

Opinion piece



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Natural disturbances and masting: from mechanisms to fitness consequences

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The timing of seed production and release is highly relevant for successful plant reproduction. Ecological disturbances, if synchronized with reproductive effort, can increase the chances of seeds and seedlings to germinate and establish. This can be especially true under variable and synchronous seed production (masting). Several observational studies have reported world-wide evidence for co-occurrence of disturbances and seed bumper crops in forests. Here, we review the evidence for interaction between disturbances and masting in global plant communities; we highlight feedbacks between these two ecological processes and posit an evolutionary pathway leading to the selection of traits that allow trees to synchronize seed crops with disturbances. Finally, we highlight relevant questions to be tested on the functional and evolutionary relationship between disturbances and masting.

This article is part of the theme issue 'The ecology and evolution of synchronized seed production in plants'.

1. Introduction

Offspring dispersal and survival is a key process for the evolution of reproductive strategies. In seeding plants, life-history traits that maximize propagule dispersal and seedling survival, such as flowering, fruiting and seed traits, are targeted by positive natural selection [1]. For example, trade-offs between dispersal distance and seed size determine the ability of seeds to escape unfavourable conditions or store provisions that improve chances of establishment [2]. Timing of reproduction is also crucial, and propagules are most successful if their development occurs when the environment into which they disperse is conducive to germination and establishment. A reproductive trait that has not received as much attention in this context is temporally variable and synchronous seed release, or 'masting'. Masting is widespread among trees and other perennial plants [3,4]. It is hypothesized to be an evolutionarily stable strategy that increases reproductive fitness by improving chances of survival for offspring dispersed in favourable years. This suggests that mast seeding in plants could be under positive selection.

The scientific community has been recognizing the mechanisms responsible for masting and its ecological and evolutive meaning [5]. Reproductive variability is often triggered by changing environmental conditions [6]. Weather fluctuations are the most commonly detected environmental 'cues' for masting. However, a time lag is often apparent between environmental conditions that induce flowering and fruiting, and their ultimate effect, i.e. successful seed germination, seedling establishment and sexual maturation [7]. During this time, the chances of seeds and seedlings to germinate and establish can be strongly affected by natural disturbances, i.e. discrete events in time that disrupt the ecosystem, community or population structure, and change resources, substrate availability or physical environment [8]. Fire, wind damage, floods or insect

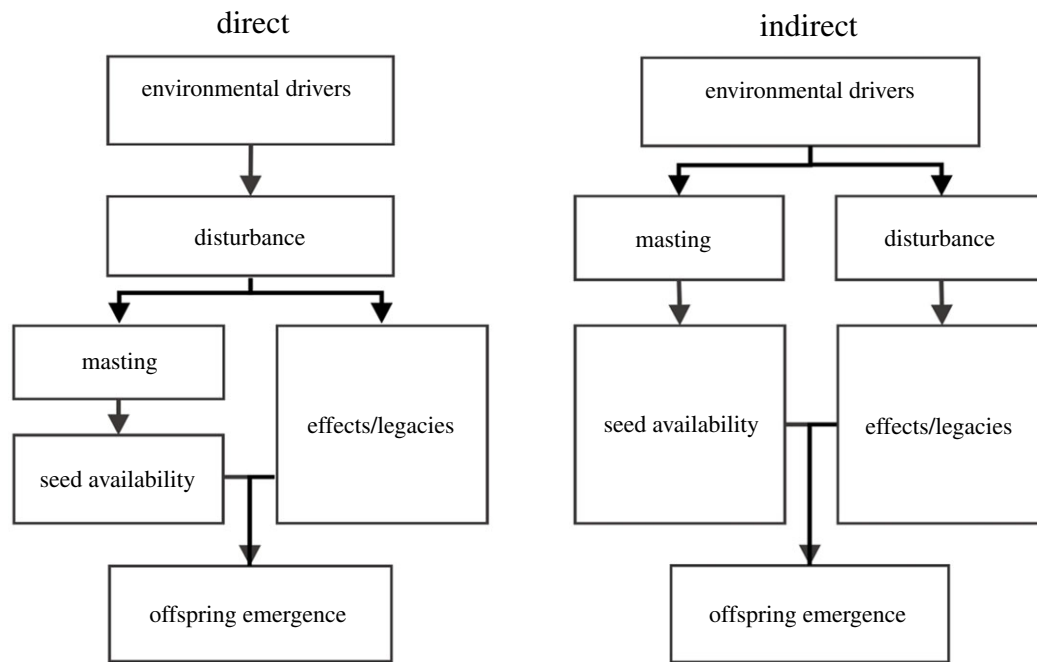


Figure 1. Conceptual diagram of direct and indirect effects of disturbances interacting with masting.

outbreaks induce abrupt changes in biomass, resources and ecological processes that alter the light regime, soil conditions, water or nutrient availability, which in turn may affect the development of plant offspring [9,10]. Likewise, abrupt events such as short-term frost or drought may change future population structure by damaging reproductive organs.

Plants have evolved strategies to increase survival and reproductive fitness in response to disturbances, and specific disturbance regimes drive selection for reproductive traits. Seed dispersal syndromes, seed dormancy, sprouting, soil and canopy seed banks and serotiny have all been linked to the timing, frequency and severity of disturbances in specific ecosystems [11–13], but the potential role of disturbances in selecting masting has been overlooked. Several observational studies have reported evidence for co-occurrence of disturbances and masting in forests around the globe (e.g. [14–17]). Is such co-occurrence merely coincidental, without any causal link? Does masting respond to environmental cues that also drive disturbance events? Or rather, is it possible that plants have evolved ways to respond to the occurrence of disturbances by timing their reproductive effort to ensure the most favourable conditions for germination?

In this paper, we hypothesize the existence of an evolutionary pathway leading to the selection of traits that allow trees to synchronize seed crops with dominant disturbance agents. We illustrate mechanisms by which disturbances can increase or hamper reproductive fitness under masting, and summarize reported evidence for interactions between disturbances and masting in global forest ecosystems, i.e. whether synchrony between the two events generates a positive or negative physiological response in terms of seed production, dispersal and seedling establishment (§2). Our hypothesis is then framed within an evolutionary framework for the emergence of masting, i.e. the environmental prediction hypothesis (EPH) (§3). We suggest under which disturbance regimes we expect the strongest selection of masting traits (§4) and explore the links between disturbances, masting and evolutionary strategies for the storage of

reproductive potential (§5). Finally, we formulate research questions needed to test our hypotheses in formal research settings (§6).

2. Interactions between masting and disturbances

To support an evolutionary explanation of masting based on disturbances as a selective force, a number of questions must be answered: Are proximate mechanisms of masting and disturbances aligned temporally and spatially? Which processes are responsible for this alignment? Does masting before, during or after a disturbance increase fitness? Two possible mechanisms link the timing of masting to that of natural disturbances, based on which we hypothesize a cause–effect relationship (figure 1). The first involves a direct link, i.e. the disturbance acts as a direct driver for both variability and synchrony of reproduction in masting species. The second implies an indirect link, whereby disturbances and masting share the same environmental cues through time and space and therefore co-occur because they respond to a common driver.

To collect evidence for direct and indirect interactions between natural disturbances and masting in perennial plants, we carried out a targeted literature search on Thomson Reuters' Web of Science, using 'Natural disturbance*' AND 'Masting OR mast seeding' as search terms. The search produced 29 records. After filtering out irrelevant results and scrutinizing the citation networks of selected papers to find additional records, we found 40 relevant studies (figure 2), 6 of which were for boreal conifer forests, 19 for temperate broadleaf and conifer forests, 1 for subtropical forests, 9 for tropical rainforest and 5 for arid or desert ecosystems. The majority of reports were from North America (14), but observations also came from Australia and Oceania (10), Europe (9), Southeast Asia (3), Central and South America (3) and Africa (1). Fire-related disturbances represented the majority of observations (30), while reports also included disturbances from wind and hurricanes, drought, frost and

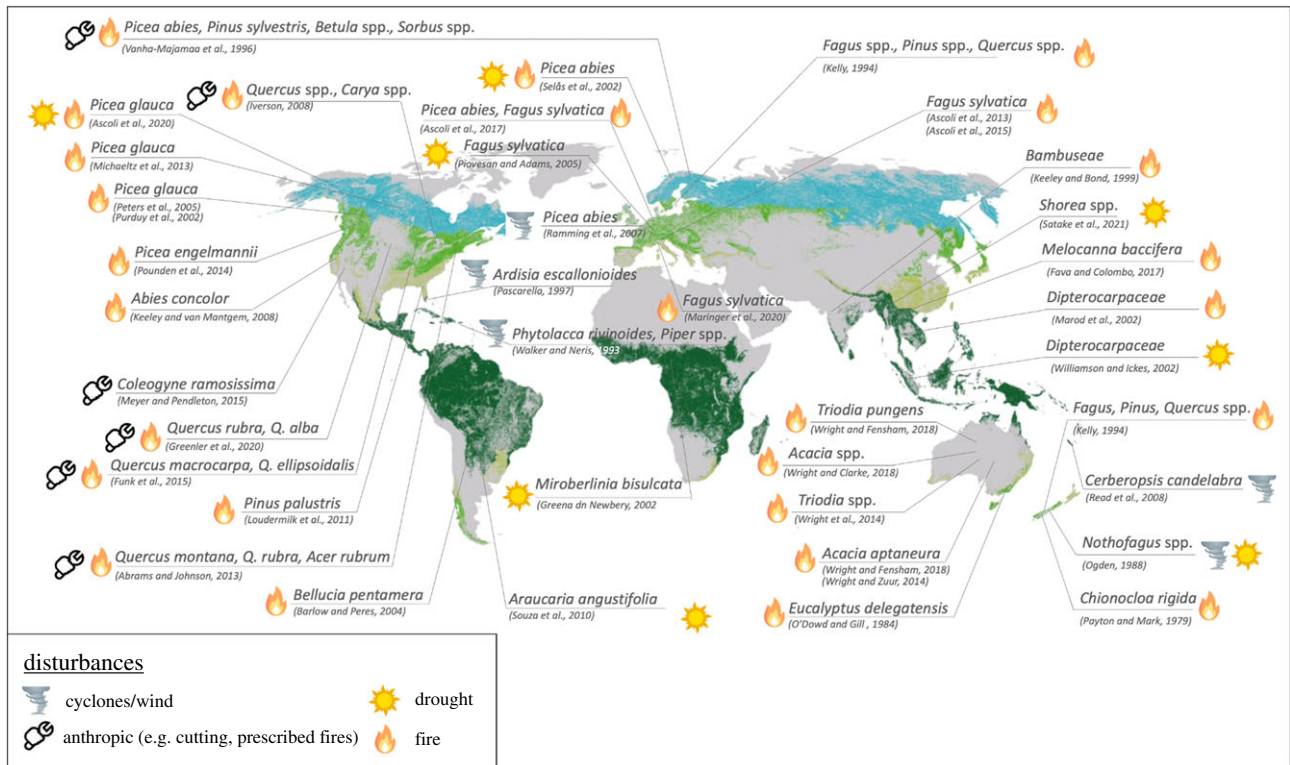


Figure 2. Map of 40 studies reporting interactions between disturbances and masting across global forests (blue: boreal, light green: temperate, sepia: subtropical, dark green: tropical forests) [14,17–56].

human-induced forest management. Disturbance regimes were heterogeneous in terms of severity (low to high) and return intervals (from 5 to more than 150 years).

(a) Direct interactions

Disturbances can affect the temporal variability of reproductive output in masting species by directly inducing physiological responses. One of the first studies showing the interaction between disturbances and masting noted a fire-triggered flowering of *Chionochloa* spp., a species that is characterized by variable and synchronous flowering patterns [56]. Flowering can be triggered directly by fire and smoke, as in Australian *Xanthorrhoea* [57] or in southern African fire-lily *Cyrtanthus ventricosus* [46]. Likewise, warmer soil temperature resulting from litter removal due to fire stimulates flowering in many grass species [58].

Variable reproduction can be triggered in response to disturbances by hormonal signals leading to shifts in resource allocation and flower bud differentiation [59]. ‘Stress crops’ following disturbance events such as hurricane-force winds or fires are sometimes interpreted as a result of hormonal signalling for allocation to reproductive pool as a consequence of plant stress [60,61]. However, such effects are usually constrained to individuals and lack synchrony among trees or stands, which is a key characteristic of masting.

Conversely, a direct effect of disturbances on reproductive synchrony occurs when seedlings or resprouted ramets establish simultaneously after a stand-replacing disturbance (e.g. [62]). Even-aged populations that have regenerated together after a disturbance reach reproductive maturity at the same time, and are more likely to synchronize their reproduction in response to relevant environmental cues [63]. In Southeast Asia, even-aged bamboo forests (*Melocanna baccifera*) experience large-scale mortality after synchronized mass

flowering and fruiting. The increased fuel load provided by dead stems increases the likelihood of stand-replacing fire [50]. Also, dense monospecific aggregations of bamboo increase the effective target area to collect lightning strikes and thus increase the probability of ignition [64]. Ensuing fires improve the germination environment and reproductive success of the new generation [48], conferring a competitive advantage versus species that are less flammable or less fire resilient [65]. In turn, synchronized regeneration after fire increases the chances for future synchronous reproduction events that reinforce the fire–reproduction feedback.

Disturbances, however, can also directly hamper tree reproduction, for example by vetoing floral development or seed maturation during a potential mast year or reducing seedling recruitment. Late spring ice storms can be responsible for flower death [66,67] and are negatively correlated with seed crops [33,68,69]. Loss of flowers following late frost or hail events has been observed for male flowers in beech [33,70] and female flowers in oaks, with related failure of fruit production over large areas [66,71,72].

(b) Indirect interactions

Variable and synchronous reproduction results from interacting mechanisms at several stages of the reproductive cycle, including resource priming, floral induction, pollination, seed dispersal, germination and seedling establishment. At each of these stages, reproduction can be triggered or vetoed by weather [6]. Weather is also a major driver of spatio-temporal patterns in natural disturbances [73,74]. Establishment of new plants can be favoured when disturbances are concurrent with seed release, by processes such as improved light availability, reduced competition above and below ground, short-term nutrient mobilization and improved germination and establishment in the vicinity of deadwood [17,75,76]. Weather

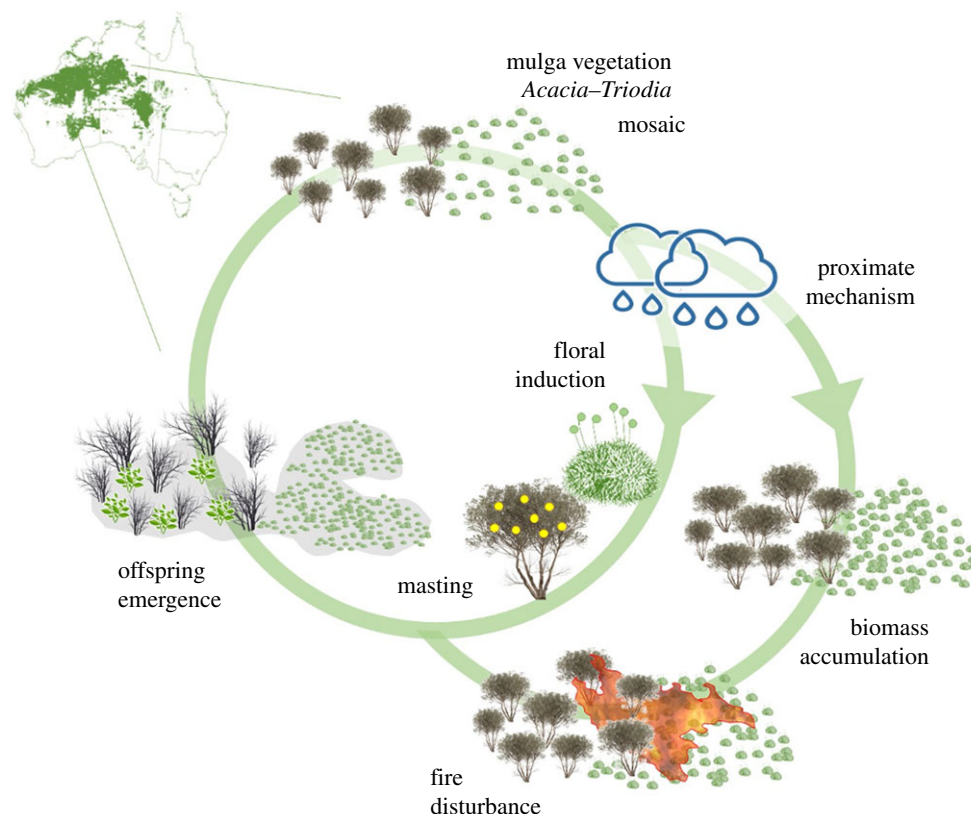


Figure 3. Example of indirect interactions between disturbance and masting in mulga vegetation in central Australia dominated by *Acacia aneura* and *Triodia* spp. (Online version in colour.)

patterns that induce variable and synchronous reproduction and at the same time increase the likelihood of disturbances can, therefore, mediate an indirect link between disturbances and masting across time and space.

In boreal areas, the reproduction success of masting species such as white spruce (*Picea glauca*) and Engelmann spruce (*Picea engelmannii*) relies on the coincidence between a fire event and seed dispersal in the same year or the year after disturbance [20,21,23]. In temperate climates, *Eucalyptus delegatensis* in Australia had higher seed production (18× increase) and higher seedling recruitment (82× increase) in burnt areas than in unburnt controls [45]. In North America's Sierra Nevada, a mast year following a fire in *Abies concolor* forests resulted in higher seedling recruitment than a mast year occurring only 1 year later [77]. Similar effects have been reported for red oak (*Quercus rubra*), white oak (*Quercus alba*) and burr oak (*Quercus macrocarpa*) in the northeastern United States [26,29,78]. Evidence of positive interactions between masting and fires is also found in the tropics, such as for *Bellucia pantamera* in Parà, Brazil [30], and in arid regions. Masting events in Australian mulga (*Acacia aptaneura*) and spinifex vegetation (*Triodia* spp.) are triggered by heavy rainfall. This also promotes vegetation growth and increases fuel loads and connectivity across the landscape, increasing the likelihood of fires in temporal proximity with a masting event (figure 3) [43,44].

Forest disturbances from wind also interact with masting. Storms may open gaps in the canopy that increase the light reaching the forest floor, or release seedlings already established after a mast year. Read *et al.* [54] observed that populations of *Cerberopsis candelabra* in New Caledonia have size distributions typical of mass recruitment following stand-replacing disturbances, and suggested that typhoons

could trigger mast events and promote post-disturbance colonization. Similarly, reproduction was more successful when masting and wind-induced disturbances were synchronized, both in New Zealand's *Nothofagus* [55] and in *Picea abies* mountain forests of Switzerland [34]. In tropical forests, shrubs such as *Ardisia escallonioides* in Florida [79] and *Phytolacca rivinoides* in Puerto Rico [37] showed increased seed production after hurricanes that abruptly reduced canopy cover.

Other than fire and wind, drought is the disturbance mostly related to masting across species and climates. Drought acts as a direct cue to flowering in spruce (*P. abies*) [31,80–82] and beech [33]. In subtropical South America, drought increased seed production of *Araucaria angustifolia* [39]. A study of masting in *Microberlinia bisulcata* in Cameroon rainforests showed a response of seed crops after drought [38]. Drought was shown to trigger mass reproduction of *Shorea* forests in Malaysia [49].

Naturally, a cue to flowering does not necessarily create a favourable environment for seedlings. However, germination and establishment for seedlings can be promoted after drought-induced mortality of parent trees, ensuring the persistence of light-demanding species such as in the *Nothofagus* community of New Zealand [55]. Notably, drought might result in improved or impaired reproduction depending on the timing of the disturbance relative to the masting event. For example, when they precede masting, droughts may induce favourable conditions for seedling recruitment (e.g. canopy gaps). However, droughts that follow a mast year may negatively affect fruit maturation, seed germination or seedling survival. For example, increased acorn abortion was found under artificial drought in holm oak (*Quercus ilex*) [83]. Also, severe drought could lead to fruit abortion, as observed in beech in Europe [84].

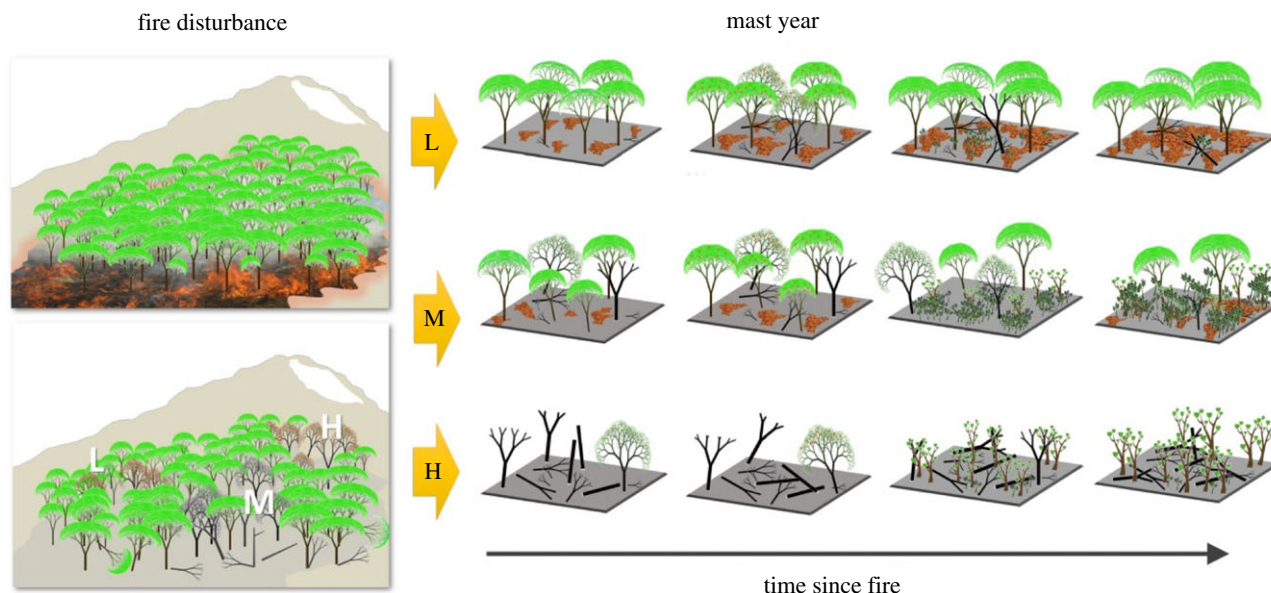


Figure 4. The post-fire regeneration of the European beech (*Fagus sylvatica* L.) illustrates the role of interactions between disturbance and masting. In beech stands, forest fires are usually of low (L) to medium (M) severity. Damaged trees experience delayed mortality, lagging up to two decades after the fire, depending on tree size and fire severity [89]. As a result, fire-induced changes in stand structures create suitable germination conditions in terms of increased light in the understorey and reduced litter cover on the forest floor [17]. When mast years occur (the dots on tree crowns represent cupules during masting), abundant seeds are dispersed by surviving trees and abundant germination occurs thanks to the favourable conditions in the post-fire forest environment. In the case of intense post-fire mortality due to high-severity (H) fire, full light conditions may favour the establishment of fast-growing pioneer species, which in turn act as nursery crop for the shade-tolerant beech regeneration. (Online version in colour.)

Indirect interactions between masting and disturbances can also be regulated by large-scale modes of climate variability, such as the El Niño-Southern Oscillation (ENSO) or the North Atlantic Oscillation (NAO) [32,85,86]. In Southwest Asia, drought induced by the onset of the El Niño phase triggers general flowering in dipterocarp forests, large-scale canopy mortality due to water shortages [52], and fire disturbances [87]. Similarly, in western North America, the ENSO phases modulated by positive Atlantic Multidecadal Oscillation (AMO) synchronizes drought, fire disturbance and masting in white spruce (*P. glauca*) over vast areas from Alaska to Alberta [19]. In Europe, large-scale masting in beech (*Fagus sylvatica*) [88] correlates positively with consecutive NAO phases conducive to large-scale natural disturbances such as wind storms and fires [32].

In summary, the literature reports evidence of both improvement and impairment of reproduction success when disturbances occur in temporal association with masting events, across multiple forest biomes. Positive effects have been more often reported than negative effects, but this could be due to publication bias. The evidence collected herein is too sparse and heterogeneous to allow a formal meta-analysis of the direction and magnitude of disturbance effects on masting success. However, this has been addressed with a robust sampling design for selected plant species, such as European beech [36]. Here, a post-disturbance chronosequence study has shown that seedlings that germinate after masting have no chance to establish in the long term under dark and undisturbed beech canopies. By contrast, beech regenerates copiously after masting and establishes successfully in areas burnt by mixed-severity fire (figure 4). Regeneration density is highest when masting immediately follows the fire event (figure 5), but the post-fire recruitment window lasts for up to two decades, creating even-aged regeneration cohorts at each subsequent masting event [17,36,92].

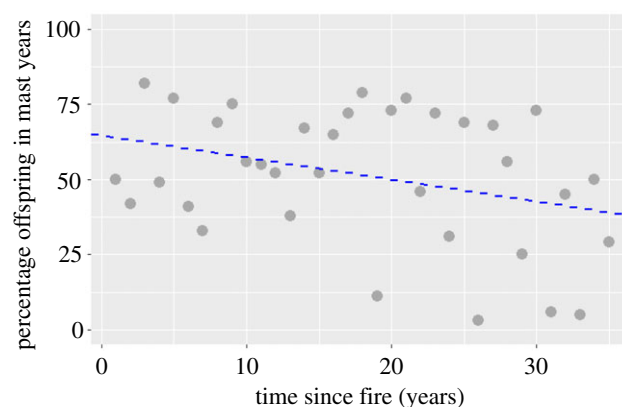


Figure 5. Percentage of established beech seedlings the year after a mast year at intermediate and high fire severity sites over the entire seedling bank, as a function of time since fire (35 years post-fire). Data for calculation were extracted from Fig. 3 in Maringer *et al.* [36]. Maringer *et al.* [36] assessed the year of germination of 2322 seedlings collected at 37 burnt sites. Since mast years were known for each study site, as reported by the MASTREE dataset [90], it was possible to assess for each seedling if it emerged after a mast year or not. Fig. 3 in Maringer *et al.* [36] shows the mean number of established seedlings (both those that emerged after a mast year and those that did not) as a function of time since fire. By using data from mid- to high-severity sites, we calculated for each year since fire the ratio between seedlings emerged after a mast year in burnt sites and the entire seedling bank (i.e. including seedlings not established after a mast year). This variable is directly proportional to the efficacy of a mast year at disturbed sites. The dashed line is the linear regression of the ratio versus time since fire ($p < 0.01$) after accounting for the autocorrelation structure (lag 1 year, $p < 0.01$) of the response variable with dynamic regression modelling [91]. (Online version in colour.)

3. Selection of masting under disturbances

Simply reporting the existence of positive or negative interaction between masting and disturbances is not yet enough

to hypothesize an evolutionary link between the two processes. Co-occurrence of disturbance and masting confers adaptive advantages under certain circumstances, but could such interaction have an evolutionary value? Can plants inherit the ability to take advantage of disturbance–masting synergies?

Research on the adaptive significance of masting has mostly focused on processes inducing an economy of scale, which has been empirically demonstrated for pollination, predation and, to some degree, dispersal [3,93]. A less tested hypothesis for the evolutionary emergence and persistence of masting postulates that environmental variability acts not only as a cue for increased reproductive output but also as a driver for selection of masting in plant populations [94]. This environmental prediction hypothesis (EPH) affirms that plants can ‘predict’ the best future environmental conditions for germination based on weather cues, and regulate the timing of masting to ensure favourable conditions for seed germination, seedling emergence, and survival [95]. This hypothesis has so far received little empirical support, mostly because it relies on unlikely ‘weather forecast’ abilities by plants, i.e. an ‘abstract’ future prediction of environmental characteristics. However, when grounded in disturbance ecology, the EPH is consistent with biologically and evolutionarily sound mechanisms. Selection for masting occurs if the offspring reaches sexual maturity; in fact, disturbances not only act as cues for seed production but may also promote (or hamper) survival of the post-disturbance generation, which will experience evolutionary filtering. Under this perspective, it appears that disturbances can act both as proximate drivers (directly or indirectly, see §2) and—via environmental prediction—as ultimate causes of masting [96]. For the well-documented case of white spruce in boreal ecosystems of North America, Ascoli *et al.* [19] provided strong evidence that the existing large-scale synchrony between seed masting and drought-induced fire seasons share the same weather drivers, thus supporting the EPH.

Finding evidence for drivers that can select for masting traits and at the same time shape disturbance regimes is challenging (e.g. [86]). However, the regulatory mechanisms for masting need not rely on absolute environmental conditions (i.e. temperature), but rather on recognizable environmental patterns (e.g. [7,86,97]) that are independent of specific site conditions or climate variability, including ongoing climate change (but see [98,99]). This could generate hypotheses on the evolution of masting under disturbances that would be testable within and across different biomes.

In order to emerge, an evolutionary linkage between disturbances and masting must have been in play over time-scales much longer than individual tree longevity. This is not unlikely, since many plant species have coevolved with their disturbance agents (biotic and abiotic) for very long times, and have experienced a recurrent disturbance regime. Fossil evidence of forest fire [100] and insect outbreaks [101], and climatological reconstruction of atmospheric circulation (e.g. [102]), confirm that forest disturbance agents have been acting over long time periods. This has also been suggested for other ultimate drivers of masting, such as the more established predator satiation hypothesis: a prolonged evolutionary interaction between arboreal rodents and the reproductive organs in Pinaceae is consistent with the fossil record, justifying coevolution between squirrels and conifer cones [103].

The implicit assumption of the EPH is that masting traits are heritable [104] and can be selected by disturbance regimes.

Independent evidence for genetic regulation of masting [105], field transcriptomics controlling flowering time [106,107] and phylogenetic stability of masting traits [108] all suggest that masting can be subject to evolutionary selection. Moreover, scientific evidence for the evolutionary significance of post-disturbance flowering in annual plants [109] and established connections between disturbance regimes and other reproductive traits [110] are robust hints that an EPH involving disturbances and masting can indeed occur in the plant kingdom. Once again, the heritability of genes responsible for masting critically depends on seedling survival, which is still a neglected aspect in most masting studies.

4. Masting and disturbance regimes

Every ecosystem is subject to a variety of types of disturbance, each with a characteristic regime. How do the features of a disturbance regime, such as frequency, severity or extent, influence their selective pressure on masting? What are the disturbance regimes under which we expect the strongest selection of masting traits?

Disturbances can vary extensively in frequency, from a few to several hundred years [8]. In general, selection for adaptive reproductive strategies is strongest when disturbances are more frequent and/or predictable [111]. The relative magnitude of selection also depends on the growth rate of the organism: disturbances must recur with a frequency comparable to or shorter than the organism’s lifespan to elicit an evolutionary response [112–115]. Conversely, when disturbances are infrequent relative to a species’ lifespan, or unpredictable, individuals cannot adapt to the disturbance regime [111]. Indeed, life-history traits of organisms that have fast growth and mature quickly do not respond to disturbance selection as strongly as slow-growing, long-lived organisms [111]. For the former species, the best strategy is to invest in early and continuous reproduction: it is unlikely that an individual will experience a disturbance during its lifetime; therefore, holding back reproduction to save resources for seeding in specific years would not pay off [111]. The reproductive fitness of long-lived trees, on the other hand, is heavily dependent on disturbance-induced regeneration opportunities; it is enough for these species to synchronize reproduction and suitable environmental conditions once in their lifetime for selection to favour masting.

Masting, however, can provide plants with an adaptive strategy even in the face of unpredictable or erratic disturbances: if a species or population masts over a large area, it can increase the chance to take advantage of improved opportunities for regeneration at any place where a disturbance could hit within the species or population range [86]. Long-distance masting synchrony can then be hypothesized as a strategy to buffer the unpredictability of disturbances in space. The evolutionary link between disturbance frequency or predictability and synchronized plant reproduction needs to be further researched, for example by analysing similarities or differences in natural disturbance regimes across the phylogenetic tree of masting traits in perennial plants [108], or by looking for relationships between disturbance frequency and the spatial extent of masting synchrony.

Similarly to frequency, the severity and extent of disturbances vary widely. At one extreme are very rare, catastrophic events that alter substrates and disrupt mechanisms of

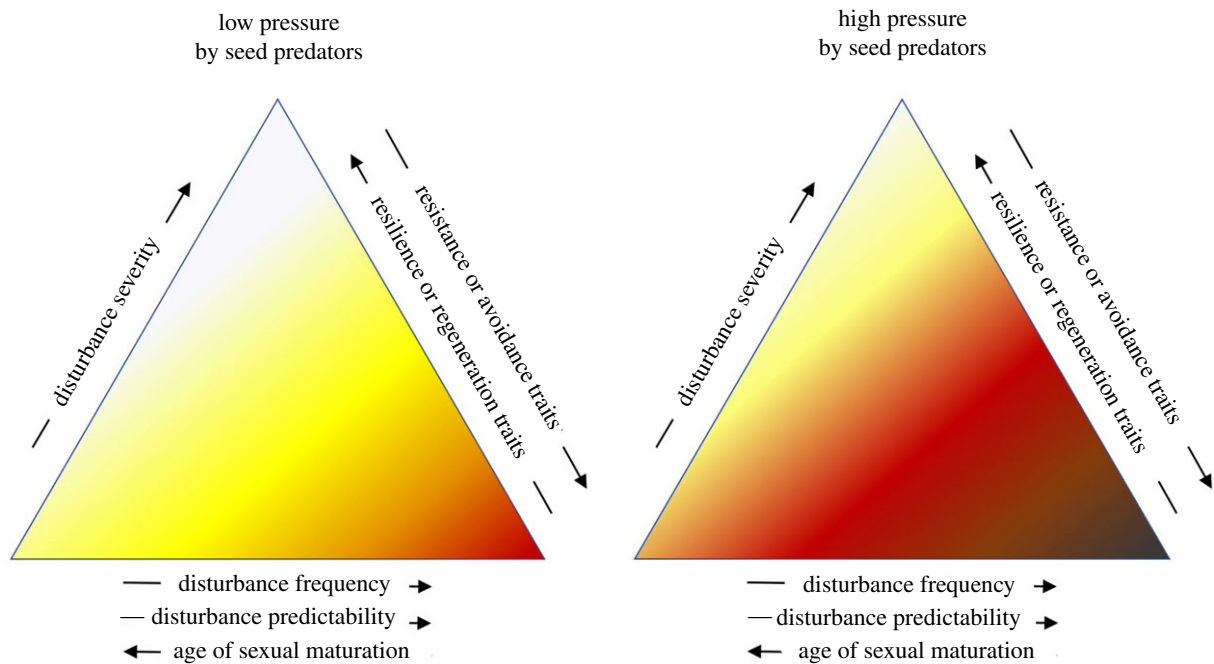


Figure 6. Conceptual hypothesis for interactions between features of a disturbance regime, predator satiation and selection of masting traits. Darker colours represent larger evolutionary advantages and stronger selection for masting under the environmental prediction hypothesis. (Online version in colour.)

persistence and recovery. It is rare that these disturbances have selective consequences relevant to the fitness of future generations. In fact, the success of masting depends on the capacity of the plant species to produce large seed crops in the immediate post-disturbance period, when an optimal recruitment window is open. This implies the need for seed-bearing individuals to survive on site, or at least within the seed dispersal distance of the species. Accordingly, disturbance severity and extent should allow some masting individuals to survive and/or reproduce. Models developed for animal populations suggest that synchronous reproduction could evolve when the spatial scale of disturbances is much smaller than the range of the breeding population. On the contrary, asynchronous breeding is expected if disturbed areas are similar or larger than those occupied by the population [116].

In summary, we expect the strongest selection in plant species with fewer opportunities for frequent reproduction (i.e. late sexual maturity, preference for resistance over resilience traits compared with disturbances) and under high-frequency, low- or mixed-severity disturbance regimes (figure 6). All else being equal, we expect other evolutionary mechanisms for masting (e.g. predator satiation) to strengthen the selection of masting traits under EPH.

In the opposite case (i.e. high-severity, low-frequency disturbance) we expect the selection of masting to be weaker, while other reproductive strategies should be favoured. An illustrative example is provided by masting versus serotinous reproductive syndromes under fire disturbance regimes. Serotinous species store and protect their mature seeds in cones or fruits in the crowns until a fire event or drought induces a synchronous seed release [13]. In serotinous species, the survival of mature seed-bearing individuals is not a prerequisite for post-fire recruitment, making serotiny a well-recognized adaptive trait in crown fire regimes [117]. This strategy is particularly effective in ecosystems where the mean fire return interval lies between the time required for a serotinous species to reach sexual maturity and its mean

longevity [118]. Under such conditions, serotinous species take advantage from severe, stand-replacing fires providing optimal post-fire recruitment conditions for the abundant seed rain following the event (e.g. [119]). Masting species, on the contrary, are advantaged most under mixed-severity fire regimes, where low-to-medium severity fire allows fire-resistant, seed-bearing individuals to survive *in situ*.

The EPH does not need to be an exclusive explanation for the evolutionary emergence of masting. We expect selection of masting traits by disturbances to be stronger if additional benefits of masting are operating, such as predator satiation [120]. If seedling survivorship is small, the parent will have to produce its offspring every year, regardless of disturbance events. By contrast, if seedling survivorship is sufficiently high, such as under high selective pressure by predators and consequent emergence of predator satiation mechanisms, reproducing every year becomes less important, and producing a greater total number of surviving offspring becomes key, thus favouring masting evolution under disturbance pressure (figure 6).

5. Evolution of masting and storage of reproductive potential

We have shown that plant reproduction is more successful when propagules are available at the time of or shortly after a disturbance. In case adaptive tracking of environmental change is not at hand, the storage of reproductive potential in soil seed banks, crown seed banks or seedling banks until a disturbance occurs enhances chances for successful establishment and thus fitness. Filling these pools and persisting until disturbances trigger reproduction, however, comes at a cost: reducing the temporal variance of fitness is traded against a lower (arithmetic) mean fitness. Under uncertainty of reproductive success, such bet-hedging strategies spread the risks over time and maximize the geometric mean fitness (but reduce the arithmetic mean fitness) [16,121–124].

Bet-hedging strategies occur in hundreds of species [16,123,124]. By analysing a global seed bank database of over 2300 angiosperm species, Gioria *et al.* [125] found that higher rates of disturbances increased the likelihood of persistent seed banks, thus corroborating the evolutionary relevance of storing reproductive potential in habitats with low disturbance predictability. Assessing how masting can contribute to reproductive storage can therefore hold potential for better explaining its evolutionary emergence, especially if storage is associated with increased fitness and selectable reproductive strategies.

Different types of disturbances select for different storage pools: large-scale disturbances select for persistent seed banks, while disturbances with low severity promote seedling banks [126] such as those produced by masting. The continued persistence of live individuals in the different storage pools also depends on the decay rate of the seed and sapling banks and their refilling rates. Seeds in soils may survive for decades, in rare cases for centuries and even millennia [127]. Most seeds in persistent seed banks show constant mortality (Deevey type II survivorship curve), although some show a slow initial mortality rate and a rapid increase of mortality thereafter (Deevey type I curve) [127]. Whelan & Ayre [128] show an exponential decline of germination rates of a *Banksia* species that forms a canopy seed bank. Besides strong variation in seed longevity, they showed that the accumulated canopy seed bank was very small (two to four seeds per plant) and that most (82–94%) of the viable seeds were not older than 6 years.

For storage effects to function, germination from soil seed banks, release from crown seed banks or enhanced growth from seedling and sapling banks has to be triggered by disturbances. Soil seed banks are either triggered directly, such in the case of fire-induced heat or smoke [129,130], or right after disturbance, owing to higher light or nutrient availability [127,131]. Seeds of serotinous species that are stored in an aerial or crown seed bank are triggered by the disturbance itself, in most cases by the heat of wildfires [13]. Juvenile trees that form a seedling or sapling bank are released from competition when disturbances open up the canopy and lead to increased radiation in the understorey [132–135].

Refilling of decayed or emptied storage pools can occur at continuous rates or in synchronized pulses through masting. Masting allows plants to concentrate reproductive efforts in specific years, thereby increasing the number of stored propagules in a mast year relative to non-masting species. However, even if masting improves seed production and/or seedling survivorship, this advantage could be greatly diminished by the intense competition among young plants [53,136–138]. Density-dependent mortality works against positive selection of masting as a strategy for adaptive reproduction under disturbances. Tachiki & Iwasa [139] concluded that, in closed-canopy forest species, masting never evolves if all vacant sites (gaps) are filled by individuals from seeds produced in the same year (i.e. if reproductive potential is not stored), despite the fact that trees reproducing intermittently enjoy a higher pollination success than trees reproducing annually. When seedlings have low survivorship, trees evolve to reproduce every year to retain their position in the seedling bank. By contrast, when seedlings have high survivorship, they can use masting to form a multi-annual seedling bank. Competition is mitigated if seedlings survive multiple years, and new recruits emerge whenever environmental resources are available.

As the survivorship of seedlings increases, a sharp and sudden transition from annual reproduction (no masting) to intermittent reproduction (masting) occurs, called 'evolutionary jumping' [140,141]. Inter-mast periods must be shorter than the maximum persistence of individuals in the reproductive pools, in order to avoid missed chances of disturbances occurring while the seed or seedling banks are empty. Given that masting intervals rarely exceed 10 years [142], this condition would be fulfilled for most ecosystems. This strategy is exploited by several masting invasive species, such as the shade-tolerant *Prunus serotina* [143], where the seedling bank strategy represents an efficient way towards site occupancy in forest understoreys with few shade-tolerant native species.

Using a dynamic model for the evolution of masting, Tachiki & Iwasa [139] showed that the ability of trees to form seedling banks, combined with predator satiation and pollen coupling, can lead to the evolution of masting. Conversely, without a persistent seed or seedling bank, even the presence of seed predators could not promote the evolution of masting. This suggests that masting, predator satiation, a transient seed bank, and the formation of a persistent seedling bank are all associated traits that promote survival in closed stands, and have a prominent role in inducing positive selection of masting in perennial plants.

6. Conclusion and open questions

Similarly to other plant reproductive traits [144–146], variable and synchronous reproduction is subject to evolutionary selection under the filtering effect of the environment where plants evolve. Among evolutionary mechanisms responsible for the emergence of masting, the environmental prediction hypothesis (EPH) is gaining new support, thanks to increased data availability and understanding of masting spatio-temporal patterns (e.g. [19,49]). Here, we have cast a new perspective on the EPH, suggesting that natural disturbance regimes can affect the fitness of masting plants either directly or indirectly, by inducing changes in light regime, soil conditions, water and nutrients available to offspring.

In this paper, we have highlighted how: (i) masting and disturbances (fire, drought, wind and possibly other agents) are observed to co-occur consistently across global forest biomes; (ii) reproductive success can be improved or hampered when masting co-occurs with disturbances, depending on the relative timing of the two events; (iii) masting and disturbances can share similar environmental triggers, which hints at active selection of masting traits due to filtering from given features of disturbance regimes; (iv) masting contributes to the storage of plant propagules, which is involved in reproductive bet-hedging strategies and plays a role in evolutionarily stable reproductive syndromes in disturbed environments.

Many questions remain open to exploration (table 1). A first group of questions is related to elements of disturbance regimes: Which types of disturbance regimes better fit and reinforce masting? How do disturbance size, frequency and severity affect the emergence and success of masting? What other elements of a disturbance regime can be responsible for masting trait selection? What kind of disturbance effects and legacies are relevant for plant reproductive success? What will be the effect of disturbance regime shifts on masting efficacy? Are there any differences between

Table 1. Open issues in masting–disturbance interactions.

process	issue
environmental prediction	support for a disturbance-based environmental prediction hypothesis for masting? heritability of masting traits? differences between ‘flowering’ and ‘seed maturation’ species? epigenetic regulation of masting response to disturbance?
disturbance regimes	what disturbance regimes are linked to the emergence of masting? role of disturbance size, frequency, severity? role of disturbance effects and legacies? effect of disturbance regime shift on masting evolution? evolution of masting under frequent large-scale disturbances?
life-history traits	trade-offs between masting and seed size, dispersal syndrome, viability and dormancy? masting complementary to disturbance resistance traits? masting complementary to serotiny?

flowering and seed-maturation masting species [147] regarding interaction with disturbances? How did masting evolve under recurrent large-scale disturbances? Is the masting response to disturbances under epigenetic regulation?

The second group of questions can generate a better understanding of similarities and trade-offs between masting and other resilience traits under selective pressure by disturbances: What are the roles of seed dispersal agents and distance in adapting to a certain disturbance regime? When is masting preferred over serotiny or other seed bank strategies? Is this preference played out at the species or at the ecosystem level? What is the role of masting in the evolutionary nexus between seed size, fecundity, dispersal distance, viability and dormancy? Is masting complementary to or partially substitutable for such other life-history responses to spatial and temporal environmental uncertainty?

And similarly, are there trade-offs between masting and other seed and plant traits that confer resistance to disturbances

(e.g. bark thickness, resprouting)? Why do fire-resistant and fire-adapted species still need masting?

Shedding light on these profound connections would improve our ability to understand and predict masting as an adaptive strategy, anticipate negative changes due to direct or indirect human modification of ecosystems and increase the effectiveness of strategies improving forest restoration and ecosystem resilience [148] in managed, disturbed and degraded forest stands.

Data accessibility. This article has no additional data.

Authors' contributions. G.V. coordinated the study and took responsibility for §§1, 4, 7; L.R. wrote §2; D.A. wrote §3 and co-designed figures; M.C. wrote §5; G.G. wrote §6; M.B.P. co-designed the study and reviewed the final draft.

Competing interests. We declare we have no competing interests.

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