






















## SYNTHESIS

# The Relationship Between Maturation Size and Maximum Tree Size From Tropical to Boreal Climates

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## ABSTRACT

The fundamental trade-off between current and future reproduction has long been considered to result in a tendency for species that can grow large to begin reproduction at a larger size. Due to the prolonged time required to reach maturity, estimates of tree maturation size remain very rare and we lack a global view on the generality and the shape of this trade-off. Using seed production from five continents, we estimate tree maturation sizes for 486 tree species spanning tropical to boreal climates. Results show that a species' maturation size increases with maximum size, but in a non-proportional way: the largest species begin reproduction at smaller sizes than would be expected if maturation were simply proportional to maximum size. Furthermore, the decrease in relative maturation size is steepest in cold climates. These findings on maturation size drivers are key to accurately represent forests' responses to disturbance and climate change.

## 1 | Introduction

The size or age at maturity is critical for tree population fitness and forest regeneration because recruitment opportunities can

occur when trees are any size or age (Dietze and Clark 2008; McDowell et al. 2020; Qiu et al. 2021). In trees, reproduction follows an extended maturation phase (Thomas 1996; Clark, LaDeau, and Ibanez 2004). Juvenile allocation to leaves and

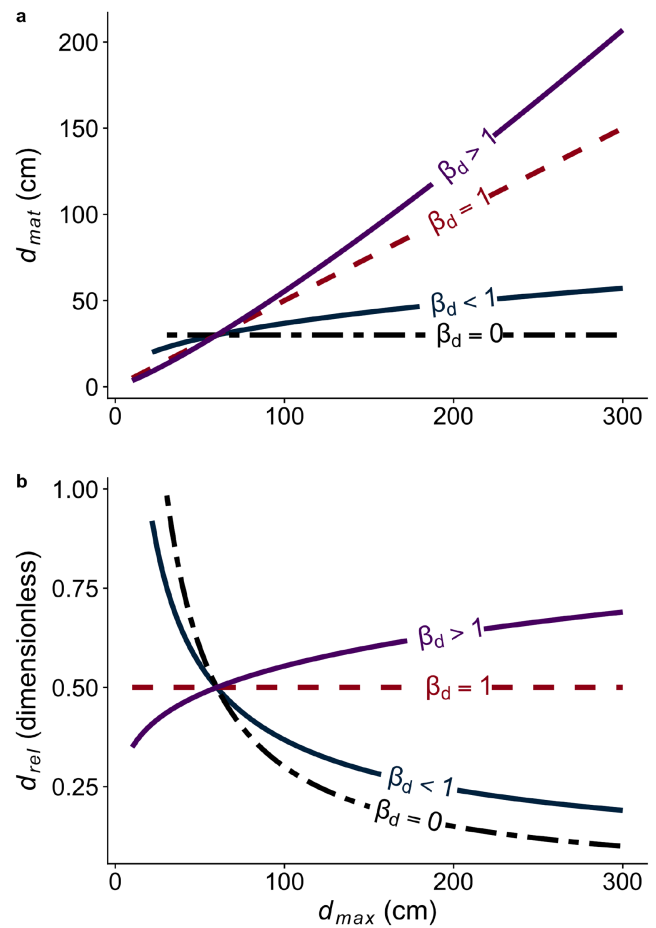
the roots and architecture that supports them build the large light- and water-harvesting capacity characteristic of the tree life form. Allocation can then shift to include reproduction. This delayed maturation of trees is linked to the fundamental trade-off between current and future reproduction (Stearns 1989).

On one hand, delayed reproduction sacrifices early seed production to reap future benefits. In environments marked by intense competition and a reliable future, delayed reproduction benefits from large size and the resources that accumulate if juveniles allocate to growth and survival (Falster and Westoby 2003; Wenk and Falster 2015). On the other hand, the advantages of large size can come with costs, including water transport high into the crown and biomechanical risk of bole fracture or windthrow (Niklas 1994; Koch et al. 2004; Dietze and Clark 2008; Lines et al. 2012). Current reproduction avoids the risks of an uncertain future, and it contributes most to fitness in non-competitive or frequently disturbed environments (Charlesworth 2000).

Among tree species, the potential trade-off between current and future reproduction might require a balance of benefits and risks and result in a positive association across species in maturation and maximum size (Loehle 1988; Thomas 1996; Davies and Ashton 1999; Westoby et al. 2002; Falster and Westoby 2003; Wenk and Falster 2015; Visser et al. 2016). Our understanding of the variation of maturation size among tree species is, however, extremely limited and there are no large-scale studies on this topic. We thus have a poor understanding of how maturation size varies with species maximum size and the relative importance of other factors such as species climate niche and functional traits.

In the absence of maturation estimates, earth system models (ESMs) incorporate assumptions that are expected to bias lifetime reproduction. Many ESMs omit impacts of life history on disturbance response entirely (see McDowell et al. 2020 for a review). In models that do accommodate life history, maturation size— $d_{\text{mat}}$  (for diameter)—is independent of maximum size— $d_{\text{max}}$  (Kohler and Huth 2004; Wallentin et al. 2008; Yang et al. 2022) (Figure 1, black dotted line). An alternative hypothesis is that maturation size is proportional to maximum size. It is consistent with a study at Barro Colorado Island in Panama; where, Visser et al. (2016) reported that  $d_{\text{mat}} = d_{\text{max}} / 2$  (red dashed line in Figure 1). This is related to the classical prediction of a proportionate increase in maturation age with increased maximum age from simple optimisation models in animals (Charnov and Berrigan 1990, 1991; Jensen 1996; Thorson et al. 2017) and trees (Clark 1991). Indeed, if the predictions for age also apply to size, then this *proportionate risk model* means that the maturation delay incurred for increased maximum size is the same for species large and small, represented by the red line in Figure 1.

In fact, it would be remarkable if this relationship was the same for species of all sizes because the constraints on the large size and the relative contribution to fitness of early seed production could vary widely depending on the species' maximum size. If mortality risks and allocation demands change with age and size (Charnov and Berrigan 1990), then the strictly proportional relationship between maturation size ( $d_{\text{mat}}$ ) and maximum size ( $d_{\text{max}}$ ) can be generalised to a power relationship,



**FIGURE 1** | Hypothesised association between maturation size ( $d_{\text{mat}}$ ) and maximum size ( $d_{\text{max}}$ ) (a) and the relative size at maturation ( $d_{\text{rel}} = d_{\text{mat}} / d_{\text{max}}$ ) (b) (Equation (1)). To highlight the effects of size (parameter  $\beta_d$ ), values of parameter  $\alpha$  are selected to yield an equivalent diameter at  $d_{\text{max}} = 60$  cm. Two ‘baseline’ hypotheses (dashed lines) are independence between  $d_{\text{mat}}$  and  $d_{\text{max}}$  (black dotted) and proportionate delay (red dotted), the latter is expected if increased size incurs the same maturation delay at all size classes. Two alternative hypotheses are increasing (purple—accelerating risk model) or decreasing (blue—diminishing risk model) maturation delays in the largest size classes.

$$d_{\text{mat}} = \alpha \times d_{\text{max}}^{\beta_d} \quad (1)$$

The proportionate model means that  $\beta_d = 1$  in Equation (1) (Figure 1a). An *accelerating risk model* refers to the case where the maturation delay required for large species to increase maximum size is greater than for small species. If  $\beta_d > 1$  (purple in Figure 1), the relative size at maturation ( $d_{\text{rel}} = d_{\text{mat}} / d_{\text{max}}$ ) continues to increase for species in the largest size classes (Figure 1b). Consider, for example, an expected fitness gain from extending end-of-life reproduction that comes with increased size and age. The early-life investments in structural support or defences needed for an incremental increase in maximum size might be especially high for the largest species.

Alternatively, a *diminishing risk model* refers to the case where the need to further delay maturation size declines for species already at large size. If  $0 < \beta_d < 1$ , then species that

reach large size do not incur the same proportionate delay risk as small species. As  $\beta_d$  approaches zero, the largest species mature at nearly the same size as the small species. Then, the relative size at maturation  $d_{rel}$  declines with maximum size (Figure 1b).

Improved understanding of maturation size confronts challenges posed by slow dynamics and limited observation. Where there is a dense canopy, the reproductive status of individual trees is often not detected, and crop failures (little or no seed production in trees that have reached maturity) are common. Likewise, seed traps often fail to recover seeds from nearby reproductive trees, especially the low seed production of newly mature individuals (LaDeau and Clark 2001). Detection error can be minimised where observations come from above the canopy or open settings like savannas, seed orchards or common gardens (LaDeau and Clark 2001; Caignard et al. 2021). Still, a time series of observations is needed because an individual reproducing this year will have matured at some time in the past. Estimates of maturation status from time series data allow for detection error similar to the way it is used in capture–recapture models. Maturation can be treated as a hidden Markov process (see detailed Supplements to Clark, LaDeau, and Ibanez 2004; Clark, Nuñez, and Tomasek 2019). As in capture–recapture models, the probability that an individual is mature in a given year depends not only on failure to detect in the current year but also on the history and future of observations on the same individual. The more times that reproduction is not detected in the past (or future), the lower the probability that a tree is mature now. In tree fecundity studies, the complexity is compounded by the ‘masting’ phenomenon, where quasi-synchronous, quasi-periodic crops require observations over several years, making a large number of observations in a single year insufficient. Most studies where maturation size has been estimated focus on open-grown trees and/or have limited taxonomic breadth, habitat variation or both (Wenk et al. 2018; Thomas 1996; Davies and Ashton 1999; Kohyama et al. 2003; Wright et al. 2005; Visser et al. 2016; Minor and Kobe 2019).

Inferring the relationship between maturation and maximum size has also to control for the environment (Wenk and Falster 2015) and species characteristics (Visser et al. 2016). While the effects of climate on maturation size are unknown, tree fecundity responds to seasonal temperature and moisture, soils and light availability, which depends on the local competitive environment (Clark et al. 2014; Caignard et al. 2017; Minor and Kobe 2019; Le Roncé et al. 2021; Qiu et al. 2022; Journé et al. 2022). Also, fast growth and accelerated competition that comes from long growing seasons in the wet tropics do not necessarily imply small or large maturation sizes.

The relationship between maturation and maximum size could be associated with other plant functional traits, that would reflect diverse plant strategies. Fast growth in open environments is often associated with low wood density and high specific leaf area (SLA) (Moles et al. 2004, 2006; Thomas, Martin, and Mycroft 2015; Visser et al. 2016; Wenk et al. 2018). However, it is unclear whether the same traits that are involved in fast growth are also associated with maturation at a small size. Furthermore, if large-seeded species need to accumulate resource reserves, then there could be a positive association between seed size and

maturation size (Moles et al. 2004). Relatedly, high reproductive expenditures, measured as seed size  $\times$  seed number (Qiu et al. 2022), might be associated with delayed maturation size. Due to their co-dependence, it is necessary to model all of these traits jointly, while accounting for the effects of habitat and phylogenetic groups (Clark 2016; Seyednasrollah and Clark 2020; Bogdziewicz et al. 2023; Qiu et al. 2023).

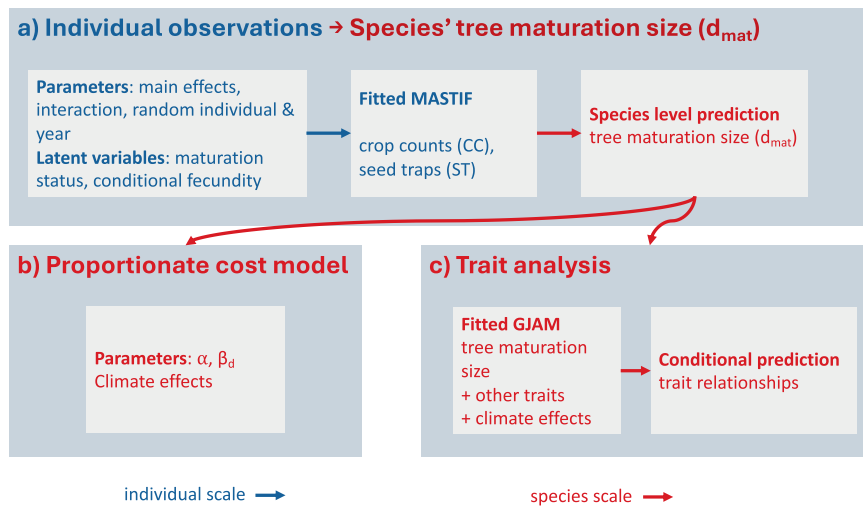
In this study, we provide the first comprehensive estimates of tree maturation size, obtained for 486 tree species on five continents, incorporating effects of the environment over a large range of tree diameters and habitats. We use the Masting Inference and Forecasting (MASTIF) network and modelling framework to accommodate the dependence between observations between trees and within trees over time (Clark et al. 2021; Sharma et al. 2022; Qiu et al. 2022; Journé et al. 2022). Based on MASTIF estimates we derive maturation size as tree diameter at the onset of female reproductive function allowing us to compare maturation sizes across species that vary in reproductive biology (e.g., *Pinaceae* commonly produce male cones earlier than female cones; many species have no such separation) and where pollen production can be hard to quantify. We first evaluate how maturation varies with species' maximum size and test the three alternative models of Figure 1 with our estimates of maturation size and estimates of species' maximum size. Then, we evaluate how the relationship between maturation size and maximum size is influenced by climate and its association with other plant functional traits.

## 2 | Materials and Methods

Our analysis includes three elements (Figure 2). We first parameterise a model for individual maturation status and fecundity based on diameter, shade conditions and environmental variables (Figure 2a). The year in which an individual achieves maturity is almost never observed. Instead, seeds counted in traps or in crowns vary from year to year. Successive observations represent a time series for every tree. This first step estimates maturation status and conditional fecundity (seeds per tree per year given that it is mature) for all trees in the network. From this fitted model, we generate predictive distributions of maturation status across diameter with other variables held at intermediate values to estimate  $d_{mat}$  from the model. Again, this prediction from the model is necessitated by the fact that true maturation status is an estimate, not a state that is directly observed. Second, we estimated the model of Figure 1 to obtain estimates of  $\alpha$  and  $\beta_d$  (Figure 2b), while controlling for other variables that could affect their relationship. Finally, we evaluate the species-level trait relationship that includes maturation size (Figure 2c). The following section describes these elements of the analysis.

### 2.1 | MASTIF Data and Model

The MASTIF model and data summarised here are detailed in Clark, Nuñez, and Tomasek (2019) and its extended Supplement (see also Qiu et al. 2021, 2022; Journé et al. 2022). Data are of two types, crop counts on trees and seed traps in mapped inventory plots (MASTIF) (Clark, Nuñez, and Tomasek 2019)



**FIGURE 2** | Three elements of the analysis include (a) an individual-scale analysis (blue) to estimate maturation status each year and to parameterise relationships that control maturation. This fitted model is the basis for species-level prediction of maturation size (red). (b) Species-level expected maturation size based on the proportionate risk model, controlling for species' differences in their climate domains. (c) Analysis of species-level trait relationships with maturation size.

(Figure S1). The initial sample size is approximately 12 million tree-years from five continents on 898 species and 112 families. The majority of observations (99%) are derived from longitudinal studies, involving repeated observations of all trees on a plot or individual trees. The remaining crop count observations (1%) are collected opportunistically through the iNaturalist project MASTIF (Clark, Nuñez, and Tomasek 2019). The number of species observed per plot ranges from 1 to 221 species. The number of species observations is larger for seed trap monitoring (476 species in total, 22,929 tree-year observations on average) than for crop count monitoring (130 species in total, 1058 tree-year observations on average). Most plots are localised in North America and central Europe (97%), whereas most species observations are coming from South America (54%). On average, 75% of individual tree-year observation are coming from the tropics. Additional information is provided in Table S1 and Supplementary Files S1 and S2. For both data types, observations include species, diameter, shade class (ranging from 'full sun', Class 1, to 'full shade', Class 5), number of fruiting structures, and an estimate of the fraction of the total crop represented by the count. For crop counts, the data model is beta-binomial, with binomial uncertainty for the counts given crop fraction, and beta uncertainty for crop fraction. The seed traps data additionally include mapped locations of trees and seed traps, which is used to jointly estimate fecundity, dispersal, and, for seeds identified only to genus, species identity. For seed traps, the data model is Poisson for counts given dispersal and species, a bivariate Student's  $t$  (i.e., 2Dt) redistribution kernel for dispersal (Clark et al. 1999; Clark, Nuñez, and Tomasek 2019), and a multinomial species probability (many seeds are identified only to genus level).

The MASTIF model is a dynamic model for year-to-year and tree-to-tree seed production. The model allows for conditional independence in crop counts and seed traps data through latent states. It estimates maturation state and conditional fecundity (seed production given the individual is mature), which depend on tree size, shading, local climate and soil conditions. Random

effects on individuals and years allow for wide variation between trees and over time. The posterior distribution includes the parameters and latent states presented in Clark, Nuñez, and Tomasek (2019), and summarised in Qiu et al. (2022) and Journé et al. (2022). Model fitting was accomplished with Gibbs sampling, a Markov chain Monte Carlo technique based on sampling from conditional distributions. Model structure and methodology are implemented with the R package Mast Inference and Forecasting (MASTIF, v1.0.1) (Clark, Nuñez, and Tomasek 2019).

## 2.2 | Derivation of Tree Maturation Size From Fitted MASTIF Model

Tree maturation size ( $d_{mat}$ ) is derived from an individual-scale model fitted to each species with MASTIF. We define tree maturation size ( $d_{mat}$ ) as the diameter when a tree is mature and has the capacity to produce enough seed to construct one fruiting structure,  $f_{min}$ . For species that produce one-seeded fruits (e.g., *Quercus*, *Juglandaceae*),  $f_{min} = 1$ . For species that produce cones (e.g., *Pinaceae*, *Cupressaceae*), pods (e.g., *Fabaceae*, *Bignoniaceae*) or other capsules that house multiple seeds (e.g., *Fagus* capsules),  $f_{min}$  is the number of seeds contained in that structure. The data and definitions we use to determine  $d_{mat}$  differ from those employed in previous studies (e.g., Visser et al. 2016), as we use both crop count and seed trap observation and not only maturation status. The estimation of individual fecundities, obtained through MASTIF model, is also included, taking into account tree characteristics and environment (Clark et al. 2021; Qiu et al. 2021; Journé et al. 2022). MASTIF models the effects of environmental predictors on conditional fecundity (given mature status), because immature trees do not respond to predictors (it is always zero) [Modelling environmental effects on (unconditional) fecundity would make no more sense than including immature individuals in studies of masting intervals or synchronicity]. Conditional fecundity  $\psi$  is represented by a log-normal distribution, which allows for the effects of the environment. The log-normal is undefined for zero seeds. Zeros

are accommodated by the fact that trees can be in the immature state ( $\rho = 0$ ), or conditional fecundity can be below the threshold  $f_{\min}$ , as in a failed seed crop (Clark, LaDeau, and Ibanez 2004; Clark, Nuñez, and Tomasek 2019),

$$f = \begin{cases} \psi & \rho = 1 \\ 0 & (\rho = 0) + (\rho = 1)(\psi < f_{\min}) \end{cases} \quad (2)$$

An individual is immature until the first time fecundity rises above the threshold for producing fruit, that is,  $(\rho_{i,t} = 1)(\psi_{i,t} > f_{\min})$ . Specifically for tree  $i$  in year  $t$ ,

$$\begin{aligned} f_{i,t} &= \psi_{i,t} \times \rho_{i,t} \\ \rho_{i,t} | \rho_{i,t-1}, \rho_{i,t+1} &\sim \text{Bernoulli}(\rho_{i,t-1} + (1 - \rho_{i,t-1})\rho_{i,t+1}\Phi(\beta_0^p + \beta_1^p d_{i,t})) \\ \log \psi_{i,t} &\sim \mathcal{N}(\mathbf{x}'_{i,t} \boldsymbol{\beta}^x + \dots, \sigma^2) \end{aligned} \quad (3)$$

where  $\Phi(\cdot)$  is the standard normal cumulative distribution function for the probit probability of transitioning to the mature state, depending on tree diameter  $d_{i,t}$ . Importantly,  $\Phi(\beta_0^p + \beta_1^p d_{i,t})$  it is the probability of making the transition for an individual that is now in the immature state. For this reason, the coefficients  $\beta_0^p, \beta_1^p$  for maturation in the second line of Equation (3) engage only for the transition tree-years,  $[\rho_{i,t} | \rho_{i,t-1} = 0, \rho_{i,t+1} = 1]$ . Predictors in the design vector for conditional fecundity  $\mathbf{x}'_{i,t}$  include the mean climate variables (defined at the species level) tested here and competition by neighbours, and  $\boldsymbol{\beta}^x$  is the estimated parameter vector. The ellipses ( $\dots$ ) in Equation (3) includes individual effects (subscript  $i$ ) and year effects (subscript  $t$ ) (Clark, Nuñez, and Tomasek 2019). The variance not assigned to predictors is  $s^2 = \sigma^2 + \text{Var}(\text{individuals}) + \text{Var}(\text{years})$ .

Setting all other fitted variables at their mean values and intermediate shade (shade class 3 on the scale from 1 to 5), we obtained (unconditional) fecundity  $f$  from the fitted model. We first factored the joint distribution of conditional fecundity and maturation,

$$[\psi > f_{\min}, \rho = 1] = [\psi > f_{\min} | \rho = 1][\rho = 1] \quad (4)$$

Using Bayes' theorem, the cumulative distribution function for maturation diameter is

$$\begin{aligned} [d_{\text{matr}} > d | \psi > f_{\min}, \rho = 1] &\propto [\psi > f_{\min}, \rho = 1 | d] [d] \\ &= [\psi > f_{\min} | \rho = 1, d][\rho = 1][d] \\ &= \Phi(z_1)\Phi(z_2)[d] \end{aligned} \quad (5)$$

where  $z_1 = \frac{\log f_{\min} - \mathbf{x}' \boldsymbol{\beta}^x}{s}$  (log normal fecundity),  $z_2 = \beta_0^p + \beta_1^p d$  (probit maturation) and again,  $s^2$  is the marginal variance for conditional fecundity. We have taken the diameter distribution  $[d]$  to be uniform. The distribution of maturation size is obtained using inverse distribution sampling from Equation (5), and we estimated  $d_{\text{mat}}$  as the mean of this distribution. We selected species for which maturation and fecundity schedules could be estimated with confidence. The selection was based on estimates of maturation status from the MASTIF model, and we retained species with at least 10 immature and 10 mature individuals. This included 486 species observed over a range of values for diameters.

### 2.3 | Trait and Climate Data

Like maximum tree height or age, maximum tree diameter is a useful concept, despite the fact that it cannot be known. To incorporate the concept of size differences, we use extreme sizes available from literature and our inventory data, recognising that the concept of a maximum becomes most meaningful with large sample sizes, which are not available for all species. For the final analysis here, we kept the highest estimates of  $d_{\text{max}}$ . Sources in Table S3 include tropical species from large plots in central Panama (189 species) and French Guyana (33 species), which together represent 45.7% of values. Estimates extracted from the internet (e.g., encyclopaedia, online flora) include 173 species (35.6%) (Table S3). For species not estimated in other sources, we used forest inventory data, evaluated by two approaches, both based on order statistics. We avoided using the absolute largest reported value in forest/MASTIF inventories due to the high noise levels associated with extremes. Order statistics were preferred over quantiles, the latter being determined by whether there are huge numbers of small trees in the data set; quantiles are based on the entire stand structure, whereas here the goal is to estimate the largest sizes, regardless of whether there are few or many small trees. For species present in national forest inventories we estimated  $d_{\text{max}}$  following Qiu et al. (2021) by using the tenth largest order statistic (38 species, 7.8%). For the remaining species present in MASTIF inventories, and with at least more than 90 unique individuals, we used the fifth largest order statistics (representing in total 8.4%). For species having only maximal plant height (Liu et al. 2019), but no  $d_{\text{max}}$ , we converted them to  $d_{\text{max}}$  using allometric equations of Feldpausch et al. (2011) (12 species, <2.5%). Observations of  $d_{\text{max}}$  coming from the internet are usually higher than data from National Forest Inventories, allometric predictions and MASTIF inventories (Figure S2). Seed size estimates came from measurements in our lab (Clark et al. 2021), the primary literature and the TRY Plant Trait Database (Kattge et al. 2011). Wood density and SLA are from the compilation of Carmona et al. (2021). We used genus- or family-level means for seed size, SLA and wood density values that were missing at the species level (15%, 28% and 26%, respectively). We defined a species' seed productivity as (mass per seed)  $\times$  (mean seeds per tree basal area) (Qiu et al. 2022).

For species' climate, we extracted average temperature (in °C) and moisture deficit (evapotranspiration minus precipitation, in mm) for each species based on all occurrences in the Global Biodiversity Information Facility (GBIF) through the R package rgbif (Chamberlain and Boettiger 2017). The GBIF request is available from reference GBIF.org (2022). For species that are absent from GBIF, we extracted temperature and deficit from the MASTIF sites where those species were reported (162 species, 33%). Climate variables were obtained from CHELSA (Karger et al. 2017).

### 2.4 | Maturation and Maximum Size

To test the alternative hypotheses that the maturation diameter decreases ( $\beta_d < 1$ ) or increases ( $\beta_d > 1$ ) with maximum species size (Figure 2b), we estimated parameters in Equation (1) with the model

$$\begin{aligned} \log_{10}(d_{\text{mat}_s}) &= \log_{10}(\alpha) + \beta_d \times \log_{10}(d_{\text{max}_s}) + \dots + \varepsilon_s \\ \varepsilon &\sim \mathcal{N}(0, \sigma^2) \end{aligned} \quad (6)$$

where for species  $s$ , where the ellipsis includes climatic variables (moisture deficit and temperature) and their interactions with  $d_{\max}$ . We tested alternative models including independence between maturation and maximum size (fitted  $\alpha$  with  $\beta_d$  fixed at zero), proportionate increase (fitted  $\alpha$  with  $\beta_d = 1$ ) and changing relationship with size (both  $\alpha$  and  $\beta_d$  estimated). Models were fitted with regression by using species average estimates of  $d_{\max}$  as a response, and we included the inverse of the standard error of  $d_{\max}$  as weights. Model selection and fit were evaluated with AIC and root mean square error (RMSE). Regression dilution could cause underestimation of the strength between here  $d_{\max}$  and  $d_{\max}$  when a predictor (i.e.,  $d_{\max}$ ) contains errors (Frost and Thompson 2000; Detto et al. 2019). We thus ran additional analyses to test the robustness of our results to the regression dilution effect (see Supplementary Material A2). First, we corrected the parameter  $\hat{\beta}_d$  from measurement error by using the R package mecor (Nab 2021) (v1.0). Secondly, we tested if the relationship between  $d_{\max}$  and  $d_{\max}$  varies depending on the origin of  $d_{\max}$ .

## 2.5 | Joint Trait Analysis

We evaluated the association between maturation size and other species' traits from the ability of  $d_{\max}$  to predict other trait values while allowing for climate and phylogeny effects (Figure 2c). The marginal correlations that are commonly used for this purpose do not account for the many ways that traits can be related to one another. For instance, maturation size might be associated with maximum size because both tend to be high in warm climates, or in the phylogenetic groups that tend to occur in warm climates. To accommodate co-dependence between trait values we used generalised joint attribute modelling (GJAM) with traits as responses (Clark 2016). To account for phylogeny in the joint traits model, we diverged from traditional assumptions concerning residual covariance. Instead, we adopted a direct inference of the effects of phylogenetic groups. Traditional approaches of phylogenetic correction build on highly specific assumptions for the residual variance (random walk, or more complex models representing stabilising selection such as the Ornstein–Uhlenbeck model). Our departure from these assumptions stems from the recognition that natural selection does not operate uniformly, neither within a given species pair nor across a broad spectrum of species. Our GJAM analysis explored phylogenetic contributions, with species groups treated as random effects and covariance that is unconstrained by assumptions on divergence rates (Qiu et al. 2023). Explanatory variables included temperature, moisture deficit and their interaction. Traits included wood density ( $\text{g m}^{-3}$ ), SLA ( $\text{mm}^2 \text{mg}^{-1}$ ), species seed productivity ( $\text{kg m}^{-2}$  basal area), seed size (g), maximum diameter ( $d_{\max}$ ) (cm) and maturation diameter ( $d_{\max}$ ) (cm). All traits were log-transformed. We included a random phylogenetic group effect in the joint trait analysis (Qiu et al. 2022, 2023; Bogdziewicz et al. 2023). For species in speciose genera (more than 10 species), genus was used as the phylogenetic group. For species in less speciose genera but belonging to families with more than five species, family was used as the phylogenetic group. For the remaining species (<25% of the total), an 'other' category was used. To estimate the direct effect of traits (i.e., SLA, wood density,

species seed productivity and seed size) and climatic variables on  $d_{\max}$ , we report conditional parameters from GJAM. Conditional parameters are estimated by extracting the parameters of the conditional distribution of traits conditioned on  $d_{\max}$ . Conditional parameters estimate the direct associations between traits while accounting for climate and phylogeny. Conditional parameters were obtained with the gjam R package (v2.6.2) (Supplementary Material, Section A1).

## 2.6 | Relation of $d_{\max}$ Along the Phylogeny

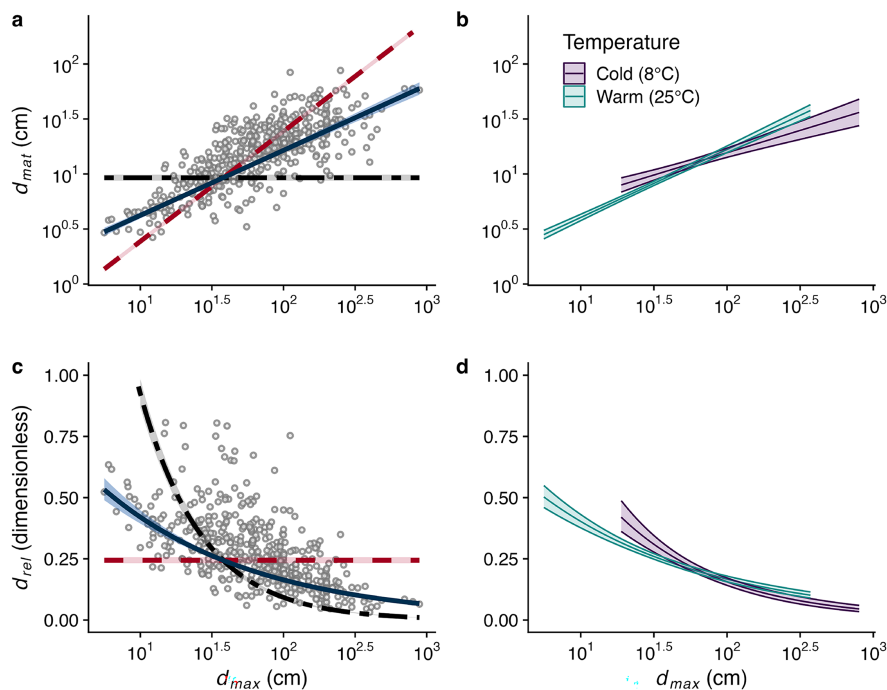
We visualised how  $d_{\max}$  varies across species phylogeny by making a phylogenetic tree plot. We used the phylogeny from Zanne et al. (2014), and retrieved phylogenetic information for 400 out of the 486 studied species. Of the species missing from the phylogeny (i.e., 86 species), the relative proportion of missing phylogenetic information is about 13.2% for temperate species and about 19.4% for tropical species. We then tested for a phylogenetic signal in  $d_{\max}$  and  $d_{\max}$  using Pagel's  $\lambda$  (Pagel 1999) (which test for a Brownian motion evolutionary signal), with values close to 0 indicating low phylogenetic signal and values close to 1 suggesting a phylogenetic correlation. We plotted the phylogenetic tree with ggtree R package (v3.8) (Yu et al. 2017). We estimated the Pagel's  $\lambda$  by using the phylosig function from phytools (v1.5) (Revell 2012).

## 3 | Results

Maturation size is associated with maximum size, but not proportionately so (Figure 3a). Large inter-specific variation in  $d_{\max}$  estimates had 95% quantiles that ranged from 4.0 to 51 cm, with relative maturation size ( $d_{\max}/d_{\max}$ ) quantiles of (0.07, 0.65). Contrary to the baseline independence model ( $\beta_d = 0$ ), trees did not start to reproduce at a constant size (dashed black line in Figure 3a). If we force proportionality (fix  $\beta_d$  at 1), the estimate of  $\hat{\alpha} = 0.24(0.23, 0.26)$  (Line 3 of Table 1) is consistent with Loehle's (1988) range for hardwoods (1/5–1/4), but far outside his range for conifers (1/15–1/10). The 95% CI that is well below 0.5. This differs from the Visser et al. (2016)'s estimate of 1/2 for Barro Colorado Island ( $N = 60$  species), Panama and with Minor and Kobe (2019) La Selva, Costa Rica ( $N = 16$  species). It is crucial to acknowledge that the aforementioned authors employed a distinct definition of  $d_{\max}$  and estimated larger  $d_{\max}$  (Figure S3). Moreover, this proportional cost model ( $\beta_d = 1$ ) fits poorly, with twice the RMSE and a higher AIC than the best-fitting model (Table 1).

Fitting both  $\alpha$  and  $\beta_d$  (Line 2 of Table 1) shows strong support for the diminishing risk model ( $0 < \hat{\beta}_d < 1$ ). Allowing for environmental predictors further decreases the estimate to  $\hat{\beta}_d = 0.30(0.15, 0.46)$ . The exponent  $0 < \hat{\beta}_d < 1$  means that relative size at maturation ( $d_{\max}$ ) decreases in large species (blue in Figure 3a).

The best-fitting model (lowest AIC and RMSE) includes a negative effect of temperature (maturation at small size for species most common in cold climates) and a positive interaction between temperature  $T$  and  $d_{\max}$  (Table 1). This positive interaction means that the relationship between maturation and maximum



**FIGURE 3** | Tree maturation size (a, b), and relative size at maturation (c, d) for 486 species. Each dot represents one species. Alternative models are dashed lines, black for independence between maturation size and maximum size ( $\beta_d = 0$ ), and red for the proportional cost model ( $\beta_d = 1$ ). The best fitting model (blue with 95%CI) supports the diminishing risk model ( $\beta_d < 1$ , Table 1). Panels b and d are predictions from the fitted model with an interaction between continuous  $d_{max}$  and temperature (Line 1 of Table 1). This model gives a continuous surface plot of maturation size as a function of maximum size and temperature (see Figure S4). However, for clarity, we represent only the prediction at cold (8°C, purple) and warm temperatures (25°C, green) spanning observed diameter ranges.

**TABLE 1** | Coefficient estimates and fit to Equation (6). The selected model with the lowest AIC (bold font at top) includes temperature ( $\beta_T$ ) and the interaction between  $d_{max}$  and temperature ( $\beta_{dT}$ ). The proportional cost model has  $\beta_d$  fixed at 1. The independence model has  $\beta_d$  fixed at 0. Additional models that include moisture deficit and temperature have higher AIC values (Table S4).

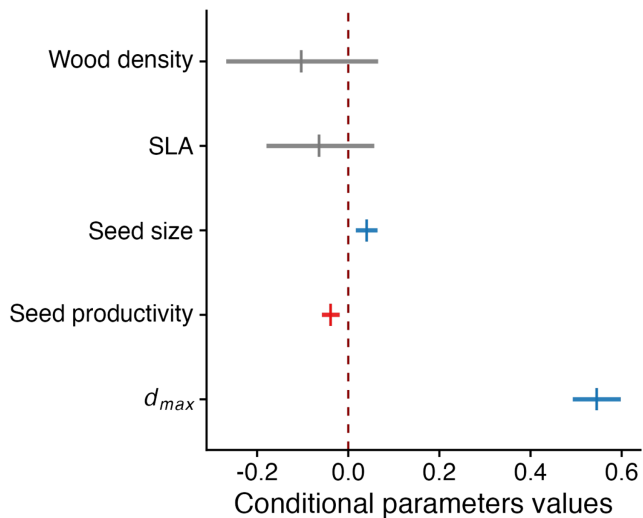
$\alpha$	$\beta_d$	$\beta_T$	$\beta_{dT}$	$\sigma$	<b>AIC</b>	<b>RMSE</b>
3.71 [1.94, 7.07]	0.30 [0.15, 0.46]	-0.023 [-0.035, -0.011]	0.012 [0.0058, 0.019]	0.089	<b>-62</b>	10.2
1.08 [0.93, 1.25]	0.59 [0.55, 0.63]	—	—	0.090	-52	10.0
0.24 [0.23, 0.26]	1	—	—	0.12	248	18.8
9.25 [8.69, 9.85]	0	—	—	0.15	447	15.4

Abbreviation: RMSE, root mean square error.

size tends to steepen for species in warm climates (Figure 3b,d), approaching the proportionate risk model (Table 1); the rise in  $d_{mat}$  with  $d_{max}$  increases with temperature. However, the main plus interaction effect remains below 1 even in warm climates showing that the diminishing risk model is supported across this temperature range. The  $\beta_d$  remained below 1 even when we restricted the analysis to a single source of  $d_{max}$  (Table S1 and Figure S1, see Supplementary Section A2). After correcting for risks of regression dilution, the average value of  $\beta_d$  remained below 1, with corrected  $\beta_d = 0.73$ ; however, the confidence interval is between 0.03 and 1.43 (Table S2, see Supplementary Section A2).

The joint trait model incorporating random phylogenetic group and climate exhibits a root mean square prediction error

1.17 units smaller compared to the model that includes only climate. Conditional parameter estimates from the joint trait analysis show that  $d_{max}$  has a stronger effect on  $d_{mat}$  than other traits. There is a weak positive association with seed size, and a negative association with species fecundity (see Methods, Trait and Climate Data section) (Figure 4). There are no meaningful associations with wood density or SLA. The joint trait analysis also confirms the absence of a direct climate effect on  $d_{mat}$  after accounting for  $d_{max}$  in the conditional trait analysis (see Table S5 for joint trait model and Table S6 for conditional parameters). Previous linear models showed that temperature was significant only in the interaction with  $d_{max}$  (Table S4). Joint trait analysis indicates that the temperature effect on maturation size in Figure 2c could be due to the abundance of small species (small  $d_{max}$ ) in warm climates (Figure S5). The trait relationships do



**FIGURE 4** | Conditional parameter estimates for the direct effect of traits on tree size at maturation diameter ( $d_{mat}$ ) while accounting for trait covariance, climate, and phylogeny. Conditional parameters are evaluated on a standardised scale (predictors are centred and standardised) making trait effects on  $d_{mat}$  respective to their variation in the data set. Shown are posterior means and 95% credible intervals. Blue and red represent positive and negative associations where 95% of the posterior does not include zero. SLA = specific leaf area.

not depend on the source of climatic data: (i) GBIF species occurrence in Figure 4 or (ii) more narrowly, where they occur in the MASTIF data network (Figure S6).

Both maturation ( $d_{mat}$ ) and relative size ( $d_{rel}$ ) show evidence of phylogenetic conservation ( $\lambda_{mat} = 0.83$ ,  $p < 0.0001$ ;  $\lambda_{rel} = 0.51$ ,  $p < 0.0001$ ,  $n = 400$ , Figure S7a), yet with substantial variation within some groups. The two-sample t-test for unequal variances shows differences between gymnosperms and angiosperms. Gymnosperms have high mean values for both  $d_{mat}$  and  $d_{max}$  and low mean values for  $d_{rel}$  (all  $p < 0.0001$ ). Within gymnosperms, *Pinales* and *Cupressaceae* mature at large size, but large  $d_{max}$  gives them lower  $d_{rel}$  than most angiosperms (Figures S8 and S9). Most *Pinaceae* (*Picea*, *Pinus*) and *Cupressaceae* (*Thuja*, *Sequoia*), *Fagaceae* (*Quercus* and *Fagus*) and *Juglandaceae* have low  $d_{rel}$  (Figure S10). Plant groups with both tree and shrub habits, such as *Rosales*, *Magnoliales*, *Rubiaceae* and *Fabaceae*, have mixed  $d_{rel}$ . However, we did not find a significant effect of tree versus shrub habit on  $d_{rel}$ , possibly due to high variation in the data (Figure S10). Shrubs may tend to have high  $d_{rel}$ , but higher  $d_{rel}$  is also observed in trees genera like *Magnolia* and *Poulsenia*.

#### 4 | Discussion

Our analysis suggests a diminishing risk model for the relationship between maturation and maximum size (i.e.,  $d_{mat}$  and  $d_{max}$ ). The novelty here comes from the low coupling we find. Indeed, the coefficient  $\hat{\beta}_d = 0.30$  in Table 1 that we found is closer to zero (no relationship) than one. In contrast, the estimated exponent values fitted to vertebrates are greater than 1/2 (Prothero 1993; Herculano-Houzel 2019), twice the value

of  $\hat{\beta}_d$  we find for trees. Nevertheless, the comparison across groups is complex due to the uncertainty on maximum size ( $d_{max}$ ), which could influence the value of the exponent  $\hat{\beta}_d$ , but this issue remained unexplored in other taxa. The biological difference of  $\hat{\beta}_d$  may arise because trees differ from other species groups in the gains that come from allocation to growth, as the gain is due to the relative difference in height with other competitive individuals. In most tree species, individuals in the understory produce no seed at all, while dominant stature can yield multi-order-of-magnitude gains in fecundity over crowded neighbours (Clark, LaDeau, and Ibanez 2004). In contrast, in vertebrates, improved parental condition and size can translate to incremental increases in clutch size or survival of well-provisioned offspring. Gestation times and physical limits on clutch size (e.g., one offspring) may allow only muted near-term benefits of reproductive delay.

In trees, large size comes with uncertainty that could weaken the potential benefit of delaying maturation. Wind exposure and risk of hydraulic failure both increase with size (Bennett et al. 2015; Jackson et al. 2021; Gardiner 2021; Barrere et al. 2023). The vanishing probability that a seed survives to large size, combined with the fact that fecundity can plateau and even decline late in life (Qiu et al. 2021) means that the competitive advantages of extremely large size can rarely make up for lost benefits of early reproduction. At a stand scale, the risk of stand-replacing disturbances can increase with stand age and development (e.g., accumulated fuels increase fire risk), such that species that fail to reach minimum reproductive size before the next disturbance can be excluded from communities (Clark 1991; McDowell et al. 2020). The fact that maturation size increases with maximum size means that the two are not independent. But the cost is not proportionate (Figure 3).

The fact that some correlation exists does not conflict with a disproportionate importance of near-term gains that can follow delayed maturation. Instead, it suggests that the benefits of large size probably do not come at the end of life. The capacity to reach a large size pays benefits throughout life, contributing with many other variables to current size and fecundity, not just as a tree approaches the maximum.

Both climate and species traits contribute to the relationships between maturation and maximum size. The negative main effect of temperature and its positive interaction steepens the relationship with maximum size in warm climates (Figure 3), where growth and mortality rates are generally higher than in temperate forests (Stephenson and Van Mantgem 2005; Locosselli et al. 2020). Abundant resources may offer a disproportionate advantage to early maturation (van Noordwijk and de Jong 1986; Kozłowski 1992; Wenk and Falster 2015). Long growing seasons in warm climates might have similar effects. However, intense competition on nutrient-rich sites might also favour delayed reproduction as trees compete for canopy access. Theoretical studies (Falster et al. 2017; Detto, Levine, and Pacala 2022) have shown that a trade-off between maximum size and maturation size can promote niche diversification and maintain species coexistence, and can be typically observed in tropical where there is a wide range of maximum sizes forests (Falster et al. 2017).



We did not find that high SLA is associated with maturation at small size (Visser et al. 2016) or early age (Wenk et al. 2018). The relationship reported in Wenk et al. (2018) includes leaf area from 1 year and one site, and the correlation estimated in that study does not appear to control for phylogeny. Similarly, lack of association with wood density in our study does not agree with suggestions that shade-tolerant species with high wood density mature at small size (Thomas, Martin, and Mycroft 2015). The inclusion of a wider range of plant species may reveal a different pattern of traits. For example, a comparison over a large number of perennial plant species such as herbs, graminoids, shrubs, and trees shows that traits that promote longevity are associated with greater variability in seed production (Journé, Hackett-Pain, and Bogdziewicz 2023). The fact that species that produce large seeds also allocate more to reproductive effort (Qiu et al. 2022) could contribute in a small way to delayed maturation. The differences between our result and previous work may be due to the larger species coverage, and to the control of the effect of climate and phylogeny in our joint analysis.

Results highlight the importance of large data sets and how they are modelled. This first compilation of tree maturation size for hundreds of species on five continents shows strong support for a diminishing risk model—trees that can get big can still mature at relatively small sizes. The result is a decline in the relative size of maturation for large trees (Figure 3d). The benefits of extensive data here parallel the shift from early theory that argued for a constant relative maturation size ( $d_{rel}$ ) in fish (Charnov and Berrigan 1990), followed by studies showing an exponent that is less than one (Froese and Binohlan 2000; Tsikliras and Stergiou 2014; Thorson et al. 2017). However, it is important to acknowledge that our coverage of tree species diversity is still patchy, with most data coming from Europe and North America and limited spatial coverage in Africa, South America, Asia and Oceania as data are concentrated in a few large plots in these areas (Daru and Rodriguez 2023).

New insight from this analysis comes first from extending observations beyond a small number of tropical sites, few species or limited sample size (Thomas 1996, 2011; Wright et al. 2005; Visser et al. 2016; Minor and Kobe 2019). The expanded coverage of species and sites permitted the incorporation of climatic drivers into the analysis of  $d_{mat}$  in relation to  $d_{max}$ , which influenced the estimation of  $\alpha$  and  $\beta_d$ . Second, this study also benefited from accommodating detection and temporal dependence to infer maturation. The estimation of  $d_{mat}$  was possible by combining diverse datasets, either based from direct crop measurement and seed trap monitoring and by the use of MASTIF model which could estimate jointly a probability of maturation and individual fecundities. For instance, estimates of  $d_{mat}$  from Visser et al. (2016) are, on average, approximately 1.8 times larger than our estimates for the species in common in the two studies (Figure S3). This discrepancy could be attributed to a different definition of size at maturation and methods of analysis, as our method also includes the number of seeds produced.

Due to the high juvenile mortality, the maturation sizes quantified here are expected to impact predictions from demographic vegetation models, including earth system models (ESMs) that include effects of maturation size. In one ESM

study that considered the effects of maturation height, variation in a single value applied to all species did not have a large impact on simulated stand productivity (Raczka et al. 2018). However, when differences in species maturation size are accounted for in models, the effect can be larger. Few individuals survive to large size and, thus, their ability to reproduce early can be important. The fact that species capable of large size tend to retain this capacity to reproduce while still small highlights the importance of understanding maturation size. Accurate estimation of maturation size ( $d_{mat}$ ) is likewise important for assessing response to disturbance regimes, especially as the time to maturity begins to exceed the interval between disturbances. For instance, several species that compared pairs of species found that species with smaller size at maturation can have better post-disturbance dynamics than species with larger maturation size (Alfaro-Sánchez et al. 2022; Andrus et al. 2020). Our results provided the data to test such hypotheses at a much larger scale. This effect can even scale up at the ecosystem scale. In boreal habitats, exposure to more frequent disturbances that exceed the tree maturation time can completely change a tree community to a grass-dominated community without a return to a forest stand within centuries (Buma et al. 2013).

Current ESMs suffer from limited information on allocation to reproduction (Wenk and Falster 2015), including empirical data (Hanbury-Brown, Ward, and Kueppers 2022b). Similarly, management actions intended to assure regeneration from seed also need to consider if the minimum harvest diameter is smaller than maturation size (Ouédraogo et al. 2018). Maturation size may play an important role in the ability of species to respond to disturbance and climate change (McDowell et al. 2020) when tree maturation can be reached faster under elevated CO<sub>2</sub> exposure (LaDeau and Clark 2001). Considering the difference in maturation size between species may be crucial, although it can be more challenging to comprehend due to the impact of CO<sub>2</sub> on maturation size. Understanding how fecundity strategies differ between species and phylogenetic groups, such as lower relative size at maturation ( $d_{rel}$ ) for gymnosperms than angiosperms, may open a new avenue to better understand species diversification and responses to disturbances (Bond 1989; Verdu 2002; Qiu et al. 2022). Developing a model that represents the size at which a species begins to produce seeds could improve the representation of the regeneration of each functional type (Hanbury-Brown et al. 2022a) and colonisation rates (Snell 2014) and improve our understanding of species coexistence. Our study contributes to the maturation sizes needed for each of these objectives.

#### Author Contributions

V.J., G.K. and J.S.C. performed analyses, led the paper and designed the study. V.J., M.B., B.C., G.K., T.Q. and J.S.C. co-wrote the paper. J.S.C. compiled the MASTIF network, and wrote the MASTIF model and software. All authors contributed data and revised the paper.

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### Conflicts of Interest

The authors declare no conflicts of interest.

### Data Availability Statement

Data and code supporting our results are archived on the Open Science Framework (OSF) Repository: <https://doi.org/10.17605/OSF.IO/U23VY>. All analyses used R Core Team (2023) (v4.3.0) and published R packages.

### Peer Review

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### Supporting Information

Additional supporting information can be found online in the Supporting Information section.