

# Fruiting Strategies of Perennial Plants: A Resource Budget Model to Couple Mast Seeding to Pollination Efficiency and Resource Allocation Strategies

Samuel Venner,<sup>1,\*</sup> Aurélie Siberchicot,<sup>1</sup> Pierre-François Péllisson,<sup>1</sup> Eliane Schermer,<sup>1</sup> Marie-Claude Bel-Venner,<sup>1</sup> Manuel Nicolas,<sup>2</sup> François Débias,<sup>1</sup> Vincent Miele,<sup>1</sup> Sandrine Sauzet,<sup>1</sup> Vincent Boulanger,<sup>2</sup> and Sylvain Delzon<sup>3</sup>

1. Laboratoire de Biométrie et Biologie Evolutive, CNRS, Unité Mixte de Recherche (UMR) 5558, Université Lyon 1, Université de Lyon, Villeurbanne, France; 2. Office National des Forêts, Département recherche, développement et innovation, Boulevard de Constance, 77300 Fontainebleau, France; 3. L'Institut National de la Recherche Agronomique, UMR 1202, BIOGECO, 69 route d'Arcachon, F-33612 Cestas, France; and Université de Bordeaux, UMR 1202, Biodiversité, des gènes aux communautés, Allée Geoffroy Saint-Hilaire, CS 50023, F-33615 Pessac, France

Submitted October 31, 2015; Accepted February 16, 2016; Electronically published May 13, 2016

Online enhancements: appendixes, zip file. Dryad data: <http://dx.doi.org/10.5061/dryad.77kj5>.

**ABSTRACT:** Masting, a breeding strategy common in perennial plants, is defined by seed production that is highly variable over years and synchronized at the population level. Resource budget models (RBMs) proposed that masting relies on two processes: (i) the depletion of plant reserves following high fruiting levels, which leads to marked temporal fluctuations in fruiting; and (ii) outcross pollination that synchronizes seed crops among neighboring trees. We revisited the RBM approach to examine the extent to which masting could be impacted by the degree of pollination efficiency, by taking into account various logistic relationships between pollination success and pollen availability. To link masting to other reproductive traits, we split the reserve depletion coefficient into three biological parameters related to resource allocation strategies for flowering and fruiting. While outcross pollination is considered to be the key mechanism that synchronizes fruiting in RBMs, our model counterintuitively showed that intense masting should arise under low-efficiency pollination. When pollination is very efficient, medium-level masting may occur, provided that the costs of female flowering (relative to pollen production) and of fruiting (maximum fruit set and fruit size) are both very high. Our work highlights the powerful framework of RBMs, which include explicit biological parameters, to link fruiting dynamics to various reproductive traits and to provide new insights into the reproductive strategies of perennial plants.

**Keywords:** masting, resource budget model, fruit set, fruit size, sex allocation, pollination efficiency.

## Introduction

Masting—or mast seeding—is a reproductive strategy characterized by seed production that varies considerably

from year to year yet is synchronized at the population level (Janzen 1976; Silvertown 1980; Kelly 1994). Masting has been reported in diverse perennial plants and is considered to evolve in various ecological contexts (Herrera et al. 1998; Kelly and Sork 2002; Koenig et al. 2003). Seeds produced by masting are a pulsed resource and, as such, are likely to greatly influence the demography and evolution of seed consumer populations and, in turn, the dynamics of the entire community (Ostfeld and Keasing 2000; Yang et al. 2010). One well-accepted selective advantage of masting is to lower the risk of seed predation: while most years of poor seed production keep consumer populations at a low level, uncommon, unpredictable mast years satiate consumers, thereby ensuring a large proportion of seeds escape from predation (Janzen 1971; Silvertown 1980; Kelly and Sork 2002). As another evolutionary issue of masting, the pollination efficiency hypothesis states that occasional high reproductive effort is concomitant with large pollen production, which increases pollination success (Smith et al. 1990; Kelly et al. 2001; Koenig and Ashley 2003; Pearse et al. 2014; Koenig et al. 2015).

While the evolutionary issue of masting and its impact on community dynamics are well documented, the proximate mechanisms governing masting are still much debated (Kelly and Sork 2002; Crone et al. 2009; Crone and Rapp 2014). A first set of hypotheses, reported in many studies, assumes that individual plants breed synchronously because they experience homogeneous climatic conditions and produce similar amounts of flowers and seeds in response (Inouye et al. 2002; Schaubert et al. 2002; Kelly et al. 2013; see Kelly and Sork 2002 for a review). On the other hand, studies based on resource budget models (RBMs) propose an al-

\* Corresponding author; e-mail: [samuel.venner@univ-lyon1.fr](mailto:samuel.venner@univ-lyon1.fr).

ternative to the explanation that masting is due to the effects of weather cues alone. Two factors are combined: (i) the intrinsic resource dynamics of the tree, that is, the way resources are allocated toward either storage or flowering and then fruiting; and (ii) the outcross pollination process that synchronizes fruiting among trees (see details below; Isagi et al. 1997; Satake and Iwasa 2000, 2002a; Crone and Rapp 2014).

RBM makes four statements: (i) Each year, an individual tree (or perennial plant) accumulates and stores energy or resources from photosynthesis or essential nutrient uptake from the soil. (ii) The tree does not reproduce unless it accumulates enough reserves. Once its reserves exceed a given threshold, the tree allocates all its excess reserves to flowers. (iii) Female flowers are fertilized by outcross pollen, with a success rate that is positively related to the amount of pollen produced by the neighboring trees (outcross pollination). (iv) Pollinated flowers then develop into mature fruits and incur resource depletion whose severity is governed by the resource depletion coefficient (DC), that is, the fruiting-to-flowering cost ratio (called  $k$  in Satake and Iwasa [2000], [2002a], [2002b] and  $R_c$  in Isagi et al. [1997]).

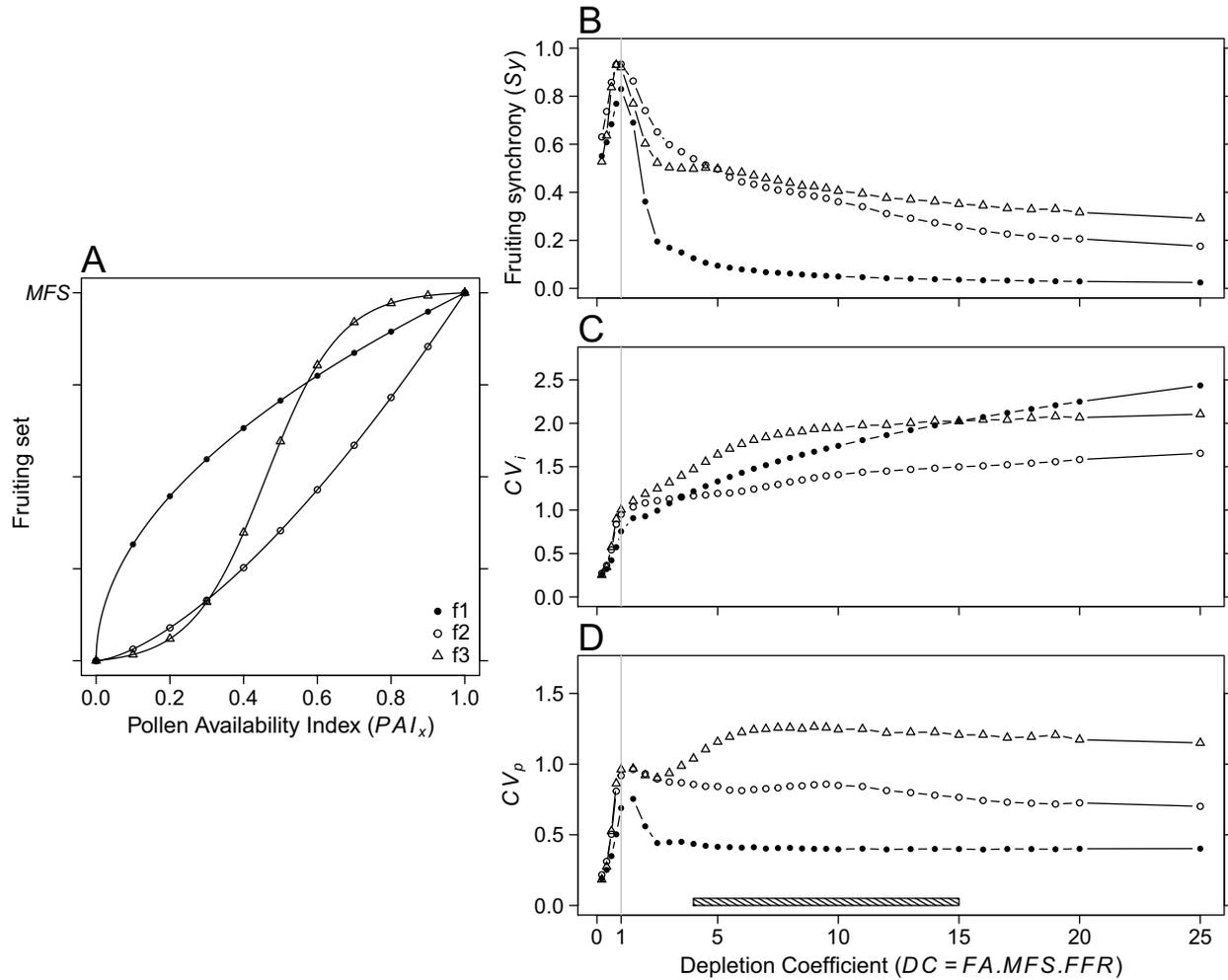
RBM can produce some outputs similar to real masting data sets (Isagi et al. 1997; Satake and Iwasa 2000, 2002a, 2002b; Crone and Rapp 2014). In RBMs, fruiting fluctuates from one year to the next when the tree produces costly seed crops (with high DC values) that subsequently severely deplete resource reserves (Isagi et al. 1997). The outcross pollination, combined with pollen limitation, is considered to be one major force governing fruiting synchrony among trees. The few trees that may breed asynchronously and invest heavily into flowering while outcross pollen is rare are likely to have their flowers mostly unpollinated. Subsequent to fruiting failure, they may save resources, which may be invested in flowering the following year, possibly reaching synchrony with the other trees of the population (Satake and Iwasa 2000). Further theoretical investigations show that the synchrony level among trees is positively related to the spatial scale of pollen dispersal and may be strengthened by the Moran effect (i.e., environmental forcing; Rees et al. 2002; Satake and Iwasa 2002b).

Besides these investigations, we revisited RBMs to better understand how masting patterns articulate with other key reproductive characteristics of trees associated with pollination efficiency and resource allocation toward flowering and fruiting. In this perspective, we reconsidered the two key ingredients in RBMs, resource depletion and outcross pollination, which govern fruiting fluctuation at the tree level and fruiting synchrony among trees, respectively.

First, we modeled the outcross pollination process as a logistic function by determining, for a given individual tree, the probability for a female flower to develop into a mature fruit (fruit set) based on the amount of outcross

pollen available. Previously, only power functions had been used to calculate this probability, even though such functions require the relationship between pollen availability and fruit set to be either strictly convex or strictly concave, depending on the power value (see fig. 1A). We hypothesized that a logistic relationship would better reflect reality because it would simultaneously capture both pollen dilution when pollen is sparse (associated with a convex increase in pollination success for power functions) and pollen saturation when pollen is abundant (a concave increase; see fig. 2A). In addition, pollination efficiency may also strongly impact tree resource dynamics and synchrony level and, hence, masting. Pollination efficiency may vary considerably depending on the mechanisms involved in gamete encounters (e.g., airborne vs. insect pollination; Regal 1982; Ackerman 2000) and on environmental features (such as tree density, landscape fragmentation, plant species assemblages in the community, or pollinator density; Allison 1990; Kunin 1997; Aguilar et al. 2006; Vamosi et al. 2006; Pellegrino et al. 2015). These mechanisms can be reflected through variable parameter values in a logistic function. Highly efficient pollination (fig. 2A, filled circles) is characterized by a quick, sharp increase in pollination success from very low amounts of outcross pollen in the environment. One notable example of this occurs for insect-pollinated plants when pollinators are abundant and readily and massively recruited as soon as the food resource (pollen) is detected (Rathcke 1983; Hegland 2014). By contrast, inefficient pollination creates strong inertia in the pollination success rate as long as small amounts of pollen are available (fig. 2A, open circles). Under limited pollen availability, a strong dilution effect means that very small amounts of pollen are trapped per female flower, thus leading to low fertilization success (Marshall and Folsom 1991; Wilcock and Neiland 2002; Aizen and Harder 2007; Eckert et al. 2010).

Second, we split the depletion coefficient into three biological components to explicitly link fruiting pattern to strategies of resource allocation for flowering and fruiting. The first component, hereafter called female flower allocation ratio (FA), is the proportion of the resources invested in flowering that is allocated to female flowers (vs. pollen) until fertilization. The second component, maximum fruit set (MFS), is the probability for a female flower to successfully develop into a mature fruit when pollen is not a limiting factor. The third component, fruiting-to-flowering resource demand ratio (FFR), is the ratio of the resources required to produce one mature fruit to that required for one sexually operational female flower. Considering a fixed amount of resources required to produce one flower within a tree population, FFR variation can be used as a proxy for mature fruit size variation. Trees may incur severe reserve depletion when they allocate most of their

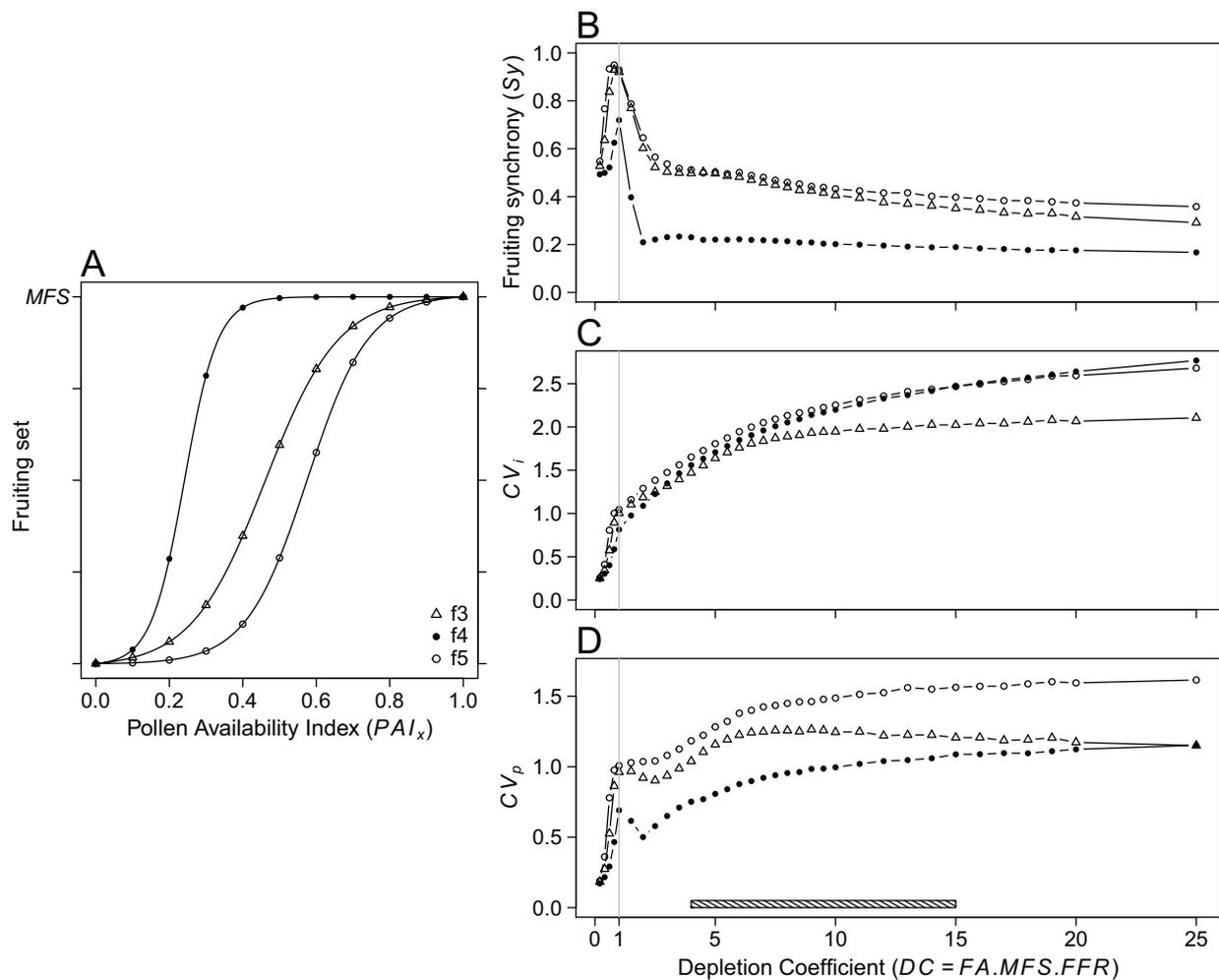


**Figure 1:** Fruiting dynamics as a function of the depletion coefficient (DC) and the shape of the outcross pollination function. *A*, The outcross pollination function determines the positive, nonlinear relationship between the amount of outcross pollen available in the neighborhood of tree  $x$  at year  $t$  ( $PAI_x(t)$ ) and the proportion of female flowers that were successfully pollinated ( $P_x(t)$ ). Pollen availability index  $PAI_x$  ranges from 0 to 1 (from no pollen produced by all the neighboring trees to the maximum amount of pollen produced; see text). Three distinct outcross pollination functions were successively included in the model: two power functions already explored in previous models (function 1:  $P_x(t) = (PAI_x(t))^{1/2}$ , function 2:  $P_x(t) = (PAI_x(t))^{3/2}$ ) and a logistic function bounded between 0 and 1 (function 3:  $P_x(t) = 1/(1 + 100e^{-10 \cdot PAI_x(t)})$ ; see eq. [3]). For each pollination function, the DC effect is shown on the fruiting synchrony among trees  $Sy$  (*B*) and on the fruiting variation across years at the individual tree level  $CV_i$  (*C*) and at the population level  $CV_p$  (*D*). The range of DC values empirically estimated for sessile oak trees is shown by the hatched horizontal bar above the  $X$ -axis.

flowering resource budget into female flowers or when they produce either a large fruit crop (i.e., associated with high pollination success and an elevated MFS value), large-sized fruits (a large FFR), or both.

To examine the relationship between fruiting dynamics and other key reproductive characteristics (e.g., outcross pollination process, resource allocation strategies for reproduction), we built a resource budget model that simulated fruiting dynamics of trees within a population (Isagi et al. 1997; Satake and Iwasa 2000, 2002a, 2002b). We examined fruiting dynamics through three distinct outputs: fruiting synchrony at the tree population level ( $Sy$ ); the co-

efficient of variation in seed production across years at the individual tree level ( $CV_i$ ), and the coefficient of variation in seed production across years at the tree population level ( $CV_p$ ). Because a high  $CV_p$  value results from high fruiting synchrony among trees within a population combined with elevated temporal fruiting fluctuation at the tree level (Herrera 1998; Koenig et al. 2003), we considered that  $CV_p$  would accurately reflect masting intensity. In addition, to improve the realism of sensitivity analyses made on fruiting dynamics, we quantified MFS and the range of FFR values to be used with data from a field survey on sessile oak (*Quercus petraea*), oak trees being among the most



**Figure 2:** Impact of outcross pollination efficiency on fruiting dynamics. A, Three logistic-shaped pollination functions. Fruiting success increases in a logistic manner with pollen availability, according to three pollination efficiency levels, functions 3–5. Function 3:  $P_x(t) = 1/(1 + 100e^{-10 \cdot PAI_x(t)})$ , function 4:  $P_x(t) = 1/(1 + 200e^{-22 \cdot PAI_x(t)})$ , function 5:  $P_x(t) = 1/(1 + 1,000e^{-12 \cdot PAI_x(t)})$ . B–D, See figure 1 legend.

emblematic mast-seeding species (Herrera et al. 1998; Kelly and Sork 2002; Koenig et al. 2003).

### Material and Methods

We built a resource budget model accounting for tree resource dynamics and the outcross pollination process.

#### Modeling Tree Resource Dynamics

In our model, the forest was defined as being composed of a large number of trees of the same species, where each tree  $x$  occupied a distinct location on a two-dimensional grid. Accordingly,  $S_x(t)$  was the level of resource reserves in tree  $x$  at the beginning of year  $t$ . Every year, each tree accumulated a fixed amount of resources from photosyn-

thesis,  $P_s$ . Unless the level of resources  $S_x(t) + P_s$  exceeded a threshold level  $L$ , the tree did not produce any flowers and stored the acquired resources until the following year. Whenever the level of resources exceeded  $L$ , tree  $x$  initiated reproduction by converting the amount of resources above  $L$  into flowering and allocating the proportion  $FA$  to female flowers, whose number was proportional to the excess reserve. Irrespective of pollen limitation, some flower abscission or fruit abortion is commonly observed in perennial plants (Stephenson 1981; Holland et al. 2004). Accordingly, we considered that, independently of any pollen limitation, only a proportion  $MFS$  of pollinated female flowers would successfully mature into fruit with the relative resource requirement  $FFR$ . The resources allocated toward fruiting then equal

$$FA \cdot MFS \cdot FFR \cdot (S_x(t) + P_s - L).$$

We assumed that fruiting might be followed by severe resource depletion, which would force the tree to replenish its reserves over several years before once again being able to flower. Overall, the absolute reserve of tree  $x$  at the onset of year  $t + 1$  can be computed as follows:

$$S_x(t + 1) = \begin{cases} S_x(t) + Ps - (1 + FA \cdot MFS \cdot FFR)(S_x(t) - L + Ps) & \text{if } S_x(t) - L + Ps > 0 \\ S_x(t) + Ps & \text{if } S_x(t) - L + Ps \leq 0 \end{cases} \quad (1)$$

(see Satake and Iwasa 2002a for details).

Equation (1) becomes nondimensionalized if  $(S_x - L + Ps)/Ps$  is replaced by  $Y_x$ , as follows:

$$Y_x(t + 1) = \begin{cases} -FA \cdot MFS \cdot FFR \cdot Y_x(t) + 1 & \text{if } Y_x(t) > 0 \\ Y_x(t) + 1 & \text{if } Y_x(t) \leq 0 \end{cases} \quad (2)$$

(Satake and Iwasa 2002a).

Here  $Y_x(t + 1)$  can be considered as the relative resource reserve of tree  $x$  at the onset of the year  $t$  once standardized per  $Ps$  unit, which is the fixed amount of resources gained yearly through photosynthesis.

We further enhanced this basic dynamic equation by accounting for outcross pollination and by introducing environmental stochasticity in the amount of resources acquired yearly by individual trees. As a result, equation (2) becomes

$$Y_x(t + 1) = \begin{cases} -FA \cdot MFS \cdot FFR \cdot P_x(t)Y_x(t) + 1 + \varepsilon_x(t) & \text{if } Y_x(t) > 0 \\ Y_x(t) + 1 + \varepsilon_x(t) & \text{if } Y_x(t) \leq 0 \end{cases} \quad (3)$$

where  $P_x(t)$  is the pollination success of tree  $x$ , and  $\varepsilon_x(t)$  is the error that results from individual tree variability added to population-wide yearly variation (see below and Satake and Iwasa 2002a).

#### The Outcross Pollination Process

Because resource dynamics in themselves do not induce fruiting synchrony among trees, and because pollination efficiency overall depends on the availability of outcross pollen (Nilsson and Wastljung 1987; Smith et al. 1990), RBMs include an outcross pollination function that precludes self-pollination (Satake and Iwasa 2000). The number of fruits produced by a single tree in any given year, therefore, depends not only on the number of female flowers it produces but also on the amount of exogenous pollen available, which itself depends on the number of neighboring trees and on the amount of pollen they pro-

duce (see below). Fruiting also depends on an outcross pollination function that reflects the link between pollen availability and pollination success.

*Determining the set of neighboring trees that might pollinate a focal tree.* We developed a spatially explicit model in which trees were regularly distributed on a two-dimensional square grid defined as a torus to avoid edge effects. The distance between two trees located at  $(x_1, y_1)$  and  $(x_2, y_2)$ , respectively, was calculated using the Moore neighborhood method. Any tree distant from focal tree  $x$  by less than a threshold value  $D$  could pollinate it; this situation occurred whenever  $\max(|x_1 - x_2|, |y_1 - y_2|) \leq D$ . At one extreme ( $D = 1$ ), only the eight trees immediately adjacent to the focal tree on the grid could pollinate it, while at the other extreme, the whole forest could potentially contribute to pollinating the focal tree. How  $D$  impacts fruiting has been explored elsewhere (Satake and Iwasa 2002a): herein, we exclusively considered intermediate situations where only trees distant from the focal tree by less than 5 units on the grid (i.e., 120 neighboring trees) could pollinate it.

*Determining the relative amount of outcross pollen available for a focal tree.* As for female flowers, the amount of pollen produced any given year by any tree is proportional to the amount of its excess reserves at the onset of the reproductive season. For each tree, we calculated its relative pollen production, that is, the ratio of the amount of pollen it actually produced to the maximum amount it would have produced if all the reserves acquired through photosynthesis had been converted into flowers. For a given focal tree  $x$ , we then computed the pollen availability index (PAI, comprised between 0 and 1) as the summed relative pollen produced by its  $z$  neighboring trees:

$$PAI_x(t) = \frac{1}{z} \sum_{y=1}^z \max(Y_y(t), 0). \quad (4)$$

*The outcross pollen function.* Following Satake and Iwasa (2000), we introduced the pollination success of tree  $x$ ,  $P_x(t)$ , to account for outcross pollen limitations on reproduction. The pollination function  $P$  describes the strength of outcrossing pollination as a function of the amount of exogenous pollen available. This function has typically been defined as a positive power function. This means that at any year  $t$ ,  $P_x$  continuously increases along with the total amount of exogenous pollen available in a concave, linear, or convex manner, depending on whether the positive coupling strength value  $\beta$  is below, equal to, or above 1, respectively (e.g., Satake and Iwasa 2002a, 2002b; Iwasa and Satake 2004). In our model, we compared the performance of two such positive power functions with several distinct logistic functions that seem to better fit the pollination process (see ‘‘Introduction’’; figs. 1A, 2A).

*Accounting for Environmental Stochasticity*

There is empirical evidence that trees, even when they are distant from each other, reproduce synchronously partly because they experience similar environmental fluctuations (Koenig and Knops 1998, 2000, 2013). As did Satake and Iwasa (2002*b*), we introduced environmental noise  $\varepsilon_x(t)$  into our model to account for the fact that the resources gained from photosynthesis by tree  $x$  may differ from one year to the next due to (i) climatic variations that evenly affect all the trees in the population and (ii) fine-scale environmental differences (e.g., soil characteristics, available nutrients, or water supply) affecting tree  $x$  only. Here  $\varepsilon_x(t)$  accounts for individual stochastic variation in the resources accumulated by tree  $x$  at the onset of the reproductive season  $t$ ; it can depart from the average population noise  $\varepsilon_{\text{pop}}$ , which itself may vary from one year to the next, so that

$$\varepsilon_x \sim N(\varepsilon_{\text{pop}}, \sigma_{\text{env}} \sqrt{1 - S_{y_{\text{env}}}}),$$

with

$$\varepsilon_{\text{pop}} \sim N(0, \sigma_{\text{env}} \sqrt{S_{y_{\text{env}}}}). \quad (5)$$

$S_{y_{\text{env}}}$  is the environmental synchrony among trees (the Moran effect) and is defined as the proportion of the total environmental variance ( $\sigma_{\text{env}}^2$ ) that is due to population-scale variance. The Moran effect has been well studied elsewhere (see Satake and Iwasa 2002*b*), so in our model, we set intermediate, fixed values for  $\sigma_{\text{env}}^2$  and  $S_{y_{\text{env}}}$  (0.2 and 0.5, respectively). Environmental stochasticity, by affecting the resources gained by trees, indirectly impacts the amount of outcross pollen produced yearly. We then modified equation (4) to introduce stochasticity into the pollen availability index as

$$\text{PAI}_x(t) = \frac{1}{\sum_{y=1}^z [1 + \varepsilon_y(t-1)]} \sum_{y=1}^z \max(Y_y(t), 0). \quad (6)$$

*Model Processing and Model Outputs:  $S_y$ ,  $CV_i$ , and  $CV_p$* 

In our model, we used a square grid comprising 400 trees. All simulations were run with a C++ algorithm. Each simulation lasted 2,000 time steps (years), but only the last 300 steps—independent from initial conditions—were used to compute parameters reflecting fruiting dynamics. We focused on three criteria classically used to describe masting: (i) the spatial synchrony of seed crop size among trees ( $S_y$ ) and the temporal coefficient of variation in fruiting at the (ii) individual ( $CV_i$ ) and (iii) population ( $CV_p$ ) levels (Herrera 1998; Koenig et al. 2003). Here,  $S_y$  is the mean of all pairwise Pearson correlations between the time series for each pair of trees (Satake and Iwasa 2002*a*),  $CV_p$  is the coefficient of variation of the mean annual seed production computed for all 400 trees in the

population, and  $CV_i$  describes individual tree between-year variability in seed production and is the mean of the coefficients of variation computed individually for the 400 trees (Herrera 1998; Koenig et al. 2003). We examined the extent to which fruiting dynamics (and, hence, masting) are sensitive to the outcross pollination function (two power and three distinct logistic functions tested; see figs. 1A, 2A) and to the depletion coefficient ( $DC = FA \cdot MFS \cdot FFR$ ). We ran 100 simulations for each set of parameters, then computed and displayed the average  $S_y$ ,  $CV_p$ , and  $CV_i$ .

*Setting Up the Range of Values for the Depletion Coefficient in RBMs*

We defined DC as the product of three biological components (FA, MFS, and FFR; see table 1). We estimated MFS and FFR based on data from a field survey of the flowering and fruiting effort of 130 sessile oak trees (*Quercus petraea*) from 13 populations distributed throughout metropolitan France (see app. A for detailed methods and results; apps. A, B available online). Assuming that oak trees invest resources equally into male and female flower production ( $FA = 0.5$ ), we found DC mean values within populations ranging from 4 to 15. Similar results were obtained when considering either dry weight, carbon, or nitrogen as the limiting resource. This range of values is shown by hatched horizontal bars above the X-axis in figures 1D and 2D.

Based on this empirical evaluation, subsequent analyses were undertaken to assess the sensitivity of the RBM outputs to extended DC values (from 0 to 25), that match DC values potentially found in various perennial plant species. Because FFR estimates were found to be highly variable among trees from the same localities ( $CV_{\text{FFR}}$  averaging 0.4 per site in our field survey; see app. A), we further examined the impact of variations in individual DC values ( $CV_{\text{DC}}$  ranging from 0 to 1) on fruiting dynamics (fig. B1, available online).

**Results***Fruiting Dynamics as a Function of the Depletion Coefficient*

Values for  $S_y$  and  $CV_i$  (fig. 1B, 1C) show similar patterns of variation along with DC values, irrespective of the outcross pollination function included in the model (see figs. 1A, 2A).

As pointed out by Isagi et al. (1997), very low DC values (near 0) indicate that almost no additional resources are required to produce a mature fruit from a female flower and that no resource depletion takes place. At the onset of each year, trees always exhibit excess reserve (eq. [1]) and therefore regularly produce flowers and fruits: as a

Table 1: Glossary

Parameter	Definition	Reference
$CV_i$	Temporal coefficient of variation of fruiting at the tree level	Figs. 1, 2
$CV_p$	Temporal coefficient of variation of fruiting at the population level	Figs. 1, 2
DC	Depletion coefficient is the fruiting relative to flowering effort (also called $k$ in Satake and Iwasa [2000], [2002a], [2002b] and $R_c$ in Isagi et al. [1997]); here, it is computed as the product $FA \cdot MFS \cdot FFR$	...
FA	Female flower allocation ratio is the proportion of resources a tree may allocate to its female flowers prior to fertilization among the excess reserves allocated to flowering	Eqq. (1)–(3)
FFR	Fruiting-to-flowering resource-demanding ratio is the ratio of the additional resources required to produce a mature fruit from a female flower to that required to produce a female flower; by extent, FFR may be considered as a proxy for fruit size; in the model, it is considered constant for individual trees	Eq. (1)
$L$	Threshold level of resources above which flowering occurs	Eq. (1)
MFS	Maximum fruit set is the probability for a fertilized female flower to develop into a mature fruit; when multiplied with $P_x(t)$ , it gives the fruiting success	Eqq. (1)–(3)
$PAI_x(t)$	Pollen availability index computes the relative amount of outcross pollen available for tree $x$ at year $t$ ; it depends on the amount of pollen produced by trees present in the neighborhood of tree $x$	Eqq. (4), (5)
$P_s$	Resources gained yearly from photosynthesis	Eq. (1)
$P_x(t)$	Pollination success of tree $x$ at year $t$ depends on PAI and on the outcross pollination function that is either a power or logistic one in this study; it is involved in the fruiting success, i.e., the probability for a female flower to develop into a mature fruit	Eq. (3); figs. 1A, 2A
$S_x(t)$	Absolute resource reserve of tree $x$ at the onset of year $t$	Eq. (1)
$S_y$	Synchrony level in fruit crop size among trees	Figs. 1, 2
$Y_x(t)$	Resource reserve of tree $x$ at the onset of year $t$ standardized per $P_s$ unit, i.e., the resources gained yearly through photosynthesis	Eqq. (1), (2)

consequence, they show low  $CV_i$  values (fig. 1C). The rather elevated fruiting synchrony observed simultaneously in the population (around 0.5) mainly results from moderate environmental forcing ( $S_{y_{env}}$ ; see eq. [5]), with only weak fruiting variation between years (low  $CV_i$  and  $CV_p$ ; fig. 1C, 1D).

When DC increases to 1, fruiting synchrony and  $CV_i$  both increase. When the fruiting cost equals that of flowering ( $DC = 1$ ), fruiting dynamics follow a very regular 2-year pattern, with 1 year of high fruiting alternating with 1 year of low (or almost no) fruiting. Such extremely regular fluctuations at the tree level promote maximum synchrony among trees (fig. 1B) due to the outcross pollination process, as has already been shown in detail in previous work (Isagi et al. 1997; Satake and Iwasa 2000).

For DC values above 1,  $CV_i$  goes on increasing monotonically—though at a lower rate (fig. 1C)—while  $S_y$  rapidly declines (fig. 1B). Such DC values are accompanied by chaotic fruiting dynamics at the tree level, thus reducing the opportunity for fruiting synchronization within the population (as shown by decreasing  $S_y$ ). For higher DC values (above 5), fruiting synchrony decreases asymptotically down to relatively stable values. The asymptotic-like synchrony level (considering strong fluctuations at the individual tree level, i.e., high  $CV_i$ ; fig. 1C) is closely related to the outcross pollination function, higher synchronization being predicted with logistic rather than power functions.

Here  $CV_p$ , resulting from the combined effects of  $CV_i$  and  $S_y$  and being positively correlated to these two parameters, shows a more complex relationship with DC (fig. 1D):  $CV_p$  first rapidly increases as DC increases up to 1 due to a concomitant increase in  $S_y$  and  $CV_i$  and then sharply and briefly declines, owing to the marked decrease in  $S_y$ , while  $CV_i$  continues to increase slightly. For higher DC values,  $CV_p$  values differ according to the outcross pollination function used.

### Fruiting Dynamics and the Shape of Outcross Pollination Function

The outcross pollination process has formerly been modeled as a power function with  $\beta$ , the power of the function. With  $DC > 3$  and small  $\beta$  values, no masting was found (fig. 1A, 1D, filled circles; function 1 [f1],  $\beta = 1/2$ ,  $CV_p$  is around 0.4). For high  $\beta$  values, moderate masting was observed (fig. 1A, 1D, open circles; f2,  $\beta = 3/2$ ,  $CV_p$  is between 0.8 and 1 for  $1 < DC < 5$  and then stays below 0.8 for  $DC > 5$ ). Neither power function was able to predict the highest  $CV_p$  values, either due to loose tree synchrony (for low  $\beta$  values; fig. 1B) or to low  $CV_i$ 's (for large  $\beta$  values; fig. 1C). Values for  $CV_p$  were the highest for the logistic-shape outcross pollination function (around 1 or above)

and remained high over a large range of DC values (from  $DC > 5$ ; fig. 1D).

#### *Fruiting Dynamics and Pollination Efficiency*

Values for  $CV_p$ , resulting from  $CV_i$  and  $Sy$ , may reach their highest through two distinct pathways depending on the efficiency of the pollination process modeled from various logistic functions (fig. 2A). Outcross pollination appears to be the key mechanism that synchronizes fruiting, as shown in previous studies with RBMs. However, our model predicts that masting should be most intense, even over a large range of DC values, only when pollination efficiency is weak (fig. 2A, 2D, open circles:  $CV_p$  around 1.5). The logistic function associated with less efficient pollination shows strong inertia in the pollination success and consequently favors homogeneous pollination success among the trees, as long as pollen availability remains low (e.g., for a pollen availability index between 0 and 0.3; fig. 2A). Such logistic pollination function thus should promote high fruiting synchrony among trees ( $Sy$ ; fig. 2B) together with marked fluctuations in fruiting at the tree level ( $CV_i$ ) which, taken together, explain the very high  $CV_p$  values obtained (fig. 2C, 2D).

On the contrary, when pollination is very efficient, the fruiting success of a tree may increase sharply from very small amounts of pollen available. Even if neighboring trees experience subtle differences in the amount of outcross pollen received, they may experience markedly distinct pollination success and, hence, may be easily desynchronized in their seed production (fig. 2B, filled circles: low  $Sy$  values). Despite weak synchrony, moderate masting may still occur, provided that very high DC values are reached (fig. 2C, 2D;  $CV_p$  reaching 1 for  $DC > 15$ ).

Moderately efficient pollination should be accompanied by intense masting starting at rather low DC values, with trees remaining synchronized (fig. 2B, 2D;  $DC > 5$ ,  $CV_p$  around 1.2). Yet, this situation also generates the lowest  $CV_i$  values (fig. 2C, open triangles).

#### *Fruiting Dynamics When DC Fluctuates among Trees*

Fruiting dynamics were only weakly affected by variations in the DC heterogeneity level among trees within a population (for  $CV_{DC}$  less than 0.4; see app. B; fig. B1). When DC becomes more variable among trees,  $Sy$  and  $CV_i$  both subtly decline, resulting in slightly declining  $CV_p$  (from 1 down to 0.8 for  $CV_{DC}$  varying from 0.4 to 1; see fig. B1).

#### *Discussion*

In this study, we revisited the way RBMs could generate masting by using logistic functions linking pollination suc-

cess to pollen availability to model the outcross pollination process. In addition, we split the depletion coefficient into three explicit biological parameters that reflect how trees allocate their resources to flowering and fruiting (i.e., FA, MFS, FFR; see table 1). Our results show that masting is much more often observed when the outcross pollination process is modeled using logistic functions than with the power functions used until now (Isagi et al. 1997; Satake and Iwasa 2000, 2002a, 2002b). While outcross pollination is the key process shown to synchronize fruiting in RBMs, our results point out that masting would be most intense when pollination is ineffective. Masting should nevertheless occur when pollination is very efficient yet be restricted to high depletion coefficient values: this can be the case whenever plants massively allocate their flowering effort into female items (i.e., high FA), reach high maximum fruit set under nonlimiting pollen availability (high MFS), and/or mature large-sized fruits compared to female flower size (high FFR).

Previous studies used power-like functions to link pollination success with the amount of outcross pollen available; they examined the fruiting dynamic using a rather narrow range of low depletion coefficient values ( $DC < 5$ ) and analyzed masting based on fruiting synchrony among trees (equivalent to  $Sy$  in this study; figs. 1B, 2B; Isagi et al. 1997; Satake and Iwasa 2000, 2002a, 2002b). According to these studies, opportunities for masting emergence are expected to sharply decrease as the depletion coefficient increases. Here, we estimated DC in several sessile oak populations and found them to vary from 4 to 15 on average, depending on the population studied (see app. A). This range should probably be extended even when considering other oak species or perennial plants that may produce bigger, costlier fruits. When the depletion coefficient value was realistically high ( $DC > 5$ ), our model showed that the two power-like pollination functions failed to predict intense masting ( $CV_p \lesssim 0.8$ ). Values for  $CV_p$  remained low due to either low fruiting synchrony levels (for low  $\beta$  value; fig. 1A, 1B, filled circles) or low individual fruiting fluctuation (for high  $\beta$  value; fig. 1A, 1C, open circles).

By contrast, our model showed that masting occurred frequently and was most intense (high  $CV_p$ ), even with elevated DC values ( $>5$ ), when a logistic relationship between pollen availability and pollination success was accounted for (figs. 1, 2). Our model was further able to disentangle contrasted ways leading to masting, depending on pollination process efficiency. While outcross pollination is central to fruiting synchrony in RBMs, our results counterintuitively showed that masting may be most intense (as shown by consistently high  $CV_p$  values along the DC gradient) when pollination is nearly ineffective (fig. 2D). At low or medium pollen availability, the slow increase in the pollination success (fig. 2A, f5, open circles) would en-

sure weak but homogeneous pollination among neighboring trees, leading to their close fruiting synchronization. Inefficient pollination maximizes masting also because it is associated with high  $CV_i$  values ( $CV_p \leq 1.5$  for  $DC > 10$ ). On the contrary, very efficient pollination is characterized by a rapid increase in pollination success as soon as low amounts of pollen are available (fig. 2A, f4, filled circles). This process causes trees to get desynchronized because pollen is a less limiting factor: the fruiting dynamics of each tree more closely depend on its own reserve levels than on local exogenous pollen production. However, when pollination is highly effective, medium-level masting may still occur, provided that the depletion coefficient is very high: despite poor tree synchrony, strong fruiting fluctuation is expected at the tree level (high  $CV_i$ ), which results in intermediate fruiting fluctuation at the population level ( $CV_p \approx 1$  for  $DC \approx 25$ ; fig. 2D). When pollination is moderately efficient (fig. 2A, f3, open triangles), masting intensity should be moderate and stable over a large DC gradient (fig. 2D).

The unexpected finding of intense masting under inefficient pollination could be tested in several different ways. First, comparisons could be made between plant species with markedly distinct pollination mechanisms. For example, pollination should be more efficient—and masting, therefore, less intense—under low pollen density in insect-pollinated species than in wind-pollinated species. Insect pollinators, at least when their populations are dense, may be actively and even exponentially recruited as soon as a small amount of food (pollen) is detected (Rathcke 1983; Hegland 2014). In agreement with this prediction, insect-pollinated species seem to exhibit overall less intense masting than do wind-pollinated species (Kelly and Sork 2002). Among wind-pollinated species, higher pollination efficiency and less intense masting would also be expected in species that have evolved organs to accumulate pollen close to stigmata (e.g., conifer ovulate cones [Niklas 1982]) than in those whose stigmata are passively exposed to aerial pollen. Second, comparisons could be made within a given plant species between populations undergoing various degrees of pollination efficiency owing to distinct environmental constraints. Our model indirectly predicts that intense masting would occur under low plant densities or in highly fragmented populations, since in both situations, pollination should be less efficient for a given mean plant flowering effort. Among insect-pollinated species, intense masting is expected either when density/diversity in pollinators is low or when many plant species severely compete for the same insect pollinators (Allison 1990; Kunin 1997; Aguilar et al. 2006; Vamosi et al. 2006; Pellegrino et al. 2015).

Resource budget models are not only robust predictors of masting, they may also provide an integrative theoretical framework for jointly analyzing mechanisms in perennial plants related to reproductive strategies such as sex al-

location strategies (linked to female flower allocation ratio, FA), fruit set and the trade-off between fruit number and fruit size (linked to maximum fruit set, MFS, and fruiting-to-flowering ratio, FFR), outcross pollination efficiency, and fruiting dynamics over time and space (described from Sy,  $CV_i$ , and  $CV_p$ ). Introducing explicit biological parameters into RBMs also offers the opportunity to provide realistic scenarios for possible changes in plant fruiting patterns under climate change by examining the sensitivity of RBM parameters to climate variables. RBMs with explicit biological parameters, therefore, open new paths and testable predictions to explore the diversified mechanisms operating on the fruiting processes of perennial plants, their complex interactions, and, by extension, the proximate and ultimate causes of fruiting strategies.

### Acknowledgments

We are very grateful to D. Kelly and one anonymous reviewer for their constructive comments on the manuscript. This work was funded by the French National Research Agency (ANR; project JC09 470585), by the Centre National de la Recherche Scientifique, and by the Potentchène program (Gip ECOFOR, BGF). Simulations were performed using the computing cluster CC LBBE/PRABI.

### Literature Cited

- Ackerman, J. D. 2000. Abiotic pollen and pollination: ecological, functional, and evolutionary perspectives. *Plant Systematics and Evolution* 222:167–185.
- Aguilar, R., L. Ashworth, L. Galetto, and M. A. Aizen. 2006. Plant reproductive susceptibility to habitat fragmentation: review and synthesis through a meta-analysis. *Ecology Letters* 9:968–980.
- Aizen, M. A., and L. D. Harder. 2007. Expanding the limits of the pollen-limitation concept: effects of pollen quantity and quality. *Ecology* 88:271–281.
- Allison, T. D. 1990. Pollen production and plant density affect pollination and seed production in *Taxus canadensis*. *Ecology* 71:516–522.
- Crone, E. E., E. Miller, and A. Sala. 2009. How do plants know when other plants are flowering? resource depletion, pollen limitation and mast-seeding in a perennial wildflower. *Ecology Letters* 12: 1119–1126.
- Crone, E. E., and J. M. Rapp. 2014. Resource depletion, pollen coupling, and the ecology of mast seeding. *Annals of the New York Academy of Sciences* 1322:21–34.
- Eckert, C. G., S. Kalisz, M. A. Geber, R. Sargent, E. Elle, P. O. Cheptou, C. Goodwillie, et al. 2010. Plant mating systems in a changing world. *Trends in Ecology and Evolution* 25:35–43.
- Hegland, S. J. 2014. Floral neighbourhood effects on pollination success in red clover are scale-dependent. *Functional Ecology* 28:561–568.
- Herrera, C. 1998. Population-level estimates of interannual variability in seed production: what do they actually tell us? *Oikos* 82:612–616.
- Herrera, C., P. Jordano, and J. Guitián. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. *American Naturalist* 152:576–594.

- Holland, J. N., J. L. Bronstein, and D. L. DeAngelis. 2004. Testing hypotheses for excess flower production and low fruit-to-flower ratios in a pollinating seed-consuming mutualism. *Oikos* 3:633–641.
- Inouye, D. W., M. A. Morales, and G. J. Dodge. 2002. Variation in timing and abundance of flowering by *Delphinium barbeyi* Huth (Ranunculaceae): the roles of snowpack, frost, and La Niña, in the context of climate change. *Oecologia* (Berlin) 130:543–550.
- Isagi, Y., K. Sugimura, A. Sumida, and H. Ito. 1997. How does masting happen and synchronize? *Journal of Theoretical Biology* 187:231–239.
- Iwasa, Y., and A. Satake. 2004. Mechanisms inducing spatially extended synchrony in mast seeding: the role of pollen coupling and environmental fluctuation. *Ecological Research* 19:13–20.
- Janzen, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2:465–492.
- . 1976. Why bamboos wait so long to flower. *Annual Review of Ecology and Systematics* 7:347–391.
- Kelly, D. 1994. The evolutionary ecology of mast seeding. *Trends in Ecology and Evolution* 9:465–470.
- Kelly, D., A. Geldenhuis, A. James, E. P. Holland, M. J. Plank, R. E. Brockie, P. E. Cowan, et al. 2013. Of mast and mean: differential-temperature cue makes mast seeding insensitive to climate change. *Ecology Letters* 16:90–98.
- Kelly, D., D. E. Hart, and R. B. Allen. 2001. Evaluating the wind pollination benefits of mast seeding. *Ecology* 82:117–126.
- Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics* 33:427–447.
- Koenig, W. D., and M. V. Ashley. 2003. Is pollen limited? the answer is blowin' in the wind. *Trends in Ecology and Evolution* 18:157–159.
- Koenig, W. D., D. Kelly, V. L. Sork, R. P. Duncan, J. S. Elkinton, M. S. Peltonen, and R. D. Westfall. 2003. Dissecting components of population-level variation in seed production and the evolution of masting behavior. *Oikos* 102:581–591.
- Koenig, W. D., and J. M. H. Knops. 1998. Scale of mast-seeding and tree-ring growth. *Nature* 396:225–226.
- . 2000. Patterns of annual seed production by northern hemisphere trees: a global perspective. *American Naturalist* 155:59–69.
- . 2013. Large-scale spatial synchrony and cross-synchrony in acorn production by two California oaks. *Ecology* 94:83–93.
- Koenig, W. D., J. M. H. Knops, W. J. Carmen, and I. S. Pearse. 2015. What drives masting? the phenological synchrony hypothesis. *Ecology* 96:184–192.
- Kunin, W. 1997. Population size and density effects in pollination: pollinator foraging and plant reproductive success in experimental arrays of *Brassica kaber*. *Journal of Ecology* 85:225–234.
- Marshall, D. L., and M. W. Folsom. 1991. Mate choice in plants: an anatomical to population perspective. *Annual Review of Ecology and Systematics* 22:37–63.
- Niklas, K. J. 1982. Simulated and empiric wind pollination patterns of conifer ovulate cones. *Proceedings of the National Academy of Sciences of the USA* 79:510–514.
- Nilsson, S. G., and U. Wastljung. 1987. Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. *Ecology* 68:260–265.
- Ostfeld, R. S., and F. Keasing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution* 15:232–237.
- Pearse, I. S., W. D. Koenig, K. A. Funk, and M. B. Pesendorfer. 2014. Pollen limitation and flower abortion in a wind-pollinated, masting tree. *Bulletin of the Ecological Society of America* 95:462–464.
- Pellegrino, G., F. Bellusci, and A. M. Palermo. 2015. Effects of population structure on pollen flow, clonality rates and reproductive success in fragmented *Serapias lingua* populations. *BMC Plant Biology* 15:222.
- Rathcke, B. 1983. Competition and facilitation among plants for pollination. Pages 305–329 in L. Real, ed. *Pollination biology*. Academic Press, New York.
- Rees, M., D. Kelly, and O. N. Bjørnstad. 2002. Snow tussocks, chaos, and the evolution of mast seeding. *American Naturalist* 160:44–59.
- Regal, P. J. 1982. Pollination by wind and animals: ecology of geographic patterns. *Annual Review of Ecology and Systematics* 13:497–524.
- Satake, A., and Y. Iwasa. 2000. Pollen coupling of forest trees: forming synchronized and periodic reproduction out of chaos. *Journal of Theoretical Biology* 203:63–84.
- . 2002a. Spatially limited pollen exchange and a long-range synchronization of trees. *Ecology* 83:993–1005.
- . 2002b. The synchronized and intermittent reproduction of forest trees is mediated by the Moran effect, only in association with pollen coupling. *Journal of Ecology* 90:830–838.
- Schauber, E. M., D. Kelly, P. Turchin, C. Simon, W. G. Lee, R. B. Allen, I. J. Payton, P. R. Wilson, P. E. Cowan, and R. E. Brockie. 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology* 83:1214–1225.
- Silvertown, J. W. 1980. The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society* 14:235–250.
- Smith, C. C., J. L. Hamrick, and C. L. Kramer. 1990. The advantage of mast years for wind pollination. *American Naturalist* 136:154–166.
- Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics* 12:253–279.
- Vamosi, J. C., T. M. Knight, J. A. Steets, S. J. Mazer, M. Burd, and T.-L. Ashman. 2006. Pollination decays in biodiversity hotspots. *Proceedings of the National Academy of Sciences of the USA* 103:956–961.
- Wilcock, C., and R. Neiland. 2002. Pollination failure in plants: why it happens and when it matters. *Trends in Plant Science* 7:270–277.
- Yang, L. H., K. F. Edwards, J. E. Byrnes, J. L. Bastow, A. N. Wright, and K. O. Spence. 2010. A meta-analysis of resource pulse-consumer interactions. *Ecological Monographs* 80:125–151.

### References Cited Only in the Online Appendixes

- Arceo-Gomez, G., and T.-L. Ashman. 2014. Patterns of pollen quantity and quality limitation of pre-zygotic reproduction in *Mimulus guttatus* vary with co-flowering diversity. *Oikos* 123:1261–1269.
- Ashman, T. L., T. M. Knight, and J. A. Steets. 2004. Pollen limitation of plant reproduction: ecological and evolutionary causes and consequences. *Ecology* 85:2408–2421.
- Stone, J. L., J. D. Thomson, and S. J. Dent-Acosta. 1995. Assessment of pollen viability in hand-pollination experiments: a review. *American Journal of Botany* 82:1186–1197.
- Venner, S., A. Siberchicot, P.-F. Péllisson, E. Schermer, M.-C. Belvenner, M. Nicolas, F. Débias, et al. 2016. Data from: Fruiting strategies of perennial plants: a resource-budget model to couple mast seeding to pollination efficiency and resource allocation strategies. *American Naturalist*, Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.77kj5>.

Associate Editor: Jürgen Groeneveld  
Editor: Alice A. Winn