Do trees with larger seeds produce fewer of them and how does this impact forest regrowth and species dominance?

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

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Is the number of tree seeds produced limited by the size of the seeds? Do some circumstances favor vegetative growth over reproduction? Are differences related to soil fertility?

For recolonization after extreme weather events and disturbances, tree species depend on seed production and dispersal from surviving individuals. The authors evaluated whether species seed production (SSP) was constrained by a trade-off between the size and number of seeds produced, and whether SSP differences were related to resource allocation between growth/defense and seed production. They investigated whether individual standardized production increased with soil fertility and whether this depended on resource allocation differences. Finally, they examined whether community seed production was positively or negatively related to soil fertility.

Did seed production decrease proportionally with increasing seed size? What variables affected the relationship?

- Species seed production was not constrained by size. Seed number declined with seed size, but at less than half the expected proportionate rate.
- Seed production was related to phylogeny, tree species fecundity was higher, on average, for some taxonomic groups regardless of seed size. However, there appears to be a cost associated with producing large seeds such as cones, in some taxonomic groups.

Did soil fertility affect seed production? Were there other factors that were more important?

- Individual standardized production (ISP) differed across soil fertility levels and varied among species. Increasing cation exchange capacity decreased ISP in some phylogenetic groups and increased ISP in other groups. Differences were not related to foliar nutrients.
- Community seed productivity was not related to soil fertility. Within species that occur over a range of soil fertility levels, responses to soil cation exchange capacity differed. Species composition also differed across soil fertility gradients.

Is there a general relationship to describe the total seed production for a given size tree?

- For seeds 1g in size, the expected number of seeds per m^2 of basal area was 19,700±2920 for seed size across 714 tree species. This benchmark provides researchers a way to estimate fecundity of individual trees when tree and seed sizes are known.
- Researchers can use deviation from the general tree size seed size fecundity relationship as a starting point for investigations into tradeoffs or limitations that occur for specific seed types or under certain conditions.

Do species with specific nutrient requirements differ from the general pattern?

- Species that require high levels of P tend to have lower SSP. High foliar P levels can stimulate vegetative growth instead of reproductive output, and if P levels in seeds increase with levels in foliage, reproduction can have increased costs.

What do the model results tell us about the cost of seed production and seed size?

- The shallow slope between seed number and size provides evidence that there is a lower cost associated with packaging reproductive output in fewer larger seeds. However, this may differ among phylogenetic groups. Within the angiosperms, those with large seeds do not have lower SSP but gymnosperms, which all produce large cones, have generally lower SSP.

How does tree fecundity impact the forest community as a whole?

- Forest success or failure after extreme disturbances will depend on species fecundity as well as on the potential for vegetative regrowth and resprouting. Understanding fecundity of trees by species and phylogenetic groups will be important for natural regeneration and reforestation plantings.
- The large numbers of seeds produced by trees play an important role in forest food webs. Masting, variability in the seed production among years, is likely driven by selection pressures to balance seed input with survival at a tree level. At the forest level seed production must be great enough to sustain seed loss and predation and balance tree mortality for species to sustain population densities.

Research Approach/Methods

- The authors modeled conditional fecundity and maturation for 714 tree species with a Bayes state-space hierarchical model that inferred the effects of tree attributes and environmental factors. Variable inclusion and model fit were based on deviance information criterion (DIC).
- Researchers used two types of fecundity data from the Masting Inference and Forecasting (MASTIF) network: seed trap counts, which are the number of seeds collected in a forest plot in

a year, and crop counts, which enumerate reproductive structures in a portion of the crop and extrapolate to the entire crop.

- The authors included model covariates that might explain differences among trees and species, including diameter, shading, temperature, moisture deficit, soil and terrain. These represented individual, climate, and habitat attributes.
- For each tree species, the authors used actual or estimated seed dry mass, foliar nitrogen, P concentration, leaf habit, fruit type, and wood density.
- The researchers investigated whether there were phylogenetic differences in SSP, the use of soil nutrients, and the relationship between foliar nutrients and seed production.

Keywords tree species fecundity, seed size-number trade-offs, forest recovery, forest regeneration, individual standardized production, species seed production, community seed production, cation exchange capacity

Images

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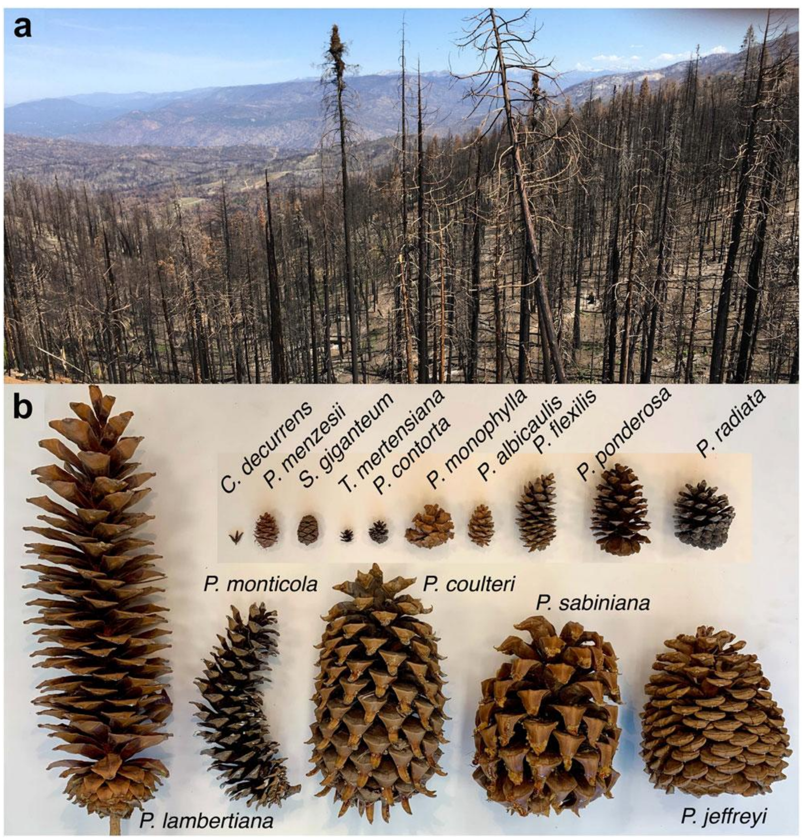

Figure 1 in Qui et al. 2022. Seed production quantifies forest regeneration potential. Regeneration of forests devastated by multi-year drought and fire depend on a vastly diminished seed supply. a Seed production is limited to unburned landscape fragments in the Sierra Nevada mixed conifer zone following 2020 burns at a Masting Inference and Forecasting network (MASTIF) and National Ecological Observatory Network (NEON) site (Shaver Lake, CA). b Total reproduction includes not only seeds, but also defenses, including wood, spines, and resin flow in conifer cones; examples from the heavily burned

Sierra Nevada and Coast ranges include Calocedrus decurrens, Pinus albicaulis, P. contorta, P. coulteri, P. flexilis, P. lambertiana, P. monophylla, P. monticola, P. ponderosa, P. radiata, P. sabiniana, Pseudotsuga menzesii, Sequoiadendron giganteum, and Tsuga mertensiana. Mass fractions for seeds to seeds plus cones ranges from 3% for P. radiata, P. contorta, P. coulteri, and P. sabiniana to 61% for C. decurrens. The largest cone in b (Pinus lambertiana) is 46 cm. Photo credits: James S. Clark and Jordan Luongo.

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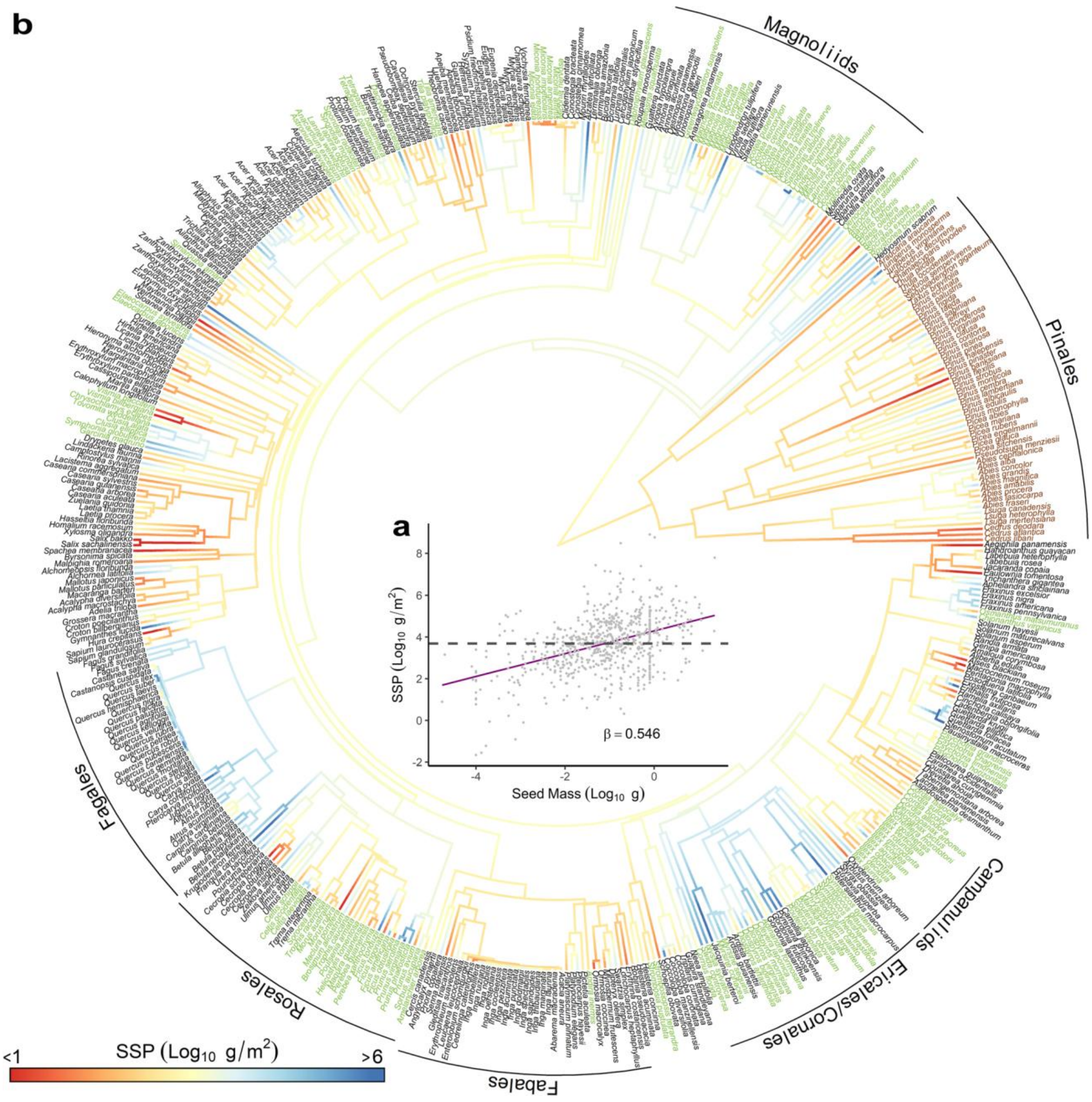

Figure 2 in Qui et al. 2022. Seed size-number trade-offs and species seed production. a Species seed production (SSP, g seed per m2 tree basal area) is not constrained by the strict size-number trade-off (dashed line with a slope of zero). Instead, it varies over ten orders of magnitude and has a positive correlation with seed mass across 714 tree species (log10SSP ¼ 4:29 þ 0:546 _ log10m, R2 =0.189, p <

10−15, n = 714). b SSP exhibits phylogenetic coherence for 482 species having phylogeny data (68% of species). Brown and green text highlight species that produce coniferous cones and fleshy fruits, respectively. The phylogenetic signal is estimated using Pagel's λ = 0.60 (p < 10−9, n = 482).

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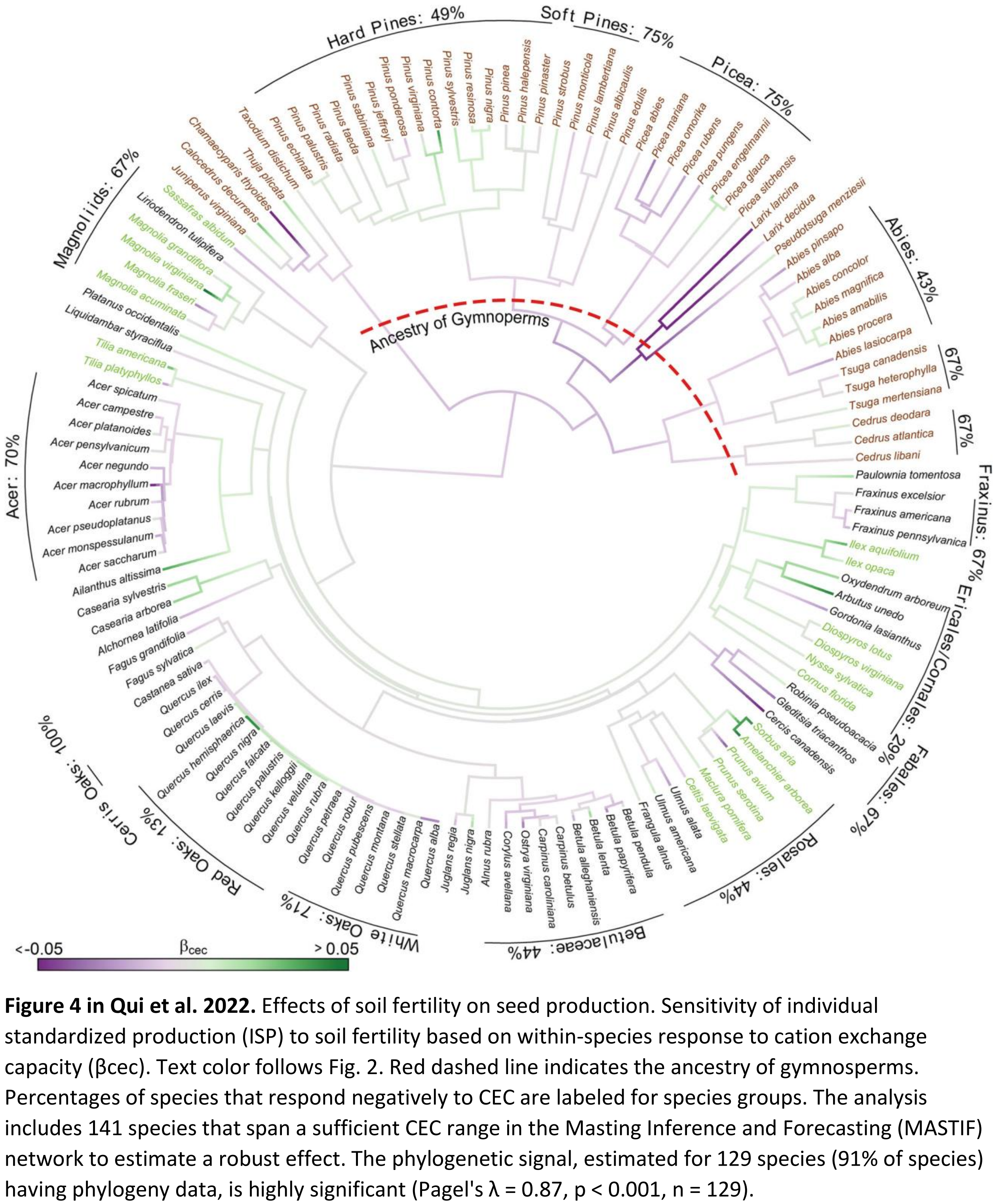

Figure 4 in Qui et al. 2022. Effects of soil fertility on seed production. Sensitivity of individual standardized production (ISP) to soil fertility based on within-species response to cation exchange capacity (βcec). Text color follows Fig. 2. Red dashed line indicates the ancestry of gymnosperms. Percentages of species that respond negatively to CEC are labeled for species groups. The analysis includes 141 species that span a sufficient CEC range in the Masting Inference and Forecasting (MASTIF) network to estimate a robust effect. The phylogenetic signal, estimated for 129 species (91% of species) having phylogeny data, is highly significant (Pagel's λ = 0.87, p < 0.001, n = 129).

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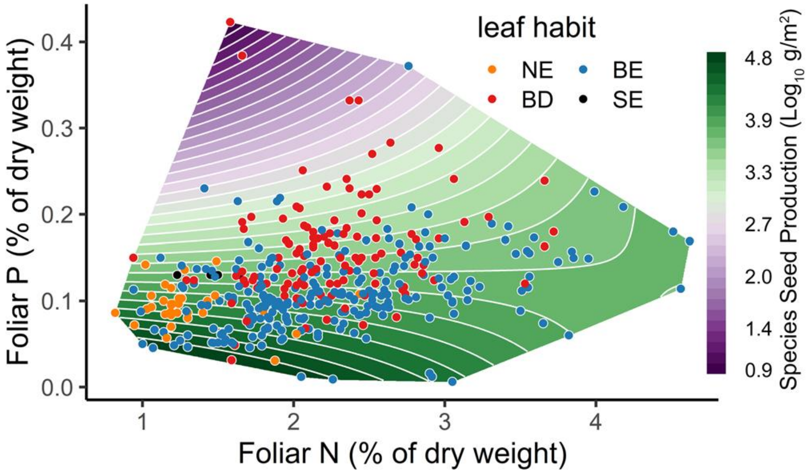

Figure 3 in Clark et al. 2022. Effects of foliar nutrients on seed production. Effects of foliar nitrogen (N) and phosphorus (P) on SSP (g seed per m2 tree basal area) from the model in Supplementary Table 1 plotted for the broadleaf deciduous leaf habit (other leaf types exhibit same patterns). The 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).