Limits to reproduction and seed size-number trade-offs that shape forest dominance and future recovery

The relationships that control seed production in trees are fundamental to understanding the evolution of forest species and their capacity to recover from increasing losses to drought, fire, and harvest. A synthesis of fecundity data from 714 species worldwide allowed us to examine hypotheses that are central to quantifying reproduction, a foundation for assessing fitness in forest trees. Four major findings emerged. First, seed production is not constrained by a strict trade-off between seed size and numbers. Instead, seed numbers vary over ten orders of magnitude, with species that invest in large seeds producing more seeds than expected from the 1:1 trade-off. Second, gymnosperms have lower seed production than angiosperms, potentially due to their extra investments in protective woody cones. Third, nutrient-demanding species, indicated by high foliar phosphorus concentrations, have low seed production. Finally, sensitivity of individual species to soil fertility varies widely, limiting the response of community seed production to fertility gradients. In combination, these findings can inform models of forest response that need to incorporate reproductive potential.
The emergence of extreme disturbance as a global change phenomenon\textsuperscript{1,2} highlights the need to understand how tree fecundity influences forest regeneration. Drought-induced forest diebacks are now observed in regions where they were rare in the past\textsuperscript{3}. Forest stands shaped by non-destructive surface fires are experiencing catastrophic crown fires, with post-burn seed production limited to survivors in unburned fragments (Fig. 1a). Species capable of vegetative regrowth will contribute to production limited to survivors in unburned fragments (Fig. 1a). Since Darwin pondered the rapid ascendance of angiosperms in from more than 12.1 million tree-years of observations on species differences in seed size are readily observed and the differing nutrient requirements of species play important roles. While species differences in seed size are readily observed and the subject of a large literature\textsuperscript{7}, differences in auxiliary structures like fruits and cones are considered a fundamental component of fitness\textsuperscript{12–15} that lacks systematic quantification for trees, the planet’s dominant life form\textsuperscript{16–18}. Here, we provide a global quantification of tree reproduction from more than 12.1 million tree-years of observations on 714 species. Results show that species differences are not bound by a strict size-numbers trade-off, instead ranging over ten orders of magnitude and mediated by foliar nutrients and soil fertility, with phylogeny accounting for some of the broad variation in fecundity.

A size-numbers trade-off could limit variation between species through allocation constraints associated with producing big seeds versus many of them\textsuperscript{5,19,20}. Because seed production depends on tree size\textsuperscript{21}, we standardize seed production per m\textsuperscript{2} of tree basal area. We define individual standardized production (ISP) as (mass per seed) × (mean seeds per tree basal area) or

$$ISP = m_i \times F_i$$

(1)

to for tree of species \(i\) with standardized seed production \(F_i = f_i / b_i\) for a tree with basal area \(b_i\). The estimate of seed number \(f_i\) incorporates year-to-year variation in seed production. Species seed production (SSP) is the expectation of ISP over trees of a given species (\(SSP = E_i(ISP_i) = m_i \times E_i(F_i)\), Methods). If the benefits of large seeds for attracting mutualist dispersers and increased seedling survival\textsuperscript{22} is offset by the cost of producing fewer of them, then SSP does not vary with seed size. But it does vary if producing larger seeds increases or decreases the net reproductive output summarized as ISP. This departure from the 1:1 trade-off is expressed on the proportionate (log\textsubscript{10}) scale as

$$SSP \propto m_i^\beta$$

(2)

$$\log_{10}SSP = \alpha + \beta \log_{10}m_i$$

where \(F_i = E_i(F_i)\) is the expected seeds per basal area for species \(s\), \(\alpha\) is the \(\log_{10}F\) for a species having seed size equal to 1 g, and \(\beta\) is the proportionate change in \(F_i\) for a proportionate increase in seed size. [Subscripts are hereafter omitted to reduce clutter.] The size-numbers trade-off predicts that \(\beta = 0\) or, equivalently, a slope of \(-1\) for \(\log_{10}m_i\) in Eq. (2). A value of \(\beta > 0\) means that numbers do not decline with seed size as steeply as predicted by the trade-off, i.e., a net (proportionate) gain in reproductive effort of \(\beta - 1\). Values of (\(\alpha,\beta\)) are unknown, as attempts to quantify species differences in SSP have been limited geographically and to few species\textsuperscript{20,23} due to missing information on numbers of seeds produced. Because large seeds may confer a competition benefit to seedlings within a crowded understory, while small seeds that are wind-dispersed can promote colonization of distant sites\textsuperscript{14,24}, we further evaluated the potential for a competition-colonization trade-off, examining the hypothesized link between competitive ability and wood density\textsuperscript{25,26}.

Species differences in seed size versus numbers could be affected by the costs of auxiliary reproductive structures\textsuperscript{27}. Total reproductive effort includes seeds and flowers supplied with nectar and nutrient-rich fleshy fruits that attract dispersers (e.g., Rosales, Ericales, Cornales, Aquifoliaceae, Magnoliids, and Lamiales). It includes cones defended with wood, armaments, and prodigious resin flows (e.g., Pinales) (Fig. 1b). Comprehensive mass and nutrient data for cones, fleshy fruits, nuts, capsules, and samaras are absent from trait data bases like TRY\textsuperscript{28}, nor is there a transparent means for comparing reproductive costs across diverse structures and provisioning. For these reasons, species differences in auxiliary structures like seeds and cones are compared here on a qualitative basis.

Limits to SSP could depend not only on the cost of auxiliary structures associated with seed production, but also on resources. Studies of nutrient effects are limited geographically and taxonomically, and results are equivocal\textsuperscript{29–33}. Through the assumption that reproductive allocation scales with net primary production (NPP)\textsuperscript{34–37}, current models assume that resources stimulate fecundity, without consideration of responses that
might come from variation within species (here, ISP) versus between species (here, SSP). Nutrient additions in orchard practice use ratios intended to balance demands for nitrogen (N), phosphorus (P), and potassium (K)29,38, the latter being especially important for fruit yield in agriculture, but less frequently reported in ecological studies39. Agricultural experience makes it clear that high-N fertilization can decrease reproductive yield40,41 due to allocation to vegetative growth. Variation between species could come from their differing nutrient demands, wherein species with high average foliar nutrients tend to occupy fertile sites34,42,43 and, thus, might be expected to produce more seed. Alternatively, species with high nutrient demands might preferentially allocate to growth and defense. Variation within species could come from phenotypic plasticity as genotype × environment (G × E) interactions. Species bearing large seeds and nutrient-rich fleshy fruits might be especially responsive to fertility variation, but data are lacking. Observed positive correlations between foliar nutrients and seed production in the same individuals over time44,45 does not mean that there is a positive association in nutrients and seed production taken over trees growing at different fertility levels. Our use of ISP (standardized for tree size) controls for responses that come from the fact that fertilized trees grow faster and thus are larger21,46, thus helping to isolate fertilization responses47 that are caused by increased seed production for a given tree size. Taken together, reproductive responses to fertility might be positive or negative, depending on allocation to growth and reproduction. As mentioned above in the context of current model assumptions, the implications of fecundity for landscape recruitment has to combine ISP with the turnover of species across environmental gradients, here termed community seed production (CSP) for the amount of seed produced per area of forest or woodland. Trees of the same species might produce more or less seeds on the richest sites, depending on partitioning between reproduction and growth.15 Species turnover influences CSP if the resource-conservative species that dominate nutrient-poor sites42,43,48 differ in their ISP from those on fertile sites. To be clear, we do not obtain CSP as an extrapolation of counts in seed traps. That practice would generate huge error due to the precise locations of seed traps, especially their siting directly below an individual that produces large seeds that almost never enter seed traps were they not directly below the tree. Reliable estimates of seed production per ha requires summing the production over all trees in the plot divided by the area of the plot (see Methods); this is the method used here for CSP. This synthesis addresses four basic questions, framed as hypotheses: (A) A size-numbers trade-off constrains species differences in SSP; (B) high auxiliary costs related to fleshy fruits and cones (Fig. 1b) and high nutrient requirements result in high or low SSP, depending on allocation trade-offs involving vegetative growth and defense; (C) ISP increases with soil fertility or not, again depending on species-specific resource allocation trade-offs; and (D) CSP increases or decreases with soil fertility due to the combined effects of within-species sensitivity (hypothesis C) and species turnover across gradients. Confirmation or rejection of these hypotheses is central to understanding the evolutionary selection pressures that have shaped the dominant forest trees of the world and is likely key to mitigating their future losses and recovery with global change. To test these hypotheses, we synthesize tree fecundity, foliar nutrients, and cation exchange capacity (CEC) (Supplementary Fig. 1)49, a widely used fertility indicator related to soil capacity to bind exchangeable ions (e.g., calcium, magnesium, sodium, potassium, ammonium, and iron) that are essential to plant function50,51. CEC has an advantage over soil carbon or nitrogen that are high not only on fertile sites, but also in saturated, nutrient-poor peatlands that dominate many important ecosystems52. The Masting Inference and Forecasting (MASTIF) network provides a global synthesis of individual tree-year observations and modeling framework that estimates effects on fecundity that accounts for dependence in data. Low signal-to-noise in seed production data requires massive sample sizes to estimate effects21, represented here by 12.1 M observations on 714 species from all vegetated continents. Valid estimates of fecundity responses to foliar nutrients and CEC accommodate dependence in seed observations between trees and seed traps and within trees and seed traps over time, the quasi-synchronous, quasi-periodic variation known as masting. Individual tree-year observations are modeled jointly in a hierarchical Bayesian state-space model detailed in Clark et al.53. Results Rather than being constrained to constant values by a size-numbers trade-off (hypothesis A), species seed production per basal area (SSP) spans ten orders of magnitude and increases with seed size (β = 0.546 ± 0.042, Fig. 2a). Across all species in the synthesis, the expected seed number per m² of basal area for a seed size of 1 g is \( E(10^4) = 19,700 ± 2920 \) (Eq. (2) and Methods section). For a small-statured species this amounts to 0.62 kg at a diameter of 20 cm. For a large species, this is 15 kg for a diameter of 100 cm. For a small-seeded species of, say, 0.001 g (e.g., Betula), this amounts to annual averages of >50,000 seeds at 40 cm and >300,000 seeds at 100 cm. If SSP is regulated by a proportionate sacrifice in seed size as the cost of producing more of them, then SSP would not vary with seed size (dashed line in Fig. 2a). Equivalently, there would be a proportionate decline in seed numbers with seed size (slope = −1, dashed line in Supplementary Fig. 2). Instead, seed numbers decline with seed size at less than half the proportionate rate for a slope of \( \beta = -1 = -0.454 ± 0.042 \) (Supplementary Fig. 2). This departure from expectation comes from variation in SSP that is related to species traits and partly captured by phylogeny. Species differences in SSP include a phylogenetic component (Fig. 2b, Pagel’s λ = 0.60, p < 10⁻⁵, n = 482). Group seed production (GSP, methods) was used to compare fecundity between different taxonomic groups, with higher average values for angiosperms than gymnosperms (Supplementary Fig. 3a). The possibility that auxiliary costs weigh against SSP (hypothesis B) is consistent with low SSP for cone-bearing Pinales (brown labels in Fig. 2b). In angiosperms, the Fagales have uniformly high SSP, despite seeds ranging from small Betula (1–6 × 10⁻⁴ g) to large Quercus (0.7–7 g). Cecropia, Miconia and the Fabales have notably low SSP. Angiosperms with fleshy fruits (green labels in Fig. 2b) do not exhibit lower SSP than other angiosperms on the whole (Supplementary Figure 3b). Some groups are predominantly high (e.g., Ericales/Cornales), low (e.g., Vismia, Cordia, and Campanulids) or mixed (e.g., Rosales and Magnoliids). At the species level, SSP declines with increasing mean foliar P after controlling for phylogeny and leaf habits (hypothesis B). The surface in Fig. 3 decreases four orders of magnitude from >10,000 at the lowest foliar P levels to <10 g per m² basal area at the highest foliar P. By contrast, foliar N has no discernible effects on SSP. Broadleaf species span the widest range of concentrations and contribute most to the declines in SSP with increasing P. Wood density did not explain SSP variation (Supplementary Table 5). Within species (hypothesis C), phenotypic plasticity in ISP to soil fertility, hereafter \( \beta_{ISP} \), varies widely between species, but with phylogenetic coherence (Fig. 4). In the well-represented Fagales, fertility responses in Castanea and the white and cerris oaks (sections Quercus and Cerris) are negative, while red oaks (section...
Lobatae) are positive. This divergence coincides with the tendency for many red oaks (Lobatae) to occupy more fertile soils. Increasing CEC reduces ISP in the angiosperm groups Fabales, Magnoliids, Acer, and Fraxinus, while stimulating ISP in Ericales/Cornales, and having mixed effects in Rosales and Betulaceae. Gymnosperm responses are primarily decreasing for Tsuga, Picea, Cedrus, and soft pines (section Haploxylon), and mixed for hard pines (section Diploxylon) and Abies. Despite species variation, the reconstructed ancestral lineage for gymnosperms is negative (purple ancestral branches marked by red dashed line in Fig. 4). By contrast, there is no angiosperm-wide tendency to produce fewer seeds on high-fertility sites. Foliar nutrients do not explain these species differences in response to fertility gradients.

Community seed productivity (CSP) does not respond to soil fertility (hypothesis D), due to the neutralizing effects of diverging responses within species that occupy a range of CEC levels (Supplementary Fig. 4) and to the turnover of species across gradients. The differing sensitivity to CEC within species combined with the species turnover results in seed production that is as high on low-fertility as on high-fertility sites.

**Discussion**

Species seed production (SSP), measured as seed size × seed number per basal area, varies over ten orders of magnitude (Fig. 2), far from the equity expected from a strict size-numbers trade-off. Ecologists have long recognized a potential trade-off...
Fig. 3 Effects of foliar nutrients on seed production. Effects of foliar nitrogen (N) and phosphorus (P) on SSP (g seed per m² tree basal area) from the model in Supplementary Table 1 plotted for the broadleaf deciduous leaf habit (other leaf types exhibit similar patterns). The convex hull for the surface is restricted to the data coverage. Symbols indicate leaf habit, including broadleaf deciduous (BD), broadleaf evergreen (BE), needleleaf evergreen (NE), and scalelike evergreen (SE).

between producing few large seeds, each provisioned to attract dispersers and/or promote high seedling survival, versus many small seeds that might offset low survival with expanded opportunities to reach suitable sites. Evaluating whether or not this compromise between size and numbers limits species variation in SSP is made possible by a large representation of 12.1 M tree-years from 714 species and an analytical framework that admits tree attributes (size and competition), environmental variation, and dependence between trees and within a tree across years. Results show that the increased seed-mass production realized by species that invest in large seeds is mediated by resource access and the auxiliary costs of woody cones.

The expected annual productivity of 19,700 ± 2920 seeds per m² basal area at a seed size of 1 g provides a benchmark for basic demographic and life-history understanding that has thus far been absent for trees. For a moderate size tree (e.g., 30 cm diameter) that produces seeds of a moderate size (e.g., 10⁻² g) this amounts to annual mean production of > 10,000 seeds. The magnitude of this estimate puts this life form far outside the range of most species, including most herbaceous plants. It is expected to drive inordinate selection pressures to offset seed input with mortality rates that would be needed for quasi-stable population densities over time.

There is a size-numbers trade-off, but it is not symmetric: species that invest in large seeds produce more seeds than expected from a strict 1:1 trade-off. The shallow slope between seed number and size (Supplementary Fig. 2), roughly half that expected for a strict trade-off, suggests a cost savings as reproductive investment is packaged into a smaller number of seeds. If the cost of reproduction increases as reproductive investment is packaged into a smaller number of seeds, then the benefit for large seeds increases according to the slope in Fig. 2a. A fixed cost associated with the production of each seed would be consistent with this shallow slope; the diversity of structures used to support reproduction suggests multiple contributing factors.

Of course, the slope of the size-numbers relationship between species does not represent strength of selection for size and numbers within species, which depends on a broad range of traits summarized in part, by phylogeny. The advantages of producing larger/fewer acorns in Quercus cannot be equated with the advantages of producing larger/fewer fleshy fruits or cones, due to the differing costs and benefits associated with each of these structures. Low SSP in gymnosperms is consistent with the investment in cones that can exceed seed mass by 30-fold in Fig. 1b. But the generally low SSP in gymnosperms does not imply a fitness disadvantage for large cones. Well-defended seeds certainly arose under selection pressure for the advantages they confer against predation. The divergent evolutionary options available to angiosperms and gymnosperms may have constrained reproductive potential for these two groups in different ways; there is no evidence that angiosperms that produce expensive, fleshy-fruits realize lower SSP than other angiosperms (Fig. 2b and Supplementary Fig. 3).

Phylogenetic differences (Fig. 2b and Supplementary Fig. 3) bear on Darwin’s ‘abominable mystery,’ the advantages that might explain the explosion of angiosperms in the Cretaceous. The rise of angiosperms has been attributed to rates of growth, photosynthesis, and diversification, all of which tend to be higher than in gymnosperms. Capacities to harbor nutrients and generate positive feedbacks with soil fertility through litter production and to reproduce vegetatively could contribute to angiosperm success. Aridification at the end of the Eocene may have contributed to gymnosperm extinctions. While all of these differences are plausible contributions to angiosperm success, the fact that angiosperms dominate gymnosperms in SSP represents a more direct connection to fitness than most of these mechanisms.

The negative effect of fertility on seed production emerges in the low SSP for P-demanding species (Fig. 3). Global change studies have steadily improved our understanding of fertility effects on tree growth, foliar nutrients, and primary productivity, suggests that angiosperms could contribute to SSP. The species-level association between high foliar P and low SSP is consistent with a species-level trade-off between growth and reproduction. P-rich ribosomal RNA required for rapid cell division can stimulate growth at the expense of reproduction. Moreover, seed production is expensive in resource-acquisitive species if nutrient concentrations in seeds increase with foliar nutrients. The decline in SSP with foliar P is consistent with the fact that angiosperms dominate gymnosperms in SSP represents a more direct connection to fitness than most of these mechanisms.
Understanding future forests requires integration of seed production estimates here with drought- and fire-tolerance, ability to resprout following dieback, and changes in forest structure and composition. While tree growth and survival have long been quantifiable using traditional methods, they cannot be used to anticipate reforestation potential without knowledge of fecundity. Seed limitation takes on new urgency, as highlighted by fires of uncommon severity in fuels cured by multi-year droughts that leave only remnants of reproductive trees. The relative benefits of size versus numbers of seeds for seedling success in natural regeneration will shift under novel combinations of temperature and moisture. The positive effects of nutrient availability on reproduction assumed in current models are sensible for tree growth and NPP, but not for seed production. The global relationships quantified from this synthesis bring not only a previously unmeasured dimension of forest response; they also will allow us to leverage existing knowledge of growth and survival with the missing link to regeneration, that of tree fecundity.

Methods

Fecundity data. Fecundity data from the Masting Inference and Forecasting (MASTIF) network include two types of raw data, seed traps (ST) and crop counts (CC). Each observation references a tree-year. Data include longitudinal (repeated) observations on individual trees and opportunistic observations that come through the iNaturalist project. ST data consist of numbers of seeds that accumulate annually in mapped seed traps on forest inventory plots. A fitted dispersal kernel relates seed counts to mapped trees, accounting for uncertainty in seed transport and Poisson seed counts. Fecundity production (Fig. 4). The global relationships quantified from this synthesis bring not only a previously unmeasured dimension of forest response; they also will allow us to leverage existing knowledge of growth and survival with the missing link to regeneration, that of tree fecundity.
Fig. 5 The MASTIF model, summarized from Clark et al.33, includes three levels, observed responses (above), process, and parameters (part of the posterior distribution, middle), and predictors (below). The data model for observed responses includes uncertainty that comes from seed dispersal (seed traps), the fraction of the crop that can be observed (crop counts), and detection of mature status. The process model describes change in maturation status $p_{ijs}$, and, once mature, conditional fecundity $\psi_{ijs}$. Fitted coefficients for conditional fecundity $\beta^f$ and maturation probability $\beta^m$ describe how predictor variables in red affect maturation and fecundity. Error in the process model is absorbed by process error variance $\sigma^2$. Predictors are held in a design matrix $x_{ijs}$ for conditional fecundity. Diameter $d_{ij}$ is the predictor for maturation status. Additional subscripts for location $j$ and species $s$ in the main texts are suppressed to reduce clutter.

- **Seed traps**: Crop counts: Maturation status: $\{y_{ijs}, x_{ijs}, d_{ij}\}$
- **Conditional fecundity**: Maturation: $\psi_{ijs}$
- **Parameters**: $\{x_{ijs}, d_{ij}\}$
- **Environment, individual**: $x_{ijs}$, $d_{ij}$

**Fecundity modeling and inference.** We estimate tree fecundity with a hierarchical Bayes state-space model33 that incorporates effects of tree attributes with environment to infer effects on maturation and conditional fecundity (Fig. 5). The methodology detailed in33 builds on models that have provided reliable estimates in many forest types107−105. The analysis in33 goes further in showing that the MASTIF model recovers the parameters controlling maturation and fecundity in simulated data, and it accurately predicts the seed-trap data that are used to estimate parameters. To allow for uncertain identification of seeds from trees of the same genus and for dependence within trees over time and between trees, all tree-years of a genus are modeled jointly136,98. For each tree $i$ of species $s$ at stand $j$ in year $t$, the expected fecundity is the product of maturation probability and conditional fecundity,

$$E(f_{ijs}) = \bar{p}_{ijs} \psi_{ijs}$$

(4)

Once a tree has been observed to produce seed in a given year $t$, then it is known to be mature in subsequent years $t > t$. A tree never having been observed to produce seed in the past could be immature or not. Maturation probability $\bar{p}_{ijs}$ is the probability that an individual is in the mature state,

$$\bar{p}_{ijs} \sim \text{Bernoulli}\left(\rho_{0,0,1} + (1 - \rho_{0,0,1})\rho_{1,0,1} + \Phi(\beta^m_{s}\rho_{0,0,1} + \beta^m_1 d_{ij,1})\right)$$

(5)

where $\Phi(\cdot)$ represents the standard normal cumulative distribution function (CDF) of the probit model, which is determined by tree diameter $d_{ij,1}$. Note that coefficients for intercept and diameter $\beta^m_{s} = \gamma_{s} + \beta_{s,1}$ influence $\rho_{0,0,1}$ only at the transition to the mature state, i.e. $[\rho_{0,0,1} > 0, \rho_{0,0,1} = 1]$. Conditional fecundity depends on predictors, individual effects, year effects, and error,

$$\log(\psi_{ijs}) = \gamma_{s} + \beta^m_{s} d_{ij,1} + \gamma_{js} + \gamma_{ts} + \epsilon_{ijs}$$

(6)

where $x_{s,js}$ is a design matrix holding individual attributes and environmental conditions (see Individual, habitat and climate covariates), and $\beta^m_{s,1}$ are fixed-effects coefficients. $\beta^m_{s}$ is the random effect for tree $i$ of species $s$ at stand $j$. $\gamma_{js}$, $\gamma_{ts}$ are year effects that are random across groups $g$ and fixed for year $t$ to account for interannual variation that is not fully captured by climate anomalies. Group membership for year effects ($g|y_i$) is defined by the species-ecoRegion combination35; quasi-synchronicity can vary between species and ecoRegions. There is a noise term $\epsilon_{ijs}$. The primary components are summarized in Fig. 5. Variable selection is based on model fit using the Deviance information criterion (DIC) and data coverage, which depends on the range of variation in each predictor and species. Model implementation is open-access with R package MASTIF, with full algorithm details provided in135.

**Individual, species, group, and community seed production.** Individual standardized production (ISP) is expressed as relative to basal area standardized for tree size12; it is the product of mass per seed $m_i$, times seeds per tree divided by tree basal area, having units $g \cdot m^{-2} \cdot yr^{-1}$. Each tree-year has an associated posterior mean estimate $f_{ijs}$ at stand $j$. ISP combines posterior mean estimates with their uncertainties, as an expectation over years:

$$\text{ISP}_{ys} = m_i \frac{w_y}{b_y} \sum_{j} w_y f_{ijs}/2 \omega_y w_y$$

(7)

where $m_i$ is seed mass (g), $b_y$ is basal area (m$^2$), and weight $w_y$ is the inverse of the coefficient of variation (CV) for the estimate,

$$w_y = CV^{-1}_{yijs} = \bar{f}_{ijs}^\gamma/b_y$$

(8)

and $\gamma_{ys}$ is the standard error of the estimate. The CV$^{-1}$ is used instead of the inverse of variance, because the mean tends to scale with variance. Low values for $f_{ijs}$ are noisy and less important than high values, which are emphasized by the CV. Estimates of seed number $\hat{f}_{ijs}$, its standard error $\gamma_{ys}$, and CV are all dimensionless. All estimates are time averages across annual estimates, so we hereafter omit yr$^{-1}$ from dimensions. Therefore, ISP has the units of g$\cdot$m$^{-2}$.
Species seed production (SSP) is the expectation taken over individual tree ISP values for a species $i$,

$$\text{SSP}_i = \frac{\sum_{j=1}^{n_k} w_{ij} \text{ISP}_{ij}}{\sum_{j=1}^{n_k} w_{ij}}$$

where $w_{ij}$ is defined as the inverse $CV_{ip}$ for individual $i$. Analyses of SSP are done on the proportionate (log) scale to avoid dominance of results by species having highest seed production. Visualizations are based on log$_{10}$ to facilitate interpretation of scale.

Group seed production (GSP) was evaluated to determine differences between angiosperms versus gymnosperms and between the cone-producing Pinales, large-seeded Fagales, fleshy-fruited members of all groups, and remaining species. For comparisons of species groups $k$, we evaluated means and uncertainties:

$$\text{GSP}_k = \frac{\sum_{i,j} w_{ij} \text{ISP}_{ij}}{\sum_{i,j} w_{ij}}$$

with standard error,

$$\text{SE}(\text{GSP}_k) = \frac{1}{n_k} \sqrt{\sum_{i,j} w_{ij}^2 \text{ISP}_{ij}^2}$$

where $n_k$ is the number of observations included in the estimate. The comparisons between the groups is shown in Supplementary Fig. 3.

To understand the collective impacts of soil fertility on seed production, we calculated community seed production (CSP) by extending tree reproduction to the stand level by summing fecundity over all trees and species and dividing by plot area:

$$\text{CSP} = \frac{1}{A_1} \sum_{i=1}^{n} \text{ISP}_{ij}$$

where $A_1$ is plot area ($ha$) for each plot. Note that we did not standardize ISP by basal area to yield instead seeds per area of forest floor. The CSP thus represents stand production, much like NPP represents stand vegetative production. Because calculation of CSP requires plot area, analysis on CSP is based on inventory plots.

**Phylogeny, foliar nutrients, and soil fertility.** Phylogeny was obtained for 482 species (67% of total) from [16]. To determine if SSP can be explained by shared ancestry, we estimated the phylogenetic signal using Pagel’s $\lambda$ [17], which ranges from 0 (independence over species) to 1 (related species completely resemble each other). Continuous character mapping was used to visualize the phylogenetic signal in Fig. 2 using R package phytools [18]. We explored the linkage between foliar nutrients and species difference in seed production using the phylogenetic regression to account for species relatedness, where the correlation between species increases proportionally with the branch length (i.e., from the root to the most recent common ancestor) in the phylogeny [19,128]. Phylogenetic regression was implemented using R package phylolm [21] for 427 species that has foliar nutrients data (89% of the 482 species with phylogeny).

We estimated within-species response to CEC, that is, $\beta_{c}$ in Eq. (6), for 141 species that has sufficient range of variation across the soil fertility (CEC) gradient; $\beta_{c}$ coefficients cannot be estimated for species that are limited to one or a few sites. We quantified phylogenetic coherence in $\beta_{c}$ (Fig. 4) between species following the same procedure used for SSP. To determine how the ability to estimate $\beta_{c}$ depended on the range in CEC over which it was observed, we plotted predicted seed production against CEC while holding all other covariates constant (i.e., half of maximum diameter, medium shade, and mean temperature and predicted seed production against CEC while holding all other covariates constant). Finally, we evaluated the effects of soil fertility on stand productivity (i.e., CSP) using regression. The analysis is restricted to sites having all trees sampled within a known area, which is true for all inventory studies with seed-traps.

**Calculation of seed number per g.** Provided the estimate of $a$ does not have large error, the expected seeds per basal area at seed mass = 1 g & for the log$_{10}$log$_{10}$ regression is approximated with two terms from the Taylor expansion

$$E(10^4) = 10^4 \left[1 + \frac{\ln 10}{2} \pm 10^4 \sigma_j^2 \right]$$

where $a = 4.29$ and $\sigma_j = 0.065$ are the estimate and standard error for parameter $a$, and the constant $l = \log(10)$. For this model $a > 3p$, this approximation is confident at 19,720 ± 2,920. For a tree of given size, its seed production is 19,720 x its basal area.

**Seed size-number trade-offs within orders.** We have included taxonomic rank (i.e., order) as a factor level, including an interaction with seed size, in the regression. We found that SSP was not constrained by the strict 1:1 trade-off within each order (Supplementary Table 4).

### References

1. Curtis, P. G., Slay, C. M., Harris, N. L., Tyukavina, A. & Hansen, M. C. Classifying drivers of global forest loss. Science 361, 1108–1111 (2018).
2. Duane, A., Castellnou, M. & Brotons, L. Towards a comprehensive look at global drivers of novel extreme wildfire events. Clim. Change 165, 43 (2021).
3. Allen, C. D. et al. A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. For. Ecol. Manag. 259, 660–684 (2010). Adaptation of Forests and Forest Management to Changing Climate.
4. Franklin, J. F., Mitchell, R. J. & Paik, B. J. Natural disturbance and stand development principles for ecological forestry. General Technical Report. NRS-19. Newtown Square, PA: US Department of Agriculture, Forest Service, Northern Research Station. 44. p. 19 (2007).
5. Westoby, M., Jurado, E. & Leishman, M. Comparative evolutionary ecology of seed size. Trends Ecol. Evol. 7, 368–372 (1992).
6. Smith, C. C., & Fretwell, S. D. The optimal balance between size and number of offspring. Am. Nat. 108, 499–506 (1974).
7. Lord, J., Westoby, M. & Leishman, M. Seed size and phylogeny in six temperate floras: Constraints, niche conservatism, and adaptation. Am. Nat. 146, 349–364 (1995).
8. Moles, A. T. et al. Global patterns in seed mass in Germany - distribution patterns and environmental correlates. Geobiota 31, 457–468 (2008).
9. Tautenhahn, S. et al. On the biogeography of seed mass in Germany - distribution patterns and environmental correlates. Geobiota 31, 457–468 (2008).
10. Lidgard, S., & Crane, P. R. Quantitative analyses of the early angiosperm radiation. Nature 331, 344–346 (1988).
11. Crisp, M. D. & Cook, L. G. Cenozoic extinctions account for the low diversity of extant gymnosperms compared with angiosperms. New Phytol. 192, 997–1009 (2011).
12. Stearns, S. C. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51, 3–47 (1976).
13. Grubb, P. J. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Ecol. Monogr. 57, 107–145 (1977).
14. Clark, J. S., LeDau, S. & Ilan, E. Feecundity of trees and the colonization-competition hypothesis. Ecol. Monogr. 74, 415–442 (2004).
15. Salguero-Gomez, R. et al. Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. Proc. Natl Acad. Sci. USA 113, 230–235 (2016).
16. Thomas, S. C. Age-Related Changes in Tree Growth and Functional Biology: The Role of Reproduction, p. 33–64 (Springer Netherlands, 2011).
17. Wenk, E. H. & Falster, D. S. Quantifying and understanding reproductive allocation schedules in plants. Ecol. Evol. 5, 5521–5538 (2015).
18. Bar-On, Y. M., Phillips, R. & Milo, R. The biomass distribution on earth. Proc. Natl Acad. Sci. USA 115, 6506–6511 (2018).
19. Turnbull, L. A., Rees, M. & Crawley, M. J. Seed mass and the competition/ colonization trade-off: a growing experiment. J. Ecol. 87, 899–912 (1999).
20. Moles, A., Falster, D., Leishman, M. & Westoby, M. Small-seeded species produce more seeds per square metre of canopy per year, but not per individual per lifetime. J. Ecol. 92, 384–396 (2004).
21. Qiu, T. et al. Is there tree senescence? the fecundity evidence. Proc. Natl Acad. Sci. USA 118, e2106130118 (2021).
22. Westoby, M., Falster, D. S., Moles, A. T., Vesk, P. A. & Wright, I. J. Plant ecological strategies: Some leading dimensions of variation between species. Annu. Rev. Ecol. Syst. 33, 125–159 (2002).
88. Clark, J. S. et al. The impacts of increasing drought on forest dynamics, structure, and biodiversity in the united states. Glob. Change Biol. 22, 2325–2352 (2016).

89. Gazol, A., Camarero, J. J., Anderegg, W. R. L. & Vicente-Serrano, S. M. Impacts of droughts on the growth resilience of northern hemisphere forests. Glob. Ecol. Biogeogr. 26, 166–176 (2017).

90. Stephens, S. L. et al. Managing forests and fire in changing climates. Science 342, 41–42 (2013).

91. North, M. P. et al. Tamm review: reforestation for resilience in dry western u.s. J. Ecol. 115, 85–88 (2017).

92. Revell, L. J. phytools: an r package for phylogenetic comparative biology (and other things). Methods Ecol. Evol. 3, 217–223 (2012).

93. Feinberg, J. Phylogenies and the comparative method. Am. Nat. 125, 1–15 (1985).

94. Martins, E. P. & Hansen, T. F. Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. Am. Nat. 149, 464–467 (1997).

95. Tung Ho, L. S. & Ané, C. A linear-time algorithm for gaussian and non-gaussian trait evolution models. Syst. Biol. 63, 397–408 (2014).

96. Clark, J. S. Data from: continent-wide tree fecundity driven by indirect climate effects https://doi.org/10.7924/r4348ph5t (2020).

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Author contributions

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

Competing interests

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