# Global patterns in the predator satiation effect of masting: A meta-analysis

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**Predator satiation is the most commonly tested hypothesis that explains the evolutionary advantages of masting. It proposes that masting benefits plant reproduction by reducing the proportion of seed crop that is consumed by predators. This hypothesis is widely accepted, but many theoretical notions about predator satiation have not been subjected to a robust evaluation. To address this issue, we conducted a meta-analysis of studies that quantified seed predation in relation to mast seeding. We found evidence of both numerical (starvation between mast years) and functional (satiation during mast years) response of consumers to masting. These two effects reinforced each other. Masting satiated invertebrate but not vertebrate seed predators. Satiation was more pronounced at higher, temperate, and boreal latitudes, perhaps because masting is more effective in reducing seed losses when plant communities are less diverse. The effectiveness of masting in satiating invertebrate consumers declined over time (1972 to 2018), probably reflecting the impact of climate change on the frequency and intensity of masting. If masting ceases to reduce seed losses, a crucial advantage of this reproductive strategy will be lost, and sustainability of many tree populations will decline.**

economy of scale | plant–animal interactions | global change | granivory | seed production

Reproduction of many perennial plants is characterized by synchronous interannual variation in seed production, known as "masting" or "mast seeding" (1–3). Mast seeding is a global phenomenon reported in dominant species in boreal and temperate forests of North America, Europe, Asia, and South America; in forests and herbaceous species in Oceania; and in tropical systems including tropical woodland, neotropical rainforests, and Dipterocarp forests in southeast Asia (4, 5). In masting species, recruitment occurs mainly after mast years (6–9). This reproductive strategy is intriguing because it involves forgoing reproductive opportunities between masting events (10–13). In addition to being an important reproductive trait, interannual variation in seed production impacts nutrient cycling and causes widespread perturbations that travel through food webs (14–16). Thus, masting has been generating considerable interest of ecologists for a long time (1, 2, 17–19). One of the fundamental questions that is still widely debated concerns the evolutionary advantages of this reproductive strategy (20–23). Seed production of most plants fluctuates in response to annual variation in climatic conditions (24). Yet, nonadaptive explanations of masting based on resource matching [a framework proposed in the beginning of last century (25)] are no longer favored (but see ref. 26). Instead, it is thought that synchronized, population-level, or community-level production of large seed crops is an evolved strategy that confers specific fitness advantages (27).

Predator satiation is the most widely known, the most commonly tested, and perhaps the most intuitive hypothesis for a selective benefit from masting (1, 2, 28). The basic idea is simple: abundant crops evolved to reduce seed losses by swamping seed predators with seeds. The satiation effect has two components.

First, the production of abundant crops exceeds the capacity of granivores to eat all available seeds [functional response, or the change in attack rate per predator as a function of prey density (29)]. Second, poor seed production between mast events causes famine and keeps populations of seed predators at a low level [numerical response, or the change in predator density as a function of prey density (29)]. These two mechanisms are expected to act in concert (30): when abundant crops follow poor ones, satiation should be particularly effective because it is easier to overwhelm the consumption rate when there are few seed predators. This basic summary of the predator satiation hypothesis is further complicated by the intricacies of predator life histories (21, 22, 31) and latitudinal variation in tree diversity that determines alternate resources for seed predators (4, 5).

The predator satiation hypothesis of masting has been widely accepted (1, 2, 27). However, almost 2 decades ago, Kelly and Sork (ref. 4, p. 435) remarked that this level of acceptance is "perhaps beyond what is warranted by the data." At the same time, the attention of researchers began to shift toward other (nonexclusive) explanations of masting, mostly the pollination efficiency hypothesis [stating that wind pollination is more effective when plants flower in synchrony (32–34)] but also others, such as environmental prediction [masting anticipates favorable conditions for recruitment (35)] or predator dispersal [masting attracts scatterhoarding seed dispersers (9)]. With plenty of other explanations, the venerable hypothesis of predator satiation was no longer the center of researchers' attention, but data on seed crops and levels of seed predation kept

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**Significance**

Masting, or synchronous production of large seed crops, is widespread among plants. The predator satiation hypothesis states that masting evolved to overwhelm seed predators with an excess of food. Yet, this popular explanation faced few rigorous tests. We conducted a meta-analysis of studies that related the magnitude of seed production to the intensity of seed predation. Our results validate certain theoretical notions (e.g., that predator satiation is more effective at higher latitudes) but challenge others (e.g., that specialist and generalist consumers differ in the type of functional response to masting). We also found that masting is losing its ability to satiate consumers, probably because global warming affected masting patterns. This shift might considerably impair the reproduction of masting plants.

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accumulating. Here we revisit this hypothesis in a more quantitative manner than it was possible ever before. The abundance of data means that we can meta-analyze many datasets from multiple studies to evaluate when, where, and how seed masting reduces seed losses to predators and gauge whether theory on how predator satiation works is supported by empirical data or not. Specifically, we tested the following predictions.

First, satiation of seed predators should depend on the sequence of high and low mast years because decrease in seed predation in the years of high seed production should be stronger if the predators were starved in the preceding year (30, 36) (see ref. 37 for other nonexclusive explanations of variation in intermast interval). While synergy between functional and numerical responses is generally expected (30, 38), an early review (2) and some of more recent empirical studies (39) failed to find evidence for the numerical response to masting.

Second, theory predicts that invertebrate seed predators are relatively easier to satiate than vertebrate consumers (4, 22, 31, 40). This is because invertebrate seed predators tend to be specialized and less mobile and display type II functional response (where the proportion of seeds predated declines linearly with seed production), while vertebrate seed predators tend to be highly mobile food generalists with type III functional response [where the proportion of seeds predated is a quadratic, hump-shaped function of seed production (41, 42)]. In fact, mobile consumers might be attracted to sites with abundant seed crops, increasing seed losses [predator attraction hypothesis (8, 43, 44)]. Note that this set of predictions requires that the spatial scale of synchrony among masting plants does not exceed the dispersal ability of the mobile consumers.

Third, it has been suggested that masting is more efficient at satiating consumers at higher latitudes than at lower latitudes. Domination by one tree species in low-diversity temperate and boreal forests should enhance the effects of synchronized seed production on predator populations and reduce alternative food sources for predators in the years of famine (1, 4, 5). Yet, this prediction has been evaluated only indirectly: Dalling et al. (45) noted that the effectiveness of masting should be negatively associated with resource allocation in individual seed defenses, but physical seed defenses do not show a latitudinal gradient (46). Direct tests are still lacking.

Finally, mast seeding is sensitive to climate change (19, 47). Growing evidence suggests that the changes in interannual variability and synchrony of masting are underway (47–50). There is a concern that lowered interannual variability and synchrony of masting might weaken the satiation effect and consequently lower plant recruitment (11, 47, 51) (see refs. 52, 53 for potential mechanisms of such change). In English populations of European beech (*Fagus sylvatica*), global warming resulted in less synchronized and more even seed production, which in turn increased losses to seed predators (47). The effectiveness of masting as predator avoidance strategy may be globally compromised as Earth is rapidly warming.

We conducted a meta-analysis of studies that quantified seed predation in masting plants to test the following predictions. 1) Predator satiation is stronger when mast years follow years of very poor seed production (evident as a negative relationship between predation rates and the ratio between this year's and last year's seed crop size). 2) Less mobile and more specialized invertebrate seed predators present a type II function response, while mobile and generalist vertebrates present type III functional response. 3) Numerical response to masting is stronger in less mobile and more specialized invertebrate seed predators compared to more mobile and generalist vertebrates. 4) Predator satiation and starvation are more pronounced at higher latitudes. 5) Satiation of seed predators by masting has weakened in recent decades.

## Results

Our main results are based on 725 estimates from 48 studies that gathered at least 4 y of data on the relationship between seed production and losses to consumers (see Fig. 1 for the global distribution of studies). In general, larger seed production was associated with a reduced seed predation (overall conclusions are summarized in Table 1). In agreement with prediction 1, numerical and functional responses reinforced each other. The functional response was most effective when high seed crops followed particularly low seed crops (Fig. 2 A and B and *SI Appendix,* Table S1). In fact, satiation by abundant crops required some level of starvation caused by poor crops (Fig. 2 A and B).

In contrast with prediction 2, predator type did not influence the type of functional response (Fig. 2C). Type II functional response consistently outperformed models with type III response, regardless of the predator (i.e., quadratic effects of seed production corresponding to the type III response were not significant and removed from the final models). However,
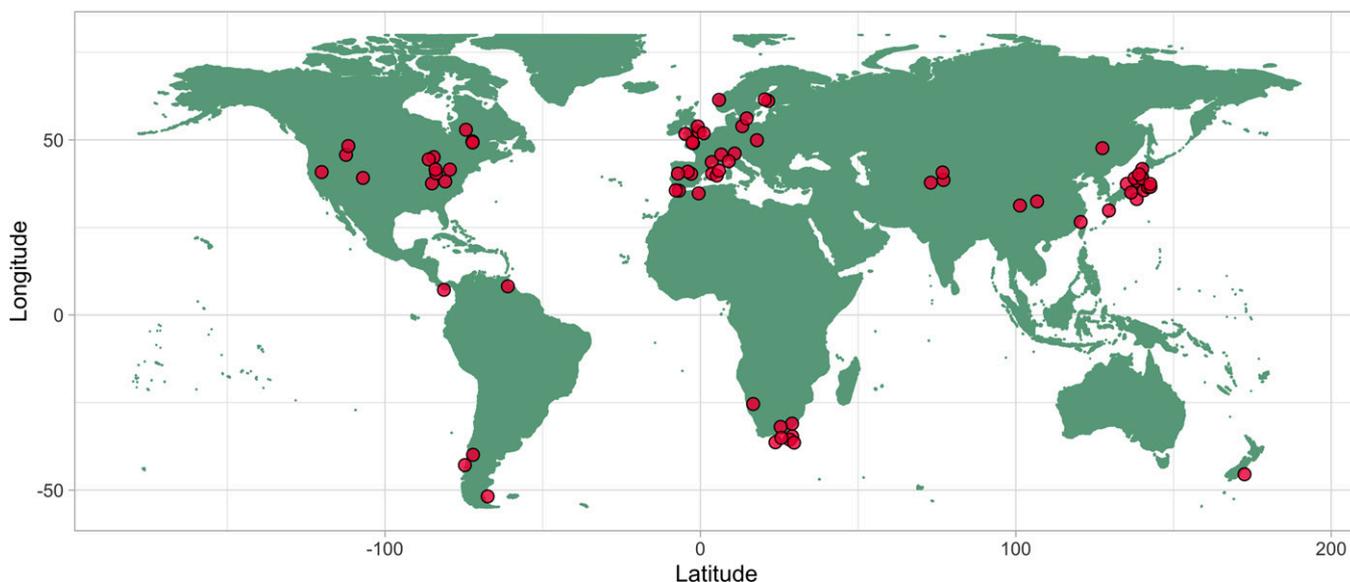


**Fig. 1.** Map of studies included in the meta-analysis. Points are study-by-plant species combinations and are jittered along both axes to increase visibility.

**Table 1. Summary of models used to test predictions on predator satiation**

| Prediction | Explanatory variables | Supported? |
|---|---|---|
| 1) Numerical response enhances functional response. | Seed production × seed production ratio* | Yes |
| 2) Functional response type differs among predator groups. | Seed production* × predator type[†] | No |
| 3) Less mobile and more specialized species show stronger numerical responses to masting. | Seed production ratio* × predator type[†] | Yes |
| 4) Satiation and starvation are more effective at higher latitudes. | Seed production or seed production ratio* × latitude[‡] | Yes |
| 5) Satiation became less effective over time. | Seed production or seed production ratio* × $(year)^2$ | Yes |

In all models, the proportion of seeds lost to predators (logit transformed) was used as a response variable, while study, plant species, and seed predator (typically species) were included as random intercepts. See *Analysis* and *SI Appendix*, Tables S1–S4, for full model descriptions and outputs.
*When analyzing functional response, we used (z-transformed seed production)$^2$ as explanatory variable ("seed production" in the table); when analyzing numerical response, we used the ratio of the crop in year T to the crop in year T − 1 ("seed production ratio").
[†]Predator type corresponded to invertebrate vs. vertebrate or predispersal vs. postdispersal seed predators (two variants).
[‡]Latitude or the absolute value of latitude (two versions of the model).

effectiveness of predator satiation, measured by the slope of the decline of seed predation with seed production, varied between predator types. Abundant seed crops satiated invertebrates (556 estimates from 37 studies) but not vertebrates (145 estimates from 13 studies) (Fig. 2*C*). Similarly, the numerical response to masting was found in invertebrates (as opposed to vertebrates: Fig. 2*D* and *SI Appendix*, Tables S2 and S3). This finding is consistent with prediction 3.

In support of prediction 4, both the functional (Fig. 3 *A* and *B*) and the numerical responses displayed a latitudinal gradient. Satiation and starvation became weaker toward the tropics (*SI Appendix*, Tables S4*A* and S5*A*). This was true also when we restricted the latitude range to >30° to avoid areas with low data coverage (*SI Appendix*, Fig. S1 and Tables S4*B* and S5*B*).

Finally, in agreement with prediction 5, the strength of predator satiation declined over time (*SI Appendix*, Table S6*A* and Fig. 4). This pattern occurred in the functional response of invertebrate seed predators (recall that vertebrate seed predators were not satiated by masting; Fig. 2*C*). The effect of masting became weaker over time and lost statistical significance after 2003 (i.e., 95% CI overlap zero in 2004 and later). The numerical response of invertebrate seed predators did not change over time (*SI Appendix*, Table S6*B*).

To verify the robustness of our findings, we examined whether the length of studies, plant taxa, or the average latitude of study locations changed during the period covered by our data and whether there was a temporal trend in association between finding predator satiation effect and publishing in higher-impact journals. We found that more recent studies tended to be longer, but their average location (latitude) has not changed (*SI Appendix*, Table S7 and Fig. S3). To test whether the temporal increase in average study length could influence our results, we rerun our models with study length included as a covariate in our models. In all models, this predictor was not significant. We did not detect any apparent temporal changes in the studied taxa. Studies that supported and those that rejected the predator satiation hypothesis tended to be published in journals with a similar impact factor, and temporal trends in the impact factor were similar for these two groups of studies (*SI Appendix*, Table S8 and Fig. S4).

## Discussion

We tested several long-standing theoretical predictions on how masting starves and satiates seed predators. They were mostly supported. Our results corroborate the notion that numerical and functional responses reinforce each other and that satiation is most pronounced at higher latitudes. They also confirm the view that satiation strength (but not the type of functional response) differs between vertebrate and invertebrate seed predators. In addition, we examined a concern that ongoing

changes in masting patterns driven by anthropogenic global change may undermine the effectiveness of masting as an antipredator strategy (47, 49, 51, 54, 55). Our analysis of global, multispecies datasets suggests that this concern is valid.

We detected a significant numerical response of seed predators to seed crops. We also found that it plays a vital role in satiating predators by making the functional response markedly more effective. Thus, both years of high production and periods when consumers are starved matter in reducing seed losses. This has consequences for selection: seed consumers likely select both for concentration of reproduction in large seeding years and for years of seed scarcity (36, 56). Such a strategy results in smaller predator populations being swamped with seeds during high-crop years.

Predator type influenced some but not all analyzed aspects of satiation. Both vertebrates and invertebrates displayed a type II functional response (the proportion of seeds predated declined linearly with seed production). Yet, satiation strength depended on predator type. When averaged across studies, only invertebrate seed predators displayed detectable functional and numerical responses to masting, while the proportion of seeds consumed by vertebrate seed predators was unaffected by fluctuations in seed crop. As a caveat, fewer studies investigated seed predation by vertebrates relative to invertebrates, potentially limiting our ability to detect patterns in the data.

Sometimes it is assumed that the numerical response works against specialist predators, which are highly susceptible to starvation, while the functional response works against generalist predators, which switch to other food items in the intermast period (31, 57). However, this is likely a simplification. Even generalist predators suffer population crashes when seed crops fluctuate (8, 14, 15), and even specialist predators are susceptible to satiation during mast years (30, 58, 59). Furthermore, masting plants can be synchronized over hundreds or even thousands of kilometers (60, 61). Even when seed predators are highly mobile, such extensive spatial synchrony can reduce their ability to counteract satiation through dispersal into areas with masting. Finally, our vertebrate category included organisms that are capable of tracking populations of masting trees in space [e.g., migratory birds such as bramblings, *Fringilla montifringilla* (62)] and organisms that are comparably sedentary and highly susceptible to mast-induced cycles of starvation and satiation [e.g., granivorous rodents (63, 64)]. The invertebrate category included insects that can enter prolonged diapause, which buffers them from starvation between mast years, and insects without this ability, which are exposed to varying resource levels (56, 65, 66). These intricacies are certainly important in determining the presence and strength of satiation in particular study systems. Yet, our results suggest that as a general rule, invertebrate seed predators are susceptible to both components
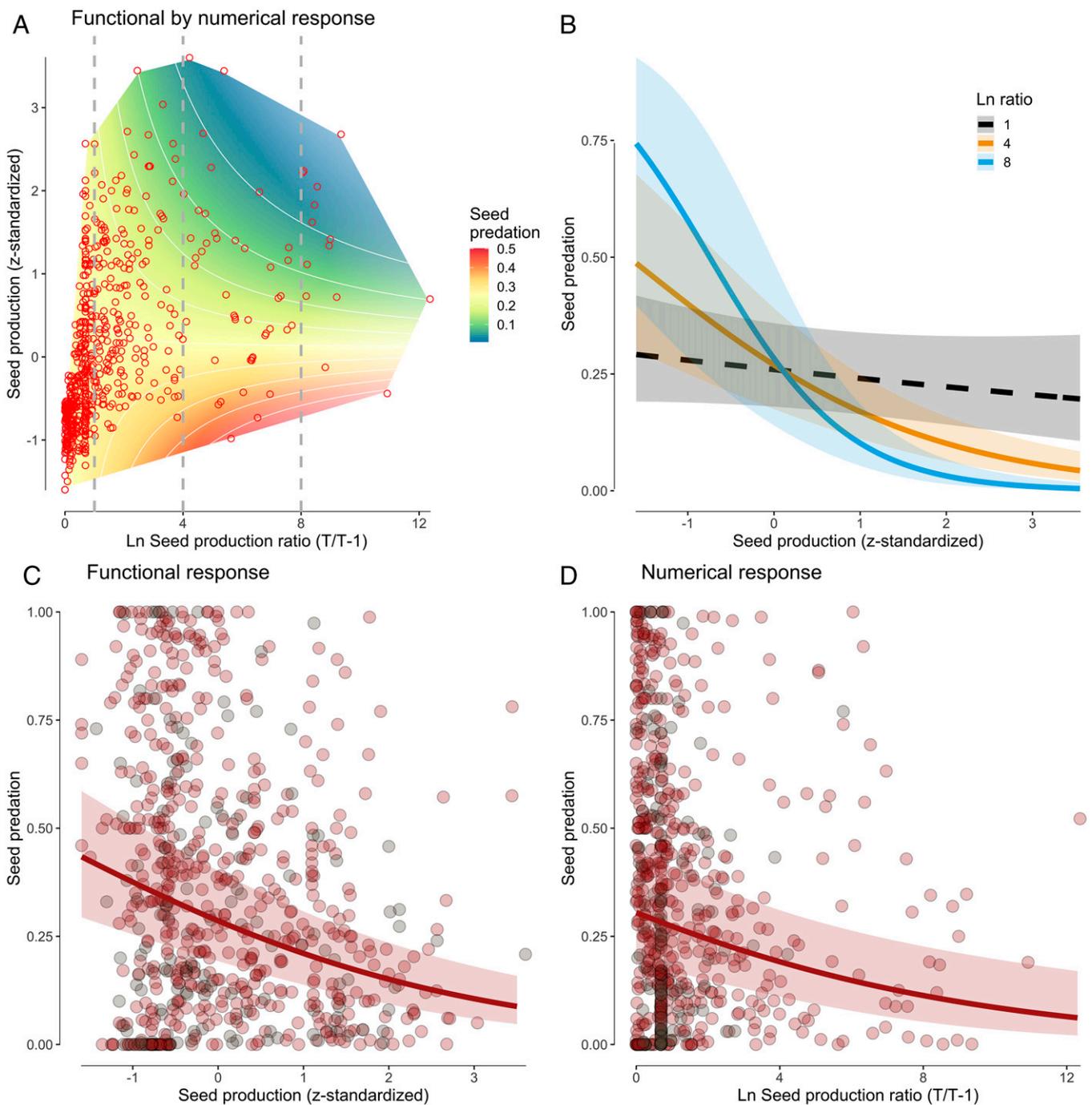
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**Fig. 2.** Starvation enhances satiation. The strategy is effective against invertebrates but not vertebrate predators. (*A* and *B*) The functional response was stronger when the seed production ratio (T/T − 1) was high. Convex hull in *A* is defined by observations (red points). Dashed lines indicate the transects plotted in *B*, i.e., the conditional relationship between seed predation and production for a selected levels of seed production ratio (see *SI Appendix*, Table S1, for model summary). Surface transparency increases as the inverse of the predictive SE; faded edges reflect increased uncertainty at data extremes. (*B*) Curves are sections through surfaces highlighted by transects at *A*, while the dashed line indicates not significant slope. (*C*) Functional response and (*D*) numerical response were significant for invertebrate (red line and dots) but not vertebrate (gray dots) seed predators. See *SI Appendix*, Tables S2 and S3, for model summary.

of the satiation effect, whereas vertebrate predators are not, probably because they are generally more mobile and have a more generalist diet.

Masting is particularly common among trees of the temperate zone and is thought to have evolved more frequently at higher latitudes, where populations are large enough to satiate seed predators when individuals produce seed crops in synchrony (1, 5, 67). In the tropics, satiation is supposed to work

mostly on the level of individual plants because high plant species diversity and their low population density makes synchrony among individuals less effective (1). Indeed, we found that the effects of population-level seed production on seed losses become stronger toward higher latitudes. However, we note that our analysis did not include studies on Dipterocarpaceae from southeast Asia. These plants solve the problem of insufficient population densities in highly diverse forests by
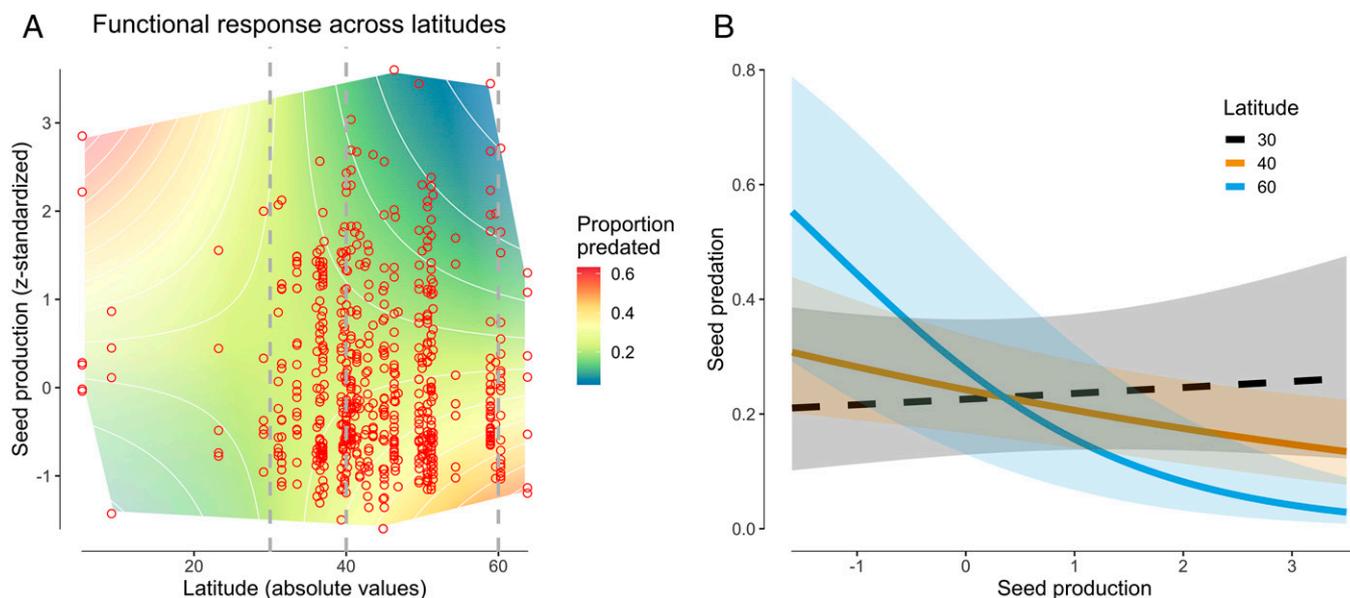
**Fig. 3.** Functional response of seed predators to masting is stronger at higher latitudes. (*A* and *B*) The functional response was stronger at higher latitudes. Convex hull in *A* is defined by observations (red points). Dashed lines indicate the transects plotted in *B*, i.e., the conditional relationship between seed predation and production for a selected levels of latitude (see *SI Appendix*, Table S4, for model summary). Surface transparency increases as the inverse of the predictive SE; faded edges reflect increased uncertainty at data extremes. (*B*) Curves are sections through surfaces highlighted by transects in *A*, while the dashed line indicates not significant slope. Numerical response presents similar pattern (*SI Appendix*, Table S5).

community-level masting. These events involve nearly all cooccurring dipterocarps and many species of other families, and flowering outside these episodes is rare (57, 68). Yet, Dipterocarpaceae studies typically do not measure seed production (69) and investigate single masting events (70); thus, they could not be included in our analysis. Incorporating such studies (8, 69–71) is a challenge for future syntheses.

Even more generally, the majority of the data in our meta-analysis come from temperate forests of Europe, North America, Japan, and New Zealand [a bias that exists more generally across ecology (72)]. To some extent, this is a pattern that originates from the biogeography of masting (5). Nonetheless, it neglects important masting-dominated systems in other regions, including African and South American tropics and boreal forest of Asia (73, 74). Clearly, there is a need to expand the geographical coverage of ecological research (75). Despite these limitations, current data indicate that predator satiation is more effective at higher latitudes. This pattern is consistent
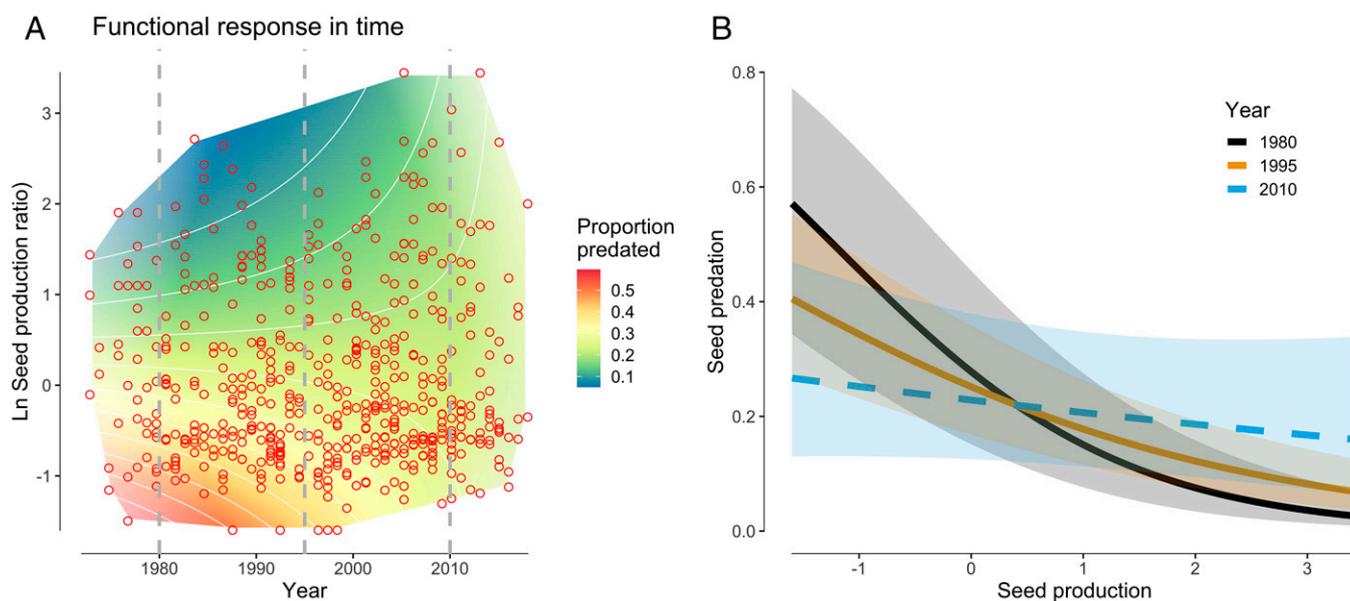


**Fig. 4.** The relationship between invertebrate seed predation and seed production (the functional response) became weaker over the period covered by our data (1972 to 2018). (*A*) Convex hull is defined by observations (red points). Dashed lines indicate the transects plotted in *B*, i.e., the conditional relationship between seed predation and production for selected years. Surface transparency increases as the inverse of the predictive SE; faded edges reflect increased uncertainty at data extremes. (*B*) Curves are sections through surfaces highlighted by transects in *A*, while the dashed line indicates not significant slope. Effect size for the numerical response did not change with time (see *SI Appendix*, Table S5, for model summaries). Models were fitted for two subsets of the data: invertebrates or vertebrates only. The effects for vertebrates were not significant.

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with the avoidance of seed predation as an evolutionary process behind the biogeographical pattern in masting occurrence.

We also found that the satiation effect became progressively weaker over time. The decline was not associated with trends in the geographical location of masting studies or publication bias and could not be explained by changes in the average study length. The most obvious reason for the trend in satiation strength is anthropogenic changes, including global warming or nitrogen deposition. Masting is sensitive to climate change because it is triggered by species-specific weather cues such as deviations from temperature or precipitation means (19). Yet, the direction of this effect is unclear, with some studies predicting or demonstrating an increase in the variability of seed crops (48, 54, 76) and others pointing toward decline (47, 49, 52). These studies agree that changes in masting patterns will affect plant ability to satiate seed predators, but direct tests of this prediction are limited to a single study (47): the decline in variability and synchrony of seed production in *F. sylvatica* was associated with increased predispersal seed predation. While our meta-analysis cannot be used to infer changes in masting patterns, it demonstrates that globally and averaged across studies, masting is losing its capacity to satiate seed predators. Reduced ability of masting to satiate predators is bound to have negative consequences for the reproduction of masting plants. Future empirical and modeling studies should examine these consequences in detail. Possible ramifications include impaired ability of plant populations to track changing climatic conditions via distribution shifts, changes in competitive hierarchies among plants, and altered community abundance patterns (77, 78). In addition, the increased destruction of seeds by invertebrates can trigger negative cascading effects on other organisms that directly (granivores) or indirectly (e.g., predators) benefit from masting (14, 16). Evolutionary responses of masting plants have the potential to restore the effectiveness of predator satiation as a defense strategy, through favoring individual plants that retain their masting intensity despite the warming (36). However, in the case of species with long generation times, such as trees, the timescale of evolutionary response is orders of magnitude slower than the pace of environmental change.

## Methods

**Data Collection.** We followed the steps outlined in the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analysis) protocol. We conducted a literature search in Scopus and Web of Science using search terms *mast** AND (*satiat** OR "*seed pred**" OR [*seed** AND *infest**]). The search was last updated in July 2021 and identified 380 papers. In addition, we searched for suitable papers among articles cited in previous reviews of masting (4, 17, 27) and articles citing several of the most widely known reviews (forward searches of refs. 2, 4, 17, 27)

As a consequence of our search terms, we retrieved only articles that studied seed predation in the context of masting, as stated by authors of the papers. Thus, we relied on opinions of researchers working on their plant species, but we note that masting encompasses a gradient of seed production strategies, without a clear boundary between masting and nonmasting species. Instead, species range widely in their masting strategy, which likely reflects the varying selective pressures for different combinations of interannual variation and synchrony (5, 31, 77, 79).

We included only studies that were published after 1980 because our coverage of older studies would probably be incomplete and because many earlier studies were quantitatively reviewed by Silvertown (2). To be included in our analysis, the studies needed to present yearly data on seed predation (presented as the proportion of seeds consumed, infested, or removed) and on seed production. We required at least 4 y of data that covered at least one mast event (as defined by the authors). Data were extracted from the text, tables, or graphs using WebPlotDigitizer (80). When results were presented in a format that we could not use (e.g., averaged across years), we contacted corresponding authors to obtain the raw data.

When studies presented data averaged over multiple sites (e.g., refs. 81, 82), we worked with the average; when data were presented for each site

separately (e.g., refs. 83–85), we selected one site randomly or selected a site with the longest time series. While averaging across sites could be fine in some cases, in others, when study sites are too remote to be synchronized, averaging would flatten masting patterns and associated fluctuations in predation rates. Choosing a single random site allowed us to avoid arbitrary decisions whether to average data or not.

Some studies investigated masting by several cooccurring species that indirectly affected each other by shared seed predators (86, 87). In such cases, we extracted data for single species rather than try to calculate total seed crop. Particular species differ in seed size and nutritional value; thus, their seeds cannot be simply summed. However, masting by nonfocal species can affect predator satiation, so we coded such studies with a dummy variable to examine their influence on the results.

We did not include studies where data were collected only during mast or only during nonmast years. We did not include studies on fruit removal vs. fruit production because it does not have a clear relation to predator satiation hypothesis (17). We included studies on scatterhoarders and used the proportion of seeds harvested as a proxy for seed predation. Some harvested seeds might be dispersed rather than eaten (88), but the general principles of predator satiation apply to scatterhoarding species (see refs. 9, 89 for more detailed discussion).

These selection criteria resulted in 78 datasets (study × plant × seed predator combinations) from 48 studies, representing 60 plant species, 27 genera, and 16 families of masting plants, conducted on six continents (Fig. 1; see *SI Appendix*, Table S9, for the list of studies). However, not all data were used in every analysis (*Analysis*).

**Analysis.** Data were analyzed in R (R Core Team 2018), and models were fitted using package *glmmTMB* (90). Model fit was assessed with package *DHARMa* (91). We tested all predictions by constructing generalized linear mixed models with logit-transformed proportion of seed loss as the response variable (see Table 1 for a summary). When testing for the functional response, explanatory variables included seed production (converted to z-scores to allow comparisons between studies that used different measures of seed crop). When testing for the numerical response, explanatory variables included the ratio of the seed crop in year T to the crop in year $T - 1$ (30). The ratios were $\ln(x + 1)$ transformed to improve model convergence. Random intercepts always included plant species, study ID, seed predators (usually species), and a first-order temporal autocorrelation structure. We also explored models with plant genus and family as random effects to control for phylogenetic covariance above the species level (92) and models that included spatial autocorrelation. However, these effects did not improve model fit (according to Akaike Information Criterion). We found moderate heteroskedasticity, with response more variable for lower values of seed production. We accounted for this effect by allowing dispersion to change along predictors. We did not weight studies because few of them provided measures necessary to calculate sampling error. Average effect sizes in unweighted meta-analyses are unbiased (93). In models in which predictors were included both as linear and quadratic terms, we removed the quadratic terms from the final model if not significant.

We tested the first prediction (i.e., the functional response is enhanced by the numerical response) with a model that included seed production in interaction with seed production ratio as predictors. Seed production was included as both linear and quadratic terms.

We tested the second prediction (types of functional response differ by predator type) with models that included seed production [linear and quadratic term, corresponding to type II and type III functional response (42)] in interaction with seed predator type (vertebrate vs. invertebrate) as predictors. The third prediction (that strength of the numerical response to masting differs by predator type) was tested similarly, but we replaced seed production with the seed production ratio.

We tested the fourth prediction (predator satiation and starvation weaken toward the tropics) with models that included either seed production (linear and quadratic terms) or the seed production ratio in interaction with latitude (linear and quadratic term). To address sparse coverage of the global south in our dataset, we constructed two versions of the models: with absolute values of latitude as predictors and with data filtered only to latitudes > 30 where the data coverage was highest.

We tested the fifth prediction (predator satiation and starvation weakened over the recent decades) with a model that included either seed production (linear and quadratic terms) or seed production ratio in interaction term with study year (linear and quadratic term). Models were fitted for two subsets of the data: invertebrates or vertebrates only.

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