Evolutionary ecology of masting: mechanisms, models, and climate change

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Abstract

Many perennial plants show mast seeding, characterized by synchronous and highly variable reproduction across years. We propose a general model of masting, integrating proximate factors (environmental variation, weather cues, and resource budgets) with ultimate drivers (predator satiation and pollination efficiency). This general model shows how the relationships between masting and weather shape the diverse responses of species to climate warming, ranging from no change to lower interannual variation or reproductive failure. The role of environmental prediction as a masting driver is being reassessed; future studies need to estimate prediction accuracy and the benefits acquired. Since reproduction is central to plant adaptation to climate change, understanding how masting adapts to shifting environmental conditions is now a central question.

keywords: | climate change | plant demography | economies of scale | environmental prediction | plant reproduction

Declaration of interests

No competing interests to declare.

What is masting and why it is relevant

Numerous perennial plant species show **mast seeding** (see Glossary), where reproduction is highly variable across years and synchronized among individuals in a population [1, 2, 3]. Peak seed production years are often orders of magnitude above the long-term mean (Fig. 1), and reproductively mature plants can forgo reproduction for years [4, 1]. Understanding the ecology and evolution of mast seeding is important for diverse groups, including plant and animal ecologists, foresters, and land managers [5, 6]. Masting has effects on plant population dynamics, and is also a dramatic example of an ephemeral pulsed resource [7]. Peaks in seed crops disrupt food webs, drive animal outbreaks and migrations [8], cause spikes in wildlife-borne human diseases [9], and peaks in allergenic pollen concentrations [10]. Masting alters carbon and nutrient allocation which affects tree growth and ecosystem-scale nutrient cycling [11, 12, 13]. Understanding masting is needed in the era of rapid climate change to which many masting systems may be sensitive. Here we show how recent discoveries can be applied to better understand and manage masting in the future.

Masting covers variation in flower and seed (or cone) crops, but for brevity, we use seeds for reproductive effort generally, except where specifically detailed.

Masting is fundamentally population-level, relative, and quantitative. Masting is population-level because it is an emergent property (variation in population seed production, CVp) which is the product of individual variation (CVi) and **synchrony** between individuals (S).
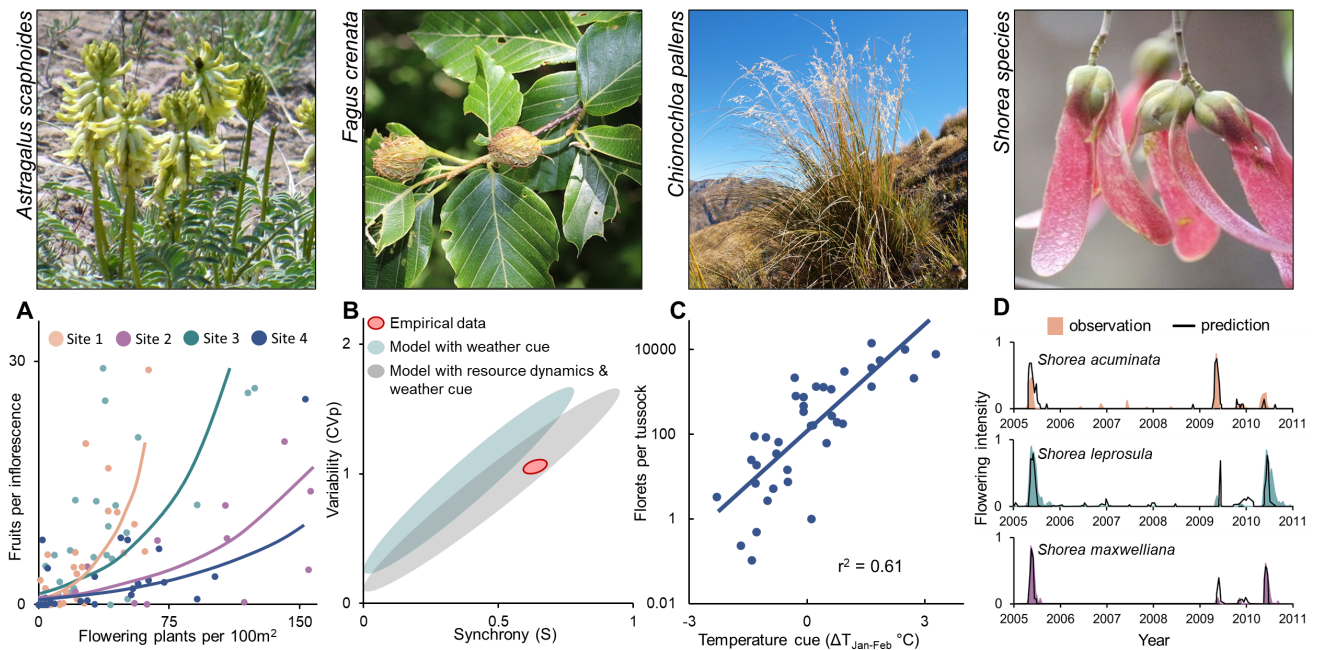
Figure 1: **Types of masting**. Masting species vary in their life histories, and in factors from Fig. 2 that drive masting [14, 15, 2]. (A) Bitterroot milkvetch (*Astragalus scaphoides*) is a short-lived herb in which masting is generated by internal resource dynamics, synchronized by density-dependent pollen limitation; weather plays a minor role (graph shows fruit set increases with population flowering density; updated from [16]). (B) Japanese beech (*Fagus crenata*) is a long-lived tree in which resource dynamics create variability, synchronized by a weather veto (graph shows that only models combining resource dynamics and weather cues match the observed dynamic behavior) [17]. (C) Snow tussocks (*Chionochloa spp.*) are alpine, long-lived grasses in which masting is driven almost entirely by a weather cue (the temperature-difference Δ**T cue**) (updated from [18]). (D) multiple *Shorea* species in Malaysia show synchronous masting at irregular intervals, cued by a combination of drought and cool temperatures (graph shows the match between predicted and observed flowering for three species) [19].

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Masting is relative because it is primarily about the proportional seed investment across years, not the long-term mean number of seeds produced [1]. Consequently, the core question is how seed production can be distributed across years to maximize **reproductive efficiency**. This could be heavier reproduction every second year, some mixture of smaller and occasional larger years, or being monocarpic.

Masting is quantitative at many levels. Firstly, the distribution of seed crop sizes among years is nearly always continuous [1], not dichotomous (mast and non-mast years) (Fig. 1). Hence the best definition of masting is quantitative: synchronous and highly variable seed production among years by a population of perennial plants [2]. Dichotomous definitions (e.g. large seed crops at irregular intervals) are misleading and best avoided. Secondly, the strength of masting varies continuously among species, from **strong masting** (high CVp) to weak (low CVp), so there is no clear boundary between masting species and non-masting species [20]. Thirdly, in a particular species, multiple factors can favor (or oppose) masting by quantitative amounts [14, 21], so assigning a single selective cause of masting may not be possible (see Fitness Benefits). Finally, while masting is only the relative temporal allocation of reproductive effort, it has downstream effects at later stages (such as seed predation) (Box 1).

Reproduction in masting is postponed. Plants skip opportunities for reproduction, waiting to concentrate reproduction in a subsequent year (hence, only perennial plants can mast). Delay imposes costs (see Costs of masting), so masting is unlikely without compensating advantages. Currently, no masting definitions explicitly mention **delayed reproduction**. Since proving delay is difficult, including a delay in the definition could make it hard to apply. Also, purely environmentally-driven masting (resource matching: [2], Fig. 2) represents special cases with no delay. For example, in arid environments, reproduction may be possible only after rare rainfall events [22]. Such datasets are uncommon, but it is not known whether few plants do this, or few biologists document it. Most masting studies are from less extreme environments, and seeding variation is usually higher than environmental variation (Fig. 2), so delays driven by selection are common. Hence masting generally requires an evolutionary explanation.

Fitness benefits

Two kinds of fitness advantages can select for masting, making CVp higher than environmental variation: **economies of scale (EOS)** and **environmental prediction**. Economies of scale are caused by events that the plants create (high seed density), whereas for environmental prediction the plants try to anticipate external events, like wetter springs.

Economies of scale are density-dependent processes in which plants gain fitness benefits by synchronizing reproduction in fewer, high-density seeding events [1]. The key feature of economies of scale is that heavy reproduction generates lower costs per surviving offspring [23], through predator satiation and/or improved pollination efficiency. Predator satiation posits that periods of alternating seed scarcity and abundance starve and then satiate seed consumers; this is

Glossary

- **Alternate bearing** - a special case of masting characterized by alternation between low and high seed production years

- **CV - Coefficient of variation** (standard deviation/mean), frequently used to quantify interannual variation in seed production either at the population level (CVp) or at the individual level (CVi). CVp is the product of the mean temporal variation of individual plants (mean CVi) and the synchrony among individuals within a population (S).

- **Delayed reproduction** - when mature plants skip viable opportunities for reproduction, to concentrate reproductive effort in a subsequent year.

- **ΔT cue** - a weather cue based on a difference (Δ) in temperature (T) from one growing season to the next, e.g. temperature difference between the two previous summers (ΔT).

- **Economies of scale (EOS)** - A positively density-dependent process that increases reproductive efficiency, such as predator satiation or pollination efficiency.

- **Environmental prediction** - A density-independent process in which the weather cue that triggers reproduction is also correlated with future environmental conditions that favor recruitment.

- **Masting or Mast Seeding** - synchronous and highly variable reproduction among years by a population of perennial plants. Masting is about the relative, rather than absolute, reproductive investment each year.

- **Mast year or Mast event** - a term for a year of high population seed crop. Separating high from medium seed crops is arbitrary, but can be repeatable.

- **Reproductive efficiency** - the cost of reproduction per surviving offspring. Typical metrics include the proportion of flowers that ripen a fruit, the proportion of fruits that escape predation, or the proportion of all seeds that produce a living seedling.

- **Resource matching** - variation in seed production that matches variation in the environment.

- **Strong masting** - a term for "high interannual variation in population-level seed production" i.e. high CVp. Weak masting is low CVp.

- **Synchrony (S)** - among-plant (or among-population) synchrony of interannual variation in seed production. Synchrony within a population is required by definition; synchrony at broader scales is not.

- **Veto** - a weather cue that decreases reproduction, e.g. by damaging developing fruits.

> • **Weather cue** - weather conditions that synchronize reproduction, typically by promoting heavy flowering. Individuals are synchronized with weather events, and indirectly with each other.

now widely supported [1, 24]. The pollination efficiency hypothesis states that cross-pollination is enhanced in large synchronized flowering events, and is also widely supported [25, 26]. These economies of scale measure the current benefits of masting, but also point to the possible origin of masting in a population that has modest initial weather-driven inter-annual variation in seed crops [27, 28].

Environmental prediction is not density-dependent; instead, the plant reproduces in anticipation of favorable conditions that plants cannot affect directly. One example is fire-stimulated flowering [1, 29]. Fire induces plants to reproduce, and seeds are subsequently dispersed into an environment favoring seedling establishment. Plants that produce more of their seeds immediately after fire have higher average seedling survival [30].

As an example of a more indirect type of environmental prediction, white spruce (*Picea glauca*) masting is triggered by dry summers that simultaneously increase the likelihood of fire, increasing the chances of seed release into disturbed areas where the establishment is enhanced [31]. This pattern is created by recurrent large-scale climate variability such as El Niño Southern Oscillation (ENSO) [32, 30]. Similarly, in five *Shorea* species (Dipterocarpaceae), cooling and drought trigger flowering, and that environmental signal is often followed by favorable wet conditions during seedling establishment months later [33], due to the autocorrelation in climate created by ENSO [32].

Plant reproduction is sometimes cued by events that are significantly correlated with favorable future conditions. However, the strength of these effects is unknown (how much does fitness increase?). The strength of benefits under masting is the effect size of an event (e.g. the change in seedling establishment under higher rainfall) multiplied by the probability that the event is successfully anticipated (e.g. how often is the high-seed year followed by higher rainfall?). The "probability of the event" therefore represents how accurately the plants predict future conditions, and reproduce heavily just before favorable conditions.

Prediction accuracy for an EOS will be high because the plants generate the key variable (seed crop size). The degree of synchrony among plants is unknown, but synchrony is under ongoing selection [34]. For environmental prediction through fire-stimulated flowering, prediction accuracy is high as each plant responds after it experiences the fire. For more indirect environmental prediction, effect sizes and prediction accuracy are largely unquantified. In *Shorea*, the prediction accuracy is good (correlation between the masting cue and subsequent wetter conditions is 0.2 - 0.4) [33], but the effect size on the seedling establishment is unknown. In contrast, for *P. glauca*, masting is more likely to occur in years with more fires [31], but the probability of a masting spruce being close to a fire (but not burned by it), as this hypothesis requires, is low. While prediction accuracy in this case is low, for plants next to a fire the

effect size (increase in seedling establishment into a large burnt area) is probably massive, and long-lived trees have multiple masting events, each of which might have an adjacent fire.

In *P. glauca* and *Shorea*, the primary benefit of the weather cue is as a synchronizing cue to allow predator satiation and/or increase pollination efficiency [35, 36]. Secondarily, the cue means masting events occur at times with a higher probability of subsequent favorable conditions, an environmental prediction benefit. If synchronizing cues provide multiple benefits (as in these cases) they might be more strongly selected for. The relative benefits from economies of scale versus environmental prediction are beginning to be explored, but lower prediction accuracy suggests the latter might have weaker effects than economies of scale. The challenge for environmental prediction is to move from statistical significance (e.g. correlations with plausibly favorable conditions) to quantifying the effect sizes and probabilities of a masting plant obtaining that benefit.

Costs of masting

The costs of masting are well known [37, 38], but studies showing how masting patterns respond to these costs are rare [15, 39]. Masting costs are of four types. First, delayed reproduction reduces population growth rates which lowers fitness [37], and creates a risk of dying before the next reproductive opportunity. These costs are important in short-lived plants (a decade or two), but negligible in plants that live for centuries, like *Shorea leprosula* [40]. Also, delaying reproduction can result in ephemeral reproductive windows (e.g. treefall gaps) being missed, and reaped by regularly reproducing individuals. Models indicate this cost can prevent masting from evolving [28]. However, many common strategies let plants store reproductive potential until a disturbance occurs (soil seed banks, seedling banks [41]), and synchronizing reproduction with disturbances (the environmental prediction hypothesis) can reduce these costs [30]. Overall, for long-lived masting species, the costs of delay are probably small.

Second, masting can increase negative density dependence, through competition between seedlings and/or aggregation of herbivores or pathogens [1], although these effects might be offset if investment in high numbers of seeds is accompanied by increased reserves invested in each seed [42]. Few studies measure whether high-seed years create higher seedling mortality [42, 43]. In two species, rowan (*Sorbus aucuparia*) and *Shorea leprosula*, masting still gave net benefits after allowing for increased seedling competition [40, 43]. More data on seedling mortality rates is needed, but we predict that higher seedling mortality rarely counterbalances the benefits of masting, otherwise masting would not be observed. Third, mutualist species could be satiated, including pollinators and seed dispersers. That cost is implicit in masting being less strong in animal-pollinated plants and plants with endozoochorous dispersal [44, 15, 45].

Fourth, masting diverts resources and can temporarily reduce allocation to growth and defense [46, 47]. Such trade-offs are well documented, but their impacts on plant performance are not. In *Shorea leprosula*, of all masting costs considered (such as density-dependent seeding

mortality) reductions in growth associated with masting had the weakest effects on demographic performance [40]. Life history theory predicts strong selection in long-lived plants to avoid reproduction which lowers survival, so such effects are more likely in shorter-lived perennials, or when masting coincides with other stressors [48, 49].

Comparing masting benefits and costs would improve understanding of why the strength of masting varies among species with some phylogenetic conservatism (e.g. masting being more common in pines, variable in oaks [39, 45]). Understanding fitness impacts throughout the lives of long-lived plants is difficult, but one approach is incorporating masting into models covering entire tree life cycles [50, 51] (Box 1).

Box 1: Demographic consequences of seed production strategies: life after masting

Recent decades have seen great progress documenting masting consequences for reproduction from flower initiation to seed survival. Nonetheless, processes acting at subsequent life stages, from germination to adults, also affect plant demography [52]. Producing viable seeds is part of successful reproduction (defined as producing offspring that themselves survive to reproduce), so seed success is a useful measure of masting success. Viable seeds are tickets in a subsequent lottery, and masting gives some plants more tickets. At the same time, later demographic stages can affect masting, and vice versa, for example through density-dependence in seedling survival [42, 43]. Moreover, when masting depletes resources, it can affect the plant's subsequent growth and survival [46, 48]. Nevertheless, quantifying the benefits and costs of masting usually stops with seedlings, as later processes are less strongly affected by masting (Fig. I). Decades-old saplings are more affected by current herbivore densities and rainfall than by previous densities of seed or seedlings.

Measuring reproductive success through the entire life cycle is necessary for understanding regeneration and coexistence. Variation in masting strategies will be important in this wider picture [50, 51]. Incorporating models of masting into whole-life-cycle demographic models can show the lifetime net benefits (or costs) of masting, and reveal how masting affects population dynamics across life stages, environmental contexts, disturbance regimes, and species traits. Stand dynamic models that integrate spatiotemporal heterogeneity at all stages of plant life history provide a way forward, including testing competition dynamics with species differing in seed production strategies [50]. Similarly, simulation models that integrate the spatial genetic structure of plant populations can improve our understanding of selective forces acting at the seedling stage on masting species [53].

Generally, there are three scales of masting studies: the narrow effects of masting on individual plants' reproductive efficiency, the wider effects of masting on the demography of plant populations, and community-level effects of masting in food webs (as mentioned in the Introduction).
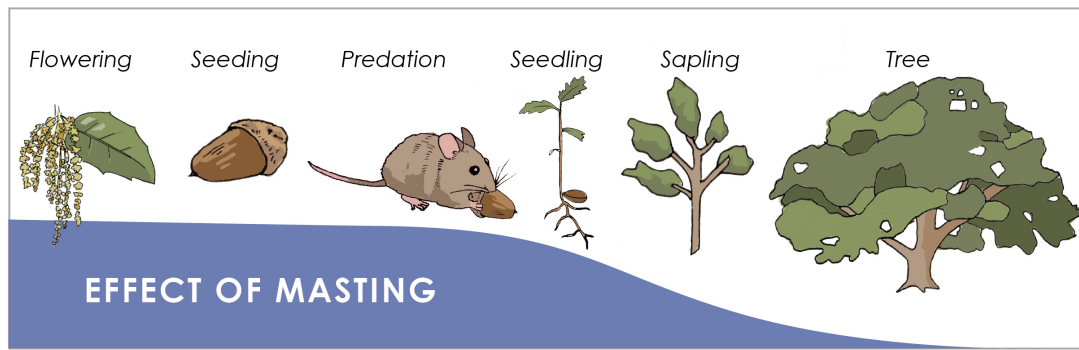
Figure I: Masting effects are strongest at early life history stages. Masting produces benefits and costs at different life history stages, which together determine reproductive efficiency and the net selective benefit of masting. The largest masting effects are predicted on early reproductive stages (pollination success, seed maturation, pre- and post-dispersal seed predation, and early seedling survival) through density-dependent processes. Masting effects become progressively weaker in later life stages. Nonetheless, since masting determines how many sound seeds are produced, it likely plays an essential role in overall regeneration processes and community dynamics. Illustration: Emily Underwood.

General Model of Masting

Past attempts to explain masting focused on either proximate or ultimate factors. But some factors have effects at both levels, and factors interact [2]. Any general model of masting, therefore, must evaluate the relative impact of all three major factors proposed as drivers of masting: weather through its effect on plant resources (resource matching: [23]), selective benefits like economies of scale [1], and internal resource dynamics (resource budget models: [54]). Resource matching was proposed first, but fell from favor because seed crops vary more than plausible weather drivers [55], and plants could be selected to be hypersensitive to weather cues [18]. Economies of scale theories stressed the selective benefits of synchrony, with weather largely reduced to a cue, and resources mainly capping the maximum possible level of reproduction. Resource budget models initially made it seem possible that masting could be the non-selective result of physical internal resource limits.

Rather than them being mutually exclusive, we propose a General Model that integrates all three factors. In this model of masting, the important question is the quantitative importance of each factor for any given species or population (Fig. 2). Pearse et al. [2] argued that in resource budget models, the threshold for reproduction (without which resource constraints do not increase CVi: [56]) generally depends on an EOS, and that in EOS models internal resources still have some role. Weather is both a cue (for the synchrony that an EOS requires) and a modifier of resource gain. So all three factors are involved, but masting in each species is affected to varying degrees by each factor (Fig. 2). For example, in Fig. 1 both bitterroot (*Astragalus scaphoides*) and Japanese beech (*Fagus crenata*) have strong resource budget effects [57, 17], while snow tussocks (*Chionochloa sp.*) are driven mainly by a strong weather cue [18].

Almost all the factors in Fig. 2 are subject to selection, including selection for hypersensitivity of plants to weather cues which promote seeding [18] and/or decrease seeding (**vetoes**, see Glossary) [58, 59]. Clarifying these drivers is a major achievement of the field, and the General Model provides the foundation for understanding the molecular basis of masting [60], creating predictive models of mast seeding (Box 2), and assessing risks from climate change (see Climate change section).
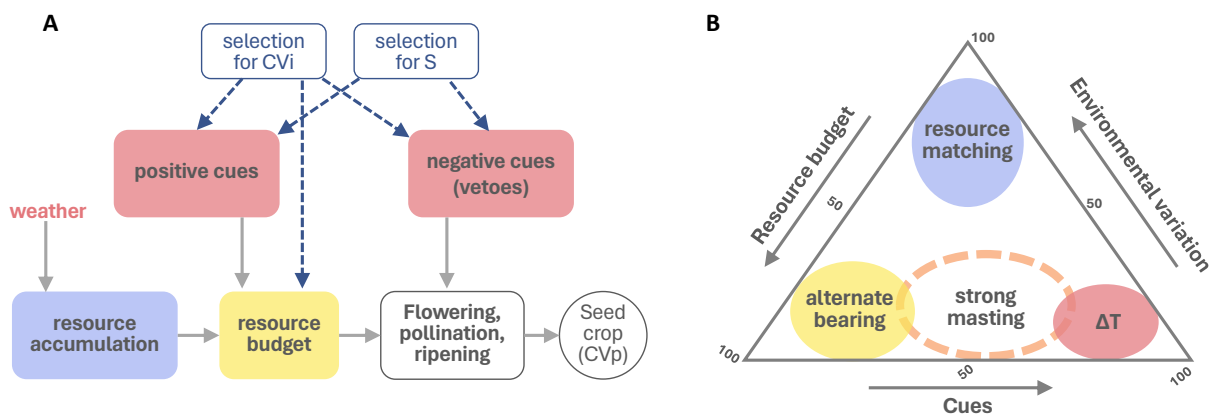
Figure 2: **A general model of masting**. (A) The key question is the relative influence on seed crop variability (CVp) of three factors: the underlying environment (blue), weather cues (red), and internal resource dynamics (yellow). The effect of each will vary across species (examples in Fig. 1). Weather variation drives resource accumulation (key parameters: mean accumulation rate $\bar{A}$ and its variation CVa) which sets the level of variation in seed production equal to CVa if there is no selection for greater variation. Selection for individual variation CVi or synchrony S can make plants more sensitive to weather cues (parameters: slope and goodness of fit) and vetoes (sensitivity P_{veto}, and fit), and/or create resource budget dynamics (relative flower cost Rc and threshold for reproduction T [28]). Cue sensitivity and resource dynamics can both increase CVi, resulting in CVp > CVa. Even without selection for resource dynamics to increase CVi, resources could cap responses to flowering cues. Vetoes block reproduction at later stages, reducing resource demands. (B) With suitable parameter values, this model could potentially match the masting patterns of any perennial species, including resource matching, **alternate bearing**, and cue-driven masting (ΔT), where colors match the factors in (A). Strong masting (high CVp) usually involves both resource dynamics and cues, so its color is intermediate. In rare cases with extreme environmental variation, resource matching can also lead to high variability in reproduction.

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New opportunities

Molecular basis of mast seeding

Genetic methods can distinguish between alternative mechanisms of masting in a particular species. Measuring gene expression can reveal whether masting in snow tussocks is driven by the ΔT temperature difference cue [61], or the previous summer temperatures plus prior flowering effort [62]. Genetic studies will enable confirmation of the apparent ability of plants to measure their environment with remarkable precision, such as comparing mean temperatures between consecutive summers perhaps using epigenetics [18], or detecting the exact date of the summer solstice [63]. Secondly, monitoring of gene expression (molecular phenology) can identify the timing of reproductive events, such as the floral transition by the floral integrator gene [64]. That allows precise time-localization of the weather cues for flowering. Without such tools, the complex weather cues that trigger general flowering in *Shorea* spp. [65] might have remained unresolved. Together, such methods enable the characterization of cues, improving the estimation of climate change responses and mast forecasting (Box 2). Genetic methods can also help reveal the basis for inter- and intraspecific variation in masting. They have already demonstrated that masting traits are heritable [66, 67].

Open data for synthesis

Compiling seed crop datasets for comparative analysis has long been useful, providing early support for the role of economies of scale as the ultimate drivers of masting [55]. Recent developments include open access data, better species and biome coverage, and high replication of individual species [75, 45]. The synthesis has enabled several previously impractical tests, generating new ideas, and opening sub-disciplines (e.g. in mast forecasting, see Box 2). For example, masting is phylogenetically conserved [15, 45, 39]. In other words, masting has been passed down from a common ancestor to its descendants, adding additional evidence that masting provides selective benefits. Species bearing traits associated with low adult mortality, such as high wood density, have stronger masting [39], consistent with a long lifespan reducing the costs of masting (see "Costs of masting"). Revisiting how the Moran effect generates large-scale synchrony of masting has been enabled by better spatial data coverage [76, 77].

Increased data availability may allow the effects of environmental gradients on masting strength to be untangled, including across and within species. At both scales, multiple factors confound each other, challenging progress. For example, across species, masting is stronger in temperate regions than tropical ones [44]. The temperate zone has lower tree species diversity, which favours masting by making predator satiation a more effective defense for plants [24]. Also, lower diversity is associated with a higher incidence of wind pollination, which favors masting [25]. But there could also be confounded direct effects of climate on masting (e.g. higher seasonality), or other, unknown factors operating.

Box 2: New challenges: mast forecasting

Because the relative timing of management and conservation efforts in ecosystems dominated by masting species often determines their success, there is a need to study masting mechanisms and develop forecasting tools for seed production. The time-series nature of masting data and the often tight association with weather predictors suggest that masting may be predictable into the future, and the capacity to forecast masting already exists for some species [68, 69]. Probably the best-known example is using mast forecasts to determine control operations for invasive mammal populations in New Zealand [68]. Other applications of mast forecasts have been discussed [5], indicating the need for the development of other operational systems. For example, as masting predicts the population dynamics of ticks, their hosts, and consequent pathogen transmission dynamics [9], mast forecasts can be incorporated into existing disease risk forecast models.

Existing work on mast forecasting has focused on near-term predictions, seeking high-accuracy forecasts typically 6-18 months ahead. These usually use statistical models to predict seed crops based on known weather cues and vetoes of masting. Sometimes, information on the previous year's seed crops is included [69], but that requires field seed production monitoring which can delay forecasts until field samples are counted. Remote sensing of masting may provide faster, cheaper alternatives to seed counting [70]. Nevertheless, one reason the New Zealand Department of Conservation finds the ΔT model so useful is that it works without information on previous seed crops [68], showing how forecast systems need to balance prediction accuracy with the needs of potential users and the costs of data collection.

The next steps for mast forecasting include the development of iterative modeling frameworks that enable continued refinement of models, including by incorporating newly available data and testing previous predictions. Other challenges include understanding how predictable masting might be in different species ("intrinsic predictability", [71]), and the timeframes over which useful predictions might be possible ("forecast horizon", [72]). The models must consider the varying needs and priorities of diverse potential users, and will be especially informative if they are capable of identifying changes in masting behavior, including masting breakdown [73, 74].

The patterns of species turnover across climates are further complicated by large within-species variation in masting; populations of the same species can show markedly different strengths of masting [78]. Internal resource dynamics are a key proximate driver of masting (Figure 2), leading to the prediction that resource-poor or stress-inducing sites will have stronger masting, as it should take a longer time to replenish resources after large seeding events (the environmental stress hypothesis)[44]. Support for that hypothesis is inconsistent, perhaps due to difficulties in defining stress [79]. Where stress can be clearly defined, such as in arid ecosystems, masting is stronger in drier habitats [80, 81]. Nonetheless, environmental gradients are complex, and in addition to climate include soils, land use history, and plant density [82]. These additional factors often co-vary with climate, and climate gradients may also influence the frequency of weather cues [83]. With larger datasets available, a better understanding of how environmental variation affects masting is within reach.

Further insights have also emerged where longitudinal monitoring of reproduction is integrated with genetic and ecophysiological monitoring [83, 84], or when combined with experimental manipulation [85].

Sensitivity of masting to changing climate

Ongoing global warming has altered masting patterns in some species [86, 73], but not others [87]. Understanding species sensitivity to climate change is a priority, as the consequences of changes in masting can be profound. In European beech (*Fagus sylvatica*), warming resulted in declining CVi and synchrony, which weakened predator satiation and pollination efficiency, leading to a decline in viable seed production by half in small trees and 83% in large trees [88, 89]. Similar warming-related changes in masting may explain global declines in the effectiveness of predator satiation [24]. The resulting limited seed supply may cause extinction debts, reduce migration rates, hinder restoration projects, and in combination with changes in variability of reproduction, disrupt food web functioning [90, 91]. Therefore, masting breakdown, defined as periods of lowered synchrony and variability (CVi and CVp, Box 3), is of concern. Advances in the reconstruction of masting over decadal to centennial scales, using tree-rings [47], can improve understanding of historical variability in masting behavior and its drivers, and clarify the role of climate change in recent trends.

The different factors controlling masting (the general model of masting, Fig. 2) make species more or less sensitive to climate change [18, 87, 83]. At one extreme is the ΔT cue [18], where flowering is proportional to the temperature difference between consecutive summers before flowering. Because gradual increases in mean temperature have little effect on temperature differences, species using ΔT cues should be largely insensitive to climate warming. Confirming this, masting was unaffected by 0.5°C warming in conifers where ΔT appears to drive masting [87]. Low risk from climate change is also likely when masting is decoupled from weather cues. For example, in *A. scaphoides*, synchrony comes from pollen coupling, and weather variation

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only impacts seed production indirectly through resource acquisition rates [57].

Nevertheless, sensitivity to cues does not always translate into low sensitivity to climate change (Fig. 2). When flowering effort is sensitive to deviations in absolute temperature (rather than relative temperatures, i.e. ΔT), sensitivity to climate change is likely. For example, where reproduction is promoted by low temperatures or inhibited by high temperatures, warming will decrease conditions that favor heavy flowering, which could decrease the frequency of high-seed years, lowering CVp and annual mean reproductive effort. In tawa (*Beilschmiedia tawa*), seeding is promoted by low winter and summer temperatures that now happen less often. This resulted in widespread failure of reproduction at warmer sites [92], though colder sites still produce high-seed years. Similarly, in dipterocarp species, flowering is promoted by a combination of low temperatures and drought. Warming reduces the cueing frequency and consequently the frequency of 'general flowering' (masting) events [74].

Fortunately, some species which might otherwise be sensitive are apparently able to adjust cue thresholds. Flowering in Japanese beech is inhibited if spring temperatures exceed the long-term mean by $1°C$ [93]. While such a degree of warming is now observed, the threshold at which flowering inhibition happens is positively correlated with local mean temperatures [94], suggesting an acclimation mechanism for adjusting the temperature thresholds. Similarly, rainfall-reduction experiments indicate that masting (CVp) can adjust to lower mean rainfall, even if mean seed production is reduced [95, 85]. Nonetheless, even apparently resilient species may have tipping points.

The sensitivity of species where multiple factors interact to control masting is complicated. For example, in such cases, under climate warming cues may occur more frequently than plants can replenish resources depleted during the last reproductive event [28], decreasing synchrony [96]. In *F. sylvatica*, an increase in mean summer temperatures of only $1°C$ resulted in a 5-fold increase in cue occurrence, disrupting CVi and synchrony [96, 97].

This leads to three conclusions on the differential effects of climate change on masting across species. First, species that do not rely on weather cues, because masting is mainly controlled by resource dynamics (e.g. *A. scaphoides*) (Fig. 2), will be at low risk. Second, species whose weather cues are based on temperature differences (e.g. ΔT) or adjustable absolute thresholds will be at lower risk than those using an absolute temperature cue. Third, species with an absolute cue will likely experience climate-driven changes in masting, but the response depends on whether warm or cold weather increases reproduction. If warmer weather promotes flowering, viable seed production would decrease even while reproductive effort remains high, because decreasing synchrony causes the loss of economy of scale benefits [88]. If colder weather promotes flowering, viable seed production decreases because the reproductive effort is inhibited (e.g. [74, 92]). Exploring patterns of cue sensitivity within species and across climates is vital to understanding their adaptive potential [84]. Moreover, investigating how past changes in cue frequency at decadal scales translated into masting patterns [47] can confirm whether and in what species cue sensitivity covaries with mean climatic conditions.

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One question is how many species have weather cues with flexible thresholds (through ΔT or an adjustable absolute threshold) versus fixed thresholds. We could find cautious optimism in the fact that current species have survived large-scale climate fluctuations over the millennia, which may have favored flexible thresholds. That plasticity might prove vital because the current rate of climatic change exceeds anything in the past 10,000 years.

Concluding Remarks

Recent research has resulted in the identification of a suite of separate masting drivers. By integrating these drivers into a unified general model, we show how these factors interact to determine masting patterns. Under the unified theory, determining the relative importance of these factors for particular masting species will help guide responses to challenges and opportunities in the coming decades. Challenges include understanding climate change risks for masting species. This requires information on mechanisms and weather cues, including whether they give species inherent adaptability to warming temperatures. Opportunities include improved forecasting from the availability of open datasets and genetic mechanisms. These concepts, tools, and data will help resolve some of our Outstanding Questions. We predict that, while recent decades were about clarifying the drivers of masting, the next few decades will be about integrating multiple drivers into an understanding of how masting will respond to a rapidly changing planet.

Acknowledgements

Box 3: Measuring masting

Masting is simple in principle - reproductive effort varying across years - but quantifying it is complex [78]. Here we provide an overview of the most commonly used metrics, which serves to reemphasize the characteristic reproductive patterns that are the hallmark of masting. The three common masting metrics, i.e. indices used to describe reproduction time series, are coefficient of variation at a population level (CVp), at CV at an individual level (CVi), and synchrony (S). These metrics are simple and widely used, and their behavior across various time series is well understood.

For variability, **CV** increases with the concentration of total reproductive effort into a smaller proportion of years. That correlates with the costs of masting, but makes CV sensitive to zero (or very low) years in the data [78]. For some applications that pose difficulties [98]. Alternative metrics to estimate variability have been proposed. A modification of the CV, called Kvalseth CV (CVk), is backward compatible and offers benefits of higher sensitivity in analyses (making shorter seed production time series more informative) [99]. Another metric, volatility, overcomes the problem of zero dominance, measuring variation in the frequency domain with a focus on the long intervals between large seeding years (measured by periodicity) [45, 98]. However, unlike CV, volatility is dependent on units of seed production measurements, which limits its applications. More problematically, the proportional variability (PV) index and consecutive disparity (D) assess the proportional difference between all pairs of values within a time series (PV), or proportional differences between consecutive values (D) [100]. These treat rare failures and rare reproduction as equivalent and are sensitive to minute variation that is biologically meaningless [99].

Synchrony is usually quantified by mean cross-correlations among pairs of individuals or populations throughout the time series [14].

Mast years is a term that implies a dichotomy that does not exist [1]. The best approach is to replace the term with high-seed year, and use quantitative analyses. If a categorical analysis is desired, the choice of cutoff is fundamentally arbitrary, but can be made consistent. The best is the standardized deviate method [101], which is clear and repeatable.

Autocorrelation (usually with a one-year lag; AR1) is used to quantify the tendency of large-seeding years to be followed by low years. AR1 describes the relationship between pairs of data. If there are few high-seed years in the time series (high CVp), then pairs of years with little seed production dominate, diluting the "resource depletion" signal.

It is important to understand the properties of different metrics. The metric should be chosen to suit the question being asked, and the interpretation should be constrained by the metric's

known features and limitations.

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