Dynamic pollinator networks maintain pollination efficiency during mast flowering in an insect-pollinated tree

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Abstract

Mast seeding, the synchronous and highly variable reproduction across years, is common among perennial plants, enhancing reproductive success through predator satiation and improved pollination. Animal-pollinated species generally show lower interannual variability in seed production then wind-pollinated plants, often explained by pollinator satiation reducing selection for masting. However, numerous animal-pollinated species mast strongly, challenging this view. We examined pollination dynamics in insect-pollinated *Sorbus aucuparia* over four years of varying flowering intensity. Pollination efficiency was generally high (mean 68%) across years and increased from 20% to 80% with increasing tree-level flower abundance, showing no decline in high-flowering periods. Instead, pollinator visitation networks shifted significantly: *Bombus* species, capable of quick numerical and functional responses, dominated visits during abundant flowering years. In contrast, bees such as *Andrena* and *Lasioglossum subg.Evylaeus*, limited by univoltine life cycles, were proportionally more important during low-flowering years. Our findings highlight that pollinator life histories shape visitation networks and stabilize pollination across mast cycles. More generally, our results suggest that animal pollination does not prevent the evolution of masting but rather reduces its selective pressure, emphasizing wind pollination as the primary driver behind the evolution of strong masting due to its high pollen transfer requirements.

keywords: bumblebee | mast seeding | pollination efficiency | pollinator networks | reproductive efficiency | Sorbus aucuparia |

Introduction

Numerous perennial plant species exhibit mast seeding, a reproductive phenomenon characterized by highly variable reproduction across years synchronized among individuals within populations (Pearse *et al.*, 2016; Journé *et al.*, 2023; Bogdziewicz *et al.*, 2024b). Mast seeding influences ecosystem functioning, affecting wildlife, plant, and fungal population dynamics, as well as carbon stocks and nutrient cycling (Hacket-Pain *et al.*, 2018; Clark *et al.*, 2019; Mund *et al.*, 2020; Michaud *et al.*, 2024). At the ultimate level, mast seeding confers fitness benefits through reproductive efficiency being enhanced by economies of scale: reduced seed predation rates and improved pollination efficiency (Kelly & Sork, 2002; Zwolak *et al.*, 2022; Pesendorfer *et al.*, 2021). Specifically, alternating periods of seed scarcity and abundance reduce seed predation by subsequently starving and satiating seed consumers (Zwolak *et al.*, 2022), while concentrated flowering efforts during mast events improve pollination efficiency (Kelly *et al.*, 2001; Rapp *et al.*, 2013). However, mast seeding can potentially trap mutualistic partners into similar starvation-satiation cycles, much like it does with seed consumers (Kelly & Sork, 2002; Qiu *et al.*, 2023). Consistent with this, interannual variability in seed production tends to be ~30% lower in animal-pollinated species compared to wind-pollinated ones, a broad-scale pattern interpreted as selection against masting in plants reliant on animal pollinators (Kelly & Sork, 2002; Pearse *et al.*, 2016; Qiu *et al.*, 2023). Yet, considerable variation within these groups exists, with numerous animal-pollinated plants exhibiting strong masting (Pearse *et al.*, 2020). This variability appears contradictory, as pronounced masting cycles in these plants would be expected to reduce pollination efficiency due to starvation and satiation of pollinators, selecting for weaker masting.

Pollinator responses to mast flowering events remain poorly understood, leaving unclear how animal-pollinated species maintain pronounced masting (Bogdziewicz *et al.*, 2024b). A notable exception is studies in dipterocarps, which address why pollination efficiency does not strongly select against community-level mass flowering in these animal-pollinated plants (Kelly & Sork, 2002). Dipterocarp species rely on thrips (Thysanoptera), small insects with rapid reproductive cycles that quickly increase in abundance during mast events by utilizing scattered floral resources or vegetative structures between mast years (Appanah & Chan, 1981; Ashton *et al.*, 1988; Kondo *et al.*, 2016). Beetles (Coleoptera) also serve as important dipterocarp pollinators, sustaining populations on vegetative tissues during non-flowering years, then shifting rapidly to floral resources during mast events (Momose *et al.*, 1998). Social bees, such as *Apis dorsata*, maintain pollination efficiency by migrating long distances to flowering areas during general flowering periods (Momose *et al.*, 1998). In another system, animal-pollinated *Astragalus scaphoides* maintains high pollination efficiency during mast events, as evidenced by reduced pollen limitation in high-flowering years (Crone & Lesica, 2006). In that species, social bumblebees exhibit immediate numerical and functional responses, ensuring effective pollination despite large interannual fluctuations in flower abundance (Crone & Lesica, 2006; Crone, 2013). Beyond these few systems, however, it remains uncertain how widespread or consistent such pollinator adaptations are across animal-pollinated masting plants. Yet, understanding pollinator responses to mast flowering is essential for predicting the occurrence and intensity of masting across species and biomes, which has significant implications for ecosystem functioning (Pearse *et al.*, 2020).

Fluctuations in flower abundance, such as those driven by mast flowering, can substantially alter the structure of plant–pollinator interaction networks, including within populations of a single plant species. For example, in years of high flowering, networks can expand with more pollinator species interacting with more individual plants (Alarcón *et al.*, 2008; CaraDonna *et al.*, 2017). Such structural shifts may promote pollen transfer and buffer pollination efficiency during peak reproductive output. However, high floral density can also lead to pollinator dilution, where individual flowers receive fewer visits due to the overwhelming abundance of flowers, reducing per-flower pollination success (Knight *et al.*, 2005; Mitchell *et al.*, 2009). In contrast, poor flowering years can show reduced pollinator interactions, as pollinators concentrate on fewer individuals, which can lead to uneven or insufficient pollen transfer and reduced pollination efficiency at the population level (Petanidou *et al.*, 2008; Ebeling *et al.*, 2008; Burkle *et al.*, 2013). Yet, under some conditions, pollination can be maintained in low-flowering years through, for example, the persistence of central, generalist pollinators that continue pollinating multiple plants despite resource scarcity (Alarcón *et al.*, 2008). These dynamics suggest that network rewiring, i.e., shifts in which pollinators visit which plants (CaraDonna *et al.*, 2017), can either stabilize or disrupt pollination, depending on how foraging behavior and network structure respond to variation in floral resources. Yet, empirical evidence from mast-seeding species remains limited, including at the within-species level, where effective pollen transfer among individuals is critical for reproductive success.

We investigated how interannual variation in flower abundance influences pollinator visitation and pollination efficiency within a population of the insect-pollinated tree *Sorbus aucuparia*. We monitored 30 marked individuals over four consecutive years, two of which can be broadly categorized as low- and two as high-flowering years (Fig. 1). Each tree was equipped with insect traps to quantify flower visitation and identify pollinator assemblages. Using these data, we tested how mast flowering affects pollination dynamics at the individual and network levels. First, we asked whether pollination efficiency exhibits a hump-shaped relationship with flower abundance, as would be expected under positive density dependence at low flower densities and pollinator satiation at high flower densities (Kelly & Sork, 2002). Alternatively, we hypothesized that pollinator responses—numerical, functional, or behavioral—lead to interaction network rewiring that buffers plants from pollen limitation during mast events, maintaining high pollination efficiency even when floral resources peak. By integrating plant-level reproduction, pollinator identity, and network structure, our study provides rare insight into how animal-pollinated masting species sustain reproductive success under extreme interannual variability in flowering.

Methods

Study species

Rowan (*Sorbus aucuparia*) is a long-lived, insect-pollinated, fleshy-fruited deciduous tree widespread across Europe, Asia Minor, the Caucasus, western Siberia, and North Africa. Individuals can reach heights of 15–20 meters and typically live 100–150 years. Rowan exhibits large, synchronous interannual variation in fruit production (mean across-individuals synchrony = 0.57, mean coefficient of variation in fruit production at a tree level = 1.71; Fig. 1), with flowering triggered by high summer temperatures in the year before reproduction (Żywiec *et al.*, 2012). The species is the primary host for larvae of the apple fruit moth *Argyresthia conjugella*, a pre-dispersal seed predator responsible for substantial seed losses. However, in high-fruiting years that follow years of low fruiting, predation rates drop sharply due to predator satiation followed by starvation: from an average of 75% to below 20% (Kobro *et al.*, 2003; Seget *et al.*, 2022a). Seeds are dispersed by frugivorous animals, and dispersal rates increase in high-fruiting years, likely driven by the attraction of migratory birds (Paulsen & Högstedt, 2002; Seget *et al.*, 2022b). Long-term monitoring combined with parentage analysis has shown that this highly variable and synchronized reproduction enhances seedling establishment, indicating increased reproductive efficiency driven by masting (Bogdziewicz *et al.*, 2024a).

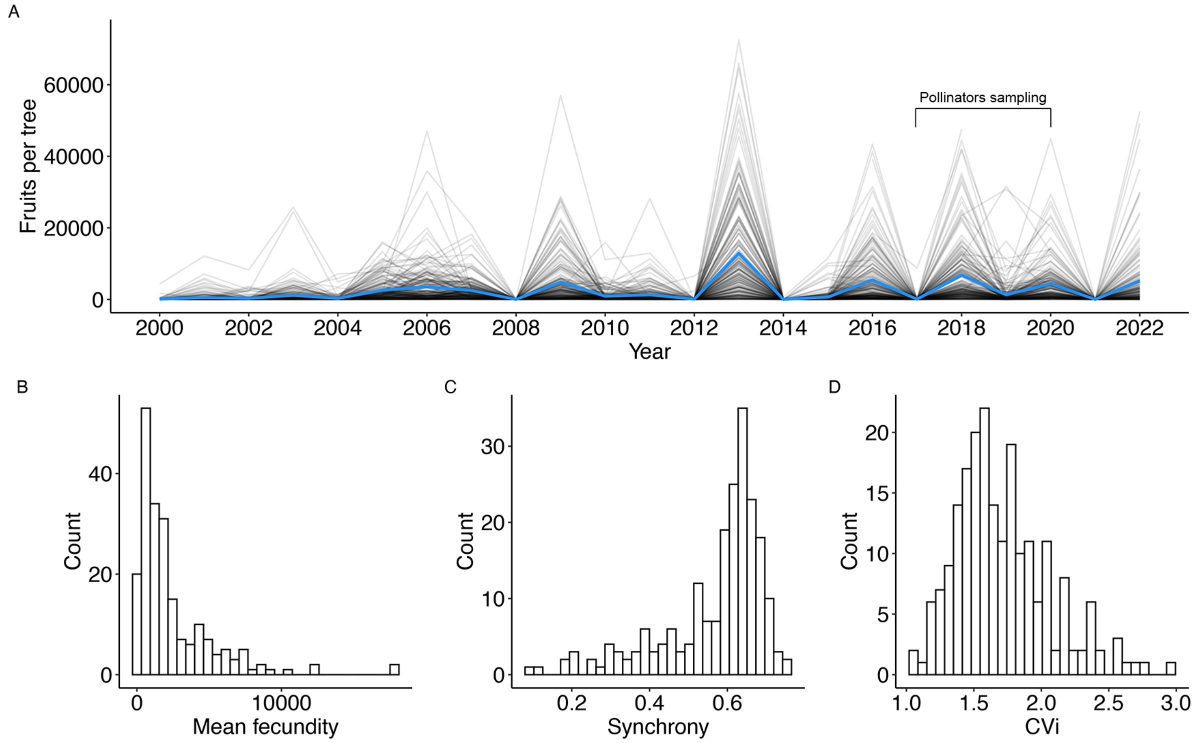

Figure 1: Temporal patterns of fruit production of *Sorbus aucuparia* monitored at Babia Góra, Poland (A). Each black line is an individual tree, while the blue line shows the population-level average fruit production in a given year. Histograms show the distribution of individual-level (B) mean fruit production, (C) mean fruiting synchrony with other individuals, calculated as mean pair-wise correlation in seed production across all pairs of trees, (D) coefficient of variation at an individual-level (CVi, sd/mean). The graph shows fruit production patterns across a larger sample of trees monitored at our population (N = 180-209 individuals depending on the year), with the period of additional inflorescences and pollinator sampling (2017-2020) highlighted at (A).

Study site

The study was conducted in a 27-ha plot (564×480 m, 1170–1310 m a.s.l) located in the subalpine spruce forest in the Babia Góra massif of the Western Carpathian Mountains in Poland. This forest has been under protection since

1930. *S. aucuparia* occupies mainly tree stand gaps caused by windstorms and bark beetle outbreaks (Żywiec & Ledwoń, 2008; Holeksa *et al.*, 2017).

Field sampling

Fruit and flower production. In 2000, all *S. aucuparia* trees with a diameter at breast height (DBH) >4 cm were mapped and marked (N=367), and subsequent fruit production was recorded during annual visits in September before fruit removal by birds was initiated. To estimate the annual fruit production of each tree, we counted all the infructescences on a tree using binoculars. This number was then multiplied by the mean number of fruits counted on five infructescences of that individual in that year to obtain the total estimate (Pesendorfer *et al.*, 2019).

For this study, we randomly selected 30 individuals from that larger population. All inflorescences were counted in those trees from June 2017 to 2020. Inflorescences were counted using binoculars, using similar methods as in the case of infructescences.

Insect assemblages We installed entomological traps in the crowns of 30 selected trees in early June, several days before the flowering period, adjusting the exact dates according to annual phenology. We suspended white Moericke traps, matching the color of rowan flowers, on ropes approximately 4–6 meters above ground level within the tree crowns. Each trap contained a mixture of water, glycol, and detergent. Approximately three weeks later, once all flowers on the studied trees had faded, we removed the traps. We transferred captured insects into plastic containers filled with alcohol and subsequently identified all collected Hymenoptera species in the laboratory.

Analysis

We tested for density dependence in pollination efficiency using generalized linear mixed models (GLMM). The proportion of inflorescences producing infructescences (measured at the tree-level annually) was modeled as the response variable, with log-transformed inflorescence counts (tree-level, annual) as the predictor. Tree ID was included as a random intercept, whereas year was excluded to avoid blocking the comparison to within-year effects (Fletcher *et al.*, 2010). We used a binomial error distribution with a logit link.

To model variation in insect visitation across inflorescence production, we used a GLMM with a Tweedie error distribution and a log link. Here, the annual, tree-level insect visitation counts were a response variable, and log-transformed annual, tree-level inflorescence counts were a predictor. All models were fitted using the glmmTMB package (Brooks *et al.*, 2017) in R version 4.2.3. In both models, predictors (inflorescences) were included in the model as natural cubic splines to allow non-linear relationships.

For pollination networks visualization and network metrics calculation, we used the bipartite R package (Dormann *et al.*, 2008).

Results

Flowering intensity varied considerably across the study period, with the lowest flowering observed in 2017 (mean of 13 inflorescences per tree), moderate flowering in 2019 (mean of 68), and higher flowering in 2018 and 2020 (means of 141 and 215 inflorescences per tree, respectively) (Fig. 2A). Pollination efficiency remained generally high across years, averaging approximately 68%. Even during the poor flowering year of 2017, mean population-wide pollination efficiency was around 35%, whereas in other years, it remained relatively stable at approximately 78% (Fig. 2B). Despite substantial interannual variation in flowering abundance, the mean number of insect visits per tree showed less variation, with approximately 20 visits in both 2017 and 2018, 14 visits in 2019, and 9 visits in 2020 (Fig. 2C).

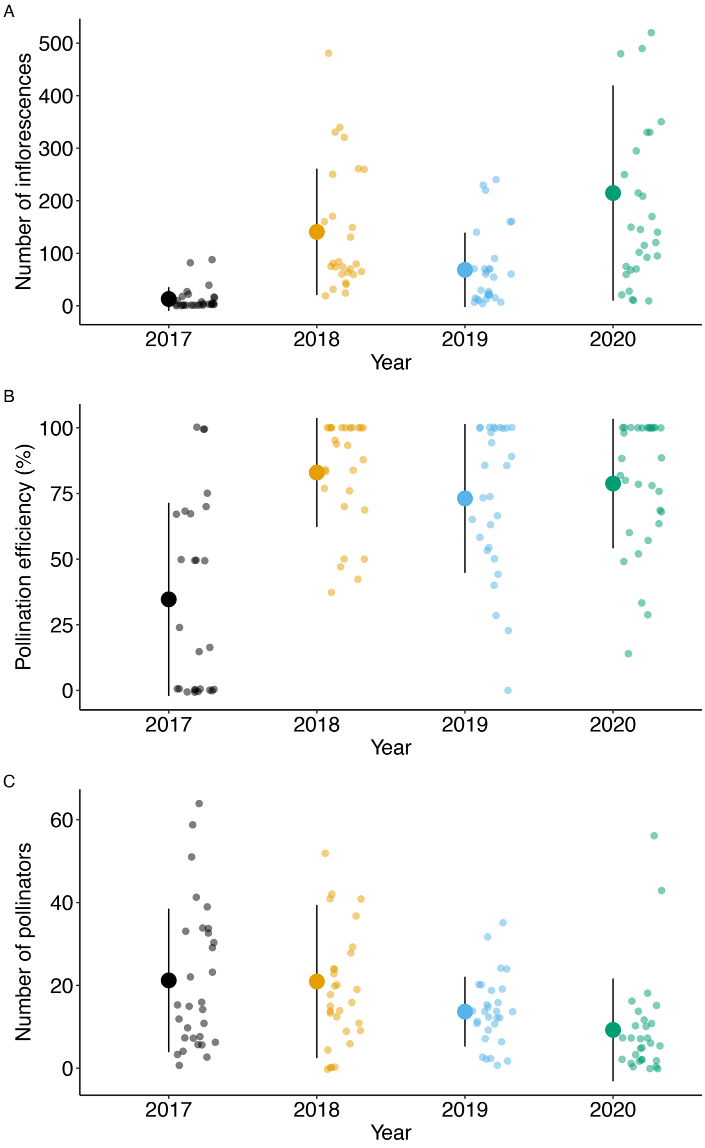

Figure 2: **Annual variation in flowering (A), pollination efficiency (B), and pollinator visits (C).** Small points show annual, tree-level observations, while large points and associated whiskers show mean and standard deviations. Pollination efficiency is calculated as the proportion of inflorescences that produced infructescences. Insect visits were estimated using Moericke traps installed at individual tree canopies.

Positive density-dependence in pollination efficiency was evident (Fig. 3A, Table 1). Efficiency increased markedly from about 15% at low flowering levels (few inflorescences per tree) to approximately 90% when inflorescence counts reached around 90 per tree. Above this threshold, pollination efficiency stabilized and remained at about 85-90%, even when flowering intensity reached as high as 750 inflorescences per tree (Fig. 3A). Thus, there was no evidence of pollinator saturation leading to a decrease in pollination efficiency. Notably, across the entire 23-year monitoring period, only one year (2013) exhibited substantially higher fruiting intensity, approximately twice the reproductive effort of 2020 (Fig. 1), suggesting that pollinator saturation is likely uncommon in our study population.

Pollinator visitation per tree declined with increasing flowering intensity (Fig. 3B, Table 1). Trees producing very few inflorescences received an estimated mean of 14 insect visits, a visitation rate that was sustained up to approximately 80 inflorescences per tree. In trees producing more than 80 inflorescences, visitation rates started to decline, down to approximately 5 insect visits per tree if inflorescences exceeded 600 (Fig. 3B). Despite this decrease, pollination efficiency did not diminish (Fig. 3A), indicating that visitation rates remained sufficient to sustain effective pollination even at high flowering levels.

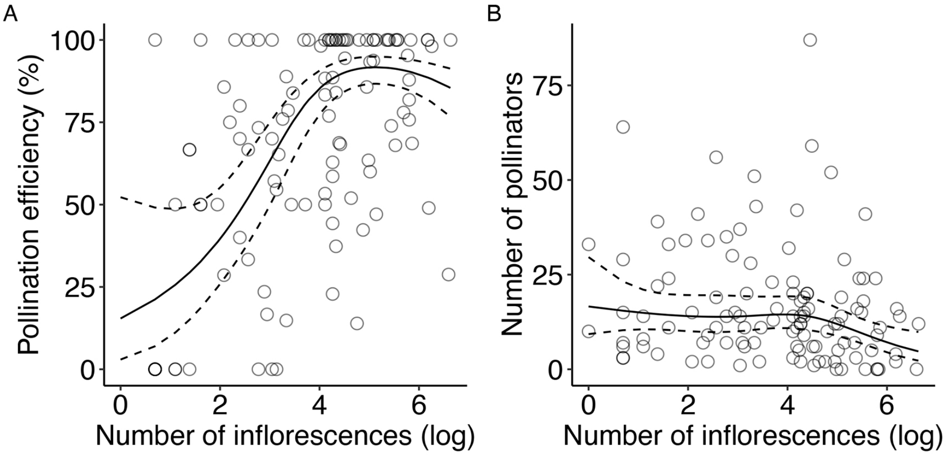

Figure 3: **Positive density-dependence in pollination efficiency is sustained despite a decrease in insect visitation rates at high flowering intensity.** Pollination efficiency (A) and insect visits (B) across tree-level (log-transformed) inflorescence production. Each dot shows annual, tree-level observations. The fitted lines and associated 95% CI are derived from a GLMMs that included treeID as a random intercept.

Analysis of insect visitation rates across years demonstrates shifts in pollinator networks associated with flowering intensity. In high-flowering years (2018, 2020), a number of *Bombus* species (*B. lucorum*, *B. pratorum*, *B. pascuorum*, *B. pyrenaeus*, *B. soroeenis*) dominated insect visitation, accounting for approximately 91% (2018) and 65% (2020) of total visits. The extensive presence of *Bombus* is clearly evidenced by wide, dense connections between trees and *Bombus* species nodes (Fig. 4).

In contrast, during low-flowering years (2017, 2019), *Bombus* visitation decreased to roughly 40% of total visits. During these periods, *Andrena* (including *A. carantonica*, *A. haemorrhoa*, *A. helvola*, *A. lapponica*, *A. subopaca*) and *Lasioglossum* (including *L. calceatum*, *L. albipes*, *E. fratellum*) species showed increased visitation proportions (Fig. 5). Specifically, *Andrena* visitation increased to around 30% from 2-10%, and *Lasioglossum* to approximately 15-20% from 5%, making both genera more important than in high-flowering years. Finally, *Apis mellifera* displayed variable presence, noted in 2017, 2018, and 2019 but was completely absent in 2020. When present, *A. mellifera* played a secondary role, accounting for about 5-10% of total visits, indicating a relatively minor but consistent contribution to pollination dynamics in those years.

The rewiring of the pollination network was also evident from changes in network metrics. Connectance, the proportion of realized interactions out of all possible interactions between plant and pollinator species, varied between low- and high-flowering years. Specifically, connectance was lower in high-flowering years (0.17 in 2018 and 0.19 in 2020) and higher in low-flowering years (0.27 in 2017 and 0.24 in 2019). This pattern reflects the increased dominance of *Bombus* species in the pollination network during periods of low flowering. Similarly, interaction evenness decreased from 0.74 (2017) and 0.73 (2019) in low-flowering years, to 0.58 (2018) and 0.64 (2020) in high-flowing years.

Discussion

Our study shows that pollination efficiency in *Sorbus aucuparia* increases with flower abundance and stabilizes, with no evidence of a decline at high floral densities. This pattern indicates that even during high-flowering years plants

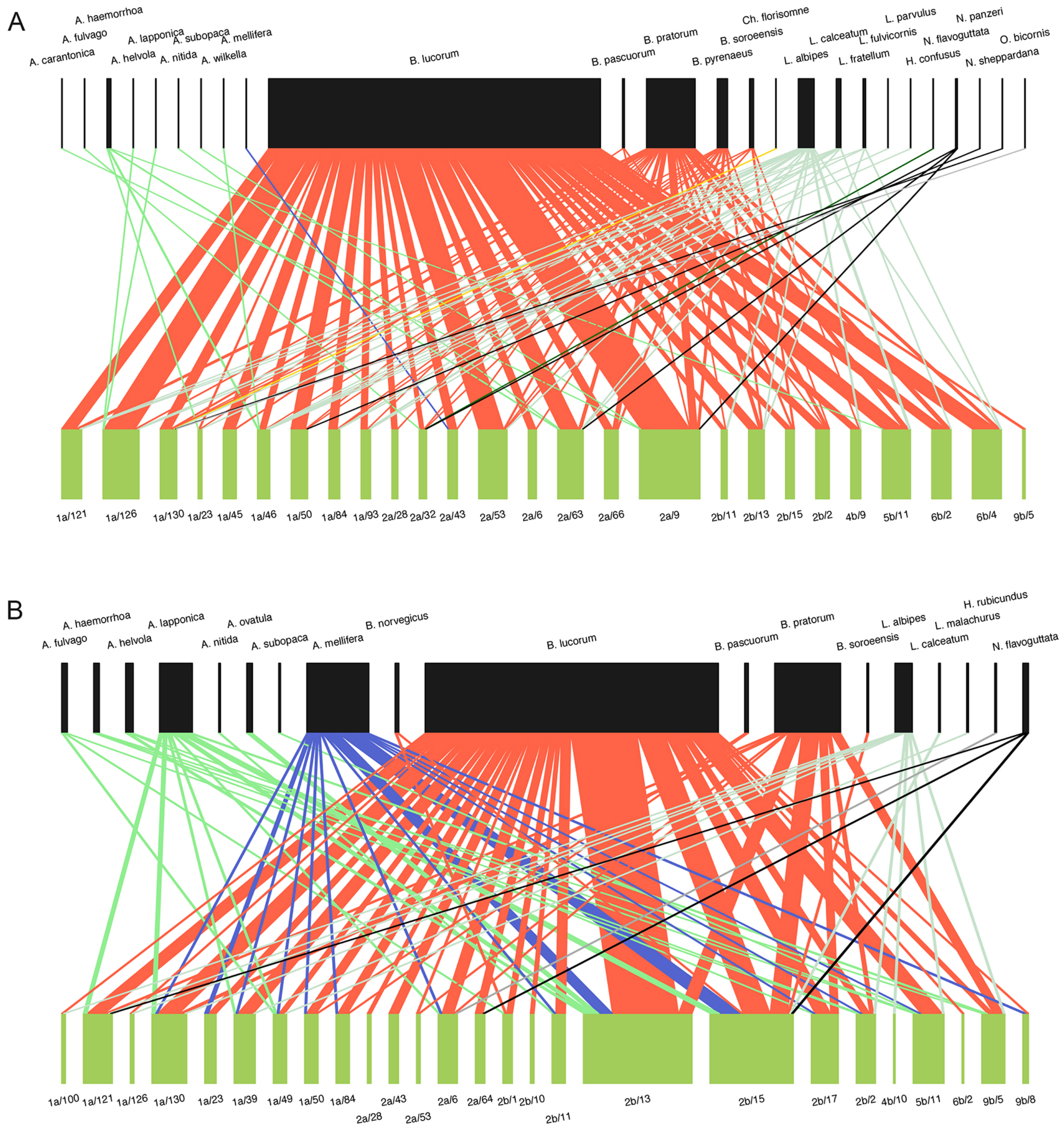

Figure 4: Bipartite network of *S. aucuparia* and pollinators interactions in 2018 (A) and 2020 (B), characterized by high flowering intensity. Bottom bars indicate 30 trees at which insect visitations were monitored, while upper panels represent different pollinator species, with different colors delineating different genus.

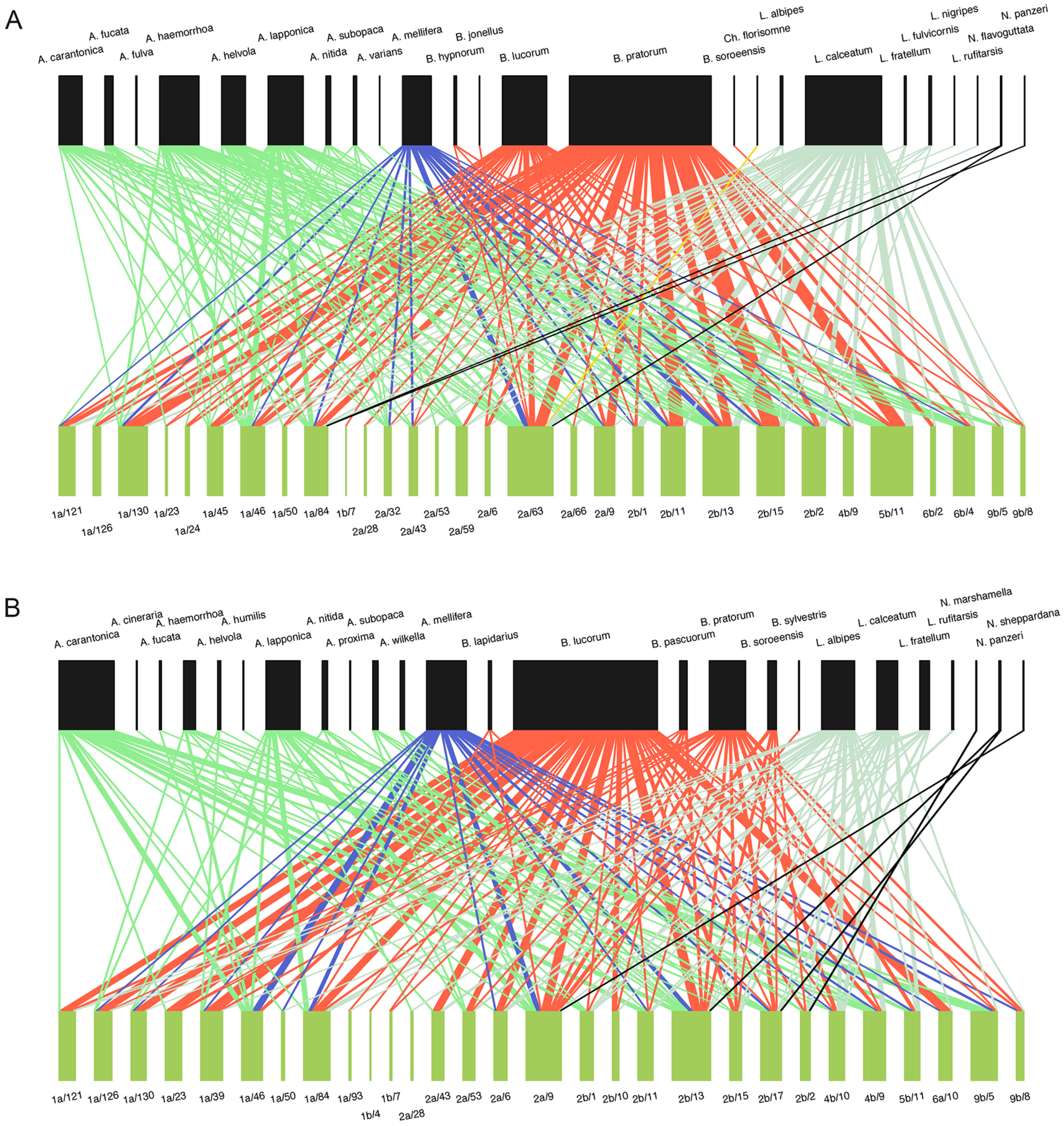

Figure 5: Bipartite networks of *S. aucuparia* and pollinators interactions in 2017 (A) and 2019 (B), characterized by low flowering intensity. Bottom bars indicate 30 trees at which insect visitations were monitored, while upper panels represent different pollinator species, with different colors delineating different genus.

Table 1: Summary of the generalized linear mixed model testing the effects of flowering intensity on pollination efficiency and insect visitation rates. The models included the proportion of inflorescenses producing infructescences (pollination efficiency model) or the total number of insect visits per tree (pollinator visits model) as the response, and the log-transformed number of inflorescence fitted as a natural cubic spline as a predictor. Both models included tree ID as random intercept.

Effect	β	SE	Z	p
Pollination efficiency				
Intercept	-1.70	0.91	-1.86	0.062
log(no. of inflorescence)	4.20	0.53	7.98	<0.001
log(no. of inflorescence^2)	5.15	1.81	2.84	<0.001
log(no. of inflorescence^3)	2.70	0.38	7.08	<0.001
Pollinator visits				
Intercept	2.81	0.30	9.50	<0.001
log(no. of inflorescence)	0.07	0.26	0.27	0.789
log(no. of inflorescence^2)	-1.02	0.71	-1.44	0.150
log(no. of inflorescence^3)	-1.11	0.37	-3.05	<0.001

are not subject to pollinator satiation. Instead, pollination efficiency remains high, suggesting that the pollinator community responds in ways that maintain reproductive success; through behavioral flexibility and interaction network rewiring. Despite limited per-plant visitation rates, effective pollen transfer is sustained, highlighting the capacity of the pollinator community to adjust to fluctuating floral resources. These findings challenge the assumption that mast flowering in animal-pollinated plants inherently risks mutualist disruption (Kelly & Sork, 2002; Pearse *et al.*, 2020; Qiu *et al.*, 2023) and support the idea that flexible foraging behavior and dynamic interaction structures enable the maintenance of reproductive function across mast cycles.

Pollinator network structure differed significantly between high- and low-fruiting years. During high-fruiting years, key pollinators such as *Bombus spp.* established extensive connections across the plant population, likely facilitating widespread and consistent pollen transfer (Crone, 2013). Low-fruiting years exhibited a greater diversity of insect species visiting individual trees, resulting in relatively stable visitation rates despite large interannual fluctuations in fruit production. These structural variations indicate that mast flowering events trigger functional and numerical responses among pollinators, causing network reorganization that enhances connectivity and boosts pollination efficiency (CaraDonna *et al.*, 2017). However, during exceptionally poor flowering periods, such as 2017, the limited availability of outcross pollen likely reduced pollination efficiency, highlighting that positive density dependence is an important driver of pollination efficiency in our system.

The rewiring observed in pollination networks between high and low-flowering years can be largely explained by the life histories of the insect species involved. In high-flowering years, *Bombus* species dominated. Their social structure, large size and mobility, and generalist diet allow both functional and numerical responses to pulsed flowering (Westphal *et al.*, 2006; Crone, 2013; Spiesman *et al.*, 2017). In contrast, solitary bees such as *Andrena* and *Lasioglossum*, which are univoltine (Packer, 1991; Bossert *et al.*, 2024), are marginalized in high-flowering years. Their one-generation-per-year life cycles appear to limit their ability to mount rapid demographic responses to floral pulses. Thus, in low-flowering years, *Bombus* remain key pollinators, but *Andrena* and *Lasioglossum* play a proportionally larger role. With overall flower density reduced, even low-density solitary bee populations can cover a greater share of available resources, increasing their relative importance in the network. **Apis mellifera** showed variable presence, the causes of which may be due to anthropogenic factors (e.g., translocation of apiaries in the vicinity of Babia Góra).

Our results, together with limited evidence from other systems, suggest that the prevailing paradigm, i.e., that animal-pollinated plants exhibit lower interannual variability in reproduction (CVp) due to selection against pollinator satiation (Kelly & Sork, 2002; Pearse *et al.*, 2016; Qiu *et al.*, 2023; Bogdziewicz *et al.*, 2024b), may need to be reconsidered. Rather than selecting against masting per se, animal pollination may reduce the need for the extreme reproductive variability observed in wind-pollinated species. In wind-pollinated plants, high flower densities are required to ensure successful pollen transfer, which favors strong reproductive synchrony and high CVp (Kelly *et al.*, 2001; Bogdziewicz *et al.*, 2020). For example, in European beech (*Fagus sylvatica*) or black beech (*Nothofagus solandri*), population-wide pollination efficiency declines to 5% in poor flowering years but can exceed 60-80% in years characterized by large and synchronous flowering effort (Kelly *et al.*, 2001; Szymkowiak *et al.*, 2024b; Pesendorfer *et al.*, 2024). In contrast, animal-pollinated species can maintain effective pollination even at relatively low floral densities due to the targeted delivery of pollen by animal vectors. In our system, even the very poor flowering year (2017) was characterized by a mean pollination efficiency of 35%, and estimated pollination efficiency reached 65% when tree-level flowering was still relatively low (20 inflorescences). Growing evidence, including our findings, shows that pulsed flowering often triggers numerical or behavioral responses in pollinator communities that buffer against pollinator satiation and pollen limitation (Momose *et al.*, 1998; Crone, 2013; Kondo *et al.*, 2016). Moreover, pollen addition experiments in several animal-pollinated masting species report no signs of pollen limitation during mast years, indicating that pollination remains effective even under highly variable flowering (e.g., Pías & Guitián, 2006; Brookes & Jesson, 2007; Griffiths *et al.*, 2010; Crone, 2013). Therefore, the generally lower CVp observed in animal-pollinated species may reflect a reduced reliance on extreme flowering variation, made possible by inherently higher pollination efficiency, rather than selection against masting itself.

In summary, our findings help clarify how animal-pollinated species can sustain pronounced masting without compromising pollination success. This sheds light on a key uncertainty in the literature: how mutualistic interactions persist under extreme flowering variability. Careful generalization based on available evidence suggests that pollinators are not satiated by masting events (Ashton *et al.*, 1988; Crone & Lesica, 2006; Pías & Guitián, 2006; Brookes & Jesson, 2007; Griffiths *et al.*, 2010; Crone, 2013). To the extent that this holds, the baseline expectation shifts: rather than interpreting low CVp in animal-pollinated species as a trade-off imposed by mutualism, we may instead interpret high CVp in wind-pollinated species as an adaptation to inefficient pollen transfer. This repositions animal-pollinated species within masting theory: they are not exceptions constrained by pollinator dynamics, but taxa in which selection for masting is simply weaker. If wind pollination is the key enabler of strong selection for high CVp, then the evolution of wind pollination itself may represent a macroevolutionary precondition for the emergence of pronounced masting. This would make masting a more clade-specific trait, contingent on particular evolutionary innovations such as abiotic pollen dispersal (Dale *et al.*, 2021). Where masting does occur in animal-pollinated lineages, it may be better explained by other selective agents, such as economies of scale in seed predation or environmental prediction (Ascoli *et al.*, 2020; Satake *et al.*, 2021; Szymkowiak *et al.*, 2024a), operating independently of pollination mode. Comparative analyses might, therefore, shift from treating pollination mode as a constraint to testing whether wind pollination acts as a precursor to the evolution of strong masting (high CVp).

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