_{it}(z_{i,t+1} = 0) = 0$, although a mature tree may still have failed crops in some years]. Expected fecundity for a tree year is $E[f_{it}] = \rho_{it}\psi_{it}$. Random effects on individual and year allow for wide variation between trees and over time that is typical of seed production (44). The posterior covariance between trees and years can take any form, avoiding assumptions of standard time-series models, important due to the quasi-periodic variation in time and varying levels of synchronicity between individual trees (44, 52).

To allow for size-based change in the relationship with diameter, including potential declines, we use the model having expectation

$$E(\log f) = \log \rho + \log \psi \quad [3]$$

$$= \log \rho + \beta_0 + \beta_D D + \beta_{D^2} D^2 + \dots$$

where \dots refers to other variables that control for the year-to-year variation in climate and the tree-to-tree differences related to competition from neighbors, local habitat, and species differences (SI Appendix, section S3 and Table S4). Note that this model includes a D^2 term that allows for changes related to size. Taken together, this form does not enforce the dynamic constraint on change in Eq. 2, instead allowing for exponentially increasing fecundity ($\beta_{D^2} = 0$) as well as eventual declines at large size ($\beta_{D^2} < 0$).

Fecundity change with tree size does not necessarily follow a simple quadratic pattern on the log scale (Fig. 1) as specified conditionally in Eq. 3. Predictive distributions from this hierarchical state-space model can vary in shape due to the distribution of coefficients across predictors that include shading from neighbors and climate variables. Like most high-dimensional models, the posterior surface can be complex (118). In the MASTIF model (44) there will be combinations of maturation statuses, fecundity values, and dispersal distances that explain seed-trap dispersion better than other combinations. As the Markov chain Monte Carlo (MCMC) chains mix over different combinations of maturation status and conditional fecundity for each tree, the species-level β parameters can find multiple modes. This behavior in the MCMC is, in fact, desirable, ensuring that the algorithm is indeed visiting the range of combinations of maturation/fecundity that each have differing capacity to explain the data. Predictive distributions from the fitted model display the range of behaviors that are consistent with the uncertainty and richer than the conditional relationship in Eq. 3.

We summarize results from hundreds of species in terms of three main groups of response. In type A, eventual decline with tree size means that $\beta_{D^2} < 0$, and the optimum diameter where maximum fecundity occurs,

$$D_{opt} = \frac{-\beta_D}{2\beta_{D^2}} \quad [4]$$

is smaller than the maximum diameter for the species. In type B, sigmoid increase continues to increase with diameter but at a decreasing rate; there is an inflection above which the rate of increase declines with diameter. Like type A, sigmoid increase has $\beta_{D^2} < 0$, but the inflection in Eq. 4 occurs above the maximum diameter. In type C, continuous increase without inflection occurs when $\beta_{D^2} \geq 0$.

If tree biomass data were available, Eq. 4 could be expressed on a mass basis. Diameter is typically translated to mass using allometric equations of the form $M = bD^c$ for fitted coefficients (b, c), in which case the inflection occurs at $M_{opt} = \left(\frac{-b\beta_D}{2\beta_{D^2}}\right)^c$. We work with diameter, because data are widely available, whereas individual tree biomass data are not. For example, there are no species-specific allometric equations for most tropical species (119).

To determine whether fecundity declines in large trees can be explained by shared ancestry, we obtained phylogenies for the 398 (66% of total) species that are included in ref. 120. We further estimated the phylogenetic signal in D_{opt} for the type A species (SI Appendix, section S6).

Data Availability. Previously published data were used for this work (121) (data from this study are available at the Duke Data Repository [<https://doi.org/10.7924/r4348ph5t1>]).

ACKNOWLEDGMENTS. This project has been funded continuously since 1992 by the National Science Foundation (NSF), most recently Division of Environmental Biology (DEB)-1754443, and by the Belmont Forum (1854976), National Aeronautics and Space Administration (Advanced Information Systems Technology 16-0052, AIST18-0063), and the Programme d'Investissement d'Avenir under Project Forecasting Biodiversity change (18-MPGA-0004) (*Make Our Planet Great Again*). Jerry Franklin's data remain accessible through NSF Long Term Ecological Research DEB-1440409. Polish data were funded by the W. Szafer Institute of Botany of the Polish Academy of Sciences and Polish National Science Foundation 2019/33/B/NZ8/0134. Puerto Rico data were funded by NSF grants, most recently, DEB 0963447 and Long Term Research in Environmental Biology (LTREB) 11222325. Data from the Andes Biodiversity and Ecosystem Research Group were funded by the Gordon and Betty Moore Foundation and NSF LTREB 1754647. For access to sites and logistical support we thank the National Ecological Observatory Network. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the US Government. Forest service research was funded by the United States Department of Agriculture (USDA) Forest Service.

- C. Ollier, F. Cardoso, M. Dinu, "Summary results of the eu-27 orchard survey" in *Eurostat Statistics in Focus*, (2009), vol. 41, p. 4.
- United States Department of the Treasury, *Report to Congress on the Depreciation of Fruit and Nut Trees* (Department of the Treasury, Washington, DC, 1990), p. 2.
- N. K. Meena, R. Asrey, Tree age affects postharvest attributes and mineral content in Amrapali mango (*Mangifera indica*) fruits. *Hortic. Plant J.* **4**, 55–61 (2018).
- Z. Zhang, Y. Jin, B. Chen, P. Brown, California almond yield prediction at the orchard level with a machine learning approach. *Front. Plant Sci.* **10**, 809 (2019).
- FAO, Food and Agriculture Organization of the United States, New food balances. <http://www.fao.org/faostat/en/#data/FBS>. Accessed 9 November 2020.
- H. Ritchie, Diet compositions. *Our World in Data*. <https://ourworldindata.org/diet-compositions>. Accessed 9 November 2020.
- M. Mencuccini, S. Munné-Bosch, "Physiological and biochemical processes related to ageing and senescence in plants" in *The Evolution of Senescence in the Tree of Life*, R. P. Shefferson, O. R. Jones, R. Salguero-Gómez, Eds. (Cambridge University Press, Cambridge, UK, 2017), pp. 257–283.
- M. Mencuccini et al., Size-mediated ageing reduces vigour in trees. *Ecol. Lett.* **8**, 1183–1190 (2005).
- J. Matsuzaki, M. Norisada, J. Kodaira, M. Suzuki, T. Tange, Shoots grafted into the upper crowns of tall Japanese cedar (*Cryptomeria japonica* d. don) show foliar gas exchange characteristics similar to those of intact shoots. *Trees (Berl.)* **19**, 198–203 (2005).
- B. J. Bond, N. M. Czarnomski, C. Cooper, M. E. Day, M. S. Greenwood, Developmental decline in height growth in Douglas-fir. *Tree Physiol.* **27**, 441–453 (2007).
- M. G. Ryan, B. J. Yoder, Hydraulic limits to tree height and tree growth. *Bioscience* **47**, 235–242 (1997).
- S. Rust, A. Roloff, Reduced photosynthesis in old oak (*Quercus robur*): The impact of crown and hydraulic architecture. *Tree Physiol.* **22**, 597–601 (2002).
- N. Phillips, B. J. Bond, N. G. McDowell, M. G. Ryan, A. Schauer, Leaf area compounds height-related hydraulic costs of water transport in Oregon white oak trees. *Funct. Ecol.* **17**, 832–840 (2003).
- G. W. Koch, S. C. Sillett, G. M. Jennings, S. D. Davis, The limits to tree height. *Nature* **428**, 851–854 (2004).
- H. T. Ishii, E. D. Ford, M. C. Kennedy, Physiological and ecological implications of adaptive reiteration as a mechanism for crown maintenance and longevity. *Tree Physiol.* **27**, 455–462 (2007).
- R. Rani, K. Abramowicz, D. S. Falster, F. Sterck, Å. Brännström, Effects of bud-flushing strategies on tree growth. *Tree Physiol.* **38**, 1384–1393 (2018).
- N. Osada, R. Tateno, F. Hyodo, H. Takeda, Changes in crown architecture with tree height in two deciduous tree species: Developmental constraints or plastic response to the competition for light? *For. Ecol. Manage.* **188**, 337–347 (2004).
- R. M. Lanner, K. F. Connor, Does bristlecone pine senesce? *Exp. Gerontol.* **36**, 675–685 (2001).
- M. S. Greenwood, Phase change in loblolly pine: Shoot development as a function of age. *Physiol. Plant.* **61**, 518–522 (1984).
- J. Rebeck, K. F. Jensen, M. S. Greenwood, Ozone effects on grafted mature and juvenile red spruce: Photosynthesis, stomatal conductance, and chlorophyll concentration. *Can. J. For. Res.* **23**, 450–456 (1993).
- M. E. Day, M. S. Greenwood, A. S. White, Age-related changes in foliar morphology and physiology in red spruce and their influence on declining photosynthetic rates and productivity with tree age. *Tree Physiol.* **21**, 1195–1204 (2001).
- M. S. Greenwood, M. E. Day, J. Schatz, Separating the effects of tree size and meristem maturation on shoot development of grafted scions of red spruce (*Picea rubens* Sarg.). *Tree Physiol.* **30**, 459–468 (2010).
- W. D. Koenig, J. M. H. Knops, W. J. Carmen, M. B. Pesendorfer, Testing the terminal investment hypothesis in California oaks. *Am. Nat.* **189**, 564–569 (2017).
- J. M. Field, Variations in Monterey pine. *Aust. For. Timber. Bur. Bull.* **31**, 1–43 (1953).

25. V. M. Healy, The collection and extraction of *P(inus) radiata* seed at Mt. Burr, South Australia. *Austral. Forestry* **5**, 103–105 (1940).
26. J. Pino, E. de Roa, Population biology of *Kosteletzkya pentacarpos* (malvaceae) in the Llobregat delta (Catalonia, NE of Spain). *Plant Ecol.* **188**, 1–16 (2007).
27. H. Van Dijk, Ageing effects in an iteroparous plant species with a variable life span. *Ann. Bot.* **104**, 115–124 (2009).
28. R. P. Shefferson, D. A. Roach, Longitudinal analysis in *Plantago*: Strength of selection and reverse-age analysis reveal age-indeterminate senescence. *J. Ecol.* **101**, 577–584 (2013).
29. E. J. H. Corner, The durian theory or the origin of the modern tree. *Ann. Bot. (Lond.)* **13**, 367–414 (1949).
30. J. A. Lutz *et al.*, Global importance of large-diameter trees. *Glob. Ecol. Biogeogr.* **27**, 849–864 (2018).
31. R. L. Chazdon, Tropical forest recovery: Legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.* **6**, 51–71 (2003).
32. E. Ribbens, J. A. Silander Jr., S. W. Pacala, Seedling recruitment in forests: Calibrating models to predict patterns of tree seedling dispersion. *Ecology* **75**, 1794–1806 (1994).
33. J. S. Clark, E. Macklin, L. Wood, Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecol. Monogr.* **68**, 213–235 (1998).
34. P. T. LePage, C. D. Canham, K. D. Coates, P. Bartemucci, Seed abundance versus substrate limitation of seedling recruitment in northern temperate forests of British Columbia. *Can. J. For. Res.* **30**, 415–427 (2000).
35. F. A. Jones, H. C. Muller-Landau, Measuring long-distance seed dispersal in complex natural environments: An evaluation and integration of classical and genetic methods. *J. Ecol.* **96**, 642–652 (2008).
36. H. C. Muller-Landau, S. J. Wright, O. Calderon, R. Condit, S. P. Hubbell, Interspecific variation in primary seed dispersal in a tropical forest. *J. Ecol.* **96**, 653–667 (2008).
37. R. J. Petit, A. Hampe, Some evolutionary consequences of being a tree. *Annu. Rev. Ecol. Evol. Syst.* **37**, 187–214 (2006).
38. F. M. Roka, R. E. Rouse, Comparison of yields by tree age and rootstock in southwest Florida orange groves. *Proc. Annu. Meet. Fla. State Hort. Soc.* **113**, 115–119 (2000).
39. M.-M. Antofie, I. Barbu, C. Sand, R. Blaj, Traditional orchards in Romania: Case study Fântânele, Sibiu County. *Genet. Resour. Crop Evol.* **63**, 1035–1048 (2016).
40. D. F. Greene, E. A. Johnson, Estimating the mean annual seed production of trees. *Ecology* **75**, 642–647 (1994).
41. K. A. Kainer *et al.*, Liana loads and their association with *Bertholletia excelsa* fruit and nut production, diameter growth and crown attributes. *J. Trop. Ecol.* **22**, 147–154 (2006).
42. Y. Naito *et al.*, Size-related flowering and fecundity in the tropical canopy tree species, *Shorea acuminata* (Dipterocarpaceae) during two consecutive general flowerings. *J. Plant Res.* **121**, 33–42 (2008).
43. J. S. Clark *et al.*, High-dimensional coexistence based on individual variation: A synthesis of evidence. *Ecol. Monogr.* **80**, 569–608 (2010).
44. J. S. Clark, C. Nunez, B. Tomasek, Foodwebs based on unreliable foundations: Spatiotemporal masting merged with consumer movement, storage, and diet. *Ecol. Monogr.* **89**, e01381 (2019).
45. M. Bogdziewicz *et al.*, Does masting scale with plant size? High reproductive variability and low synchrony in small and unproductive individuals. *Ann. Bot.* **126**, 971–979 (2020).
46. A. A. Downs, Estimating acorn crops for wildlife in the southern Appalachians. *J. Wildl. Manage.* **8**, 339–340 (1944).
47. N. Jacob *et al.*, Red oak acorn yields in green-tree reservoirs and nonimpounded forests in Mississippi. *Wildl. Soc. Bull.* **43**, 491–499 (2019).
48. R. H. Whittaker, G. M. Woodwell, Structure, production and diversity of the oak-pine forest at Brookhaven, New York. *J. Ecol.* **57**, 155–174 (1969).
49. K. Niklas, B. Enquist, An allometric model for seed plant reproduction. *Evol. Ecol. Res.* **5**, 79–88 (2003).
50. J. S. Clark *et al.*, Continent-wide tree fecundity driven by indirect climate effects. *Nat. Commun.* **12**, 1242 (2021).
51. K. J. Niklas, The allometry of plant reproductive biomass and stem diameter. *Am. J. Bot.* **80**, 461–467 (1993).
52. J. S. Clark, S. LaDeau, I. Ibanez, Fecundity of trees and the colonization-competition hypothesis. *Ecol. Monogr.* **74**, 415–442 (2004).
53. R. H. Peters *et al.*, The allometry of the weight of fruit on trees and shrubs in Barbados. *Oecologia* **74**, 612–616 (1988).
54. P. S. White, Corner's rules in eastern deciduous trees: Allometry and its implications for the adaptive architecture of trees. *Bull. Torrey Bot. Club* **110**, 203–212 (1983).
55. J. S. Clark, M. Silman, R. Kern, E. Macklin, J. HilleRisLambers, Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology* **80**, 1475–1494 (1999).
56. C. D. Canham, W. A. Ruscoe, E. F. Wright, D. J. Wilson, Spatial and temporal variation in tree seed production and dispersal in a New Zealand temperate rainforest. *Ecosphere* **5**, 49 (2014).
57. J. S. Clark, Density-independent mortality, density compensation, gap formation, and self-thinning in plant populations. *Theor. Popul. Biol.* **42**, 172–198 (1992).
58. N. L. Stephenson *et al.*, Rate of tree carbon accumulation increases continuously with tree size. *Nature* **507**, 90–93 (2014).
59. S. C. Sillett *et al.*, How do tree structure and old age affect growth potential of California redwoods? *Ecol. Monogr.* **85**, 181–212 (2015).
60. I. J. Wright *et al.*, Relationships among ecologically important dimensions of plant trait variation in seven neotropical forests. *Ann. Bot.* **99**, 1003–1015 (2007).
61. A. B. Leslie, J. M. Beaulieu, P. R. Crane, M. J. Donoghue, Cone size is related to branching architecture in conifers. *New Phytol.* **203**, 1119–1127 (2014).
62. J. N. Owens, Constraints to seed production: Temperate and tropical forest trees. *Tree Physiol.* **15**, 477–484 (1995).
63. D. Barthélémy, Y. Caraglio, Plant architecture: A dynamic, multilevel and comprehensive approach to plant form, structure and ontogeny. *Ann. Bot.* **99**, 375–407 (2007).
64. T.-L. Ashman *et al.*, Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. *Ecology* **85**, 2408–2421 (2004).
65. D. W. Koenig, M. V. Ashley, Is pollen limited? The answer is blowing in the wind. *Trends Ecol. Evol.* **18**, 157–159 (2003).
66. I. M. Pérez-Ramos, J. M. Ourcival, J. M. Limousin, S. Rambal, Mast seeding under increasing drought: Results from a long-term data set and from a rainfall exclusion experiment. *Ecology* **91**, 3057–3068 (2010).
67. J. M. Knops, W. D. Koenig, W. J. Carmen, Negative correlation does not imply a trade-off between growth and reproduction in California oaks. *Proc. Natl. Acad. Sci. U.S.A.* **104**, 16982–16985 (2007).
68. S. J. Wright, C. P. van Schaik, Light and the phenology of tropical trees. *Am. Nat.* **143**, 192–199 (1994).
69. E. A. Graham, S. S. Mulkey, K. Kitajima, N. G. Phillips, S. J. Wright, Cloud cover limits net CO₂ uptake and growth of a rainforest tree during tropical rainy seasons. *Proc. Natl. Acad. Sci. U.S.A.* **100**, 572–576 (2003).
70. J. S. Clark, D. M. Bell, M. C. Kwit, K. Zhu, Competition-interaction landscapes for the joint response of forests to climate change. *Glob. Change Biol.* **20**, 1979–1991 (2014).
71. S. L. LaDeau, J. S. Clark, Rising CO₂ levels and the fecundity of forest trees. *Science* **292**, 95–98 (2001).
72. S. C. Thomas, Photosynthetic capacity peaks at intermediate size in temperate deciduous trees. *Tree Physiol.* **30**, 555–573 (2010).
73. D. R. Woodruff, B. J. Bond, F. C. Meinzer, Does turgor limit growth in tall trees? *Plant Cell Environ.* **27**, 229–236 (2004).
74. K. Steppe, Ü. Niinemets, R. O. Teskey, “Tree size- and age-related changes in leaf physiology and their influence on carbon gain” in *Size- and Age-Related Changes in Tree Structure and Function*, F. Meinzer, B. Lachenbruch, T. Dawson, Eds. (Springer Netherlands, Dordrecht, The Netherlands, 2011), pp. 235–253.
75. L. P. Mullin, S. C. Sillett, G. W. Koch, K. P. Tu, M. E. Antoine, Physiological consequences of height-related morphological variation in *Sequoia sempervirens* foliage. *Tree Physiol.* **29**, 999–1010 (2009).
76. D. T. Tissue *et al.*, Leaf respiration at different canopy positions in sweetgum (*Liquidambar styraciflua*) grown in ambient and elevated concentrations of carbon dioxide in the field. *Tree Physiol.* **22**, 1157–1166 (2002).
77. T. Zha, K.-Y. Wang, A. Ryyppö, S. Kellomäki, Needle dark respiration in relation to within-crown position in Scots pine trees grown in long-term elevation of CO₂ concentration and temperature. *New Phytol.* **156**, 33–41 (2002).
78. P. B. Reich, M. G. Tjoelker, J. L. Machado, J. Oleksyn, Universal scaling of respiratory metabolism, size and nitrogen in plants. *Nature* **439**, 457–461 (2006).
79. P. Meir, J. Grace, Scaling relationships for woody tissue respiration in two tropical rain forests. *Plant Cell Environ.* **25**, 963–973 (2002).
80. M. G. Ryan, Growth and maintenance respiration in stems of *Pinus contorta* and *Picea engelmannii*. *Can. J. For. Res.* **20**, 48–57 (1990).
81. H. Ishii, “How do changes in leaf/shoot morphology and crown architecture affect growth and physiological function of tall trees?” in *Size- and Age-Related Changes in Tree Structure and Function*, F. Meinzer, B. Lachenbruch, T. Dawson, Eds. (Springer, 2011), pp. 215–232.
82. C. H. Greenberg, Individual variation in acorn production by five species of southern Appalachian oaks. *For. Ecol. Manage.* **132**, 199–210 (2000).
83. D. Hirayama, S. Nanami, A. Itoh, T. Yamakura, Individual resource allocation to vegetative growth and reproduction in subgenus *cyclobalanopsis* (*Quercus*, Fagaceae) trees. *Ecol. Res.* **23**, 451–458 (2008).
84. J. J. Camarero, J. Albuixech, R. López-Lozano, M. A. Casterad, G. Montserrat-Martí, An increase in canopy cover leads to masting in *Quercus ilex*. *Trees (Berl.)* **24**, 909–918 (2010).
85. H. Davi *et al.*, Disentangling the factors driving tree reproduction. *Ecosphere* **7**, e01389 (2016).
86. D. Ascoli *et al.*, Inter-annual and decadal changes in teleconnections drive continental-scale synchronization of tree reproduction. *Nat. Commun.* **8**, 2205 (2017).
87. A. Hackett-Pain *et al.*, Temperature and masting control Norway spruce growth, but with high individual tree variability. *For. Ecol. Manage.* **438**, 142–150 (2019).
88. A. B. Berdanier, J. S. Clark, Divergent reproductive allocation trade-offs with canopy exposure across tree species in temperate forests. *Ecosphere* **7**, e01313 (2016).
89. D. M. Minor, R. K. Kobe, Masting synchrony in northern hardwood forests: Super-producers govern population fruit production. *J. Ecol.* **105**, 987–998 (2017).
90. D. M. Minor, R. K. Kobe, Fruit production is influenced by tree size and size-asymmetric crowding in a wet tropical forest. *Ecol. Evol.* **9**, 1458–1472 (2019).
91. D. W. Purves, J. W. Lichstein, S. W. Pacala, Crown plasticity and competition for canopy space: A new spatially implicit model parameterized for 250 North American tree species. *PLOS ONE* **2**, e870 (2007).
92. O. R. Jones *et al.*, Diversity of ageing across the tree of life. *Nature* **505**, 169–173 (2014).
93. M. Mencuccini, M. Oñate, J. Peñuelas, L. Rico, S. Munné-Bosch, No signs of meristem senescence in old Scots pine. *J. Ecol.* **102**, 555–565 (2014).
94. C. S. Thomas, Reproductive allometry in Malaysian rain forest trees: Biomechanics versus optimal allocation. *Evol. Ecol.* **10**, 517–530 (1996).
95. A. D. Roach, E. F. Smith, Life-history trade-offs and senescence in plants. *Funct. Ecol.* **34**, 17–25 (2020).
96. O. Kull, A. Koppel, Net photosynthetic response to light intensity of shoots from different crown positions and age in *Picea abies* (L.) Karst. *Scand. J. For. Res.* **2**, 157–166 (1987).

97. Y. Takemoto, M. S. Greenwood, Maturation in larch: Age-related changes in xylem development in the long-shoot foliage and the main stem. *Tree Physiol.* **13**, 253–262 (1993).
98. B. J. Yoder, M. G. Ryan, R. H. Waring, A. W. Schoettle, M. R. Kaufmann, Evidence of reduced photosynthetic rates in old trees. *For. Sci.* **40**, 513–527 (1994).
99. J.-C. Domec *et al.*, Maximum height in a conifer is associated with conflicting requirements for xylem design. *Proc. Natl. Acad. Sci. U.S.A.* **105**, 12069–12074 (2008).
100. D. Cohen, The optimal timing of reproduction. *Am. Nat.* **110**, 801–807 (1976).
101. Y. Iwasa, Dynamic optimization of plant growth. *Evol. Ecol. Res.* **2**, 437–455 (2000).
102. D. A. Roach, Evolutionary senescence in plants. *Genetica* **91**, 53–64 (1993).
103. W. D. Hamilton, The moulding of senescence by natural selection. *J. Theor. Biol.* **12**, 12–45 (1966).
104. P. B. Medawar, *An Unsolved Problem of Biology* (H. K. Lewis and Company, London, 1952).
105. C. G. Williams, Pleiotropy, natural selection, and the evolution of senescence. *Evolution* **11**, 398–411 (1957).
106. E. R. Everman, T. J. Morgan, Antagonistic pleiotropy and mutation accumulation contribute to age-related decline in stress response. *Evolution* **72**, 303–317 (2018).
107. D. W. Koenig, J. M. H. Knops, The mystery of masting in trees: Some trees reproduce synchronously over large areas, with widespread ecological effects, but how and why? *Am. Sci.* **93**, 340–347 (2005).
108. N. I. Lichti, M. A. Steele, H. Zhang, R. K. Swihart, Mast species composition alters seed fate in North American rodent-dispersed hardwoods. *Ecology* **95**, 1746–1758 (2014).
109. J. S. Clark *et al.*, Interpreting recruitment limitation in forests. *Am. J. Bot.* **86**, 1–16 (1999).
110. R. S. Snell *et al.*, Using dynamic vegetation models to simulate plant range shifts. *Ecography* **37**, 1184–1197 (2014).
111. R. A. Fisher *et al.*, Vegetation demographics in Earth System Models: A review of progress and priorities. *Glob. Change Biol.* **24**, 35–54 (2018).
112. W. Stephen *et al.*, Forest models defined by field measurements: Estimation, error analysis and dynamics. *Ecol. Monogr.* **66**, 1–43 (1996).
113. T. David *et al.*, Regeneration in gap models: Priority issues for studying forest responses to climate change. *Clim. Change* **51**, 475–508 (2001).
114. D. Marco *et al.*, Functional traits as predictors of vital rates across the life cycle of tropical trees. *Funct. Ecol.* **30**, 168–180 (2016).
115. S. C. Sillett *et al.*, Structure and dynamics of forests dominated by *Sequoiadendron giganteum*. *For. Ecol. Manage.* **448**, 218–239 (2019).
116. H. Liu *et al.*, Hydraulic traits are coordinated with maximum plant height at the global scale. *Sci. Adv.* **5**, eaav1332 (2019).
117. T. R. Feldpausch *et al.*, Height-diameter allometry of tropical forest trees. *Biogeosciences* **8**, 1081–1106 (2011).
118. J. S. Clark, A. E. Gelfand, *Hierarchical Modelling for the Environmental Sciences: Statistical Methods and Applications* (Oxford University Press on Demand, 2006).
119. A. Ledo *et al.*, Re-evaluation of individual diameter: Height allometric models to improve biomass estimation of tropical trees. *Ecol. Appl.* **26**, 2374–2380 (2016).
120. A. E. Zanne *et al.*, Three keys to the radiation of angiosperms into freezing environments. *Nature* **506**, 89–92 (2014).
121. Terrestrial Observation System, Data from “Woody plant vegetation structure.” National Ecological Observatory Network. <https://data.neonscience.org/data-products/DP1.10098.001>. Accessed 21 July 2021.