Growth–reproduction trade-offs are common but changing in woody plants: a meta-analysis

—

Maciej K. Barczyk*[1], Michał Bogdziewicz[1], Szymon M. Drobniak[2,3], Maria Bogdańska[1], Urszula Eichert[1], Jessie J. Foest[1], Valentin Journé[1,4], Katarzyna Kondrat [1], Jakub Szymkowiak[1,5], Andrew Hacket-Pain[6]

[1] Forest Biology Center, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Uniwersytetu Poznańskiego 6, 61-614 Poznan, Poland
[2] Institute of Environmental Sciences, Faculty of Biology, Jagiellonian University, Krakow, Poland
[3] School of Biological, Environmental, and Earth Sciences, University of New South Wales, Sydney, Australia
[4] Department of Biology, Faculty of Science, Kyushu University, Fukuoka, Japan
[5] Population Ecology Research Unit, Institute of Environmental Biology, Faculty of Biology, Adam Mickiewicz University, Poznan, Poland
[6] Department of Geography and Planning, School of Environmental Sciences, University of Liverpool, Liverpool, UK

*Corresponding author: maciejkbarczyk@gmail.com;

Abstract

Growth and reproduction draw on a common resource pool, yet empirical studies of woody plants report widely differing relationships between seed production and growth. Here we synthesize 685 estimates from 78 studies covering 79 woody species to test how growth–reproduction correlations vary across time, species, and environments. Growth and reproduction measured within the same year were negatively correlated, suggesting an immediate cost of reproduction. Lagged growth–reproduction relationships further suggest that reproduction incurs delayed constraints on growth beyond the year of investment. The strength and direction of growth–reproduction correlations showed no detectable phylogenetic signal and were not systematically related to functional traits and climate. Instead, trade-offs were strongest in species with high interannual variability in seed production and weakened markedly over recent decades in these species. Together, these results show that growth–reproduction trade-offs in woody plants are common but not fixed, and that shifts in reproductive variability under environmental change can alter how trees balance growth and reproduction, with consequences for long-term forest functioning.

keywords: growth–reproduction trade-off | cost of reproduction | life-history theory |resource allocation | secondary growth | seed production | tree rings | masting | meta-analysis |

Introduction

Individual fitness depends on survival, growth, and reproduction. These functions are constrained by resource-based trade-offs, including the growth–mortality trade-off, growth–defense trade-off, and the cost of reproduction (Williams, 1966; Obeso, 2002; Dorken *et al.*, 2025; Russo *et al.*, 2020; Cople *et al.*, 2021). In long-lived organisms such as perennial plants, growth-reproduction trade-offs are expected because the allocation of resources is a zero-sum game; reproduction reduces resources available for other functions, such as growth and survival, thereby lowering future fitness returns (Williams, 1966; Dorken *et al.*, 2025). Although the cost of reproduction in plants has been extensively discussed (Dorken *et al.*, 2025; Obeso, 2002; Thomas, 2011), meta-analytic evidence is lacking on the extent to which woody plants face a compromise between seed production and somatic growth, and how this varies across species, traits, and habitats (Dorken *et al.*, 2025; Thomas, 2011). Systematic reviews suggest that growth–reproduction trade-offs are widespread (Obeso, 2002; Thomas, 2011), yet case studies report diverse outcomes, including negative (Norton & Kelly, 1988; Woodward *et al.*, 1994; Hadad *et al.*, 2021; Braun *et al.*, 2017), positive (Garcia-Barreda *et al.*, 2021; Alfaro-Sánchez *et al.*, 2015), and absent (Knops *et al.*, 2007; Patterson *et al.*, 2023) correlations between growth and reproduction.

Perennial plants vary widely in their annual allocation to reproduction, offering a test bed for growth–reproduction trade-offs (Norton & Kelly, 1988). Numerous long-lived woody plants show irregular seed production, with years of high, low or absent production, called masting or mast seeding (Bogdziewicz *et al.*, 2024). These among-year shifts in allocation create natural contrasts: years of heavy reproductive investment can be set against lean years to detect growth costs (Norton & Kelly, 1988; Monks *et al.*, 2016). The magnitude of these contrasts varies strongly among species, reflecting differences in interannual variability in reproductive investment, commonly quantified by the coefficient of variation of seed production (CV_p) (Pearse *et al.*, 2020; Journé *et al.*, 2023). Here, we synthesize multi-year measurements of seed production and growth to test how prevalent such trade-offs are across woody plants, and whether their strength depends on phylogeny, functional traits, climate, or temporal change under anthropogenic warming.

Reproductive strategies in plants are shaped by phylogenetic history. Fruit type, for instance, shows strong conservatism: in a dataset of 9,370 species from China, phylogeny explained nearly 80% of the variation in whether species produced fleshy or dry fruits, far exceeding the influence of growth form or climate (Wang *et al.*, 2022). Seed size is also rooted in evolutionary history. An analysis of nearly 13,000 species showed that the largest divergences in seed mass were repeatedly associated with major phylogenetic splits (Moles *et al.*, 2005). Patterns of interannual variation in reproduction also carry a phylogenetic signal (Pearse *et al.*, 2020; Qiu *et al.*, 2023). In a synthesis of 517 species, the coefficient of variation of seed production, a measure of masting intensity, exhibited significant coherence across the plant tree of life, with lineages such as Fagales, Pinales, and Poales showing consistently high variability (Journé *et al.*, 2023). Together, these findings indicate that reproductive strategies are constrained by ancestry. Consequently, woody plants are expected to be evolutionary constrained in the magnitude of seed production and growth potential, resulting in weaker or stronger allocation trade-offs depending on lineage (Pearse *et al.*, 2020; Journé *et al.*, 2023; Dorken *et al.*, 2025).

Functional traits capture physiological and morphological strategies that affect fitness indirectly through their influence on growth, survival, and reproduction (Violle *et al.*, 2007; Adier *et al.*, 2014). Because traits are relatively easily measurable and comparable between taxa, they allow generalizations about life-history strategies across species and ecosystems (Díaz *et al.*, 2016; Maynard *et al.*, 2022). Analyses of tropical tree demography reveal that functional traits align with two axes of life-history variation (Rüger *et al.*, 2018; Kambach *et al.*, 2022). The fast–slow continuum, reflecting the growth–survival trade-off, and a stature–recruitment axis, which distinguishes tall, long-lived pioneer species with large seeds and low recruitment from short-lived breeders that produce numerous small seeds at the expense of growth and survival (Rüger *et al.*, 2018; Kambach *et al.*, 2022). On the other hand, nutrient-demanding species with high foliar nitrogen, high specific leaf area (SLA), and low wood density tend to produce many small seeds, whereas conservative species with dense wood, low foliar nitrogen, and low SLA produce fewer but larger seeds (Bogdziewicz *et al.*, 2023). In trees, the classic seed size–number trade-off is not strict, and species with large seeds often produce a greater total biomass of seeds (Qiu *et al.*, 2022). These results yield contrasting expectations: conservative, dense-wooded species with large seeds may experience high reproductive allocation and thus greater costs to growth (Qiu *et al.*, 2022; Bogdziewicz *et al.*, 2023). Alternatively, according to the stature–recruitment axis, tall species with large seeds may incur lower reproductive costs because they invest relatively little in recruitment while maintaining performance.

Spatial variation in temperature and precipitation often mediates reproductive allocation and growth, thereby potentially influencing the apparent strength of trade-offs between them (Hulshof *et al.*, 2012; Shestakova *et al.*, 2021; Hacket-Pain *et al.*, 2018). Across biomes, reproductive allocation tends to increase from cold to warm regions (Journé *et al.*, 2022; Ward *et al.*, 2025). Within species, seed production is also often higher in warmer parts of species' ranges. For example, North American tree fecundity peaks in the warm and moist southeastern United States (Sharma *et al.*, 2022). Parallel patterns emerge for growth. Trees in the tropics grow twice as fast as in temperate and boreal biomes (Locosselli *et al.*, 2020), and within species growth is generally faster at warmer sites (Perret *et al.*, 2024), except where water limitation prevails (Klesse *et al.*, 2024). Similarly, low precipitation and high evaporative demand are associated with stronger negative correlations between growth and reproduction (Hulshof *et al.*, 2012; Hacket-Pain *et al.*, 2017). Together, these findings suggest that accounting for local climate is needed to understand growth–reproduction trade-offs: warm and moist conditions may produce apparent positive associations between growth and reproduction, whereas hot and dry climates are expected to strengthen trade-offs through resource limitation.

Climate change affects resource allocation to reproduction and growth (Etzold *et al.*, 2020; Hacket-Pain & Bogdziewicz, 2021; Clark *et al.*, 2021). Direct effects of warming and moisture limitation often reduce both seed production and growth (Sharma *et al.*, 2022; Klesse *et al.*, 2024; Perret *et al.*, 2024), yet plant responses in many systems appear to maintain reproduction at the expense of growth (Dohrenbusch *et al.*, 2002; Rowland *et al.*, 2018; Bogdziewicz *et al.*, 2020; Hacket-Pain *et al.*, 2025). In European beech, warming has shifted reproduction towards more frequent seed crops, depleting stored reserves and causing a 28% decline in mean radial growth (Hacket-Pain *et al.*, 2025). That change was associated with a weakening of the negative growth–reproduction correlation because, in poor seed years, trees with depleted reserves cannot mount strong growth responses (Hacket-Pain *et al.*, 2025). Experimental evidence supports this mechanism, for example, *Picea abies* maintained allocation to reproduction at the expense of growth under experimental drought in Germany (Hesse *et al.*, 2021). Alternative mechanisms can also relax trade-offs when resource inputs increase through nitrogen and CO_2 fertilization. Rising atmospheric CO_2 enhances photosynthetic productivity and increases both wood production and reproductive output (e.g., FACE experiments on oaks) (Norby *et al.*, 2024; Esquivel-Muelbert *et al.*, 2025; Jablonski *et al.*, 2002). Long-term nitrogen addition often increases aboveground wood biomass and seed production (Magill *et al.*, 2004; Bogdziewicz *et al.*, 2017). Anthropogenic change can alter not only the magnitude of demographic rates but also the relationships among them, with particularly strong indirect effects expected in masting species where interactions among resource reserves, growth, and intermittent large seed crops are pronounced (Sala *et al.*, 2012; Han *et al.*, 2017; Hacket-Pain *et al.*, 2017).

Interannual variation in reproductive allocation raises the question of whether growth–reproduction trade-offs operate within years or emerge across years (Knops *et al.*, 2007; Pearse *et al.*, 2016). Resource-budget models of masting predict that reproduction draws on reserves accumulated in previous years, while reserve replenishment after mast events can compete with other carbon sinks such as growth (Isagi *et al.*, 1997; Kabeya *et al.*, 2017, 2021; Kelly *et al.*, 2025). Because reproduction is temporally autocorrelated (Koenig *et al.*, 2003; Foest *et al.*, 2025), high reproductive output in a given year generates a null expectation of reduced reproduction—and thus relatively higher growth—both in the preceding and the following year. Under this expectation, elevated growth in the year preceding and following mast events simply reflects low reproductive investment and associated growth release. Failure to observe elevated growth in the year following mast events represents a deviation from that null expectation and is consistent with delayed costs of reproduction expressed after reproductive investment. Empirical support for such lagged costs is mixed: some studies report reduced subsequent growth or storage following reproduction (Obeso, 2002; Sala *et al.*, 2012), whereas others find that trade-offs are largely confined within the same year (Hadad *et al.*, 2021; Hacket-Pain *et al.*, 2017). Explicitly accounting for null expectations imposed by reproductive autocorrelation is therefore important for correctly interpreting temporal growth–reproduction relationships and for linking allocation dynamics with demographic performance (Hacket-Pain *et al.*, 2018).

To disentangle these mechanisms, we compiled evidence from studies that jointly measured interannual seed production and aboveground, somatic growth across woody plants. We tested five hypotheses related to a broad context of factors that can influence trait trade-offs, including phylogenetic history, functional trait syndromes, spatial variation, and climate-driven effects. (1) Carry-over effects: growth-reproduction trade-offs are strongest within years, but negative effects on growth are expected in the year following high reproductive investment. (2) Phylogeny: trade-off strength is phylogenetically structured, with some lineages showing consistently stronger allocation conflicts. (3) Traits: functional traits mediate allocation patterns; species with conservative syndromes (dense wood, low SLA) exhibit higher reproductive allocation (Qiu *et al.*, 2022; Bogdziewicz *et al.*, 2023), so they should pay larger growth costs reflected in stronger negative growth–reproduction correlations. Alternatively, tall species with large seeds should display weaker trade-off correlations under the stature–recruitment axis of life history variation (Rüger *et al.*, 2018; Kambach *et al.*, 2022). (4) Climate: the trade-off depends on local climate, weakening under warm–moist conditions that promote resource accumulation and strengthening under hot–dry conditions that increase carbon and water limitation. (5) Reproductive variability and time: growth-reproduction trade-offs are stronger in species with high interannual variability in seed production (high CV_p), reflecting large, episodic reproductive investments that impose greater demands on resources (Norton & Kelly, 1988), but weaken over time under anthropogenic change as more frequent seed years and rising resource inputs (elevated CO_2, nitrogen deposition) decouple annual reproductive effort from short-term growth responses.

Results

Our meta-analysis of 78 studies, 79 species (Fig. 1), and 685 effect sizes across time lags shows that the strength and sign of growth–reproduction correlations depend on their temporal alignment (Fig. 2A,B, Supplementary Table S3). When growth and reproduction were correlated in the same year, the pooled effect size was negative (effect size = -0.194, 95% CI = $[-0.239, -0.148]$, $N = 308$), consistent with the within-year trade-offs between growth and reproduction. Hereafter, we refer to negative growth–reproduction correlations as trade-offs, following their common interpretation as signatures of allocation constraints, while acknowledging that the underlying evidence is correlational (see Discussion).

Higher growth in year $t-1$ was associated with greater reproduction in year t (effect size = 0.143, 95% CI = $[0.090, 0.197]$, $N = 199$), consistent with the expectation that years preceding high reproductive output tend to be characterized by low reproductive investment and, thus, relatively higher growth (Fig. 2B). This association was strongest in populations with stronger within-year trade-offs (Fig. 2C, Supplementary Table S4), consistent with reproductive autocorrelation generating strong growth contrasts between years of reproductive suppression and preceding low-investment years; particularly in populations with strong growth–reproduction

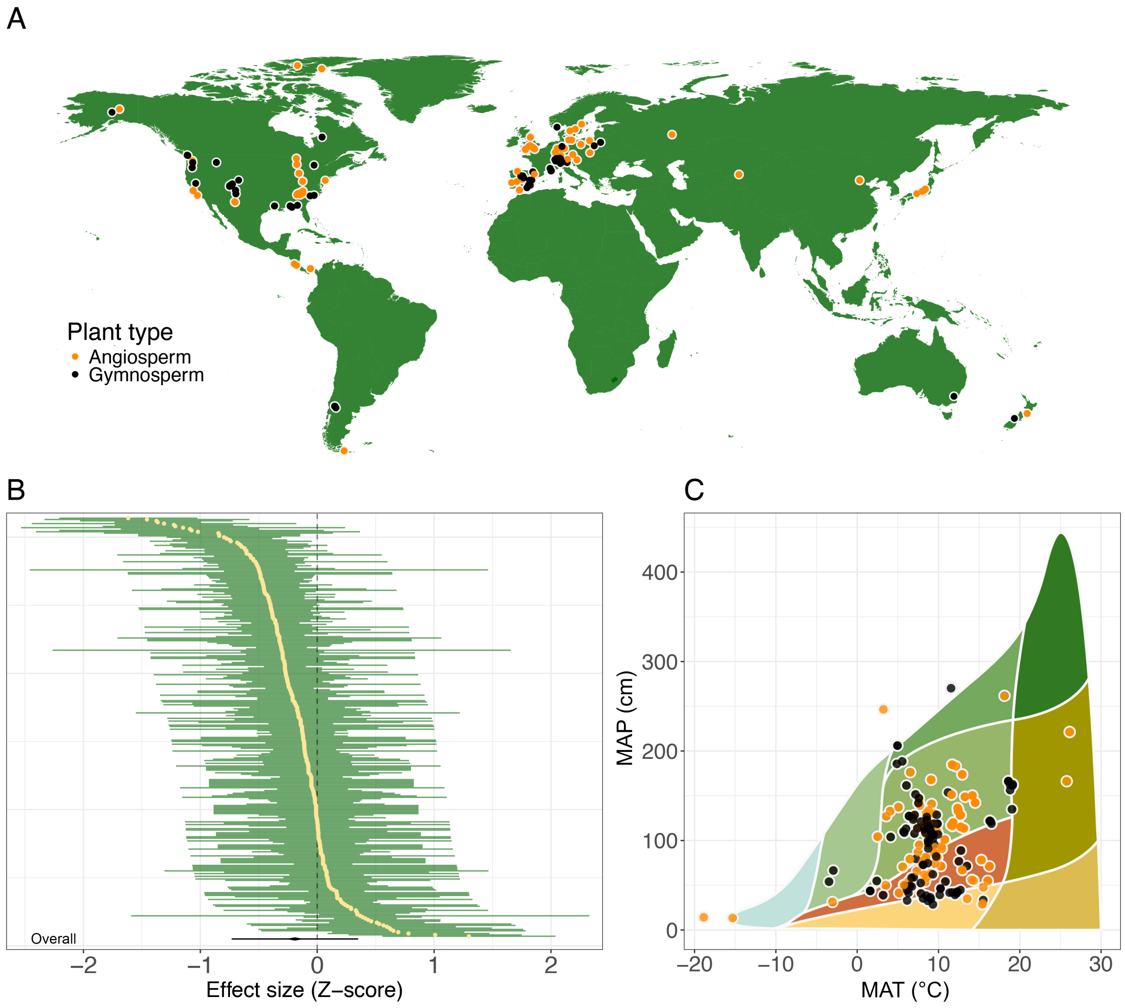

Figure 1: **Data distribution and effect size.** (A) The location of population-level observations of growth-reproduction correlations. (B) Population-level effect sizes (Z-scores, see Methods) for the relationship between reproduction and growth in the same year (t) with associated 95% confidence intervals (for lagged effects and their framework see Fig. 2A,B). The yellow points indicate the mean of each effect size. The estimated effect size of the null model with the confidence and prediction intervals is shown below (k = 308 observations and $n_{species}$ = 79). (C) Whittaker biome plot with observations distributed along mean annual temperature [°C] and mean annual precipitation [cm]. Orange points indicate species belonging to angiosperms, while black points indicate species belonging to gymnosperms. Background colors refer to the Whittaker Biome classification ranging from tundra (pale blue) through temperate forests in the middle to tropical seasonal and tropical rain forest (olive and dark green).

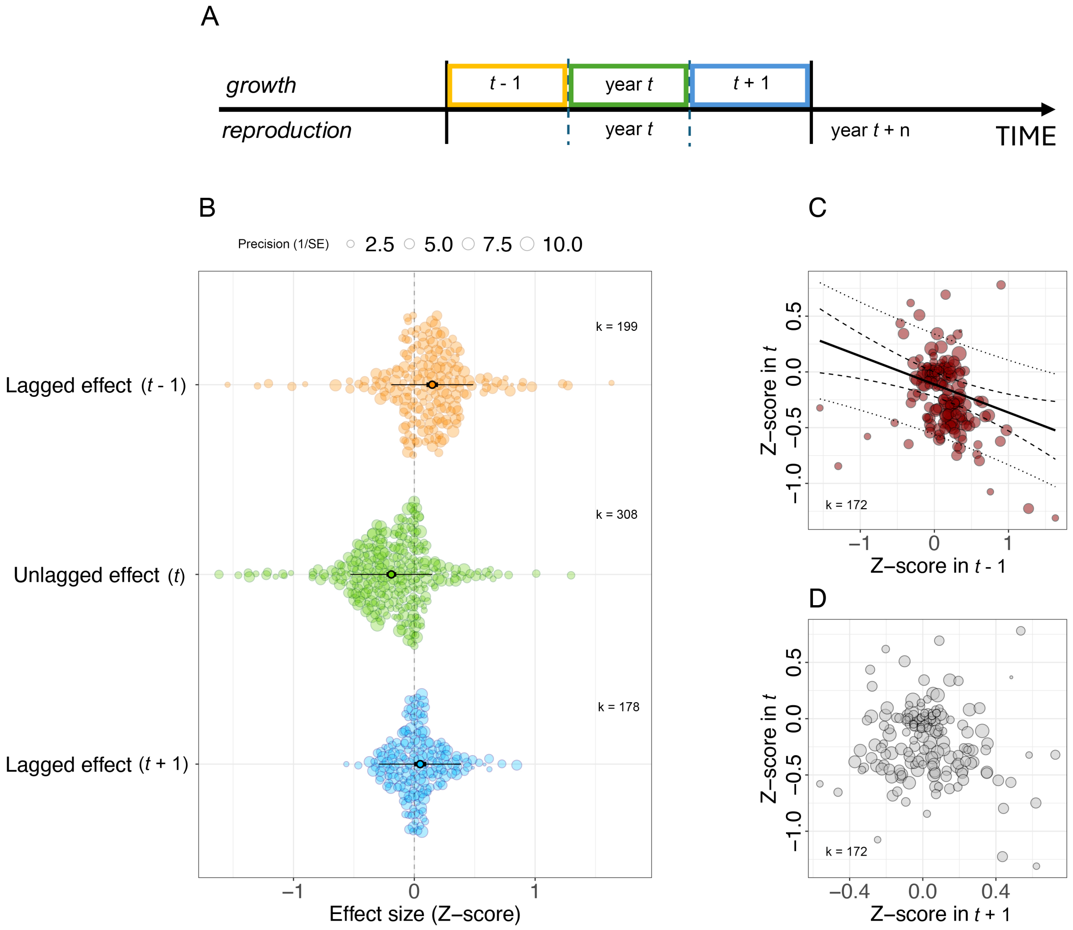

Figure 2: Growth is reduced in years of high seed production. (A) The temporal framework to study growth-reproduction correlations across multiple years, accounting for the within-year and lagged effect of growth ($t-1$, t, and $t+1$ in relation to reproduction in year t). (B) Relationships between reproduction and growth in the preceding year ($t-1$), same year (t), and the subsequent year ($t+1$). Black points show estimated effect sizes with 95% confidence intervals (CI; thicker bars) and 95% prediction intervals (PI; thinner bars). The relationship between the growth-reproduction correlation (Z-score) in the same year (t) and C) reproduction and growth in the preceding year ($t-1$), and D) reproduction and growth in the following year ($t+1$). Line at C) shows the relationship as estimated with phylogenetically informed multilevel meta-analytic model, associated 95% confidence intervals (dashed line), and 95% prediction intervals (dotted line). Points represent population-level effect sizes (k), with point size proportional to their precision (inverse SE). Model summary provided in Supplementary Table S3.

trade-offs. In contrast, reproduction in year t was not associated with growth in year $t+1$ (effect size $= 0.041$, 95% CI $= [-0.016, 0.099]$, $N = 178$) (Fig. 2B). The absence of a positive association contrasts with the expectation of elevated growth in years adjacent to high reproductive output, indicating an asymmetry around reproductive events. Such a pattern is consistent with delayed costs of reproduction expressed through constrained post-reproductive growth.

The growth-reproduction trade-off (within-year/unlagged effect) based on the effect sizes averaged for each of the 79 species was not significantly related to phylogeny (Pagel's $\lambda = 0.001$, $p = 0.99$, Fig. 3). Thus, closely related species do not have more similar effect sizes than expected by chance. This lack of signal reflects the heterogeneous distribution of effect size across the phylogeny: positive and negative effects occur intermixed within most major clades, with no large clusters of uniformly positive or negative values. Even within genera for which a larger number of species were sampled, such as *Quercus*, *Pinus*, and *Fagus*, the direction and magnitude of effects vary widely among species. Some adjacent taxa differ sharply in effect size, indicating contrasting growth–reproduction correlations despite close evolutionary relatedness. Within oaks, for example, *Quercus robur* had a positive effect size on average, while *Q. suber* or *Q. velutina* negative. Similarly, the negative effect sizes in *Fagus sylvatica* and *F. crenata*, contrasted with near-zero correlation in *F. grandifolia*. Closely related *Pinus nigra* and *P. sylvestris* were characterized by negative and positive effect sizes, respectively. The weak phylogenetic structure arises from repeated, independent expression of both negative and positive correlations between growth and reproduction across the plant tree of life.

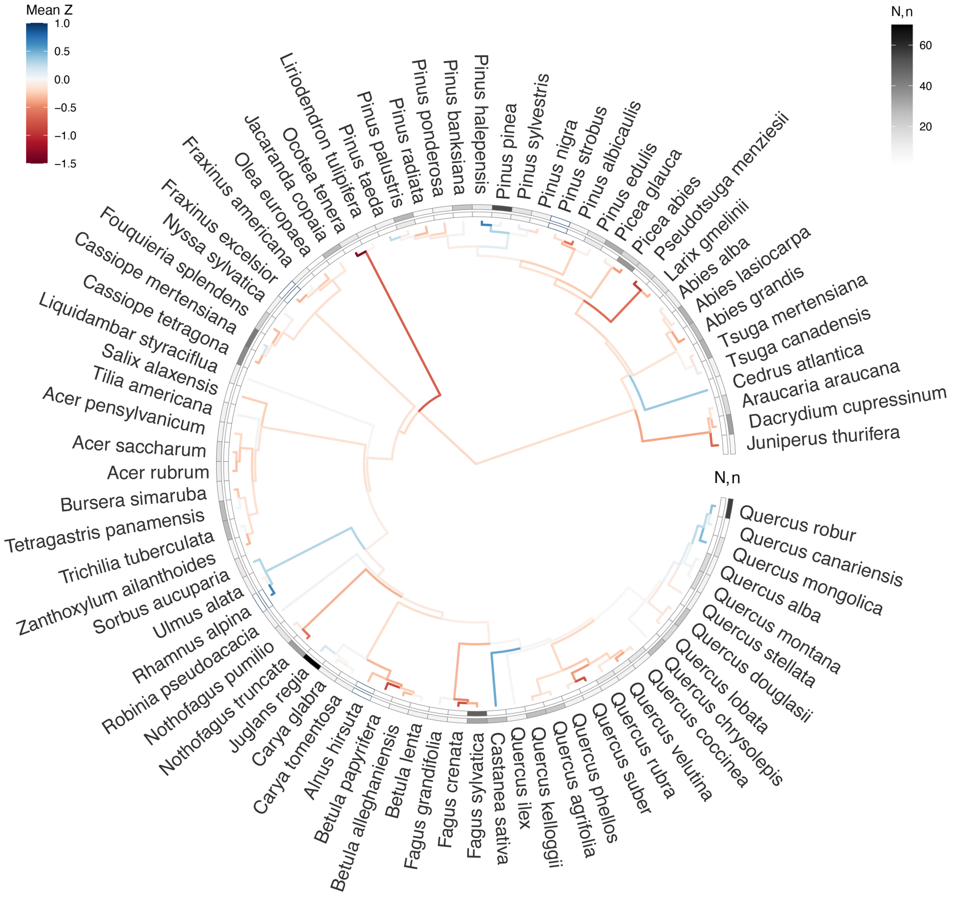

Figure 3: **Growth–reproduction correlation does not exhibit phylogenetic coherence.** Red indicate negative, and blue indicate positive correlations between reproduction and growth in the same year (t). Phylogenetic signal, estimated from species-level mean effect sizes, is negligible (Pagel's $\lambda = 0.001$, $p = 0.99$, $n_{\text{species}} = 79$). The gray-scale circle indicates sampling intensity, with shade proportional to the number of populations sampled (inner ring, N) and mean number of years per species (outer ring, n) for each species.

While we expected the negative correlation between growth and reproduction to be weaker in warm-moist sites, the interaction between mean annual temperature (MAT) and mean annual precipitation (MAP) was not significant (estimate = 0.003, $p = 0.9$). The trade-off did not vary systematically across sites differing in MAT ($p = 0.62$) and MAP ($p = 0.63$) (Fig. 4,

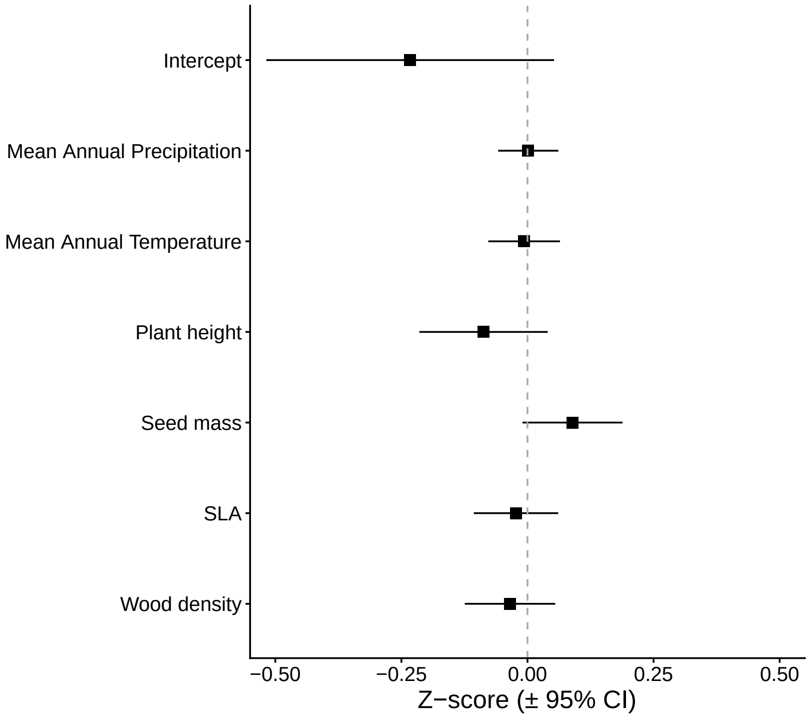

Figure 4: Growth–reproduction correlation shows no associations with climate or functional traits. Effect sizes and their 95% confidence intervals are derived from a phylogenetically informed multilevel comparative model ($n_{observations} = 307$, $n_{species} = 79$), with sampling variance incorporated at the observation level. All predictors were centered and scaled to facilitate direct comparison of effect sizes. Model summary provided in Supplementary Table S6.

Supplementary Table S6).

Wood density ($p = 0.37$) and specific leaf area (SLA, $p = 0.85$), two key traits reflecting the fast-slow continuum, were not significantly related to the trade-off between growth and reproduction (Supplementary Table S6). Likewise, the maximum height, which is reflecting the stature-recruitment trade-off, was not associated with the trade-off between growth and reproduction ($p = 0.17$). Seed size, the key trait related to reproduction, exhibited only a weak positive tendency to moderate growth-reproduction trade-off ($p = 0.06$), such that larger seed sizes were associated with weaker trade-offs.

The correlations between growth and reproduction became weaker over time, especially for species with high interannual variation in reproduction (year × CV_p interaction: $\beta = 0.021$, $p < 0.001$, $n = 261$) (Fig. 5, Supplementary Table S7). For example, in a species with an intermediate $CV_p = 1$, the estimated correlation between growth and reproduction was -0.16 in both 1980 and 2020. In contrast, in a species characterized by higher interannual variation in reproduction ($CV_p = 1.6$), the estimated correlation declined more than 8-fold over the 40 years, from -0.58 in 1980 to -0.07 in 2020 (Fig. 5B).

At the same time, in earlier decades of the dataset, species with high CV_p in seed production exhibited stronger negative growth–reproduction correlations than species with low CV_p (Fig. 5C). For example, in species with high reproductive variability ($CV_p = 1.6$), the estimated correlation was -0.8, whereas in species with relatively regular reproduction ($CV_p = 0.6$)

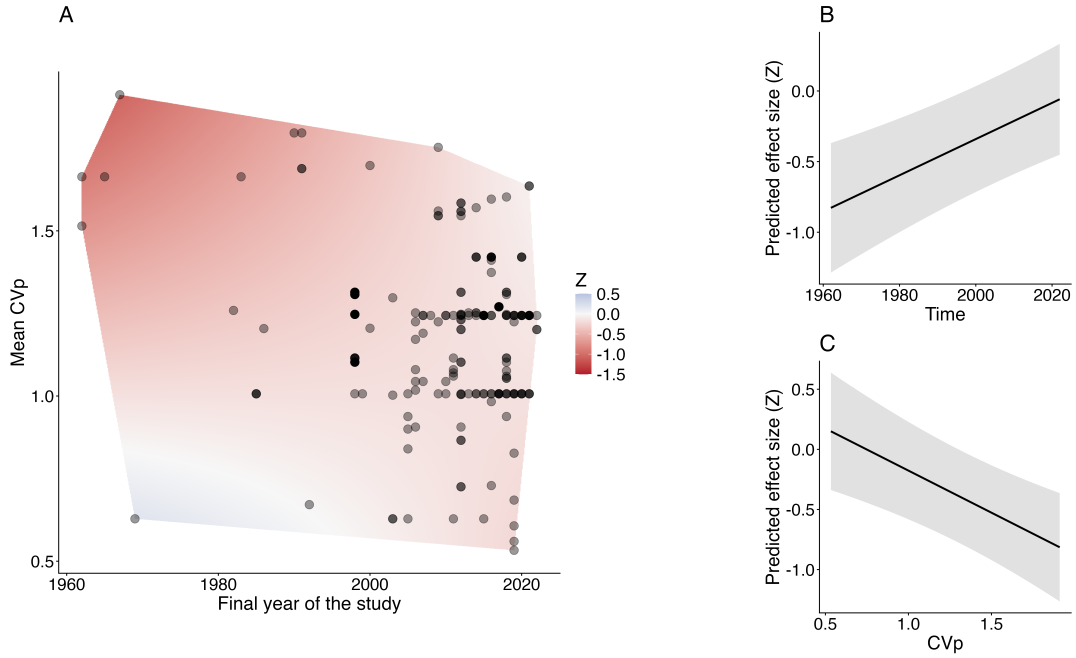

Figure 5: Negative growth–reproduction correlations weaken over time in strongly masting species. The surface plot at A) shows the estimated (unlagged) growth–reproduction correlation across combinations of population-level interannual variation in seed production (CV_p) and the final monitoring year of the study from which each effect size was extracted. Black dots denote data points that define the convex hull of the prediction space ($n_{populations}$ = 261, $n_{species}$ = 48. B) Temporal weakening of negative correlation between growth and reproduction, as estimated for CV_p = 1.6. C) The negative correlation between growth and reproduction is stronger in species characterized by higher CV_p, as estimated for year 1980. All predictions are derived from phylogenetically informed multilevel meta-analytic model, summarized in Supplementary Table S7.

the corresponding estimate was 0.27. Over time, however, growth–reproduction correlations converged across levels of reproductive variability.

Discussion

Our meta analysis indicate a trade-off between growth and reproduction in woody plants: growth and seed production are negatively correlated within the same year. In addition, the temporal structure of these correlations reveals asymmetric carry-over effects across years, consistent with delayed costs of reproduction expressed as constrained growth following high reproductive investment. The trade-off exhibits no detectable phylogenetic signal. Although the absence of signal contrasts with our predictions, the result aligns with demographic syntheses indicating that allocation strategies are only weakly constrained by lineage (Salguero-Gómez *et al.*, 2016; Rüger *et al.*, 2018). Furthermore, neither spatial variation in climate nor functional traits systematically explained variation in effect sizes, suggesting that species resolve allocation conflicts in ways that are not tightly linked to biome, climatic regime, or ecological strategy. Notably, the trade-off was strongest in species with high interannual variability in reproduction but diminished over recent decades in these species, suggesting that changing resource dynamics under warming are reshaping the balance between growth and reproduction (Hacket-Pain *et al.*, 2025; Macias &

Redmond, 2025). Our results indicate that while growth–reproduction trade-offs are widespread, their expression is flexible and responsive to contemporary environmental change (summarized in Supplementary Table 1).

Within-year trade-offs dominated growth-reproduction dynamics, but lagged correlations revealed a pronounced asymmetry around reproductive events. Growth and seed production were negatively correlated in the same year. Growth in year $t - 1$ was positively associated with reproduction in year t, a pattern that scaled with the strength of within-year growth suppression. This scaling indicates that the pre-reproductive growth signal primarily reflects large contrasts between years when growth is strongly suppressed by reproductive investment and preceding years when reproduction is minimal (Koenig *et al.*, 2003; Foest *et al.*, 2025). In contrast, reproduction in year t was not associated with growth in year $t + 1$. Given the temporal autocorrelation of reproduction, the absence of elevated growth in the post-reproductive year contrasts with the expectation of low reproductive investment and indicates constrained growth following reproduction. These results support resource-budget models in which reproduction draws on resources accumulated in previous years and replenishment after mast events competes with growth, such that delayed costs are expressed as asymmetric temporal patterns around reproductive events rather than as a consistent lagged reduction in growth (Satake & Iwasa, 2000; Han *et al.*, 2017; Kelly *et al.*, 2025). This interpretation, by adjusting the null expectation to account for the autocorrelation in reproduction, contrasts with earlier interpretations of positive growth anomalies at $t - 1$ indicating resource accumulation, or a lack of growth response at $t + 1$ as indicating an absence of delayed costs of reproduction (Hacket-Pain *et al.*, 2017; Drobyshev *et al.*, 2010; Nussbaumer *et al.*, 2021).

The lack of phylogenetic signal in the growth–reproduction correlation contrasts with the evolutionary conservatism reported for reproductive traits such as seed size, fruit type, and interannual variability in seed production (Moles *et al.*, 2005; Wang *et al.*, 2022; Journé *et al.*, 2023). While lineages such as Fagales and Pinales show coherent patterns of masting intensity (Journé *et al.*, 2023), or conserved seed size (Moles *et al.*, 2005), our results indicate that the strength and even the sign of growth–reproduction correlations vary markedly among closely related species. Positive and negative correlations occur side by side within genera including *Quercus*, *Fagus*, *Pinus*, and *Tsuga*, implying repeated divergence in allocation strategies within clades. This suggests that, although key reproductive traits are constrained by ancestry, the balance between growth and reproduction remains evolutionarily labile.

We also found no evidence that spatial variation in climate modulates the trade-off. Neither mean annual temperature, mean annual precipitation, nor their interaction predicted variation in the growth–reproduction correlation. This result contrasts with the expectation that warm–moist sites should weaken trade-offs by easing resource limitation, while hot–dry climates should strengthen them. Several mechanisms may explain this mismatch. First, coarse annual climate metrics may not capture the within-season water stress and extreme events that drive resource limitation or sink activity (Espelta *et al.*, 2008; Körner *et al.*, 2023; Cabon, 2025). Second,

Table 1: Summary of results across hypotheses. Hypotheses are stated in shortened form; results summarize the direction and support in the meta-analysis.

Hypothesis	Result summary
Within-year allocation trade-off	Growth and reproduction are negatively correlated within the same year, indicating a widespread immediate cost of reproduction.
Lagged costs of reproduction	Growth is higher in the year before reproduction but not elevated after reproduction, consistent with delayed post-reproductive growth constraints.
Phylogenetic constraint	Growth–reproduction correlations show no phylogenetic signal; closely related species often differ strongly in trade-off strength and sign.
Trait mediation	Functional traits (wood density, SLA, height) do not explain variation in trade-off strength; seed mass shows at most a weak tendency toward weaker trade-offs.
Climatic modulation	Trade-off strength is not systematically related to mean annual temperature or precipitation across sites.
Reproductive variability (CV_p)	Species with high interannual reproductive variability exhibit stronger negative growth–reproduction correlations.
Temporal change	Negative growth–reproduction correlations weaken over recent decades, particularly in species with high reproductive variability.

growth and reproduction may respond in parallel to local climate, so that their correlation is conserved even when absolute rates change (Locosselli *et al.*, 2020; Ward *et al.*, 2025). Third, local edaphic variation and stand structure can buffer or amplify climatic effects (Barringer *et al.*, 2013), reducing the signal of broad-scale climate drivers in meta-analytic models.

Similarly, functional traits associated with the fast–slow continuum and the stature–recruitment axis did not show associations with the growth–reproduction correlation. Wood density, specific leaf area, and maximum height were all poor predictors of trade-off strength, and seed size showed only a weak, marginally significant tendency toward more positive correlations. This suggests that simple trait syndromes, while powerful for predicting demographic rates and fecundity (Rüger *et al.*, 2018; Qiu *et al.*, 2022; Bogdziewicz *et al.*, 2023), may not map directly to how plants partition resources between growth and reproduction from year to year, especially under variable environmental conditions (Augusto *et al.*, 2025). In fact, a recent global analysis failed to detect the expected links between acquisitive trait syndromes and high growth rates in natural forests, as environmental constraints override trait-based growth potential across species (Augusto *et al.*, 2025). Trade-offs may instead be governed by unmeasured axes of variation, such as non-structural carbohydrate storage dynamics (Trugman & Anderegg, 2025) or phenological strategies (Journé *et al.*, 2021; Etzold *et al.*, 2021; Wolkovich *et al.*, 2025), which are rarely quantified across many species but may determine how plants buffer or transmit resource limitations into growth and seed output.

The temporal trend in our dataset reveals that in strongly masting species, the negative growth–reproduction correlation has weakened over recent decades. First, the strong relationship between the interannual variation in reproduction (CV_p) and growth-reproduction trade-off supports an early, but so far untested, prediction that high variation in reproductive allocation in strongly masting species should render the detection of costs of reproduction more likely in such species (Norton & Kelly, 1988). The weakening of the trade-off over time aligns with the long-term evidence from European beech and Japanese oak (*Quercus crispula*), in which warming increased the frequency of weather cues that trigger reproduction, leading to more frequent seed crops, and in the case of beech, reserve depletion, and an erosion of the growth–reproduction trade-off (Foest *et al.*, 2024; Hacket-Pain *et al.*, 2025; Shibata *et al.*, 2020). Our results indicate that this weakening of the growth–reproduction trade-off is not unique to beech, implying a more general disruption of how trees balance competing demands on limited resources. Such disruption matters because growth–reproduction correlations reflect underlying resource allocation processes. Warming can push these processes out of balance, with consequences that extend from growth and reproduction to survival, defense, and overall resilience (Lauder *et al.*, 2019; Macias & Redmond, 2025). A weakening trade-off therefore does not necessarily signal relaxed resource limitation. Rather, it may indicate that trees are increasingly unable to convert the opportunity for compensatory growth in years of reduced reproductive investment because reserves are depleted or physiological stress constrains recovery (Hacket-Pain *et al.*, 2025). In strongly masting species, this creates conditions where reproduction remains frequent while growth declines — a combination shown to reduce carbon storage, diminish future reproductive potential, and increase mortality (Qiu *et al.*, 2021; Hacket-Pain *et al.*, 2025; Bordin *et al.*, 2025). These temporal shifts suggest that climate change is altering the resource dynamics that underpin masting, weakening a fundamental component of demographic regulation in many forest trees.

Our findings come with several limitations. While the database include a large geographic range, it is largely composed of temperate and boreal tree species, reflecting the current scarcity of long-term seed production data for tropical systems (Hacket-Pain *et al.*, 2022). While allocation strategies and environmental constraints may differ under such conditions, community-level studies suggest reduced growth during general flowering events in tropical Dipterocarp forests (Nakagawa *et al.*, 2012). Similarly, a larger species sample with broader trait and climate coverage could reveal patterns that were not detected here, despite the reasonable trait coverage of our dataset (Supplementary Figure S5). Measures of growth and reproduction also vary across studies—ranging from basal area increment and ring width to fruit counts and seed traps—introducing methodological heterogeneity that our models only partly capture (Supplementary Table S5). Potentially important sources of variation, such as ontogenetic stage (Thomas, 2011), stand age (Genet *et al.*, 2009; Ward *et al.*, 2025), or competitive environment (Clark *et al.*, 2014; Augusto *et al.*, 2025), were often unreported and could not be incorporated despite their possible influence on allocation patterns. Our analysis also largely focuses on secondary growth of the main stem, whereas primary growth may be more directly affected by reproductive investment, especially given the partial resource autonomy of branches (Hoch, 2005; Han *et al.*, 2011). Negative growth–reproduction relationships may also arise not from direct competition for shared resources but from independent sink limitation by external drivers—for example, weather conditions that favor reproduction while suppressing growth (Knops *et al.*, 2007; Mund *et al.*, 2020). Growth can also be actively down-regulated in years with high reproductive investment to maintain storage (Dietze *et al.*, 2014; Trugman & Anderegg, 2025). While such mechanisms could contribute to the patterns we detect, the meta-analysis was not designed to disentangle them. A further limitation is that most studies rely on among-year correlations averaged across individuals, even though trade-offs evolve and operate at the level of individual plants (Cople *et al.*, 2021). Many estimates of trade-offs therefore reflect aggregated data on growth and reproduction from different trees; if resource allocation depends strongly on individual-level resource acquisition, such aggregation could obscure or inflate underlying relationships. Finally, the 'decline effect' in meta-analyses, caused by an increasing tendency to publish null results (Nakagawa *et al.*, 2022), may overestimate temporal effects on trade-offs caused by a changing climate. Together, these limitations highlight the need for long-term datasets that jointly track individuals, multiple tissues, demographic stages, and environmental covariates to fully resolve how growth–reproduction relationships operate across species and biomes.

Taken together, our results show that growth–reproduction trade-offs in woody plants are common and weakly constrained by lineage, climate, or functional traits, yet are changing over time in strongly masting species. The consistent same-year cost of reproduction, combined with asymmetric lagged effects in which high reproductive investment is followed by reduced growth, supports a resource-budget view in which allocation conflicts are expressed within years and lagged costs emerge following high reproductive investment (Satake & Iwasa, 2000; Koenig *et al.*, 2003). The absence of strong phylogenetic, climatic, or trait controls indicates that trade-off strength is not a fixed property of lineages or life-history syndromes, but emerges from local conditions and species-specific resource dynamics (Hacket-Pain *et al.*, 2017). The temporal weakening of the trade-off in high-$\mathrm{CV_p}$ species links these dynamics to climate change, suggesting that more frequent cueing and altered reserve trajectories can decouple growth responses from annual reproductive effort (Hacket-Pain *et al.*, 2025). Our meta-analysis calls for further research on resource-based individual-level quality of phenotypic correlations between growth and reproduction in woody plants in relation to the changing climate.

Materials and Methods

Meta-analysis To identify relevant studies, we conducted keyword searches in Web of Science and Scopus following the PRISMA guidelines (Preferred Reporting Items for Systematic Reviews and Meta-Analyses); (O'Dea *et al.*, 2021). We evaluated three different combinations of terms related to growth and reproduction (Supplementary Table S1) inspired by two systematic reviews on the cost of reproduction in plants (Obeso, 2002; Thomas, 2011) and the referenced studies incorporated in our meta-analysis. We applied the final search string on 30 March 2024 including:

> (reproduction OR seed OR seeds OR fruit* OR cone* OR acorn*) AND ("tree growth" OR ring*) AND (tree* OR shrub*)

Given the large number of studies reporting growth (>10,000, Supplementary Table S1) in non-woody plants, we restricted the search to woody species by using "tree growth" instead of "growth". We also limited the search to trees and shrubs by including these terms directly in the string.

The search yielded 3,449 and 3,111 documents from Web of Science and Scopus, respectively. To streamline the process of literature screening we used Rayyan QCRI (`https://rayyan.ai/`). After removing duplicates (2,015), we screened abstracts of 4,545 articles, and classified 110 papers for full-text evaluation. That classification was based on a previously constructed decision tree inspired by studies from two systematic reviews (Supplementary Figure S1). We also included data from before-mentioned systematic reviews (Obeso, 2002; Thomas, 2011) and studies cited in recent publications, resulting in a total of 146 publications eligible for data extraction (Supplementary Figure S2). Studies on orchard trees and cultivated species were excluded due to the possible bias caused by horticultural selection (Supplementary Figure S1).

Out of the 146 articles reporting both annual reproduction and annual growth in woody plants, we positively classified 78 studies based on assessment of the full text. Sixty eight studies that did not contain reliable data on either growth or reproduction, or did not report appropriate statistical tests between them were excluded (68 articles in total). In case of studies lacking formal statistical analyses or raw data suitable for our analysis, we contacted 14 authors asking for the missing data. As five research groups shared their data on six species, we were able to include additional data representing over 60 tree populations. We extracted all lagged effects of reproduction on growth when reported.

We extracted data combining somatic growth and reproduction over multiple years, with a few exceptions for studies based on one year of measurements. Most studies used secondary growth and seed production, but in the final analysis, we also included 13 studies on primary growth and physiological measurements, and 6 studies that measured flower production instead of seed production (Supplementary Figure S3. Excluding these studies (based on less frequent categories of growth or reproduction measurement) did not change the qualitative outcome of the analyses despite statistically significant differences in effect sizes among growth measurement methods (Supplementary Figure S4, Supplementary Table S5).

In total, we compiled a dataset of 685 observations (species × population × time-lag effect) from 78 studies containing data on reproduction and growth of trees and other woody plants. We also extracted available effect sizes that were reported in the studies, but were not included in the final analysis, e.g. time lags exceeding one year, correlations based on flower numbers or female individuals only (70 extra effect sizes). Given that seed production in some species (e.g. *Pinus pinea* (Garcia-Barreda *et al.*, 2021)) extends over multiple years we classified correlations between time lags in respect to the species' natural history. For example, for *Pinus pinea*, *Pinus palustris* and *Cedrus atlantica* we chose the year of seed filling as the ecologically relevant year to be correlated with growth.

To standardize data for the meta-analysis, we first transformed all reported effect sizes to Pearson's correlation coefficient (r) using test-specific formulas (Supplementary Table S2). We then converted r to Fisher's Z-scores (Z_r) using

$$Z_r = \frac{1}{2} \ln\left(\frac{1+r}{1-r}\right).$$

The sampling variance of each effect size was calculated as

$$V_{Z_r} = \frac{1}{n-3}.$$

For most observations (97%), the sample size (n) was equivalent to the number of years for which reproduction and growth were correlated. In case of growth-reproduction comparisons that used different statistical tests from correlations, we used the number of years or the number of individuals as the respective sample size. If the sample size was less than four, the observation was excluded from the analysis.

Climate data We extracted mean annual temperature (MAT [°C]) and mean annual precipitation (MAP [cm]) for each unique study location, based on monthly values of temperature and precipitation (1970 to 2000) from the corresponding 2.5 minute grid cell in the WorldClim 2 dataset (Fick & Hijmans, 2017). The extracted values of MAT and MAP were plotted in a Whittaker biome diagram using the *plotbiomes* package (Stefan & Levin, 2025).

Functional traits and masting metrics We compiled functional trait data from publicly available datasets (Kattge *et al.*, 2020; Chave *et al.*, 2009). We filtered the list of species according to the World Checklist of Vascular Plants (WCVP) (Brown *et al.*, 2023). Then we compiled data on species-specific functional traits related to the fast-slow continuum and defined by the global trait analysis (Díaz *et al.*, 2016; Reich, 2014). We selected specific leaf area (SLA), wood density, seed mass, and plant height as potential predictors of the growth-reproduction trade-off. We obtained complete set of functional traits for 61 species. For each trait x species combination that was absent from the databases, we averaged the trait value at the genus level. Such a trait imputation allowed us to cover all 79 species with the relevant trait information. We log-transformed all trait values to approximate a normal distribution, and to facilitate comparisons, we scaled and centered these values prior to the analysis.

To obtain the coefficient of variation of seed production (CV_p), we filtered MASTREE+, a global database of annual records of population-level reproductive effort (Hacket-Pain *et al.*, 2022; Foest *et al.*, 2024). We estimated the species-level CV_p by taking at least 5-year time series from at least 5 distinct populations for each species. We were able to extract the mean CV_p of seed production for 48 species. If information on population-specific seed production variability (CV_p) was reported in the study (11 species), we gave it priority over the MASTREE-derived value.

Analysis All data analysis was performed in R v. 4.5.1 (R Core Team, 2024). We used the multilevel comparative meta-analysis approach that involves phylogenetic, interspecific, and intraspecific variance partitioning (Pottier *et al.*, 2024). We built our models using the *rma.mv* function in the *metafor* package v. 4.8-0 (Viechtbauer, 2010). First, based on our species list, we built the phylogenetic tree using the Open Tree of Life with the *rotl* package v. 3.1.0 (Michonneau *et al.*, 2016). We calculated the distance between branches using Grafen's method and then built the correlation matrix of phylogenetic relatedness under Brownian motion with the *ape* package v. 5.8-1 (Paradis & Schliep, 2019). All fitted models had the same random effect structure that included effects of individual study, individual effect size, and phylogenetic relatedness. In addition to this model structure, we built two parallel models for sensitivity analyses, one using the phylogenetic relatedness adapted from Zanne et al. (Zanne *et al.*, 2014) and one simplified model replacing the phylogenetic relatedness correlation matrix with just the random effect of species. We used *orchaRd* package v. 2.0 to plot the results from the *rma* models (Nakagawa *et al.*, 2023).

To test whether growth-reproduction trade-offs occur in woody plants worldwide, we ran a multilevel comparative model with time lags included as the model predictors (n = 685). The models tested whether effect sizes (Fisher's Z) differed from zero for correlations measured in year t (a), one-year lags $t - 1$ (b), and one-year lags $t + 1$ (c) (Fig. 2A). We also quantified the relationship between growth and reproduction correlation within-year with the lagged correlations. To do so, we fitted an *rma* model using the within-year Z-scores as response, and the lagged correlations ($t - 1$ and $t + 1$) as predictors.

In further analyses, we restricted the dataset to within-year correlations (t; a; $n = 308$). We then tested for a phylogenetic signal in the trade-off expression. To this end, we averaged the Z-score at the species level and then calculated Pagel's λ (Paradis & Schliep, 2019).

To assess how climate and functional traits modulate growth-reproduction trade-offs, we fitted a multilevel comparative model. Predictors included mean annual temperature (MAT) and mean annual precipitation (MAP) as key climatic variables, and specific leaf area (SLA), seed mass, plant height, and wood density as relevant functional traits.

Finally, we fitted a model to test how trade-offs in species characterized by variable CV_p of seed production have changed over recent decades. To do so, we extracted the final year of the study for each observation and fitted a model that included the final year of the study, the average species-specific CV_p of seed production, and their interaction as predictors.

For each model, we estimated the total amount of heterogeneity (I^2) to quantify variation that is not explained by sampling error. The information on heterogeneity was given in model summaries together with the estimated variance components of random effects terms (See Supplementary Material).

We assessed potential publication bias using two methods recommended by Nakagawa *et al.* (2022). Specifically, we plotted a funnel plot with Z-scores and performed multilevel meta-regressions with standard error and sampling variance as fixed predictors of effect size. Visual inspection of the funnel plot suggests that there is no publication bias (Supplementary Figure S6). Likewise, the meta-regressions revealed that there is no bias related to studies with small sample sizes as both sampling variance and standard error were non-signifcant predictors of the effect size (Fisher's Z).

Acknowledgements

We would like to acknowledge researchers who kindly shared their data: Sabine Braun, Simon Tresch, Sven Hopf, Angelika Kölbl, Burkhard Beudert, Bruno Fady, Maxime Cailleret, Manuel Esteban Lucas Borja, and Walt Koenig. This study was funded by Polish National Science Centre grant 2019/35/D/NZ8/00050 and the European Union (ERC, ForestFuture, 101039066; EC, FECUND, 101244227). Views and opinions expressed are however those of the authors only and do not necessarily reflect those of the European Union or the European Research Council. Neither the European Union nor the granting authority can be held responsible for them. JJF was also supported by the Foundation for Polish Science (FNP).

Author Contributions Statement

AHP, MB and MKB conceived the study idea and developed research questions. MKB, MB, UE, MB, VJ, KK, JS and AHP performed the abstract screening. MKB extracted data from the literature and curated data. MKB led the analysis with the input from SMD, MB, VJ, JJF and JS. MKB wrote the first draft of the manuscript with substantial help from MB and AHP. All authors contributed to the interpretation of the analysis, revised the draft, and gave their final approval for publication.

Declaration of interests

Authors have no competing interests to declare.

Data availability statement

The data and code supporting the results are available at https://github.com/maciejkbarczyk/meta_trade-offs.

References

Adier, P.B., Salguero-Gómez, R., Compagnoni, A., Hsu, J.S., Ray-Mukherjee, J., Mbeau-Ache, C. *et al.* (2014). Functional traits explain variation in plant lifehistory strategies. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 740–745.

Alfaro-Sánchez, R., Camarero, J.J., López-Serrano, F.R., Sánchez-Salguero, R., Moya, D. & De Las Hera, J. (2015). Positive coupling between growth and reproduction in young post-fire Aleppo pines depends on climate and site conditions. *International Journal of Wildland Fire*, 24, 507–517.

Augusto, L., Borelle, R., Boča, A., Bon, L., Charru, M. *et al.* (2025). Widespread slow growth of acquisitive tree species. *Nature*, 640, 395–401.

Barringer, B.C., Koenig, W.D. & Knops, J.M. (2013). Interrelationships among life-history traits in three california oaks. *Oecologia*, 171, 129–139.

Bogdziewicz, M., Acuña, M.C.A., Andrus, R., Ascoli, D., Bergeron, Y., Brveiller, D. *et al.* (2023). Linking seed size and number to trait syndromes in trees. *Global Ecology and Biogeography*, 32, 683–694.

Bogdziewicz, M., Crone, E., Steele, M. & Zwolak, R. (2017). Effects of nitrogen deposition on reproduction in a masting tree: benefits of higher seed production are trumped by negative biotic interactions. *Journal of Ecology*, 105, 310–320.

Bogdziewicz, M., Fernández-Martínez, M., Espelta, J.M., Ogaya, R. & Penuelas, J. (2020). Is forest fecundity resistant to drought? Results from an 18-yr rainfall-reduction experiment. *New Phytologist*, 227, 1073–1080.

Bogdziewicz, M., Kelly, D., Ascoli, D., Caignard, T., Chianucci, F., Crone, E.E. *et al.* (2024). Evolutionary ecology of masting: mechanisms, models, and climate change. *Trends in Ecology & Evolution*, 39, 851–862.

Bordin, K.M., Bauman, D., Pugh, T.A., Müller, S.C., Phillips, O.L., Fortunel, C. *et al.* (2025). Growth–survival trade-off in temperate trees is weak and restricted to late-successional stages. *Journal of Ecology*, 113, 3466–3477.

Braun, S., Schindler, C. & Rihm, B. (2017). Growth trends of beech and Norway spruce in Switzerland: The role of nitrogen deposition, ozone, mineral nutrition and climate. *Science of the Total Environment*, 599, 637–646.

Brown, M.J.M., Walker, B.E., Black, N., Govaerts, R.H.A., Ondo, I., Turner, R. *et al.* (2023). rWCVP: a companion R package for the World Checklist of Vascular Plants. *New Phytologist*, 240, 1355–1365.

Cabon, A. (2025). Distal to proximal: a continuum of drivers shaping tree growth and carbon partitioning. *New Phytologist*, 249, 729–735.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009). Towards a worldwide wood economics spectrum. *Ecology Letters*, 12, 351–366.

Clark, J.S., Andrus, R., Aubry-Kientz, M., Bergeron, Y., Bogdziewicz, M., Bragg, D.C. *et al.* (2021). Continent-wide tree fecundity driven by indirect climate effects. *Nature Communications*, 12, 1–11.

Clark, J.S., Bell, D.M., Kwit, M.C. & Zhu, K. (2014). Competition-interaction landscapes for the joint response of forests to climate change. *Global Change Biology*, 20, 1979–1991.

Cople, O., Keefover-Ring, K., Kruger, E.L. & Lindroth, R.L. (2021). Growth–defense trade-offs shape population genetic composition in an iconic forest tree species. *PNAS*, 118, e2103162118.

Dietze, M.C., Sala, A., Carbone, M.S., Czimczik, C.I., Mantooth, J.A., Richardson, A.D. *et al.* (2014). Nonstructural carbon in woody plants. *Annual Review of Plant Biology*, 65, 667–687.

Dohrenbusch, A., Jaehne, S., Bredemeier, M. & Lamersdorf, N. (2002). Growth and fructification of a Norway spruce (*Picea abies* L. Karst) forest ecosystem under changed nutrient and water input. *Annals of Forest Science*, 59, 359–368.

Dorken, M.E., van Kleunen, M. & Stift, M. (2025). Costs of reproduction in flowering plants. *New Phytologist*, 147, 55–70.

Drobyshev, I., Övergaard, R., Saygin, I., Niklasson, M., Hickler, T., Karlsson, M. *et al.* (2010). Masting behaviour and dendrochronology of European beech (*Fagus sylvatica* L.) in southern sweden. *Forest Ecology and Management*, 259, 2160–2171.

Díaz, S., Kattge, J., Cornelissen, J.H., Wright, I.J., Lavorel, S., Dray, S. *et al.* (2016). The global spectrum of plant form and function. *Nature*, 529, 167–171.

Espelta, J.M., Cortés, P., Molowny-Horas, R., Sánchez-Humanes, B. & Retana, J. (2008). Masting mediated by summer drought reduces acorn predation in mediterranean oak forests. *Ecology*, 89, 805–817.

Esquivel-Muelbert, A., Banbury Morgan, R., Brienen, R., Gloor, E., Lewis, S.L., Dexter, K.G. *et al.* (2025). Increasing tree size across Amazonia. *Nature Plants*, 11, 2016–2025.

Etzold, S., Ferretti, M., Reinds, G.J., Solberg, S., Gessler, A., Waldner, P. *et al.* (2020). Nitrogen deposition is the most important environmental driver of growth of pure, even-aged and managed European forests. *Forest Ecology and Management*, 458, 117762.

Etzold, S., Sterck, F., Bose, A.K., Braun, S., Buchmann, N., Eugster, W. *et al.* (2021). Number of growth days and not length of the growth period determines radial stem growth of temperate trees. *Ecology Letters*, 25, 427–439.

Fick, S.E. & Hijmans, R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.

Foest, J.J., Bogdziewicz, M., Pesendorfer, M.B., Ascoli, D., Cutini, A., Nussbaumer, A. *et al.* (2024). Widespread breakdown in masting in European beech due to rising summer temperatures. *Global Change Biology*, 30, e17307.

Foest, J.J., Caignard, T., Pearse, I.S., Bogdziewicz, M. & Hacket-Pain, A. (2025). Intraspecific variation in masting across climate gradients is inconsistent with the environmental stress hypothesis. *Ecology*, 106, e70076.

Garcia-Barreda, S., Sangüesa-Barreda, G., Madrigal-González, J., Seijo, F., González de Andrés, E. & Camarero, J.J. (2021). Reproductive phenology determines the linkages between radial growth, fruit production and climate in four Mediterranean tree species. *Agricultural and Forest Meteorology*, 307, 108493.

Genet, H., Bréda, N. & Dufrêne, E. (2009). Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach. *Tree Physiology*, 30, 177–192.

Hacket-Pain, A. & Bogdziewicz, M. (2021). Climate change and plant reproduction: trends and drivers of mast seeding change. *Philosophical Transactions of the Royal Society B*, 376, 20200379.

Hacket-Pain, A., Foest, J.J., Pearse, I.S., LaMontagne, J.M., Koenig, W.D., Vacchiano, G. *et al.* (2022). Mastree+: Time-series of plant reproductive effort from six continents. *Global Change Biology*, 28, 3066–3082.

Hacket-Pain, A., Szymkowiak, J., Journé, V., Barczyk, M.K., Thomas, P.A., Lageard, J.G.A. *et al.* (2025). Growth decline in European beech associated with temperature-driven increase in reproductive allocation. *Proceedings of the National Academy of Sciences*, 122, e2423181122.

Hacket-Pain, A.J., Ascoli, D., Vacchiano, G., Biondi, F., Cavin, L., Conedera, M. *et al.* (2018). Climatically controlled reproduction drives interannual growth variability in a temperate tree species. *Ecology Letters*, 21, 1833–1844.

Hacket-Pain, A.J., Lageard, J.G. & Thomas, P.A. (2017). Drought and reproductive effort interact to control growth of a temperate broadleaved tree species (*Fagus sylvatica*). *Tree Physiology*, 37, 744–754.

Hadad, M.A., Roig, F.A., Molina, J.G.A. & Hacket-Pain, A. (2021). Growth of male and female *Araucaria araucana* trees respond differently to regional mast events, creating sex-specific patterns in their tree-ring chronologies. *Ecological Indicators*, 122, 107245.

Han, Q., Kabeya, D. & Hoch, G. (2011). Leaf traits, shoot growth and seed production in mature *Fagus sylvatica* trees after 8 years of CO2 enrichment. *Annals of Botany*, 107, 1405–1411.

Han, Q., Kabeya, D. & Inagaki, Y. (2017). Influence of reproduction on nitrogen uptake and allocation to new organs in *Fagus crenata*. *Tree Physiology*, 37, 1436–1443.

Hesse, B.D., Hartmann, H., Rötzer, T., Landhäusser, S.M., Goisser, M., Weikl, F. *et al.* (2021). Mature beech and spruce trees under drought – Higher C investment in reproduction at the expense of whole-tree NSC stores. *Environmental and Experimental Botany*, 191, 104615.

Hoch, G. (2005). Fruit-bearing branchlets are carbon autonomous in mature broad-leaved temperate forest trees. *Plant, Cell and Environment*, 28, 651–659.

Hulshof, C.M., Stegen, J.C., Swenson, N.G., Enquist, C.A.F. & Enquist, B.J. (2012). Interannual variability of growth and reproduction in *Bursera simaruba*: the role of allometry and resource variability. *Ecology*, 93, 180–190.

Isagi, Y., Sugimura, K., Ssumida, A. & Ito, H. (1997). How does masting happen and synchronize? *Journal of Theoretical Biology*, 187, 231–239.

Jablonski, L.M., Wang, X. & Curtis, P.S. (2002). Plant reproduction under elevated CO2 conditions: a meta-analysis of reports on 79 crop and wild species. 156, 9–26.

Journé, V., Andrus, R., Aravena, M.C., Ascoli, D., Berretti, R., Berveiller, D. *et al.* (2022). Globally, tree fecundity exceeds productivity gradients. *Ecology Letters*, 25, 1471–1482.

Journé, V., Caignard, T., Hacket-Pain, A. & Bogdziewicz, M. (2021). Leaf phenology correlates with fruit production in European beech (*Fagus sylvatica*) and in temperate oaks (*Quercus robur* and *Quercus petraea*). *European Journal of Forest Research*, 140, 733–744.

Journé, V., Hacket-Pain, A. & Bogdziewicz, M. (2023). Evolution of masting in plants is linked to investment in low tissue mortality. *Nature Communications*, 14, 7998.

Kabeya, D., Iio, A., Kakubari, Y. & Han, Q. (2021). Dynamics of non-structural carbohydrates following a full masting event reveal a role for stored starch in relation to reproduction in *Fagus crenata*. *Forestry Research*, 1, 18.

Kabeya, D., Inagaki, Y., Noguchi, K. & Han, Q. (2017). Growth rate reduction causes a decline in the annual incremental trunk growth in masting *Fagus crenata* trees. *Tree Physiology*, 37, 1444–1452.

Kambach, S., Condit, R., Aguilar, S., Bruelheide, H., Bunyavejchewin, S., Chang-Yang, C.H. *et al.* (2022). Consistency of demographic trade-offs across 13 (sub)tropical forests. *Journal of Ecology*, 10, 35.

Kattge, J., Bönisch, G., Díaz, S., Lavorel, S., Prentice, I.C., Leadley, P. *et al.* (2020). Try plant trait database – enhanced coverage and open access. *Global Change Biology*, 26, 119–188.

Kelly, D., Szymkowiak, J., Hacket-Pain, A. & Bogdziewicz, M. (2025). Fine-tuning mast seeding: as resources accumulate, plants become more sensitive to weather cues. *New Phytologist*, 246, 1975–1985.

Klesse, S., Peters, R., Alfaro-Sánchez, R., Badeau, V., Baittinger, C., Battipaglia, G. *et al.* (2024). No future growth enhancement expected at the northern edge for European beech due to continued water limitation. *Global Change Biology*, 30, e17546.

Knops, J.M.H., Koenig, W.D. & Carmen, W.J. (2007). Negative correlation does not imply a tradeoff between growth and reproduction in California oaks. *Proceedings of the National Academy of Sciences*, 104, 16982–16985.

Koenig, W.D., Kelly, D., Sork, V.L., Duncan, R.P., Elkinton, J.S., Peltonen, M.S. *et al.* (2003). Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos*, 102, 581–591.

Körner, C., Möhl, P. & Hiltbrunner, E. (2023). Four ways to define the growing season. *Ecology Letters*, 26, 1277–1292.

Lauder, J.D., Moran, E.V. & Hart, S.C. (2019). Fight or flight? potential tradeoffs between drought defense and reproduction in conifers. *Tree Physiology*, 39, 1071–1085.

Locosselli, G.M., Brienen, J.W., Leite, M.D.S., Gloor, M., Krottenthaler, S., Oliveira, A.A.D. *et al.* (2020). Global tree-ring analysis reveals rapid decrease in tropical tree longevity with temperature. *PNAS*, 117, 33358–33364.

Macias, D.S. & Redmond, M.D. (2025). Climate-warming alters resource allocation in unpredictable ways. *Trends in Ecology and Evolution*, 40, 428–430.

Magill, A.H., Aber, J.D., Currie, W.S., Nadelhoffer, K.J., Martin, M.E., McDowell, W.H. *et al.* (2004). Ecosystem response to 15 years of chronic nitrogen additions at the Harvard Forest LTER, Massachusetts, USA. *Forest Ecology and Management*, 196, 7–28.

Maynard, D.S., Bialic-Murphy, L., Zohner, C.M., Averill, C., van den Hoogen, J., Ma, H. *et al.* (2022). Global relationships in tree functional traits. *Nature Communications*, 13, 3185.

Michonneau, F., Brown, J.W. & Winter, D.J. (2016). rotl: an R package to interact with the Open Tree of Life data. *Methods in Ecology and Evolution*, 7, 1476–1481.

Moles, A., Ackerly, D., Webb, C., Tweddle, J., Dickie, J. & Westboy, M. (2005). A brief history of seed size. *Science*, 307, 576–580.

Monks, A., Monks, J.M. & Tanentzap, A.J. (2016). Resource limitation underlying multiple masting models makes mast seeding sensitive to future climate change. *New Phytologist*, 210, 419–430.

Mund, M., Herbst, M., Knohl, A., Matthäus, B., Schumacher, J., Schall, P. *et al.* (2020). It is not just a 'trade-off': indications for sink- and source-limitation to vegetative and regenerative growth in an old-growth beech forest. *New Phytologist*, 226, 111–125.

Nakagawa, M., Matsushita, M., Kurokawa, H., Samejima, H., Takeuchi, Y., Aiba, M. *et al.* (2012). Possible negative effect of general flowering on tree growth and aboveground biomass increment in a bornean tropical rain forest. *Biotropica*, 44, 720–729.

Nakagawa, S., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W.A., Parker, T.H. *et al.* (2022). Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution*, 13, 4–21.

Nakagawa, S., Lagisz, M., O'Dea, R.E., Pottier, P., Rutkowska, J., Senior, A.M. *et al.* (2023). orchaRd 2.0: An R package for visualising meta-analyses with orchard plots. *Methods in Ecology and Evolution*, 14, 2003–2010.

Norby, R.J., Loader, N.J., Mayoral, C., Ullah, S., Curioni, G., Smith, A.R. *et al.* (2024). Enhanced woody biomass production in a mature temperate forest under elevated CO2. *Nature Climate Change*, 14, 983–988.

Norton, D.A. & Kelly, D. (1988). Mast seeding over 33 years by Dacrydium cupressinum Lamb. (rimu) (*Podocarpaceae*) in New Zealand: The importance of economies of scale. *Functional Ecology*, 2, 399–408.

Nussbaumer, A., Gessler, A., Benham, S., de Cinti, B., Etzold, S., Ingerslev, M. *et al.* (2021). Contrasting resource dynamics in mast years for European beech and oak—a continental scale analysis. *Frontiers in Forests and Global Change*, 4, 89.

Obeso, J.R. (2002). The costs of reproduction in plants. *New Phytologist*, 155, 321–348.

O'Dea, R., Lagisz, M., Jennions, M., Koricheva J.and Noble, D., Parker, T., Gurevitch, J. *et al.* (2021). Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a prisma extension. *Biological Reviews*, 96, 1695–1722.

Paradis, E. & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528.

Patterson, T.W., Greenberg, C.H. & Hacket-Pain, A. (2023). Acorn production, climate, and tree-ring growth of five oak species in southern Appalachian forests. *Forest Ecology and Management*, 546, 121310.

Pearse, I.S., Koenig, W.D. & Kelly, D. (2016). Mechanisms of mast seeding: resources, weather, cues, and selection. *New Phytologist*, 212, 546–562.

Pearse, I.S., LaMontagne, J.M., Lordon, M., Hipp, A.L. & Koenig, W.D. (2020). Biogeography and phylogeny of masting: do global patterns fit functional hypotheses? *New Phytologist*, 227, 1557–1567.

Perret, D.L., Evans, M.E. & Sax, D.F. (2024). A species' response to spatial climatic variation does not predict its response to climate change. *Proceedings of the National Academy of Sciences of the United States of America*, 121, e2304404120.

Pottier, P., Noble, D.W.A., Seebacher, F., Wu, N.C., Burke, S., Lagisz, M. *et al.* (2024). New horizons for comparative studies and meta-analyses. *Trends in Ecology & Evolution*, 39, 435–445.

Qiu, T., Andrus, R., Aravena, M.C., Ascoli, D., Bergeron, Y., Berretti, R. *et al.* (2022). Limits to reproduction and seed size-number trade-offs that shape forest dominance and future recovery. *Nature Communications*, 13, 1–12.

Qiu, T., Aravena, M.C., Andrus, R., Ascoli, D., Bergeron, Y., Berretti, R. *et al.* (2021). Is there tree senescence? The fecundity evidence. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2106130118.

Qiu, T., Aravena, M.C., Ascoli, D., Bergeron, Y., Bogdziewicz, M., Boivin, T. *et al.* (2023). Masting is uncommon in trees that depend on mutualist dispersers in the context of global climate and fertility gradients. *Nature Plants*, 9, 1044–1056.

R Core Team (2024). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Reich, P.B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102, 275–301.

Rowland, L., da Costa, A.C., Oliveira, A.A., Almeida, S.S., Ferreira, L.V., Malhi, Y. *et al.* (2018). Shock and stabilisation following long-term drought in tropical forest from 15 years of litterfall dynamics. *Journal of Ecology*, 106, 1673–1682.

Russo, S.E., McMahon, S.M., Detto, M., Ledder, G., Wright, S.J., Condit, R.S. *et al.* (2020). The interspecific growth–mortality trade-off is not a general framework for tropical forest community structure. *Nature Ecology & Evolution*, 5, 174–183.

Rüger, N., Comita, L.S., Condit, R., Purves, D., Rosenbaum, B., Visser, M.D. *et al.* (2018). Beyond the fast–slow continuum: demographic dimensions structuring a tropical tree community. *Ecology Letters*, 21, 1075–1084.

Sala, A., Hopping, K., McIntire, E.J., Delzon, S. & Crone, E.E. (2012). Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytologist*, 196, 189–199.

Salguero-Gómez, R., Jones, O.R., Jongejans, E., Blomberg, S.P., Hodgson, D.J., Mbeau-Ache, C. *et al.* (2016). Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 230–235.

Satake, A. & Iwasa, Y. (2000). Pollen coupling of forest trees: Forming synchronized and periodic reproduction out of chaos. *Journal of Theoretical Biology*, 203, 63–84.

Sharma, S., Andrus, R., Bergeron, Y., Bogdziewicz, M., Bragg, D.C., Brockway, D. *et al.* (2022). North american tree migration paced by climate in the west, lagging in the east. *Proceedings of the National Academy of Sciences*, 119, e2116691118.

Shestakova, T.A., Mutke, S., Gordo, J., Camarero, J.J., Sin, E., Pemán, J. *et al.* (2021). Weather as main driver for masting and stem growth variation in stone pine supports compatible timber and nut co-production. *Agricultural and Forest Meteorology*, 298-299, 108287.

Shibata, M., Masaki, T., Yagihashi, T., Shimada, T. & Saitoh, T. (2020). Decadal changes in masting behaviour of oak trees with rising temperature. *Journal of Ecology*, 108, 1088–1100.

Stefan, V. & Levin, S. (2025). *plotbiomes: Plot Whittaker biomes with ggplot2*. R package version 0.0.0.9001.

Thomas, S.C. (2011). Age-related changes in tree growth and functional biology: The role of reproduction. In: *Size- and Age-Related Changes in Tree Structure and Function* (eds. Meinzer, F.C., Lachenbruch, B. & Dawson, T.E.). Springer, Dordrecht, pp. 33–64.

Trugman, A.T. & Anderegg, L.D. (2025). Source vs sink limitations on tree growth: from physiological mechanisms to evolutionary constraints and terrestrial carbon cycle implications. *New Phytologist*, 245, 966–981.

Viechtbauer, W. (2010). Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. *et al.* (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892.

Wang, G., Ives, A.R., Zhu, H., Tan, Y., Chen, S.C., Yang, J. *et al.* (2022). Phylogenetic conservatism explains why plants are more likely to produce fleshy fruits in the tropics. *Ecology*, 103, e03555.

Ward, R.E., Zhang-Zheng, H., Abernethy, K., Adu-Bredu, S., Arroyo, L., Bailey, A. *et al.* (2025). Forest age rivals climate to explain reproductive allocation patterns in forest ecosystems globally. *Ecology Letters*, 28, e70191.

Williams, G.C. (1966). Natural selection, the costs of reproduction, and a refinement of lack's principle. *The American Naturalist*, 100, 687–690.

Wolkovich, E.M., Ettinger, A.K., Chin, A.R., Chamberlain, C.J., Baumgarten, F., Pradhan, K. *et al.* (2025). Why longer seasons with climate change may not increase tree growth. *Nature Climate Change*, 15, 1283–1292.

Woodward, A., Silsbee David, G., Schreiner Edward, G. & Means Joseph, E. (1994). Influence of climate on radial growth and cone production in subalpine fir (*Abieslasiocarpa*) and mountain hemlock (*Tsugamertensiana*). *Canadian Journal of Forest Research*, 24, 1283–1292.

Zanne, A.E., Tank, D.C., Cornwell, W.K., Eastman, J.M., Smith, S.A., FitzJohn, R.G. *et al.* (2014). Three keys to the radiation of angiosperms into freezing environments. *Nature*, 506, 89–92.

Supplementary Information

Title: Growth–reproduction trade-offs are common but changing in woody plants: a meta-analysis

Authors: Maciej K. Barczyk, Michał Bogdziewicz, Szymon M. Drobniak, Maria Bogdańska, Urszula Eichert, Jessie J. Foest, Valentin Journé, Katarzyna Kondrat, Jakub Szymkowiak, Andrew Hacket-Pain

Table S1: **Search summary.** Each row contains set of keywords used for searching in the databases and the numbers of research items detected in the respective database. The trial search was performed at 22.03.2024. The final string was rerun at 30.03.2024 and supplied the meta-analysis (see Methods).

String	Scopus	Web of Science
(reproduction OR seed* OR cone* OR acorn*) AND (growth OR ring*) AND tree	23,244	22,733
(reproduction OR seed* OR cone* OR acorn* OR fruit*) AND (growth OR ring*) AND tree	33,863	32,367
(reproduction OR seed OR seeds OR fruit* OR cone* OR acorn*) AND ("tree growth" OR ring*) AND (tree* OR shrub*)	3,102	3,253

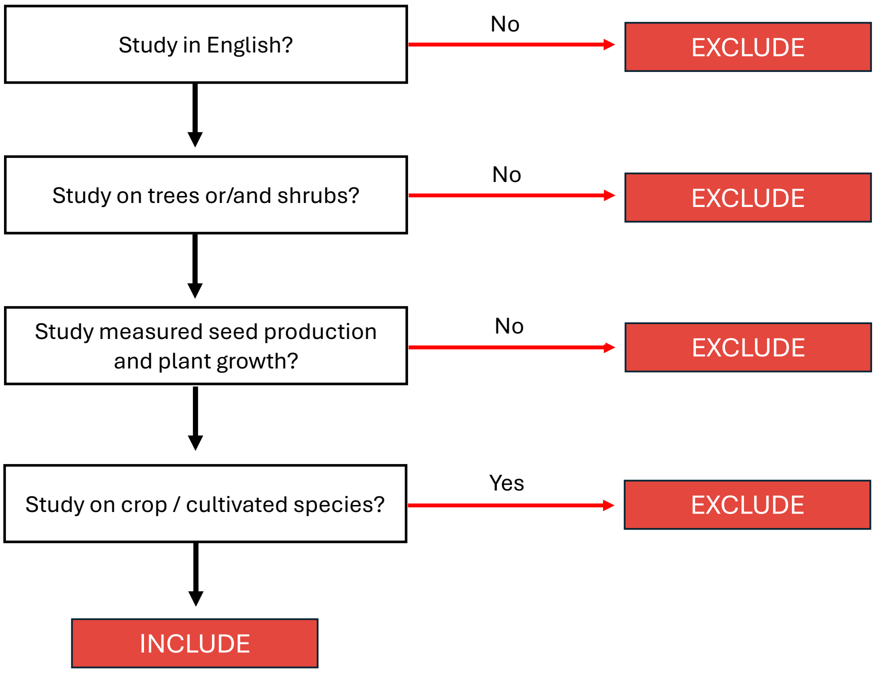

Figure S1: **Decision tree.** Decision tree with the inclusion criteria used in meta-analysis.

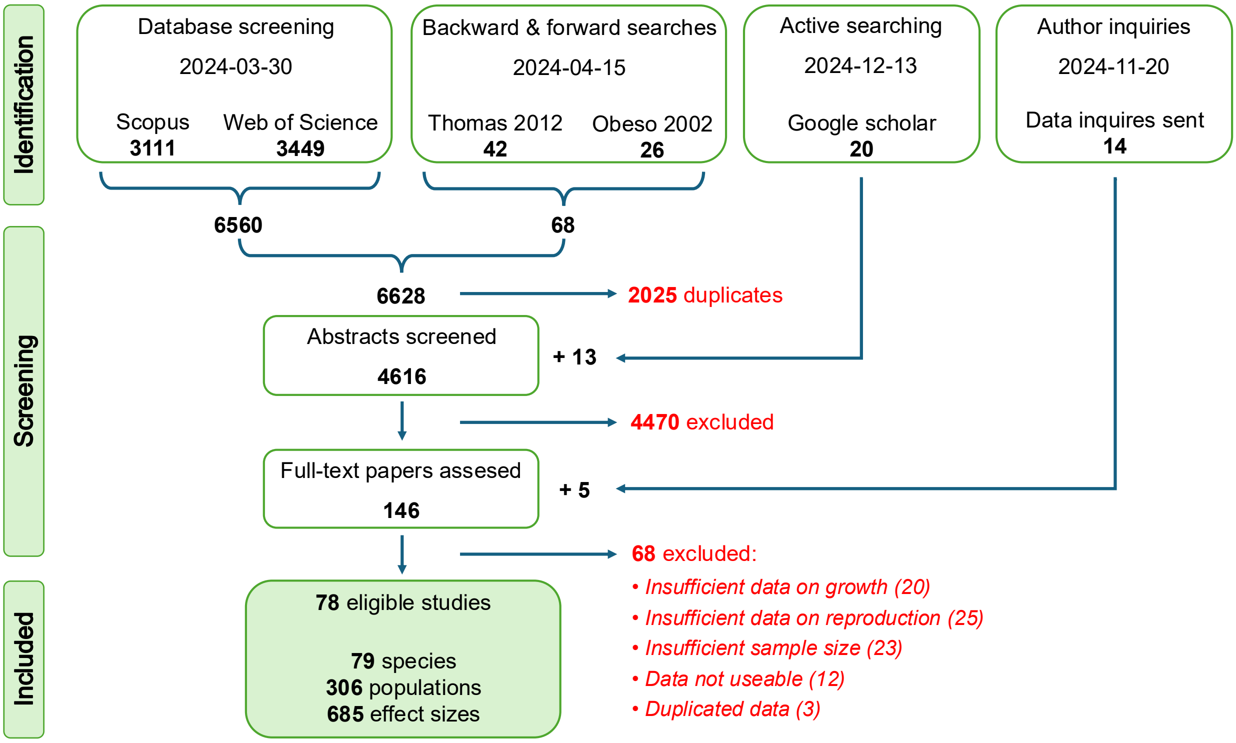

Figure S2: **PRISMA flow chart.** PRISMA graph summarizes the methods and data used in meta-analysis, including the search description, number of screened and excluded studies, the reasons for exclusion, and the final details on eligible studies.

Table S2: **Effect size formulas.** Statistical tests and equations used to calculate standardized Pearson's r correlation coefficient. Intermediate effect size (t-value) was calculated with the use of respective effect size (ES) and standard error (SE) prior to conversions to Pearson's r coefficients following $t = ES/SE$. The n refers to the sample size.

Statistical test	**Formula**
t-test	$r_P = \sqrt{t^2/(t^2 + n - 1)}$
Spearman correlations	$r_P = 2\sin(\pi r_S/6)$
Linear models	$r_P = \sqrt{(t^2/(t^2 + n - 1)}$
Multiple regressions	$r_P = \sqrt{t^2/(t^2 + n - 2)}$

Table S3: Results of the rma model testing the relationships between reproduction and growth in the preceding year ($t-1$), same year (t), and the subsequent year ($t+1$). The effect sizes are based on phylogenetically informed multilevel meta-analytic model without an intercept accounting for random effects of phylogeny, effect size ID, and study. The results are based on 685 observations and 79 species 2. Asterisks indicate significant effects. AIC = 443.63; $I^2 = 47.11$. The estimated variance components of random effects equal <0.001 for phylogeny, 0.01 for study, and 0.03 for effect size ID.

Predictor	**estimate**	**se**	**z-value**	**p-value**	**ci.lb**	**ci.ub**	
Lagged effect ($t + 1$)	0.039	0.03	1.304	0.192	-0.02	0.097	
Unlagged effect (t)	-0.199	0.024	-8.388	<.0001	-0.245	-0.152	***
Lagged effect ($t - 1$)	0.143	0.028	5.120	<.0001	0.088	0.198	***

Table S4: Summary of the rma model testing the relationship between the growth-reproduction correlation (Z-score) in the same year (t), and reproduction and growth in the preceding year ($t-1$), and reproduction and growth in the following year ($t+1$) (Fig. 2). The effect sizes are based on phylogenetically informed multilevel meta-analytic model accounting for random effects of phylogeny, effect size ID, and study. The results are based on 172 observations and 51 species for which information on population-level correlation was available. Asterisks indicate significant effects. AIC = 26.02; I^2 = 48.82. The estimated variance components of random effects equal <0.001 for phylogeny, 0.05 for study, and <0.001 for effect size ID.

Predictor	estimate	se	z-value	p-value	ci.lb	ci.ub	
Intercept	-0.107	0.056	-1.924	0.054	-0.2161	0.002	
Lagged effect ($t-1$) Z	-0.253	0.079	-3.219	0.001	-0.407	-0.099	**
Lagged effect ($t+1$) Z	-0.166	0.098	-1.702	0.089	-0.357	0.025	

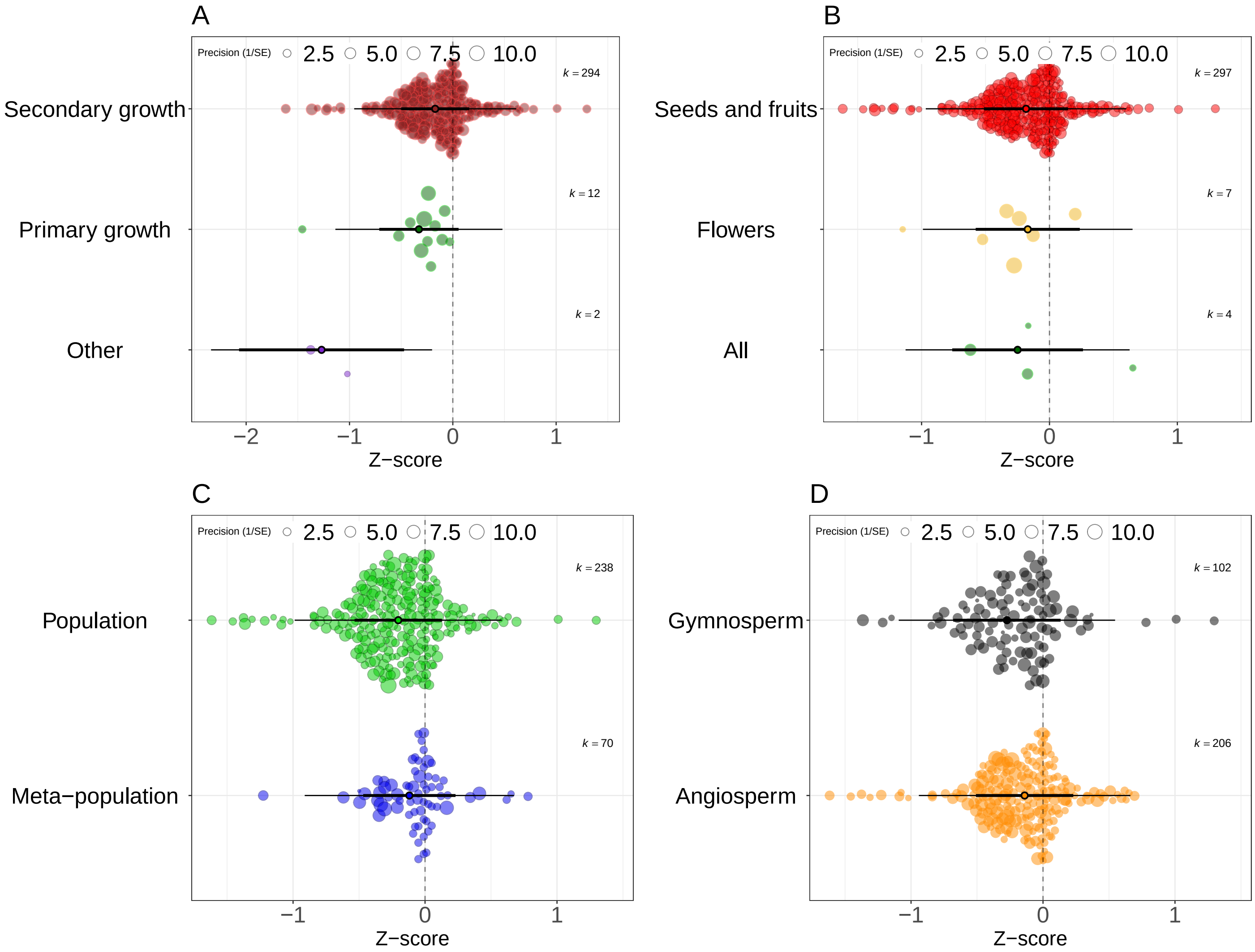

Figure S3: Category-dependent differences in population-level, within-year growth-reproduction correlations. A) Comparison of the effect sizes (Z-score) between different growth measurements. Secondary growth measurements derive mostly from tree ring data and basal area increments. Primary growth refers to measurements of buds, twigs, organs or plant height increments. Other methods ("others") refer to two studies using photosynthetic capacity [O evolution/leaf area] and root collar non-stuctural carbohydrate (NSC) levels as growth proxy. B) Comparison of the effect sizes (Z-score) between different reproduction measurements. C) Comparison of the effect sizes (Z-score) between populations and meta-populations. D) Comparison of the effect sizes (Z-score) between gymnosperms and angiosperms. Model summary provided in Supplementary Table S5.

Table S5: Summary of the rma model testing the growth-reproduction relationships in relation to the different data categories. The effect sizes are based on the phylogenetically informed multilevel meta-analytic model accounting for random effects of phylogeny, effect size ID, and study. Primary and secondary growth were compared with other growth measurements (three-level factor); flowers, seeds and fruits were compared with all reproductive organs (three-level factor); populations were contrasted with meta-populations (two-leveled factor) and gymnosperms were compared with angiosperms (two-leveled factor) in a joint rma model, as visualized in the Supplementary Fig. S3. The results are based on 308 observations derived from 78 studies on 79 species. Asterisks indicate significant effects. AIC = 194.11; I^2 = 69.08. The estimated variance components of random effects equal 0.08 for phylogeny, 0.05 for study, and <0.001 for effect size ID.

Predictor	**estimate**	**se**	**z-value**	**p-value**	**ci.lb**	**ci.ub**	
Intercept	-1.226	0.46	-2.667	0.008	-2.127	-0.325	**
Primary growth	0.942	0.402	2.343	0.019	0.154	1.73	*
Secondary growth	1.1	0.39	2.82	0.005	0.335	1.864	**
Population	-0.084	0.084	-1.005	0.315	-0.248	0.08	
Flowers	0.079	0.243	0.326	0.744	-0.397	0.556	
Seeds and fruits	0.066	0.204	0.323	0.747	-0.335	0.467	
Gymnosperms	-0.134	0.212	-0.633	0.527	-0.549	0.281	

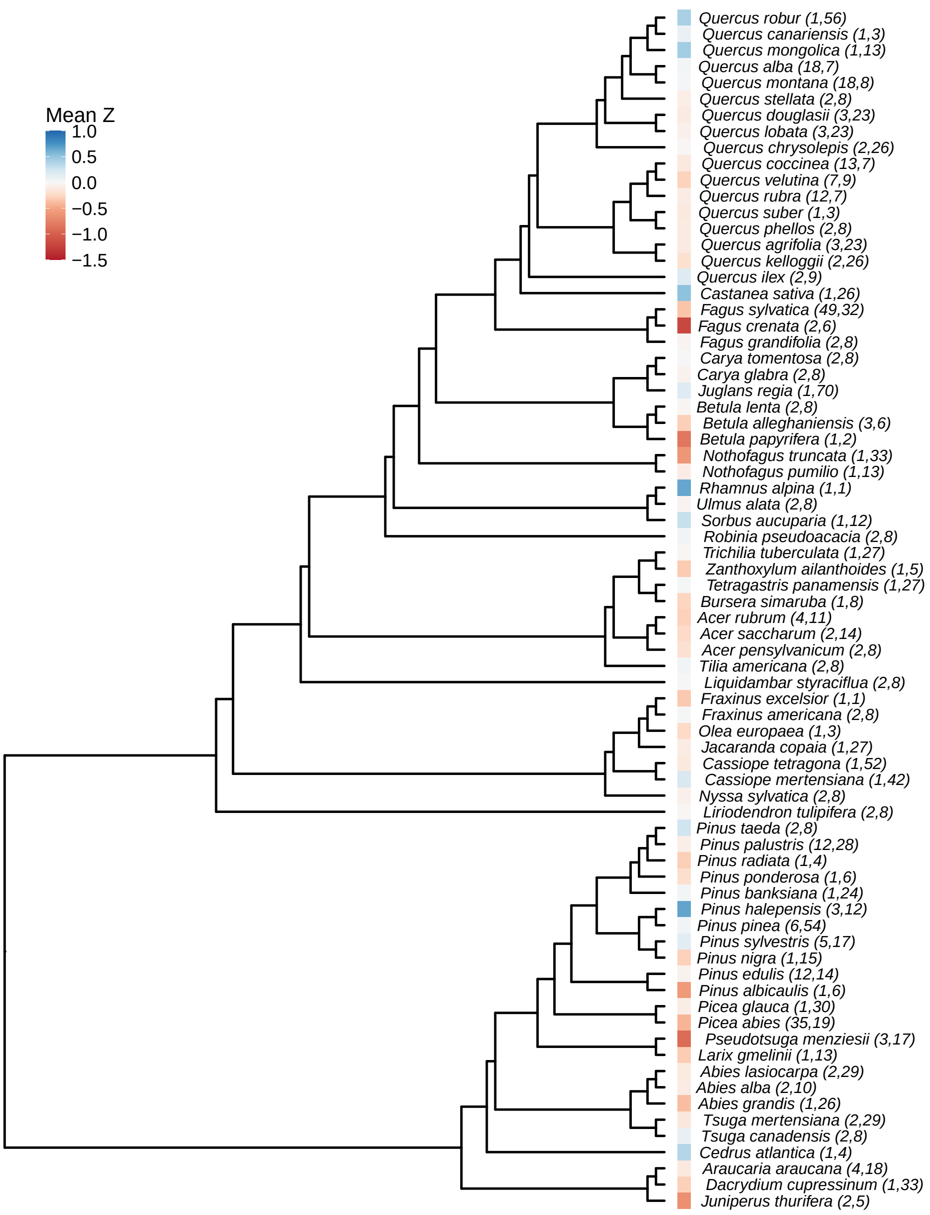

Figure S4: **Correlation between secondary growth and reproduction does not exhibit phylogenetic coherence.** Warmer colours (reds) indicate negative, and cooler colours (blues) indicate positive correlations between reproduction and growth in the same year (t). In brackets given are: the number of populations in which trade-offs were studied and the mean number of years for each species. Phylogenetic signal, estimated from species-level mean effect sizes, is negligible (Pagel's $\lambda < 0.001$, $p = 0.99$, $n = 74$ species). The data is restricted to observations based only on studies measuring secondary growth (see Supplementary Fig. S3).

Table S6: Summary of the rma model testing the effects of climate and functional traits on growth-reproduction relationships (Fig. 4). The effect sizes are based on phylogenetically informed multilevel meta-analytic model accounting for random effects of phylogeny, effect size ID, and study. MAT - Mean Annual Temperature, MAP - Mean Annual Precipitation, SLA - Specific Leaf Area. The results are based on 308 observations and 79 species. AIC = 202.09; I^2 = 65.76. The estimated variance components of random effects equal 0.06 for phylogeny, 0.05 for study, and <0.001 for effect size id.

Predictor	**estimate**	**se**	**z-value**	**p-value**	**ci.lb**	**ci.ub**
Intercept	-0.233	0.146	-1.599	0.11	-0.518	0.053
MAT	-0.007	0.036	-0.183	0.855	-0.078	0.064
MAP	0.002	0.03	0.048	0.962	-0.058	0.061
SLA	-0.023	0.043	-0.534	0.594	-0.106	0.061
Wood density	-0.035	0.046	-0.758	0.446	-0.124	0.055
Plant height	-0.087	0.065	-1.342	0.18	-0.214	0.04
Seed mass	0.089	0.051	1.765	0.077	-0.01	0.189

Table S7: Summary of the rma model testing the effect of interaction between mean CV_p of seed production and the final year of the study. The effect sizes are based on phylogenetically informed multilevel meta-analytic model accounting for random effects of phylogeny, effect size ID, and study. Asterisks indicate significant effects. The results are based on 261 observations and 48 species for which CV_p values were available (Fig 5). Asterisks indicate significant effects. AIC = 142.61; I^2 = 64.02. The estimated variance components of random effects equal 0.09 for phylogeny, 0.02 for study, and <0.001 for effect size id.

Predictor	**estimate**	**se**	**z-value**	**p-value**	**ci.lb**	**ci.ub**	
Intercept	42.64	15.9	2.682	0.007	11.477	73.803	**
Mean CV_p	-42.778	12.148	-3.522	0.0004	-66.587	-18.969	***
Final year of the study	-0.021	0.008	-2.687	0.007	-0.037	-0.006	**
Mean CV_p : Final year	0.021	0.006	3.512	0.0004	0.009	0.033	***

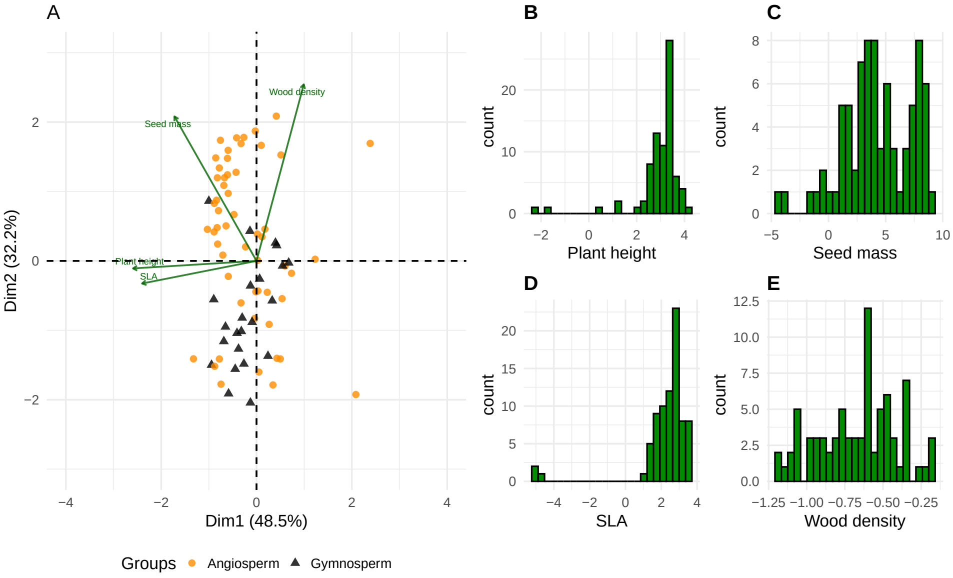

Figure S5: **Coverage of species-level functional traits investigated in the meta-analysis.** A) Principal Component Analysis. Arrow length indicate relationships between four functional traits tested in the meta-analysis (i.e. SLA, plant height, wood density, seed mass) (Fig. 4) averaged at the species level (n = 79). Each point represents single species (yellow - angiosperms, black triangles - gymnosperms). B) Histogram of log-transformed plant height. C) Histogram of log-transformed seed mass. D) Histogram of log-transformed SLA (specific leaf area). E) Histogram of log-transformed wood density (including genus-level average values).

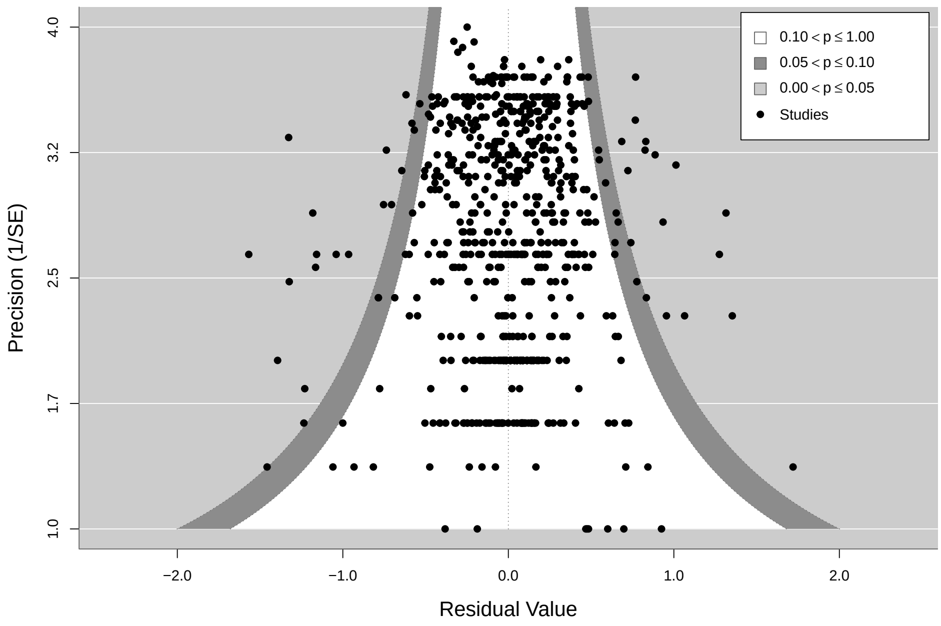

Figure S6: **Funnel plot.** Residual values from the rma model are plotted in relation to their precision (inverse standard error). Each point refers to population-level growth-reproduction correlation (based on all time lags, n = 685). Shades highlight different levels of statistical significance described in the legend.