

Spatial Dynamics of Specialist Seed Predators on Synchronized and Intermittent Seed Production of Host Plants

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ABSTRACT: Masting, the synchronized and intermittent seed production by plant populations, provides highly variable food resources for specialist seed predators. Such a reproductive mode helps minimize seed losses through predator satiation and extinction of seed predator populations. The seed predators can buffer the resource variation through dispersal or extended diapause. We developed a spatially explicit resource-consumer model to understand the effect of masting on specialist seed predators. The masting dynamics were assumed to follow a resource-based model for plant reproduction, and the population dynamics of the predator were represented by a spatially extended Nicholson-Bailey model. The resultant model demonstrated that when host plants reproduce intermittently, seed predator populations go locally extinct, but global persistence of the predator is facilitated by dispersal or extended diapause. Global extinction of the predator resulted when the intermittent reproduction is highly synchronized among plants. An approximate invasion criterion for the predators showed that negative lag-1 autocorrelation in seeding reduces invasibility, and positive lag-1 cross-correlation enhances invasibility. Spatial synchronization in seeding at local scale caused by pollen coupling (or climate forcing) further prevented invasion of the predators. If the predators employed extended diapause, extremely high temporal variability in reproduction was required for plants to evade the predators.

Keywords: mast seeding, synchrony, dispersal, spatial dynamics, predator satiation, invasibility.

Seeds and berries can be an invaluable resource for herbivores. As a consequence, there are many species—"seed

predators"—that are specialized on seeds. Plants in turn attempt to minimize their seed losses through specialized reproductive strategies. Mast seeding, or masting, the intermittent and synchronized reproduction of large seed crops by plant populations (Kelly 1994) documented across a broad group of plant species (Herrera et al. 1998), is often explained to have evolved to reduce seed losses to such seed predators (the predator satiation hypothesis; Janzen 1971; Silvertown 1980). Many studies testify to predator satiation by showing lower predation rates in high seed production years (Smith et al. 1990; Sork et al. 1993; Kelly and Sullivan 1997; Sperens 1997; Shibata et al. 1998; Kelly et al. 2000; Satake et al. 2004). In addition to enhancing seed survival through satiation of a predator's functional response, there is evidence that mast seeding can satiate a numerical response of specialized seed predators. In this case, predation risk is a declining function of the ratio of current to previous year's seed set (Kelly and Sullivan 1997; Sperens 1997; Shibata et al. 1998; Satake et al. 2004). Masting is at least partially accounted for from the point of view of plant life history. From the perspective of the seed predator, in contrast, numerous questions remain; masting provides a nutrient-rich but highly variable food resource that can lead to food shortage and extinction of seed predator. This is particularly likely if seed predators are specialists whose diet is dominated by the seeds produced by masting species.

As an evolutionary response to the unpredictable resource availability, seed predators should employ strategies for spreading risk to reduce realized variability in fitness: dispersal, dormancy, and/or generalizing the diet (Hopper 1999). If plants are patchily distributed, dispersal may reduce variation in fitness by spreading risk over space. In a temporally fluctuating environment, invertebrate seed predators may respond with an extended diapause to spread risk over time (Tauber et al. 1986; Roff 1992). According to general theory and field studies for the evolution of dispersal, dispersal among the patches is advantageous if fluctuations of local conditions are independent across space (Levin et al. 1984), but if there is positive correlation either in time or across space, dispersal is less favored (Ellner and

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Shmida 1981; Cohen and Levin 1991; Holt and McPeck 1996). Furthermore, a recent continuous-space stochastic model of population dynamics showed that the risk of extinction is reduced by dispersal, while it is increased by enhanced spatial correlation in environmental stochasticity (Harrison and Quinn 1989; Engen et al. 2002a). The advantage of dispersal is therefore influenced by spatiotemporal pattern in resource fluctuation. In the case of mast seeding, resources will be negatively correlated in time but positively correlated across space (Kelly and Sork 2002). In order to understand the ecological consequences of such a particular pattern of resource variability induced by mast seeding, a more detailed theory is needed.

Two interlinked challenges are to understand the spatiotemporal dynamics of a seed predator on a masting resource and to understand the invasibility of the predators—when is a specialist seed predator ecologically viable? Answers to these are the topic of this study. Spatiotemporal fluctuations in seeding are represented by the pollen-coupled tree model (Isagi et al. 1997; Satake and Iwasa 2000, 2002a, 2002b), in which reproductive behavior of individual plants is prompted on the level of internal energy. This mechanism of mast seeding has recently received firm empirical support (Rees et al. 2002) and is therefore a natural starting point for exploring the spatiotemporal dynamics of seed predators. We consider specialized insect seed predators with a semelparous life cycle in which adults disperse to neighboring host plants to search randomly for seeds, berries, or flower heads on which to lay their eggs. The larvae subsequently complete the life cycle through feeding on the seeds. Thus, the dynamics of the predator at a single host plant are assumed to follow a spatially extended Nicholson-Bailey model (Hassell et al. 1991; Comins et al. 1992). Our model centers on the effect of dispersal by predators. In addition, we also examine the effect of extended diapause as a strategy for predators to spread the risk in time (dispersal in time). Spatial and temporal dynamics are interwoven in a complex fashion in such a system. Temporal dynamics induce complex spatial patterns, which critically influence the dynamics and persistence of the system. Our modeling addresses the fundamental question of how variable and synchronized seed production of plants may prevent persistence and invasion of seed predator populations.

Model

Masting Dynamics: Pollen-Coupled Tree Model

Consider a forest of outcrossing plants, each of which has internal energy reserves according to the balance between net energy gain through photosynthesis and energy expenditure through reproduction (and maintenance/growth, which we will assume to be deduced from the

energy gain prior to the calculations that follows). From photosynthesis, each plant gains net energy, P_s , every year. Let $S_i(t)$ be the energy reserves of a plant located at site i at the beginning of year t . Assume further that a plant will not reproduce unless its accumulated energy reserves, $S_i(t) + P_s$, exceed some critical threshold, L_T . If $S_i(t) + P_s$ exceeds L_T , the plant produces flowers that invest energy (“flowering cost”) proportional to the excess as given by $a[S_i(t) + P_s - L_T]$, where a is constant of proportionality (Satake and Iwasa 2000). If a flower is successfully pollinated, the plant invests additional energy as a result of the cost of fruit production, $R_c a[S_i(t) + P_s - L_T]$, where R_c is the ratio of fruiting cost to flowering cost. The energy reserve level thus falls to $S_i(t) + P_s - a(R_c + 1)[S_i(t) + P_s - L_T]$, so the overall resource dynamics are

$$S_i(t+1) = \begin{cases} S_i(t) + P_s & \text{if } S_i(t) + P_s \leq L_T, \\ S_i(t) + P_s - a(R_c + 1)[S_i(t) + P_s - L_T] & \text{if } S_i(t) + P_s > L_T. \end{cases} \quad (1)$$

In a previous set of articles (Satake and Iwasa 2000, 2002a, 2002b), we introduced the nondimensional equations to characterize the dynamics of this system. Since the predator dynamics are critically dependent on the underlying reproductive dynamics of plants, we provide a brief overview of the key results here.

Considering the nondimensionalized variable $Y_i(t) = [S_i(t) + P_s - L_T]/P_s$, equation (1) is rewritten as

$$Y_i(t+1) = \begin{cases} Y_i(t) + 1 & \text{if } Y_i(t) \leq 0, \\ -kY_i(t) + 1 & \text{if } Y_i(t) > 0, \end{cases} \quad (2)$$

in which $k = a(R_c + 1) - 1$ is a reproductive depletion constant. If $a = 1$, k is equal to the ratio of fruiting cost to flowering cost, R_c . Equation (2) represents a “tent map” that predicts stable annual reproduction for $k < 1$ and chaotic reproduction for $k > 1$ (Satake and Iwasa 2000).

In outcrossing plants, fruiting rates may be restricted by pollen production of other plants in the neighborhood (Nilsson and Wästljung 1987; Smith et al. 1990). Knapp et al. (2001) reported that plants with many pollen-producing neighbors tended to produce larger acorn crops than do those that were more isolated. It is also documented that seed limitation is frequently caused by pollination failure that has been variously attributed to pollen limitation (Wilcock and Neiland 2002). To model the pollen limitation of plant reproduction, the pollen availability, $P_i(t)$, to individual i was introduced (Isagi et al. 1997;

Satake and Iwasa 2000). The nondimensionalized energy dynamics are then

$$Y_i(t+1) = \begin{cases} Y_i(t)+1 & \text{if } Y_i(t) \leq 0, \\ -kP_i(t)Y_i(t)+1 & \text{if } Y_i(t) > 0, \end{cases} \quad (3a)$$

where $P_i(t)$ is determined by the average flowering intensity of the plants in some neighborhood around the focal plant, U_p , according to

$$P_i(t) = \left(\frac{1}{m} \sum_{j \in U_i} [Y_j(t)]_+ \right)^\beta, \quad (3b)$$

where $[Y]_+ = Y$ if $Y > 0$ and 0 otherwise. The m is the number of plants included in the neighborhood U_p , and β determines the pollination efficiency; for small β , $P_i(t)$ will be close to the maximum value of 1, even when the flowering activity of neighbors is only at an intermediate level, implying that plants can set fruit even when few other plants flower. In contrast, if β is large, $P_i(t)$ depends strongly on the flowering intensity of other plants, and seeds will be set only when most of the plants in the forest bloom. Thus, we call β the pollen coupling strength. In this study, we will consider a situation of local pollen coupling in which pollination is limited to eight nearest neighbors around the focal plant ($m = 8$). Masting dynamics under an assumption of global pollen coupling, in which the neighborhood U_i is the whole forest ($m =$ total number of plants in a forest except oneself), was studied by Satake and Iwasa (2000), and we will return briefly to such a situation in "Discussion."

Population Dynamics of Seed Predators

We consider a specialized insect seed predator with a semelparous life cycle and assume an all-females model. Adults disperse to nearby host plants to search randomly for seeds, berries, or flower heads on which to lay their eggs. The larvae hatch to complete their life-cycle feeding on the seed, leave the seeds to pupate, and emerge as adults at the beginning of next generation. With randomly searching adults, the dynamics of seed predators follow the spatially extended Nicholson-Bailey model (Hassell et al. 1991; Comins et al. 1992), with the notable exception that dynamics of the consumer and the resource are decoupled. Decouplings would not necessarily be the case for herbivores that feed on floral structures. Floral herbivores influence the degree of seed limitation (Krupnick and Weis 1999; Kelly and Dyer 2002), which may change the energy dynamics of plants by reducing the amount of resource investment for seed production. The dynamics of such systems are a topic for future studies.

In the spatially extended setting, we denote the number of emerged adults at site i at the beginning of year t by $Z_i(t)$ and assume host plants are arranged on lattice points of a two-dimensional square grid. We assume that a fraction, μ , of the adults leave the plant where they were born and disperse to adjacent plants. The postdispersal number of adults at site i , denoted as $Z'_i(t)$, is given by

$$Z'_i(t) = (1 - \mu)Z_i(t) + \frac{\mu}{n} \sum_{j \in R_i} Z_j(t), \quad (4)$$

where R_i is the neighborhood of site i and n is the number of host plants included in R_i . In the numerical explorations that follow, we assume the seed predator disperses to eight nearest neighbors ($n = 8$). When the amount of seeds produced by a single plant at site i in year t is denoted as $F_i(t)$, the predispersed number of adults in the next generation ($t + 1$) is given by

$$Z_i(t+1) = \gamma F_i(t) [1 - e^{-\alpha Z'_i(t)}], \quad (5)$$

where γ is the per capita emergence rate and α is the per capita attack rate (the searching efficiency). The $F_i(t)$ itself is governed by the pollen-coupled tree model (eqq. [1]–[3]) according to

$$F_i(t+1) = \begin{cases} 0 & \text{if } Y_i(t) \leq 0 \\ ckP_i(t)Y_i(t) & \text{if } Y_i(t) > 0 \end{cases} \quad (6)$$

where c is constant, k is the depletion coefficient, and $P_i(t)$ is the pollen availability given by equation (3b). The local dynamics of seed predators represented by equation (5) include two parameters, γ and α . We can reduce the number of parameters by introducing $W_i(t) = \alpha Z_i(t)$ and rewriting equation (5) by a formula, $W_i(t+1) = hF_i(t)[1 - e^{-W_i(t)}]$, which is governed by a single compound parameter $h (= \alpha\gamma)$. Hence, in the following calculation, we will fix $\gamma = 1$ and examine the effect of the value of α (without loss of generality).

We also examine extended diapause as a potential strategy a predator may employ to cope with variable resource availability (Tauber et al. 1986; Roff 1992; Hopper 1999). Kelly et al. (2000) and McKone et al. (2001) demonstrated that extremely high levels of mast seeding in *Chinochloa* species may have evolved to satiate predators who have extended diapause. In the diapause mode, we assume no dispersal (i.e., $\mu = 0$) and that a fraction d of the pupae has extended diapause. This assumption of dormancy is further motivated by studies of the apple fruit moth *Argyresthia conjugella* Zeller, whose larvae feed on rowan berries *Sorbus aucuparia* L. and some fraction of whose pupae show extended diapause (Ahlberg 1927; Edland 1971; see Satake et al. 2003 for a detailed analysis of masting-insect

Table 1: Symbols used in the model and statistical analysis

Variables and parameters	Definition
Energy dynamics of host plants:	
S_i	Level of stored energy of individual at site i
P_s	Energy gain from photosynthate per year
L_T	Threshold of energy level for flowering
a	Coefficient of energy expenditure for flowering
R_c	Ratio of energy expenditure for fruiting to flowering
Y_i	Nondimensionalized variable of stored energy level of individual at site i
k	Scaling parameter ($k = a(R_c + 1) - 1$), called depletion coefficient
P_i	Pollen availability of individual at site i
U_i	Neighborhood of individual at site i
m	Number of plants included in the neighborhood
β	Strength of pollen limitation called pollen coupling strength
Fruiting dynamics of host plants:	
F_i	Amount of seeds produced by individual at site i
c	Constant converting energy expenditure for fruiting to number of seeds
Population dynamics of seed predators:	
Z_i	Number of predispersal adults at site i
Z'_i	Number of postdispersal adults at site i
μ	Fraction of adults disperse into adjacent sites
R_i	Neighborhood of the seed predator population at site i
n	Number of host plants included in the neighborhood
γ	Per capita emergence rate
α	Per capita attack rate or searching efficiency
Dormant model for seed predators:	
X_i	Number of pupae at site i
d	Fraction of the pupae that are capable of extended diapause
ν	Survival rate of pupae in dormancy
Statistical parameters:	
CV_i	Coefficient of variation in seed production at individual level
CV_p	Coefficient of variation in seed production at population level
$\bar{\rho}$	Degree of regional synchrony
$A(1)$	Autocorrelation at the time lag 1
$C(1)$	Cross-correlation at the time lag 1
\hat{Q}	Approximate invasion criteria
\hat{Q}'	Approximate invasion criteria with no local spatial structure

interactions in this system). The number of newly produced pupae (or larvae) that emerged from egg and survived through winter at location i in year t is then given by $X_i(t) = \gamma F_i(t)[1 - e^{-\alpha Z_i(t)}]$, where $Z_i(t)$ is the number of adults' seed predators defined in equation (5). Let the annual survival rate of pupae in dormancy be ν . The probability that pupae emerge as adults after n years dormancy is then given by $(1 - d)d^n\nu^n$, which decreases geometrically with time. The number of adults of seed predators in year t is the sum of pupae emerging from all different cohorts according to

$$\begin{aligned}
 Z_i(t + 1) &= (1 - d)X_i(t) + (1 - d)d\nu X_i(t - 1) \\
 &+ \dots + (1 - d)d^n\nu^n X_i(t - n) \dots \\
 &= \sum_{n=0}^t (1 - d)d^n\nu^n X_i(t - n). \tag{7}
 \end{aligned}$$

Table 1 summarizes all symbols used in the models.

Statistical Approach

In the computer simulations, we considered 30×30 host plants distributed regularly over two-dimensional space. We employed periodic boundary condition, that is, the lattice of a torus shape (the rightmost column is the nearest neighbor of the leftmost column, and the top row is nearest neighbor of the bottom row). We subsequently subjected the model output from numerical simulations to various statistical analyses.

Masting Measures

Spatiotemporal dynamics in mast seeding predicted by the model depend critically on the depletion coefficient, k , and

the coupling strength, β . Varying these parameters will alter reproductive strategies from stable to intermittent (and increase the coefficient of variation in seed production at individual level, CV_i) and change spatial dynamics from synchronous to asynchronous (thereby changing the degree of spatial synchrony among plants, $\bar{\rho}$). As is standard, both the CV in reproduction at a population level (CV_p) and $\bar{\rho}$ are adopted to measure key elements of mast seeding (Kelly and Sork 2002; Buonaccorsi et al. 2003). Here we use only $\bar{\rho}$ to measure masting dynamics because CV_p is tightly related to $\bar{\rho}$ when the long-term average of seed production is approximately the same among different plants (see app. B in the online edition of the *American Naturalist*). For a more detailed classification of spatio-temporal dynamics of mast seeding predicted by the model, see an article by Satake and Iwasa (2000).

Seed Predation

We measured severity of seed predation as the proportion of seeds that was attacked by seed predators. To calculate the proportion of attacked seeds, 100 independent simulations with different initial conditions were performed for a range of parameter combinations of (k, β) . For each simulation, we analyzed time series of length 1,000 in seed production and in seed predation after discarding the first 1,000 iterations to omit the long transients that are commonly seen in spatially extended models (Hastings and Higgins 1994).

Invasion

Invasibility is typically studied by asking what happens when a rare predator is introduced to a resource at its consumer plant. However, in the case of mast seeding, the resource may not be stable but may fluctuate widely across years in a cyclic or chaotic manner (Satake and Iwasa 2000, 2002a). Moreover, the dynamics of the resource may exhibit complex spatial dynamics. Because of these complexities, we have been unable to obtain exact invasion criteria. We have, however, developed an approximate invasion criterion, \hat{Q} . When a small number of predators are distributed uniformly across all host plants, a unique spatial pattern of predators is generated through the spatially extended resource fluctuation and the predator's dispersal to nearby plant. The \hat{Q} was calculated as the average growth or decline in the predator population during two generations following introduction (app. A). This approximate criterion provides key insights into how predator persistence is influenced by spatial and temporal fluctuations of the resource. The \hat{Q} is given as follows:

$$\hat{Q} = \frac{1}{T} \sum_{t=0}^{T-1} Q(t), \quad (8a)$$

where

$$Q(t) = \frac{\alpha^2 \gamma^2}{N} \left[(1 - \mu) \sum_{i=1}^N F_i(t) F_i(t+1) + \frac{\mu}{n} \sum_{i=1}^N \sum_{j \in R_i} F_i(t) F_j(t+1) \right]. \quad (8b)$$

In the above equation, N is the number of plants included in the forest stand, and n is the number of plants included in the neighborhood, R_i . The $F_i(t)$ is the amount of seed produced at site i in year t , given by equation (6). Other parameters are as defined in equations (4) and (5) (see also table 1). The first term in the right-hand side in equation (8b) arises from the seed predators that do not disperse, so their next-year offspring are left to consume seeds or berries produced by the plant where their parents were born. The second term arises from seed predators that disperse to lay eggs on seeds or berries produced by neighboring plants.

By a simple calculation, \hat{Q} is related to the time lag-1 autocorrelation $A(1)$ and time lag-1 cross-correlation $C(1)$ in seed production according to

$$\hat{Q} = \alpha^2 \gamma^2 [(1 - \mu)R(1)\sigma^2 + \mu C(1)\sigma^2 + 2\hat{F}^2], \quad (9)$$

where σ^2 is the variance and \hat{F} is the temporal mean of fruiting for each plant. The $C(1)$ is calculated across the plants in the neighborhood, R_i . The \hat{Q} is an increasing function of $R(1)$ and $C(1)$. Thus, invasibility is enhanced if seed production is not negatively correlated with previous seed production at both the same location and adjacent locations. In contrast, if seed production of each plant is negatively autocorrelated, invasibility is reduced. If the fluctuation in resources is spatially synchronized, $C(1)$ will be negative, and invasibility is reduced further. Because \hat{Q} is an approximate invasion criterion, we confirm its accuracy through numerical simulation; seed predators should be able to invade only when $\hat{Q} > 1$.

If seed production is regionally (not locally) self-organized among plants, $Q(t)$ simplifies to

$$Q'(t) = \frac{\alpha^2 \gamma^2}{N} \left[(1 - \mu) \sum_{i=1}^N F_i(t) F_i(t+1) + \frac{\mu}{(N-1)} \sum_{i=1}^N \sum_{j \neq i} F_i(t) F_j(t+1) \right]. \quad (10)$$

The second term in the right-hand side in equation (8b) is now replaced by the average of the product for all possible pairs (i, j). By taking temporal average of $Q'(t)$, we have an approximate invasion criterion with no local spatial structure, \hat{Q}' . The assumption of no localized spatial structure is crude; however, it will lead to critical insights into invasibility, as we will show later.

We evaluate \hat{Q} and \hat{Q}' numerically from the spatiotemporal patterns in seed production ($[F_i(t)]$, $i = 1, \dots, N$) generated by numerical simulation of the pollen-coupled tree model. For each parameter combination of the pollen-coupled tree model, we calculated (\hat{Q} , \hat{Q}') and spatial synchrony in seed production, $\bar{\rho}$. Invasion success is also examined directly through numerical simulation of the full consumer-resource model. We introduce a minute density of predator (10^{-4}) at each host plant and trace their population growth over the first 100 generations. If the seed predator's population is still extant at the end of the 100 generations, the plant reproductive strategy is considered invulnerable.

Spatial Dynamics

To characterize the spatial dynamics, we applied a non-parametric method to estimate the spatial correlation function (SCF) or time-lagged cross-correlation function (LCF) in the time series data generated from numerical simulations of the model. These correlation functions decompose synchrony/lagged correlation as a function of distance (Bjørnstad et al. 1999, 2002; Bjørnstad and Falck 2001). We used 100 points in time for calculation after discarding 1,000 transient iterations.

Results

Masting Dynamics

In this section, we summarize the reproductive behavior predicted by the pollen-coupled tree model. When the depletion coefficient, k , is < 1 , each plant produces seeds every year, leading to annual reproduction (fig. 1A). Annual reproduction can be further classified into "annual and constant" reproduction, in which the amount of seeds is constant, and "annual and 2-yr cyclic," in which the amount of seeds alternates between high and low (but positive) reproduction (fig. 1A). In the case of annual reproduction, perfect synchrony may be assumed, that is, $\bar{\rho} = 1$, though constant reproductive effort complicates the notion of synchrony because reproductive variance is zero. Conversely, if $k > 1$, each plant reproduces intermittently, and the time series of individual seed production includes years with no seed set. We distinguish significant synchrony ($\bar{\rho} \geq 0.8$) from weak synchrony ($\bar{\rho} < 0.8$). Sig-

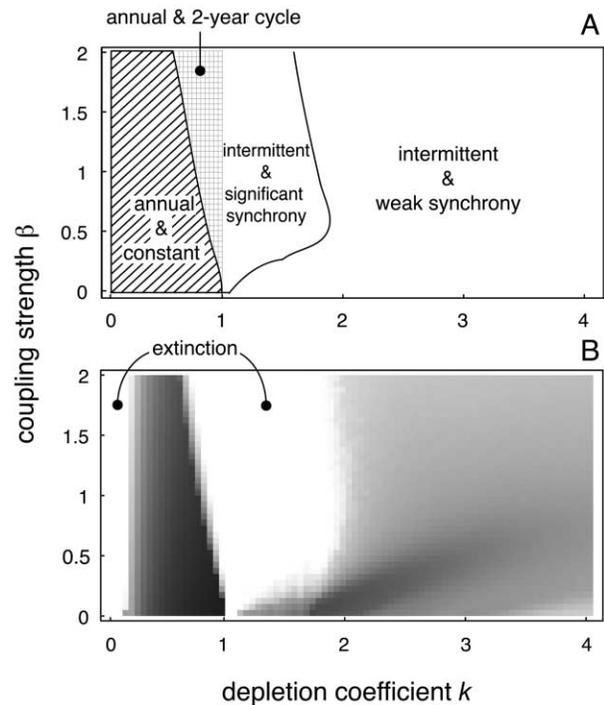
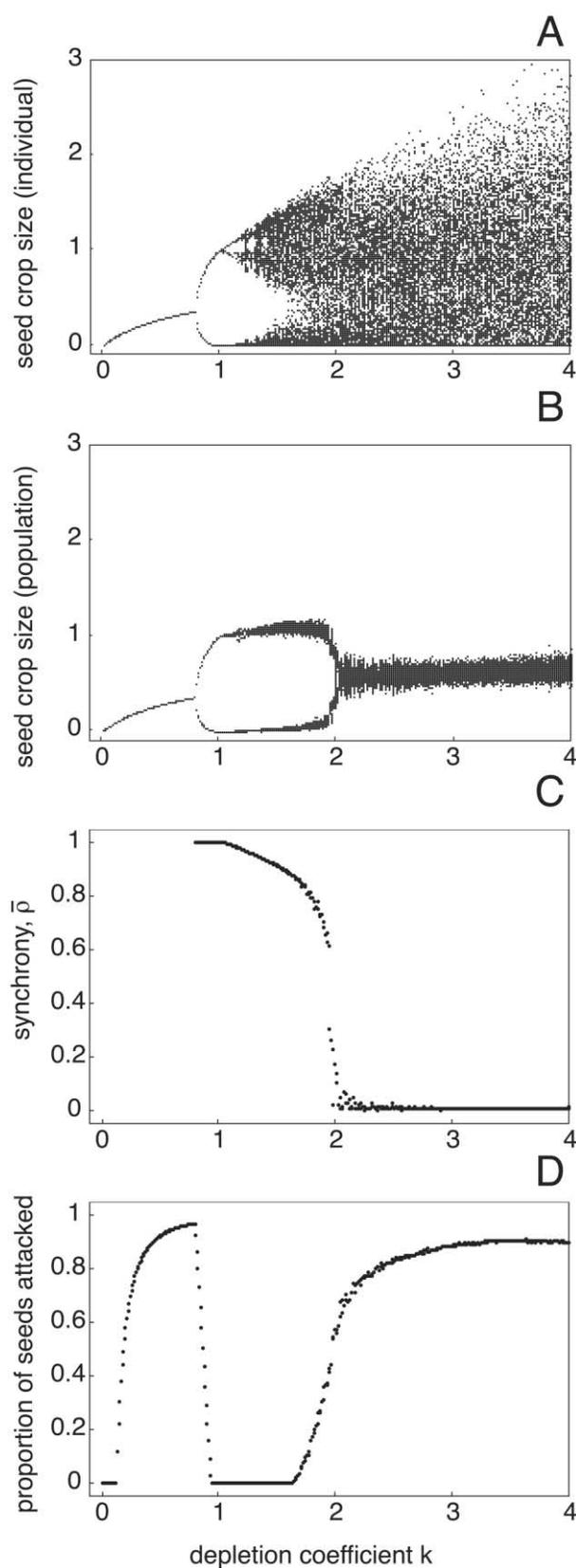


Figure 1: A, Classification of reproductive pattern of plants predicted by the pollen-coupled tree model with an assumption of local pollen coupling. We classified four types of reproductive pattern as explained in the text. B, Density plot for proportion of seeds attacked calculated by numerical simulation of the model. Darker area represents more severe seed predation. Parameters: $\mu = 0.8$, $\alpha = 10$.

nificantly synchronized reproduction with intermittence is realized only when $1 < k < 2$. In this parameter region, seed production at population level tends to exhibit a 2-yr cycle (fig. 2B; Satake and Iwasa 2002a).

Temporal dynamics in seed production at the individual and population levels are illustrated through bifurcation diagrams (fig. 2). The long-term trajectories of seed crop size, $F_i(t)$, defined in equation (6) and its mean in a population, $\sum_{i=1}^N F_i(t)$, are plotted across a range of values of k to obtain reproductive bifurcation diagrams at individual (fig. 2A) and at population levels (fig. 2B). For any given individual, reproduction is annual and constant when k is small (fig. 2A). As k increases, the reproductive orbit bifurcates into 2-yr cycles (annual and 2-yr cycle reproduction) and eventually chaotic seed production (fig. 2A; Satake and Iwasa 2000). The mean reproductive activity across the forest is governed partially by individual reproduction and partially by the self-organized spatial dynamics. In the presence of complete spatial synchrony ($\bar{\rho} = 1$; see fig. 2C), the reproductive behavior of the forest mirrors that of each plant (fig. 2A, 2B). However, as individual orbits become increasingly unstable ($k > 2$), the



collapse of spatial synchrony leads to divergence of individual-level and population-level dynamics. As k increases, mean seed crop size across the forest comes to visit two sets of high-low values in a 2-yr cycle and finally centers near a single average value (fig. 2B). In such desynchronized forests, mean reproductive activity does not change between years, and the fraction of plants that bloom, the mean pollen availability, and the total number of seeds produced in a forest are almost constant because of the averaging across independent orbits.

Seed Predation

We examined the severity of seed predation as the average proportion of seeds attacked (fig. 1B). Annual and constant seed production (*shaded area* in fig. 1A) results in severe attacks (fig. 1B). However, for very low seed production (i.e., for k close to 0), seed predators do not persist (fig. 1B), although this region diminishes with increasing searching efficiency of seed predators, α . When seed production is annual but fluctuating with a 2-yr cycle alternating between high and low reproduction levels (*checkered region* in fig. 1A), seed predators are partially satiated in their numerical response; predation rates depend on the population size of predators as controlled by seed production in previous years. Such a numerical response of seed predators can cause extinction of the predator (fig. 1B). The proportion of attacked seeds increased from 0 to 1 with increased reproductive rates within the annual and constant regime but declined sharply for the 2-yr cycle (fig. 2B, 2D). Again, increased searching efficiency may alleviate this.

Individual plants mast (i.e., produce seeds intermittently) when $k > 1$ (fig. 2A). Time series of individual seed production then includes numerous years with no seed set. In this case, “local” extinction of seed predators is inevitable, but they may nevertheless persist globally as a result of dispersal and spatial averaging. Regional persistence in the face of local instability is most likely when mast synchrony is weak (fig. 1). In this scenario, there is always some fraction of plants producing seeds within the forest. This enables seed predators to persist globally through dispersal to any asynchronous nearby plants. Seed predators are globally extinct over the parameter region in which significant reproductive synchrony is realized (fig.

Figure 2: A, Bifurcation diagram for individual seed crop sizes. B, Bifurcation diagram for population level seed crop size. C, Degree of synchrony in seed production ($\bar{\rho}$). D, Proportion of seeds attacked. The horizontal axis is the depletion coefficient, k . Parameters: $\beta = 0.8$, $\mu = 0.8$, $\alpha = 10$.

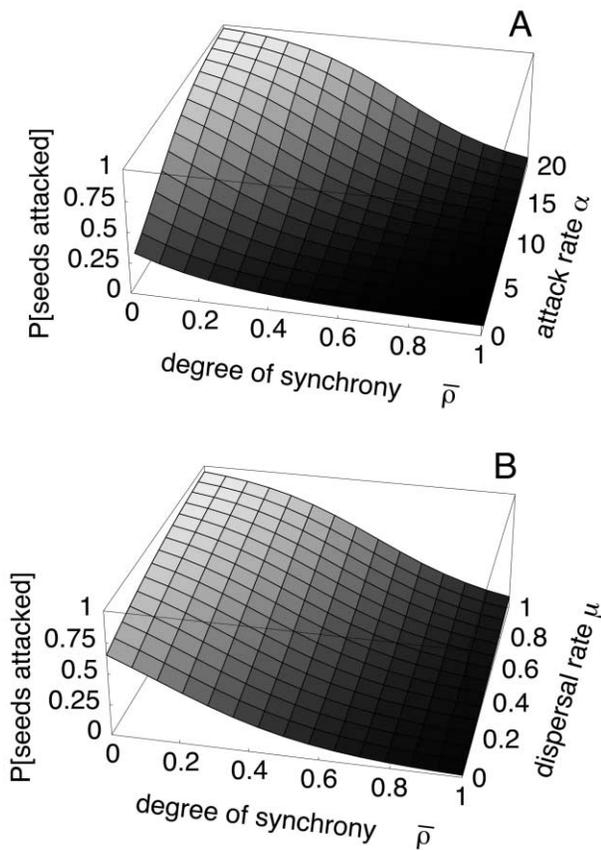


Figure 3: The logistic-regression response surface of the proportion of attacked seeds (p) as a function of A, the degree of synchrony, $\bar{\rho}$, and the per capita attack rate of seed predators, α , and B, the dispersal rate of seed predators, μ . Logistic regression analysis gives $\ln[p/(1-p)]$ as: (A) $-1.3 - 5.1\bar{\rho} + 0.24\alpha - 0.045\bar{\rho}\alpha$ and (B) $0.62 - 4.6\bar{\rho} + 2.3\mu - 0.56\bar{\rho}\mu$.

1; fig. 2C, 2D). For masting plants ($k > 1$), the proportion of attacked seeds is inversely related to $\bar{\rho}$ (fig. 2C, 2D),

We performed logistic regression analysis to synthesize how different factors such as the degree of spatial synchrony, $\bar{\rho}$, the searching efficiency, α , and the dispersal rate, μ , influence the proportion of seeds attacked. This proportion was found to be negatively related to $\bar{\rho}$ but positively related to α (fig. 3A) and μ (fig. 3B).

Invasion

Invasibility is most critically dependent on the degree of synchrony of seed set, $\bar{\rho}$ (fig. 4). Both \hat{Q} and \hat{Q}' decrease with increasing $\bar{\rho}$, meaning that invasibility decreases as the degree of spatial synchrony in seed production increases. Interestingly, \hat{Q} is almost always less than \hat{Q}' . This discrepancy highlights that seed predators suffer lower in-

vasibility when reproduction among plants is locally self-organized. To elucidate this, we depict the time lag-1 cross-correlation function (LCF) in seed production (fig. 5A). When in a weakly synchronized forest (i.e., small $\bar{\rho}$), a local spatial pattern in seeding is created, then nearby sites show a strong negative correlation at time lag 1 (*solid line* in fig. 5A), though this negative correlation erodes with increasing distance to converge to 0 for distant plants. If, in contrast, the spatial dynamics are not locally synchronized, the LCF is almost 0 throughout (*dotted line* in fig. 5A). Because of such a smaller time lag-1 cross-correlation (eq. 9), \hat{Q} fell below \hat{Q}' (fig. 4).

The approximate invasion criterion appears to give an excellent prediction of the invasion in the full spatiotemporal simulations. In simulations, establishment fails when $\hat{Q} < 1$, and it succeeds for $\hat{Q} > 1$. Intriguingly, the approximation is derived by considering only two steps in the invasion process (app. A). Its success is likely to be linked to the time lag-1 nature of dependence in masting dynamics (Kelly and Sork 2002).

Spatial Dynamics

The pollen-coupled tree model with local pollen dispersal generates nonuniform spatial patterns with local spatial clusters. The spatial scale of the clusters tends to be a few times the range of direct pollen exchange (Satake and Iwasa 2002a). The spatially correlated seed production, in combination with local pollen dispersal, induces spatial correlation in the dynamics of the seed predators. Figure 5B, 5C exemplifies the spatial correlation functions (SCFs) in seed predators as compared with the SCFs of their re-

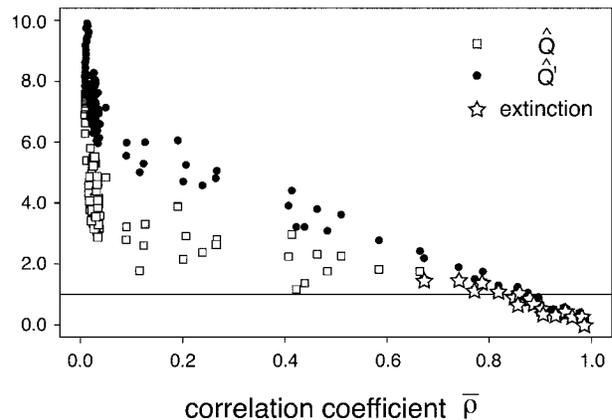


Figure 4: Plot of the approximate invasion criteria, \hat{Q} (open squares) and \hat{Q}' (solid circles), along the degree of synchrony in seed production among different plants ($\bar{\rho}$). Stars represent the values of \hat{Q} in which extinction of seed predators occurred. Parameters: $\mu = 0.8$, $\alpha = 10$.

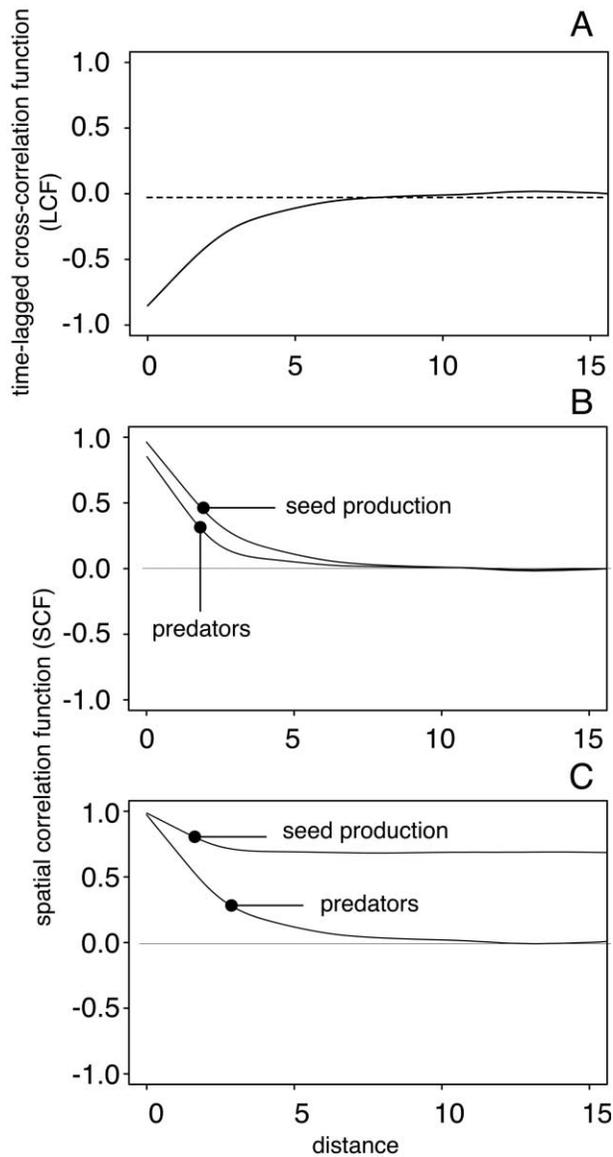


Figure 5: A, Spatial correlation function in seed production at the time lag 1 (solid line), calculated from spatial pattern predicted by the pollen-coupled tree model. Dotted line is the degree of regional synchrony. Parameters: $k = 2.1$, $\beta = 0.8$, $\bar{\rho} = 0.042$. B, C, Spatial correlation functions in seed production and predator abundance as predicted by the pollen-coupled tree model. Parameters: (B) $k = 2.1$, $\beta = 0.8$, $\bar{\rho} = 0.042$; (C) $k = 1.8$, $\beta = 0.8$, $\bar{\rho} = 0.68$.

source. If the degree of spatial synchrony is small ($\bar{\rho} = 0.04$), the SCF in seed production declines and approaches 0 for large distances (fig. 5B). However, the decrease in synchrony with distance is very shallow in a synchronized forest ($\bar{\rho} = 0.68$), and positive correlation is maintained over long distances (fig. 5C). The SCFs for seed predators also decrease as a function of distance and are always below

the SCFs for resources (fig. 5B, 5C). The discrepancy between the SCFs for seed production and those for seed predator is most distinct in a significantly synchronized forest (fig. 5C).

To fully visualize the spatial persistence of predators in the presence of highly variable mast seeding, we present three temporal snapshots (fig. 6). The upper three panels represent the temporal change of spatial distributions for seed crop size produced by individual plants. For the parameters chosen, there are distinct spatial clusters in which plants show synchronized reproduction with the 2-yr cycle, visiting high and very low reproductive levels as shown in figure 6 (this is typical reproductive behavior of plants when $k < 2$; see fig. 2B). The corresponding spatial distributions of seed predators are shown in three panels at the bottom. The seed predator's persistence is facilitated at the boundary of distinct clusters. This elucidates the importance of dispersal for spreading the risk in the face of variable resources. When host plants produce too-small amounts of seeds, successful predator reproduction requires dispersal to find resources elsewhere within the dispersal range.

We may acquire a deeper understanding of the spatio-temporal persistence through a simplifying assumption. Consider that the amount of seeds produced by i th plant in year t , $F_i(t)$, visits either H (high) or L (low) levels cyclically. When two distinct spatial clusters A and B exhibit opposite reproductive phases, as shown in figure 6, the reproductive level of any individuals belonging to cluster A, $F_{i \in A}(t)$, is simplified to

$$F_{i \in A}(t) = \begin{cases} H & \text{for } t \text{ even} \\ L & \text{for } t \text{ odd} \end{cases}, \quad (11)$$

and vice versa for the reproductive level of individuals in cluster B, denoted as $F_{i \in B}(t)$.

The population growth rate of the predator at site i , $Q_i(t)$, is then approximated using the similar calculations in appendix A, according to

$$\begin{aligned} Q_i(t) &= \alpha^2 \gamma^2 \left\{ (1 - \mu) HL \right. \\ &\quad \left. + \mu \left[\frac{(n - l_i)}{n} HL + \frac{l_i}{2n} (HH + LL) \right] \right\} \\ &= \alpha^2 \gamma^2 \left[HL + \frac{\mu l_i}{2n} (H - L)^2 \right], \end{aligned} \quad (12)$$

where l_i is the number of sites that belong to the cluster showing opposite reproductive phase within the neigh-

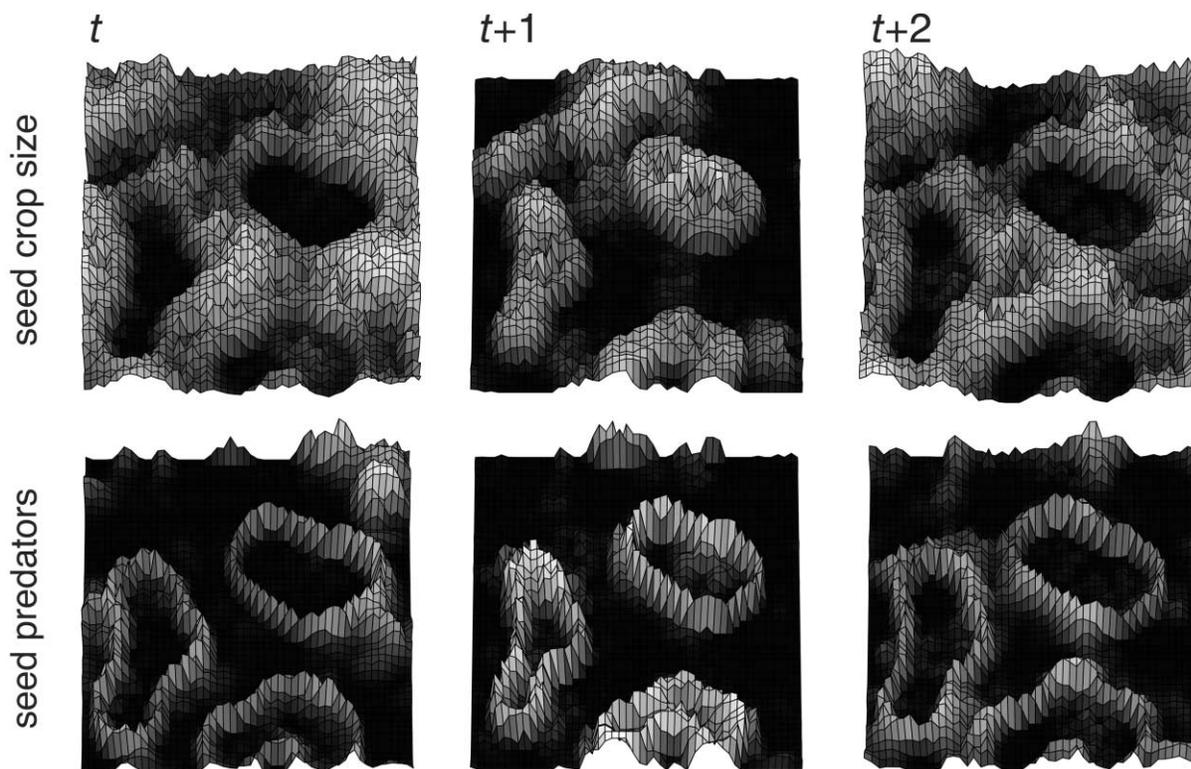


Figure 6: Spatial patterns in seed production (*upper row*) and amount of seed predators (*bottom row*). *X*- and *Y*-axes represent spatial locations, and *Z*-axis represents seed crop size (*upper three panels*) or seed predator abundance (*bottom three panels*). Time flows left to right. Parameters: $k = 1.8$, $\beta = 1.0$, $\mu = 0.8$, $\alpha = 10$. The total number of host plant is 50×50 . In order to show clear spatial patterns, we apply the pollen dispersal range larger than nearest neighbor: plants located at i th location (x_i, y_i) and j th location (x_j, y_j) can exchange pollen if $|x_i - x_j|^2 + |y_i - y_j|^2 \leq 5^2$. Overall spatial pattern is similar, but spatial scale of the pattern is larger and becomes coarse grained as pollen dispersal range increases (for details, see Satake and Iwasa 2002a).

borhood of the focal plant i and n is the total number of plants in the neighborhood. For other parameters, see table 1. Equation (12) illustrates that $Q_i(t)$ increases with μ and l_i . This means that local population of seed predators shows higher growth rate when they have a larger dispersal rate, μ , and a larger number of neighboring plants belonging to clusters that are different from the focal plant. As illustrated by the spatial dynamics in figure 6, l_i attains large value at the boundary of two distinct clusters, which provides the core areas for persistence of the seed predators. Note that these calculations are general in the sense that they hold not only for the nearest-neighbor dispersal assumed in the simulations but also for arbitrary neighborhood size.

Dormancy

Numerical simulation of the diapause model (eq. [7]) shows that plants suffer from severe seed losses over a large parameter region when seed predators exhibit an

extended diapause (fig. 7A), but large temporal variability in seeding tends to reduce losses (fig. 7B). However, the qualitative features of persistence as a function of plant reproductive synchrony bears some resemblance to the “disperse in time” and “disperse in space” strategies (cf. fig. 1B and fig. 7A).

Discussion

Mast seeding has a great impact on the dynamics of seed consumers (Wolff 1996; McShea 2000; Kobro et al. 2003; Schnurr et al. 2002; Satake et al. 2004) and herbivores (Selås et al. 2001) by generating spatial and temporal fluctuation in resource levels. Pulsed seed production may have cascading effects on ecosystems through the food web (Ostfeld et al. 1996; Liebhold et al. 2000; Ostfeld and Keesing 2000; Schmidt and Ostfeld 2003; Satake et al. 2003). This article focuses on the spatially extended dynamics of plant reproduction and seed predators to explore the effect of mast seeding on dynamics and persistence of specialist

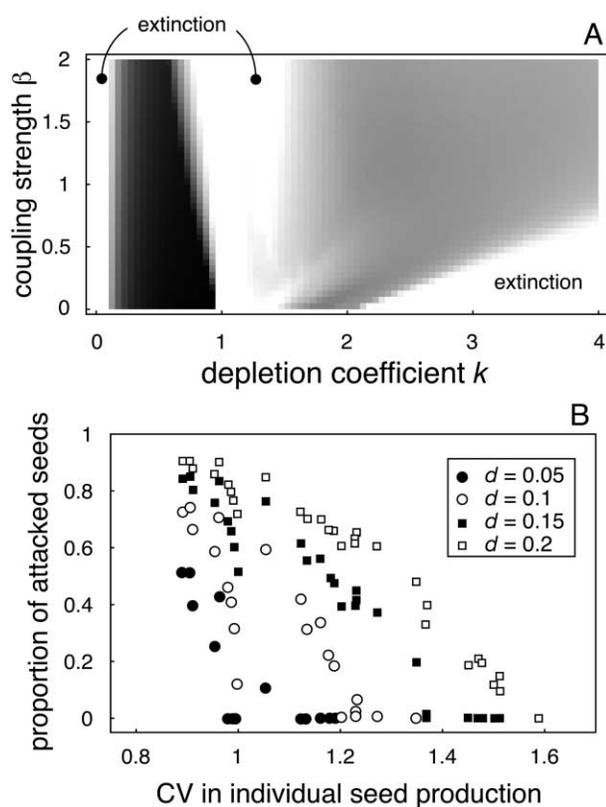


Figure 7: A, Density plot of proportion of seeds damaged predicted by the diapause model. Darker area represents more severe seed predation. Parameters: $d = 0.05$, $v = 1.0$. B, Plot of the proportion of seeds attacked by predators along the coefficient of variation (CV) of individual reproduction. d = fraction of the pupae that are capable of extended diapause. Parameters: $v = 1.0$, $\beta = 0.0$.

consumers. Population dynamics of seed predators are assumed to respond to mast seeding of host plants in a bottom-up fashion. The results of our analysis provide firm theoretical support of previous hypotheses of how mast seeding may lead to an escape from seed predation (Janzen 1971; Silvertown 1980; Kelly and Sork 2002).

Theoretically speaking, local populations of seed predators may be expected to become locally extinct when a host plant shows intermittent seed production. However, because of dispersal to adjacent host plants, global persistence of the predator may still be ensured (fig. 1). In this case, a plant population suffers from seed predation even if individual reproduction varies substantially across years, although its level of seed predation is lower than those for constant reproduction. Global extinction of seed predators results when intermittent reproduction is highly synchronized (fig. 1). According to the approximate invasion criterion, negative time lag-1 autocorrelation and cross-correlation in seeding reduce invasibility of the seed

predators (note how our study thus adds to the growing body of theory that shows how the influence of pattern on process can be approached by considering spatial correlation/cross correlation [Bolker and Pacala 1999; Keeling et al. 2002]). This means that classic mast seeding, which exhibits a seed set that is negatively correlated in time but positively correlated across space, is a good strategy to prevent invasion of the seed predators. The approximation for the invasion criterion works well because the entire forest exhibits a 2-yr cycle in seed production when the plant's reproduction is highly synchronized (fig. 2). However, as $\bar{\rho}$ slightly decreases, the 2-yr cycle becomes unclear (fig. 2), and longer intervals between mast years should be taken into account to correct slight overestimation of the invasion criterion (fig. 4).

Koenig and coworkers (Koenig and Knops 1998, 2000; Koenig et al. 1999; Koenig 2002) demonstrated that the degree of mast synchrony among temperate forests is high and may extend to as far as 1,000 km. Mast synchrony at the relatively short spatial scale (distance <10 km) at which seed predator populations operate has also been shown to be high (Rees et al. 2002; Liebhold et al. 2004). Such strong positive spatial correlation in seeding may greatly reduce losses to the predators. In addition, spatial synchrony at local scales (<100 m in the work by Liebhold et al. 2004) may further reduce losses by preventing the invasion of seed predators as predicted by the model (fig. 4).

According to the prediction of the model, the scale of spatial synchrony critically depends on the pollen dispersal range; the scale is at least a few times larger than the range of direct pollen exchange (Satake and Iwasa 2002a). Environmental fluctuations (such as temperature and precipitation level) are correlated across a large scale and may cause further synchrony in seed production over longer distances than in the case of direct pollen exchange (Koenig and Knops 1998, 2000; Koenig et al. 1999; Koenig 2002; Rees et al. 2002; Schaubert et al. 2002), or pollen coupling and environmental forces may work in concert to realize large-scale reproductive synchrony (Satake and Iwasa 2002b). The spatial scale at which synchrony in seed production effectively reduces seed losses to seed predators is influenced by the mobility of seed predators (Kelly and Sork 2002). In this study, we considered invertebrate predators that disperse over a short distance. These may contrast with highly mobile predators such as birds or mammals (Curran and Leighton 2000). Larger spatial scales of reproductive synchrony would be required to satiate such predators in order to reduce seed losses. Even in such a case, the same analysis of approximate invasion criteria given in equations (8) and (9) can be applied because they are general and hold for arbitrary neighborhood sizes not restricted to nearest-neighbor dispersal. In the model, dispersal was assumed to be isotropic. However, if predators

have advective (directional) dispersal, as in the case of the larch budmoth (Bjørnstad et al. 2002), different spatio-temporal patterns will arise from trophic interactions, which is an interesting topic for future studies.

We have examined a modification of the model to relax the range of simplifying assumptions. The core model assumes that plants exchange pollen only with adjacent plants (i.e., local pollen dispersal), which results in formation of local spatial pattern in seed production. Contrary to local pollen dispersal, a model with global pollen dispersal generates regional reproductive synchrony with no local spatial pattern (Satake and Iwasa 2000). We have applied the same range of analysis to the global pollen coupling situation. When pollen is dispersed globally, spatial reproductive synchrony is created over a larger parameter region (fig. 8A), and therefore, global extinction of seed predators occurs more frequently (fig. 8B) than is the case with local pollen dispersal (fig. 1B). However, as long as seed predators persist globally, severity of seed predation is greater (fig. 8B) than in the case with local pollen coupling (fig. 1B), meaning that a nonlocal pattern in seeding may enhance the level of seed predation. Furthermore, the diapause model shows that large temporal variability in seeding may reduce seed losses to the predators even if predators disperse in time (fig. 7).

The results of our analysis provide an interesting insight into a coevolutionary arms race between plant and seed predators in addition to insight into how economy of scale of masting explains how a larger reproductive effort is more efficient (Norton and Kelly 1988). The reproductive strategy of plants that effectively satiates seed predators is dependent on the behavior of the seed predator itself. For long-distance mobile predators, strategies that generate large-scale synchrony in seeding would be favored. In contrast, for predators with extended diapause, strategies that generate extremely variable seed set across years may be necessary. It is critical to realize that there are potential disadvantages associated with synchronized fluctuations in seed production. Mast seeding may result in increased seedling competition (Kelly 1994) and lost opportunities for colonization or increasing risk of death (Waller 1979). Plants may also face a physiological trade-off; the pollen-coupled tree model predicts that if individual plants employ extremely variable reproduction across years (i.e., a large depletion coefficient, k), synchrony in seed production among different individuals is not likely because seed production becomes more chaotic for larger k (Satake and Iwasa 2000). The tension between these forces will variously contribute to complex selective pressures on the reproductive schedules of individual plants (e.g., Rees et al. 2002). We believe that our spatially extended mechanistic model should produce a basis for future research to explore

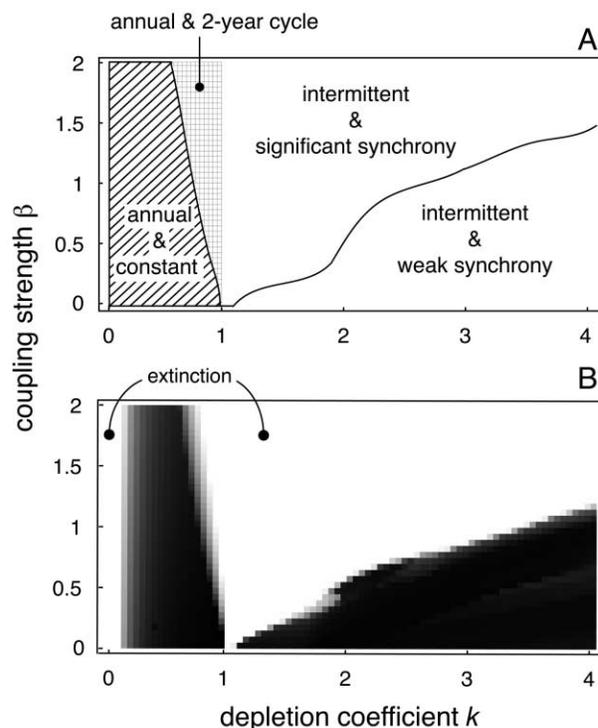


Figure 8. A, Classification of reproductive pattern of plants predicted by the pollen-coupled tree model with global pollen coupling. We classified four types of reproductive pattern as explained in the text. B, Density plot for proportion of seeds attacked. Darker area represents more severe seed predation. Parameters: $\mu = 0.8$, $\alpha = 10$.

evolution of mast seeding and evolution of life histories of specialized seed predators.

From a wider perspective, our study, in a uniquely detailed fashion, adds to the growing emphasis on the intertwined interaction among spatial pattern, temporal process, and environmental stochasticity in ecological dynamics. Theory appears increasingly to support the notion that ecological processes associated with environmental stochasticity induce self-organized spatial patterns (Bjørnstad et al. 1999; Lande et al. 1999; Engen et al. 2002a, 2002b). Such spatial patterns in turn potentially alter the ecological process (Bolker and Pacala 1999). The drawback of this realization is that spatiotemporal models will need to replace classical models for population dynamics. The benefit is the depth of ecological understanding that arises from explicit spatial embedding.

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APPENDIX A

Deriving Approximate Invasion Criterion

Consider the situation in which the number of seed predators is very small ($Z_i(t) \ll 1$ and $Z'_i(t) \ll 1$ for all i). Here, i represents the i th location in two-dimensional lattice space composed of a $n \times n$ grid. By noting $e^{-\alpha Z'(t)} \cong 1 - \alpha Z'(t)$ for small $Z'(t)$ and applying equation (4), equation (5) can be rewritten as

$$\begin{aligned} Z_i(t+1) &\cong \alpha \gamma F_i(t) Z'_i(t) \\ &= \alpha \gamma F_i(t) \left[(1 - \mu) Z_i(t) + \frac{\mu}{n_{j \in R_i}} \sum_{j \in R_i} Z_j(t) \right], \quad i = 1, \dots, N. \end{aligned} \quad (\text{A1})$$

Using matrix notation, the dynamics of seed predators are then written as

$$\begin{aligned} \mathbf{Z}(t+1) &= \mathbf{A}(t) \mathbf{M} \mathbf{Z}(t) \\ &= \mathbf{A}(t) \mathbf{M} \mathbf{A}(t-1) \mathbf{M} \\ &\quad \dots \mathbf{M} \mathbf{A}(1) \mathbf{M} \mathbf{A}(0) \mathbf{M} \mathbf{Z}(0), \end{aligned} \quad (\text{A2a})$$

where $\mathbf{Z}(t) = [Z_1(t), \dots, Z_N(t)]^T$ (the superscript T denotes matrix transpose) is a vector of abundance of adults in year t , $\mathbf{A}(t)$ is the growth matrix, and \mathbf{M} is the dispersal matrix given by

$$\mathbf{A}(t) = \begin{bmatrix} \alpha \gamma F_1(t) & 0 & \cdot & 0 \\ 0 & \alpha \gamma F_2(t) & 0 & 0 \\ \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & \alpha \gamma F_N(t) \end{bmatrix}, \quad (\text{A2b})$$

$$\mathbf{M} = \begin{bmatrix} m_{11} & m_{12} & \cdot & m_{1n} \\ \cdot & \cdot & \cdot & \cdot \\ \cdot & \cdot & \cdot & \cdot \\ m_{n1} & \cdot & \cdot & m_{nn} \end{bmatrix},$$

$$\text{where } m_{ij} = \begin{cases} 1 - \mu, & i = j \\ \mu/n, & i \neq j \text{ and } j \in R_i. \\ 0, & \text{otherwise} \end{cases} \quad (\text{A2c})$$

Seed predators can invade a plant population only if the dominant eigenvalue of the product $\mathbf{A}(t) \mathbf{M} \mathbf{A}(t-1) \mathbf{M} \dots \mathbf{M} \mathbf{A}(0)$ is >1 . Analytical calculation of the eigenvalue of this product is formidable task because the growth

matrix is dependent on time in a manner predicted by the pollen-coupled tree model, and dispersal of adults to nearby trees creates complex linkages among different trees. Thus, we developed a heuristic method to calculate the approximate invasion criterion, \hat{Q} . We assume that invasion criterion is approximated by the mean of population growth rate calculated from the process including two growth steps accompanied by one dispersal step: $\mathbf{A}(t+1) \mathbf{M} \mathbf{A}(t)$. Let $Q(t)$ be the quantity to measure the population growth rate when predators are introduced in year t . By assuming that predators are initially distributed uniformly across all host (i.e., $\mathbf{Z}(t) = \varepsilon(1, 1, \dots, 1)^T$, where ε is a small constant), $Q(t)$ is given as

$$\begin{aligned} Q(t) &= \frac{1}{N} (1, 1, \dots, 1) \left[\mathbf{A}(t+1) \mathbf{M} \mathbf{A}(t) \right] \begin{bmatrix} 1 \\ 1 \\ \cdot \\ 1 \end{bmatrix} \\ &= \frac{\alpha^2 \gamma^2}{N} \sum_{i=1}^N F_i(t) \left[(1 - \mu) F_i(t-1) \right. \\ &\quad \left. + \frac{\mu}{n_{j \in R_i}} \sum_{j \in R_i} F_j(t-1) \right] \\ &= \frac{\alpha^2 \gamma^2}{N} \left\{ (1 - \mu) \sum_{i=1}^N F_i(t) F_i(t+1) \right. \\ &\quad \left. + \frac{\mu}{n} \sum_{i=1}^N \sum_{j \in R_i} F_i(t) F_j(t+1) \right\}, \end{aligned} \quad (\text{A3})$$

which corresponds to equation (8b). Taking average of equation (A3) over time t leads to the approximate invasion criterion given by \hat{Q} in equation (8a).

Literature Cited

- Ahlberg, O. 1927. Rönnsbärsmalen, *Argyresthia conjugella* Zell. En redogörelse för undersökningar åren 1921–1926. Lantbruksentomologiska avdelningen, Stockholm. (In Swedish; English summary.)
- Bjørnstad, O. N., and W. Falck. 2001. Nonparametric spatial covariance functions: estimation and testing. *Environmental and Ecological Statistics* 8:53–70.
- Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology & Evolution* 14:427–432.
- Bjørnstad, O. N., M. Peltonen, A. M. Liebhold, and W.

- Baltensweiler. 2002. Waves of larch budmoth outbreaks in the European Alps. *Science* 298:1020–1023.
- Bolker, B., and S. W. Pacala. 1999. Spatial moment equations for plant competition: understanding spatial strategies and the advantages of short dispersal. *American Naturalist* 153:575–602.
- Buonaccorsi, J. P., J. Elkinton, W. Koenig, R. Duncan, D. Kelly, and V. Sork. 2003. Measuring mast seeding behavior: relationships among population variation, individual variation and synchrony. *Journal of Theoretical Biology* 224:107–114.
- Cohen, D., and S. A. Levin. 1991. Dispersal in patchy environments: the effects of temporal and spatial structure. *Theoretical Population Biology* 39:63–99.
- Comins, H. N., M. P. Hassell, and R. M. May. 1992. The spatial dynamics of host parasitoid systems. *Journal of Animal Ecology* 61:735–748.
- Curran, L. M., and M. Leighton. 2000. Vertebrate responses to spatiotemporal variation in seed production of mast-fruited Dipterocarpaceae. *Ecological Monographs* 70:101–128.
- Edland, T. 1971. Rognebærmøll (*Argyresthia conjugella* Zell.). Ein må rekne med sterke angrep på eple i 1971. *Gartneryrket* 61:444–445. (In Norwegian.)
- Ellner, S., and A. Shmida. 1981. Why are adaptations for long-range seed dispersal rare in desert plants? *Oecologia* (Berlin) 51:133–144.
- Engen, S., R. Lande, and B.-E. Sæther. 2002a. Migration and spatiotemporal variation in population dynamics in a heterogeneous environment. *Ecology* 83:570–579.
- . 2002b. The spatial scale of population fluctuations and quasi-extinction risk. *American Naturalist* 160:439–451.
- Harrison, S., and J. F. Quinn. 1989. Correlated environments and the persistence of metapopulations. *Oikos* 56:293–298.
- Hassell, M. P., H. N. Comins, and R. M. May. 1991. Spatial structures and chaos in insect population dynamics. *Nature* 353:255–258.
- Hastings, A., and K. Higgins. 1994. Persistence of transients in spatially structured ecological models. *Science* 263:1133–1136.
- Herrera, C. M., P. Jordano, J. Guitian, and A. Traveset. 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.
- Holt, R. D., and M. A. McPeck. 1996. Chaotic population dynamics favors the evolution of dispersal. *American Naturalist* 148:709–718.
- Hopper, K. R. 1999. Risk-spreading and bet-hedging insect population biology. *Annual Review of Entomology* 44: 535–560.
- Isagi, Y., K. Sugimura, A. Sumida, and H. Ito. 1997. How does masting happen and synchronize? *Journal of Theoretical Biology* 187:231–239.
- Janzen, D. H. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2:465–492.
- Keeling, M. J., H. B. Wilson, and S. W. Pacala. 2002. Deterministic limits to stochastic spatial models of natural enemies. *American Naturalist* 159:57–80.
- Kelly, C. A., and R. J. Dyer. 2002. Demographic consequences of inflorescence-feeding insects for *Liatris cylindracea*, an iteroparous perennial. *Oecologia* (Berlin) 132:350–360.
- Kelly, D. 1994. The evolutionary ecology of mast seeding. *Trends in Ecology & Evolution* 9:465–470.
- Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics* 33:427–447.
- Kelly, D., and J. J. Sullivan. 1997. Quantifying the benefit of mast seeding on predator satiation and wind pollination in *Chionochloa pallens* (Poaceae). *Oikos* 78:143–150.
- Kelly, D., A. L. Harrison, W. G. Lee, I. J. Payton, P. P. Wilson, and W. M. Schaubert. 2000. Predator satiation and extreme mast seeding in 11 species of *Chionochloa* (Poaceae). *Oikos* 90:472–488.
- Knapp, E. E., M. A. Goedde, and K. J. Rice. 2001. Pollen-limited reproduction in blue oak: implications for wind pollination in fragmented populations. *Oecologia* (Berlin) 128:48–55.
- Kobro, S., L. Søreide, E. Djønnne, T. Rafoss, G. Jaastad, and P. Witzgall. 2003. Masting of rowan, *Sorbus aucuparia* L., and consequences for the apple fruit moth, *Argyresthia conjugella* Zeller. *Population Ecology* 45:25–30.
- Koenig, W. D. 2002. Global patterns of environmental synchrony and the Moran effect. *Ecography* 25:283–288.
- 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.
- Koenig, W. D., J. M. H. Knops, W. J. Carmen, and M. T. Stanback. 1999. Spatial dynamics in the absence of dispersal: acorn production by oaks in central coastal California. *Ecography* 22:499–506.
- Krupnick, G. A., and A. E. Weis. 1999. The effect of floral herbivory on male and female reproductive success in *Isomeris arborea*. *Ecology* 80:135–149.
- Lande, R., S. Engen, and B.-E. Sæther. 1999. Spatial scale of population synchrony: environmental correlation versus dispersal and density regulation. *American Naturalist* 154:271–281.
- Levin, S. A., D. Cohen, and A. Hastings. 1984. Dispersal

- strategies in patchy environments. *Theoretical Population Biology* 26:165–191.
- Liebhold, A., J. Elkinton, D. Williams, and R. M. Muzika. 2000. What causes outbreaks of the gypsy moth in North America? *Population Ecology* 42:257–266.
- Liebhold, A., V. Sork, M. Peltonen, W. Koenig, O. N. Bjørnstad, R. Westfall, J. Elkinton, and J. M. H. Knops. 2004. Within-population spatial synchrony in mast seeding of North American oaks. *Oikos* 104:156–164.
- McKone, M. J., D. Kelly, A. L. Harrison, J. J. Sullivan, and A. J. Cone. 2001. Biology of insects that feed in the inflorescences of *Chinichloa* (Poaceae) in New Zealand and their relevance to mast seeding. *New Zealand Journal of Zoology* 28:89–101.
- McShea, W. J. 2000. The influence of acorn crops on annual variation in rodent and bird populations within oak dominated forests. *Ecology* 81:228–238.
- Nilsson, S. G., and U. Wästljung. 1987. Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. *Ecology* 68:260–265.
- Norton, D. A., and D. Kelly. 1988. Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. *Functional Ecology* 2:399–408.
- Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology & Evolution* 15:232–237.
- Ostfeld, R. S., C. G. Jones, and J. O. Wolff. 1996. Of mice and mast: ecological connections in eastern deciduous forests. *BioScience* 46:323–330.
- Rees, M., D. Kelly, and O. N. Bjørnstad. 2002. Snow tussocks, chaos, and the evolution of mast seeding. *American Naturalist* 160:44–59.
- Roff, D. A. 1992. *The evolution of life histories: theory and analysis*. Chapman & Hall, New York.
- 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.
- Satake, A., O. N. Bjørnstad, and S. Kobro. 2004. Masting and trophic cascades: interplay between rowan trees, apple fruit moth, and their parasitoid in southern Norway. *Oikos* 104:540–550.
- 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.
- Schmidt, K. A., and R. S. Ostfeld. 2003. Songbird populations in fluctuating environments: predator responses to pulsed resources. *Ecology* 84:406–415.
- Schnurr, J. L., R. S. Ostfeld, and D. Canham. 2002. Direct and indirect effect of masting on rodent populations and tree seed survival. *Oikos* 96:402–410.
- Selås, V., O. Hogstad, G. Andersson, and T. von Proschwitz. 2001. Population cycles of autumnal moth, *Epirrita autumnata*, in relation to birch mast seeding. *Oecologia* (Berlin) 129:213–219.
- Shibata, M., H. Tanaka, and T. Nakashizuka. 1998. Cause and consequences of mast seed production of four co-occurring *Carpinus* species in Japan. *Ecology* 79:54–64.
- 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.
- Sork, V. L., J. Bramble, and O. Sexton. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. *Ecology* 74:528–541.
- Sperens, U. 1997. Fruit production in *Sorbus aucuparia* L. (Rosaceae) and predispersal seed predation by the apple fruit moth (*Argyresthia conjugella* Zell.). *Oecologia* (Berlin) 110:368–373.
- Tauber, M. J., C. A. Tauber, and S. Masaki. 1986. *Seasonal adaptations of insects*. Oxford University Press, Oxford.
- Waller, D. M. 1979. Models of mast fruiting in trees. *Journal of Theoretical Biology* 80:223–232.
- Wilcock, C., and R. Neiland. 2002. Pollination failure in plants: why it happens and when it matters. *Trends in Plant Science* 7:270–277.
- Wolff, J. O. 1996. Population fluctuations of mast-eating rodents are correlated with production of acorns. *Journal of Mammalogy* 77:850–856.