Chapter twelve

Invasibility of seed predators on synchronized and intermittent seed production of host plants

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INTRODUCTION

The spatiotemporal distribution of resources that invaders require for their growth and reproduction is a key factor in controlling success of invasion (Davis *et al.* 2000). The abundance of abiotic resources, such as water supply and nutrient levels, may fluctuate due to variable climatic condition and disturbance regime (e.g., drought, flood, or fire regimes). Therefore the intensity of competition for these limited resources varies resulting in temporal fluctuation of a community's susceptibility to invasion (Davis and Pelsor 2001).

When invading species are consumers of biotic resources (e.g., hervivores and seed predators), successful invasion may trigger the evolution of traits of host species that enhance resistance to invaders. For example, mast seeding or masting, the intermittent and synchronized reproduction by plant populations (Kelly 1994) reported across a broad group of tree species (Herrera *et al.* 1998), is often explained to have evolved to reduce seed losses to (and hence to prevent

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invasion of) seed predators (the "predator satiation hypothesis", Janzen 1971; Silvertown 1980). Essentially, larger seed crops are synchronized among individuals and satiate seed predators and therefore experience a lower percentage of seed predation. At the same time, years with low seed production will reduce the growth of the seed predator populations. Many studies confirm predator satiation by showing lower predation rates in high seed years (Smith *et al.* 1990; Sork 1993; Kelly and Sullivan 1997; Sperens 1997; Shibata *et al.* 1998; Kelly *et al.* 2000; McKone *et al.* 2001; Satake *et al.* 2004).

The properties or adaptations of the invading consumers also play an important role, particularly the traits associated with dispersal. Even if food resources show unpredictable fluctuation at a single patch (or plant), dispersal between patches buffers variation in fitness by spreading risk over space (Hopper 1999). Dispersal among 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 Shmida 1981; Cohen and Levin 1991; Holt and McPeek 1996).

In this chapter, we discuss a resource-consumer model to understand the spatiotemporal dynamics of a seed predator on a masting resource and explore the invasibility of the predators (Satake and Bjørnstad 2004). Spatiotemporal fluctuations in seeding are represented by the pollen coupled tree model (Isagi 1997; Satake and Iwasa 2000, 2002a, 2002b) in which reproductive behavior of individual plants is constrained by the level of internal energy reserves and local pollen production. We consider specialized insect seed predators. The dynamics of the predator at a single host plant is assumed to follow a spatially-extended Nicholson-Bailey model (Hassell *et al.* 1991; Satake and Bjørnstad 2004), and the adults having a semelparous lifecycle disperse to neighboring host plants to search randomly for seeds, berries, or flowerheads on which to lay their eggs, and the larvae subsequently complete the lifecycle through feeding on the seeds. We calculate an approximate invasion criterion for the predators, which illustrates how variable and synchronized seed production of plants may prevent invasion of seed predator's population.

RESOURCE DYNAMICS OF SEED PRODUCTION

Spatiotemporal fluctuation of food resource for seed predators is modeled as follows. We consider a forest of out-crossing plants each with an internal energy reserve that changes with net energy gain through photosynthesis and energy expenditure through reproduction (and maintenace/growth). Each plant gains net energy, P_s, every year from photosynthesis. Let $S_i(t)$ be the energy reserves of a plant located at site i at the beginning of year t. A plant will not reproduce unless its accumulated energy reserves, $S_i(t) + P_s$, exceeds a critical threshold, L_T. Otherwise the plant produces flowers investing energy ("flowering cost") proportional to the excess given by $a(S_i(t) + P_s - L_T)$, where a is constant of proportionality (Satake and Iwasa 2000). All flowers are pollinated and the plant then invests additional energy due to 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 that the overall resource dynamics are

$$S_i(t+1) = \begin{cases} S_i(t) + P_s & \text{if } S_i(t) + P_s \le L_T \\ (S_i(t) + P_s - a(R_c+1)(S_i(t) + P_s - L_T) & \text{if } S_i(t) + P_s > L_T \end{cases}. \tag{1}$$

Considering the non-dimensionalized variable $Y_i(t) = (S_i(t) + P_s - L_T)/P$, equation (1) is rewritten as,

$$Y_i(t+1) = \begin{cases} Y_i(t) + 1 & \text{if } \; Y_i(t) \le 0 \\ -kY_i(t) + 1 & \text{if } \; Y_i(t) > 0 \end{cases}. \tag{2}$$

in which $k = a(R_c + 1) - 1$ is a 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). Such temporal energy dynamics at the level of the individual plant is easily illustrated through bifurcation diagrams (Fig. 1). The long-term trajectories of energy level defined in eq. (2) are plotted across a range of values of k. When $k < 1$, trajectories visit a single positive value, which represents annual and constant reproduction. For $k > 1$, the orbit eventually represents chaotic fluctuation. As k increases, the interval between non-reproductive years becomes longer because the plant needs more years to rebuild energy reserves to the threshold level.

Pollen limitation

If plants are self-incompatible, fruiting rates may depend on the flowering activity of other trees in a forest because pollination efficiency changes with the number of flowering plants (Nilsson and Wästljung 1987; Smith *et al.* 1990). To model the pollen limitation of plant reproduction, the pollen availability, $P_i(t)$, to individual i was introduced in the non-dimensionalized energy dynamics (Isagi *et al.* 1997; Satake and Iwasa 2000):

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

where $P_i(t)$ is determined by the average flowering intensity of the plants in the neighborhood around the focal plant, U_i. It is given by

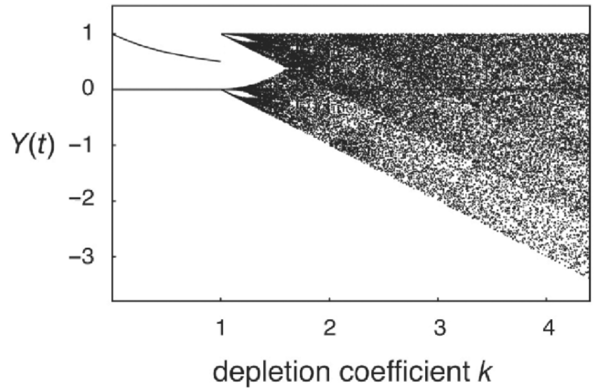

Fig. 1 Bifurcation diagram of an individual plant. Horizontal axis is depletion coefficient k, and the vertical axis is the non-dimensinalized energy level. Parameters: $\beta = 0$, $w_1 = 100$.

$$P_i(t) = \left(\frac{1}{w_1} \sum_{j \in U_i} [Y_j(t)] \right)^{\beta}, \tag{3b}$$

where $[Y]_+ = Y$ if $Y > 0$ and zero otherwise. The parameter w_1 is the number of plants included in the neighborhood U_i (note that the neighborhood does not include oneself), and β determines the degree of neighbor dependence on the pollen limitation. If β is close to 0, fruit production is almost independent of the flowering intensity of other plants. In contrast, a large β implies a strong dependence of seed and fruit production on the pollen production of other plants. Thus, we call β the pollen coupling strength. In this chapter, we consider a situation of "local pollen coupling" in which pollination is limited to the eight nearest neighbors around the focal plant ($w_1 = 8$).

POPULATION DYNAMICS OF SEED PREDATORS

A specialized insect seed predator with a semelparous lifecycle is considered in an all-females model. Adults disperse to nearby host plants to search randomly for seeds and berries on which to lay their eggs. The larvae hatch to complete their lifecycle feeding on the seed, leave the seeds to pupate, and emerge as adults at the beginning of next generation. These assumption are motivated by studies of the apple fruit moth, *Argyresthia conjugella* Zeller, which is a pre-dispersal seed predator of rowan, *Sorbus aucuparia* L. The larvae of the apple fruit moth relies heavily on rowan berries that varies substantially between years in a geographically synchronized fashion (Kobro *et al.* 2003; Satake *et al.* 2004).

We assume that host plants are arranged on lattice points of a two-dimensional square grid. The number of emerged adults at site *i* at the beginning of year *t* is denoted by $Z_i(t)$. A fraction, μ, of the adults leaves the plant where they were born and disperses to adjacent plants. The post-dispersal number of adults at site *i*, denoted as $Z'_i(t)$, is given by:

$$Z'_i(t) = (1 - \mu)\, Z_i(t) + \frac{\mu}{w_2} \sum_{j \in R_i} Z_j(t). \tag{4}$$

The parameter R_i is the neighborhood of site *i* and w_2 is the number of host plants included in R_i. For simplicity, we also assume that seed predator disperses to the eight nearest neighbors ($w_2 = 8$). When a single plant at site *i* produces a certain amount of seeds, $F_i(t)$, in year *t*, the number of pre-dispersal adults in the next generation ($t + 1$) is given by:

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

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

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

where *c* is a constant, *k* is the depletion coefficient, and $P_i(t)$ is the pollen availability given by eqn. (3b).

SEED PREDATION ON MASTING RESOURCE

The reproductive behavior predicted by the pollen coupled tree model and severity of seed predation is illustrated in Fig. 2. When the depletion coefficient, *k*, is less than 1, each plant produces seeds every year, which is annual reproduction (Fig. 2A). Annual reproduction can be further classified into "annual and constant reproduction" (shaded area in Fig. 2A) in which each plant produces seeds constantly and "annual and 2-year cyclic reproduction" (checker region in Fig. 2A) in which produced seed crop size alternates between high and low (but positive) reproductive levels. Annual and constant seed production results in severe attacks (Fig. 2B), while annual and 2-yr cyclic seed production can cause extinction of the predator (Fig. 2B). This extinction is due to the satiation of numerical response of

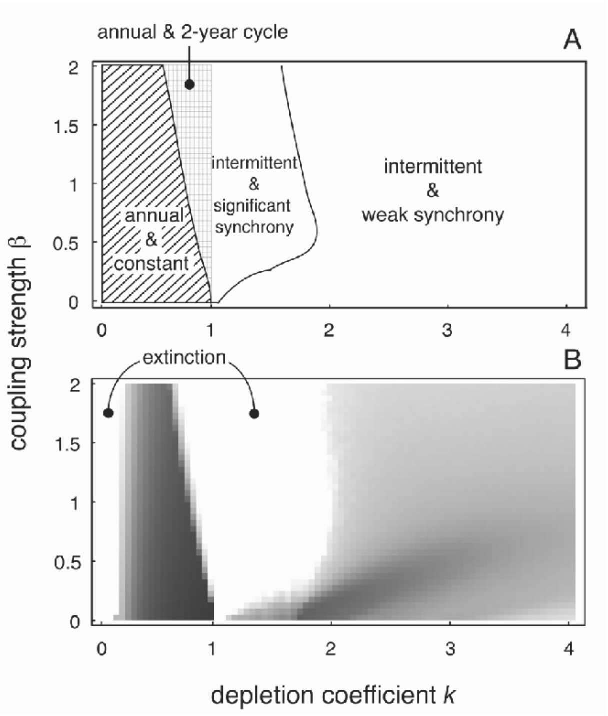

Fig. 2 (A) Classification of reproductive pattern of plants predicted by the pollen coupled tree model with an assumption of local pollen coupling. We classified four types of reproductive pattern as explained in the text. (B) The density plot for proportion of seeds attacked calculated by numerical simulation of the model. The darker area represents more severe seed predation. Parameters: $\mu = 0.8$; $\alpha = 10$. (From A. Satake and O. N. Bjørnstad, Spatial dynamics of specialist seed predators on synchronized and intermittent seed production of host plants, American Naturalist 163, (2004), 591-605. Reprinted with permission from The University of Chicago Press).

the predator — the number of the predators is heavily reduced by a very small seed production in a low reproductive year, and the predator population cannot cope with a great increase in seed production in a high reproductive year, which decreases the population size and finally leads the population to extinction.

When individual plants produce seeds intermittently with numerous years with no seed set (parameter region of $k > 1$ in Fig. 2A), "local" extinction of seed predators is inevitable. However they may nevertheless persist globally due to dispersal when mast synchrony is weak (Fig. 2). In Fig. 2, significant synchrony ($\overline{\rho} \geq 0.8$) is distinguished from weak synchrony ($\overline{\rho} < 0.8$) by calculating the degree of spatial synchrony among plants, $\overline{\rho}$. In a forest exhibiting weak synchrony in seeding, there is always some fraction of plants producing seeds. This enables seed predators to persist globally through dispersal to any asynchronous nearby plants.

In contrast, if plants in a forest produce seeds in a significantly synchronized fashion, seed predators cannot find resources elsewhere within the dispersal range and then go globally extinct (Fig. 2). For masting plants ($k > 1$), the proportion of attacked seeds is inversely related to the degree of spatial synchrony among plants, $\overline{\rho}$ (Fig. 3), meaning that spatial synchrony in seed production effectively reduces losses to seed predators.

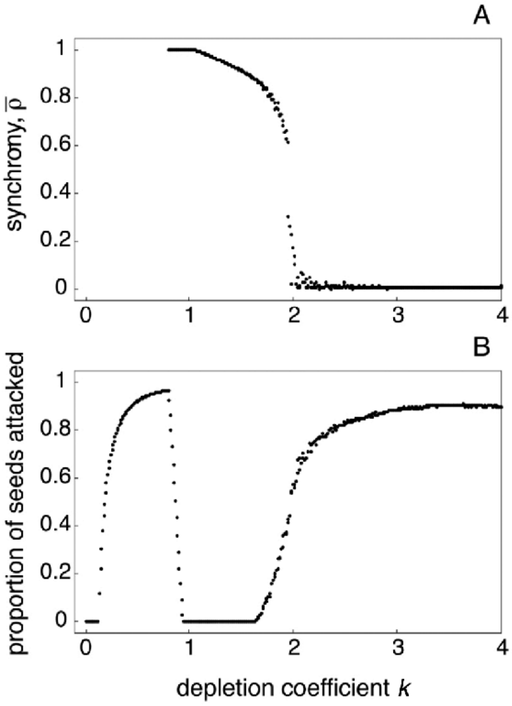

Fig. 3 (A) Degree of synchrony in seed production (ρ). (B) Proportion of seeds attacked. The horizontal axis is the depletion coefficient, k. Parameters: $\beta = 0.8$; $\mu = 0.8$; $\alpha = 10$.

INVASION

We developed an approximate invasion criterion, $\hat{Q}$, that approximately describes when seed predators can invade a system where the host plants produce seeds synchronously and intermittently (see Appendix in Satake and Bjørnstad 2004). Though we have been unable to obtain exact invasion criteria due to the nature of masting resources (i.e., fluctuation across time and space in a cyclic or chaotic manner; Satake and Iwasa 2000, 2002a). The approximate invasion criterion appears to give a good prediction of the invasion and provides key insights into how predator invasion is influenced by the manner of fluctuations of the resource. The approximate invasion criterion $\hat{Q}$ is the average growth or decline in the predator population during two generations following introduction, given as follows:

$$\hat{Q} = \frac{1}{T} \sum_{t=0}^{T-1} Q(t), \tag{7a}$$

where

$$Q(t) = \frac{\alpha^2\gamma^2}{N} \left\{ (1-\mu) \sum_{i=1}^{N} F_i(t)\, F_i(t+1) + \frac{\mu}{w_2} \sum_{i=1}^{N} \sum_{j \in R_i} F_i(t)\, F_j(t+1) \right\}. \tag{7b}$$

In the above equation, N is the number of plants in the forest, and w_2 is the number of plants included in the neighborhood, R_i. $F_i(t)$ is the amount of seed produced by a plant at site i in year t given by eqn. (6). Other parameters are as defined in equations (4) and (5). The first term in the right hand side in eqn. (7b) represents the average population increase (or decline) through two generations for the seed predators that do not disperse — their next-year offspring are left to consume seeds produced by the plant where their parents were born. The second term represents the corresponding average for the predators that dispersed to lay eggs on neighboring plants.

By a simple calculation (Stake and Bjornstad 2004), $\hat{Q}$ is related to the time lag-1 auto-correlation $R(1)$ in seed production of individual plants and time lag-1 cross-correlation $C(1)$ between neighboring plants as follows:

$$\hat{Q} = \alpha^2 \gamma^2 \{(1-\mu)\, R(1)\sigma^2 + \mu C(1)\, \sigma^2 + 2\hat{F}^2\} \tag{8}$$

where σ^2 is the variance and $\hat{F}$ is the temporal mean seedset of each plant. Eqn. (8) shows that invasibility is prompted if seed production is positively correlated in time both for a given plant and for plants within the dispersal neighborhood of the predator. In the case of mast seeding, negative time lag 1 or 2 autocorrelations in seed production are often realized (Norton and Kelly 1988; Sork *et al.* 1993; Koenig *et al.* 1994; Kelly and Sork 2002). In addition, negative cross correlation at time lag 1 often result because of spatially synchronized reproduction. Thus invasibility to the predators is reduced on masting resources.

If seed production with intermittence is synchronized at a “local” spatial scale, nearby plants show a stronger negative cross correlation in seed production at time lag 1 than distantly located plants. In a forest showing regionally (not locally) self-organized seed production, cross correlations calculated at the local spatial scale will be similar to the average across the regional spatial scale. In this case, $Q(t)$ simplifies to:

$$Q'(t) = \frac{\alpha^2\gamma^2}{N}\left\{(1-\mu)\sum_{i=1}^{N} F_i(t)\,F_i(t+1) + \frac{\mu}{(N-1)}\sum_{i=1}^{N}\sum_{j\neq i} F_i(t)\,F_j(t+1)\right\}. \qquad (9)$$

Here, the second term in the right hand side in eqn. (7b) is replaced by the average of the product for all possible pairs (i, j) of plants. By taking the temporal average of $Q'(t)$, we have an approximate invasion criterion in the absence of local spatial structure, $\hat{Q}'$.

We evaluated $\hat{Q}$ and $\hat{Q}'$ numerically by generating the spatiotemporal patterns in seed production from a numerical simulation of the pollen-coupled tree model with a range of parameters resulting in varying degree of masting (Satake and Bjornstad 2004). We confirm the accuracy of the approximate invasion criteria, through numerical simulation of the full consumer-resource model. In theory the seed predators should only be able to invade when $\hat{Q} > 1$. To investigate this, we introduced a minute density of the predator (10^{-4}) on each host plant in the model. We subsequently traced their population growth for 100 generations. If the predator's population is still extant at the end of the simulation, the plant reproductive strategy is considered invasible.

The results including the two approximate invasion criteria are illustrated in Fig. 4. Both criteria are seen to decrease with increasing synchrony of seed set, $\bar{\rho}$, meaning that invasibility is inhibited, partly or entirely, when plants show reproductive synchrony. In simulations, establishment fails when $\hat{Q}$ is below 1 and

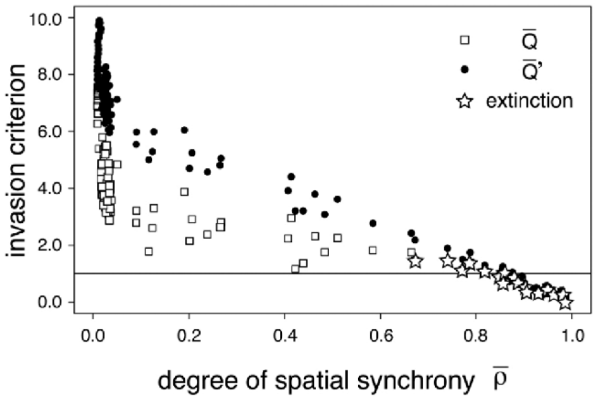

Fig. 4 Plot of the approximate invasion criteria, $\hat{Q}$ (open squares) and $\hat{Q}'$ (solid circles), along the degree of synchrony in seed production among different plants (ρ). Stars represent the values of $\hat{Q}$ in which extinction of seed predators occurred. Parameters: $\mu = 0.8$; $\alpha = 10$. (From A. Satake and O. N. Bjørnstad, Spatial dynamics of specialist seed predators on synchronized and intermittent seed production of host plants, American Naturalist 163, (2004), 591-605. Reprinted with permission from The University of Chicago Press).

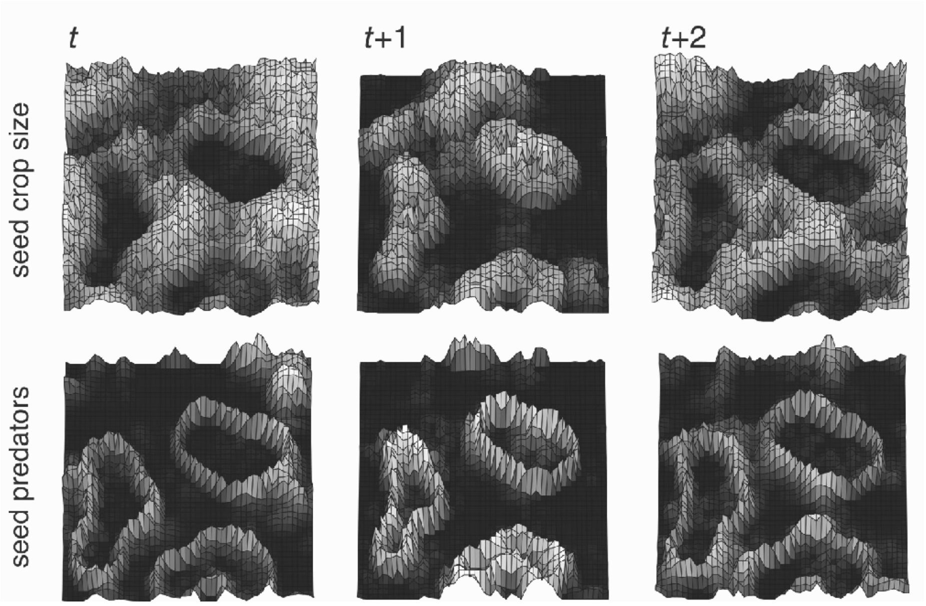

Fig. 5 Spatial patterns in seed production (upper row) and amount of seed predators (bottom row). x and y-axes represent spatial locations, and z-axis represents seed crop size (upper three figures) or seed predator abundance (bottom three figures). Time flows left to right. Parameters: $k = 1.8$; $\beta = 1.0$; $\mu = 0.8$; $\alpha = 10$. 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 ith location, (xi, yi), and jth location, (xj, yj) can exchange pollen if |xi − xj|2 + |yi − yj|2 ≤ 52. The overall spatial pattern is similar, but the spatial scale of the pattern is larger and becomes coarse grained as pollen dispersal range increases (for details, see Satake and Iwasa 2002a). (From A. Satake and O. N. Bjørnstad, Spatial dynamics of specialist seed predators on synchronized and intermittent seed production of host plants, American Naturalist 163, (2004), 591-605. Reprinted with permission from The University of Chicago Press).

succeeds for $\hat{Q} > 1$. This suggests that the approximate invasion criteria based on the population growth during two generations appears to give an excellent prediction of the invasion in the full spatiotemporal simulations. This success originates in part from how the entire forest exhibits a 2-year cycle in seed production when the plant's reproduction is highly synchronized (Fig. 2). The 2-year cyclic seed production becomes unclear at the population level as the degree of synchrony decreases. Thus longer intervals between mast years (e.g. 3 or 4 years) should be taken into account to correct the slight overestimation of the invasion criterion (Fig. 4). Interestingly, $\hat{Q}$ is almost always less than $\hat{Q}'$. This difference highlights that seed predators suffer lower invasibility when reproduction among plants is synchronized at a local spatial scale.

The spatial persistence of predators in the presence of highly variable mast seeding is visualized in Fig. 5. The upper three figures represent the temporal change of spatial distributions for seed crop size produced by individual plants. The figure illustrates how localized spatial clusters can result form local pollen coupling. Within a given cluster, plants show synchronized reproduction with a 2-year cycle visiting high and very low reproductive level. The corresponding spatial distributions of seed predators (bottom panel in Fig. 5) show how the seed predator's persistence is facilitated at the boundaries of the clusters. Seed predators can find resources to consume only when host plants showing opposite reproductive phases are within the dispersal range.

COMMUNITY LEVEL MASTING AND INVASION

In this section, we introduce a simple case study of plant-consumer system, and briefly discuss that when seed predators are generalists, masting at community level is necessary to reduce the impact of the predator. Rowan, *Sorbus aucuparia* L., is a deciduous tree, which is common in much of Europe (Tutin *et al.* 1968). The fleshy berries produced by rowan trees suffer from attack by the apple fruit moth, *Argyresthia conjugella*, that is a primary pre-dispersal seed predator whose larvae rely heavily on rowan berries (Sperens 1997a; 1997b; Kobro *et al.* 2002; Satake *et al.* 2004). The spatiotemporal data obtained from a census in southern Norway show that berry production in rowan is variable across years (mean CV = 1.02) and is spatially synchronized ($\overline{\rho} = 0.67$: bootstrapped 95% confidence interval 0.63-0.70). The degree of spatial synchrony in rowan population is lower than the level of synchrony leading to seed predator extinction (i.e., $\overline{\rho} > 0.8$; Fig. 4), and hence the apple fruit moth successfully invade and is persistent in this system.

However relatively high degree of spatial synchrony in rowan masting efficiently reduces seed losses to the apple fruit moth and suppresses the population growth rate of seed predators at a low level as illustrated in Fig. 7. The proportion of seeds predated was negatively correlated with the total number of seeds, evidencing a satiated functional response of the seed predators by masting. In addition, a negative relationship was observed between the seed predation and the ratio of berry production in successive years. This means that seed crops following poor seed crops tended to escape predations, testifying to a satiation through numerical response of the predators (Satake *et al.* 2004). The predator satiation hypothesis further predicts that the more variable populations should attain higher overall seed survival (Janzen 1971, Waller 1979, Silvertown 1980). To assess this, the total proportion of seeds lost to predation was examined as a function of temporal variability in seed production, measured by the CV. The resultant logistic regression revealed a significantly negative relationship between the proportion of berries predated and CV (the slope $= -1.03$; $p < 0.001$),

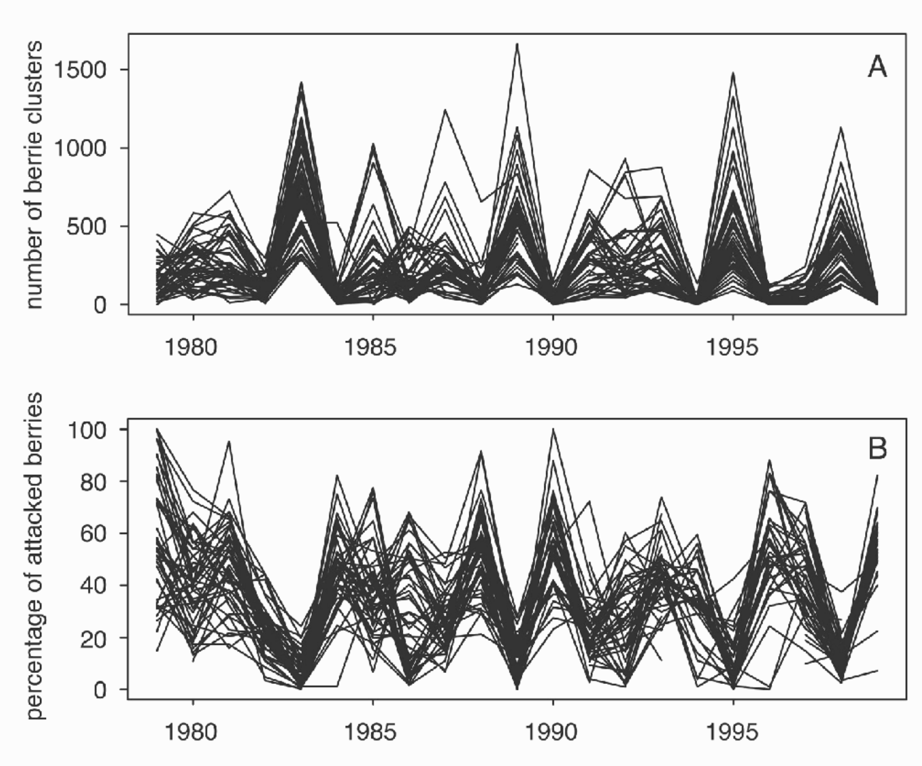

Fig. 6 Time series data of (A) annual berry production of rowan trees, and (B) percentage of attacked berries by the apple fruit moth. Each line represents the time series from one study site. (From A. Satake, O. N. Bjørnstad, and S. Kobro, Masting and trophic cascades: interplay between rowan trees, apple fruit moth, and their parasitoid in southern Norway, Oikos 104, (2004), 540-550. Reprinted with permission from Blackwell Publishing).

indicating that larger inter-annual variation in berry production resulted in smaller losses to predation. These results show that rowan masting has an adaptive foundation, which reduce seed losses to and prevent a rapid expansion in a plant population.

The persistence of the moth in the rowan-moth system is in part because of the fact that the apple fruit moth is not a strict specialist — the primary and preferred host of the apple fruit moth is rowan, but when too few rowan berries are available for egg-laying, many female moths switch the host to apple (Ahlberg 1927). If there are generalist seed predators in a plant community, variable and synchronized seed production only within a single species may not enough to prevent invasion of the seed predator and even masting species showing a significant synchrony in seed production may suffer heavy seed predation. Silvertown

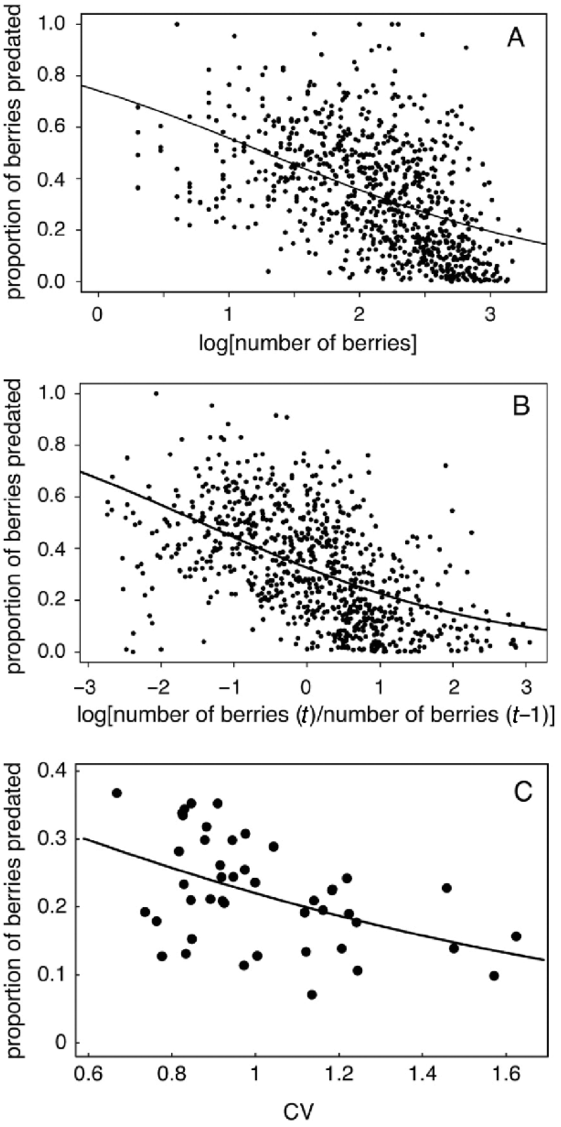

Fig. 7 Plot of proportion of seed predation in rowan as a function of (A) seed crop size and (B) the ratio of seed crop size in year t and that in year $t - 1$ (lag1). Log transformed variables are used for calculation. Lines represents the logistic regression model which have intercepts and slopes of (A) 1.06 (SE = 0.097, $p < 0.001$), –0.82 (SE = 0.055, $p < 0.001$) and (B) –0.73 (SE = 0.030, $p < 0.001$), –0.50 (SE = 0.029, $p < 0.001$). (C) Relationship between the coefficient of variation (CV) of annual seed production and the total proportion of seed predation. Each point represents the result calculated at one study site. Logistic regression analysis gave the regression line as intercept of –0.23 (SE = 0.29, p = 0.44) and slope of –1.03 (SE = 0.29, $p < 0.001$).

(1980) stated that synchronous seed production between population of different species sharing the same seed predators reduces the growth rate of the predator population by predator satiation. Spatial synchrony in seed production among species has been reported in animal-pollinated species in a relatively closed community in the rain forest (Momose *et al.* 1999; Inoue and Hamid 1997; Sakai *et al.* 1999), and in wind-pollinated species in open habitats such as temperate forest and savanna (Koenig and Knops 1998, 2000; Schauber *et al.* 2002; Shibata *et al.* 1998, 2002). Such a synchronized and episodic reproduction in a community provides an interesting insight into the evolutionary process how plant communities enhance resistance against generalist seed predators.

CONCLUSION

This chapter focuses on the spatially-extended dynamics of masting plants and their seed predators. Plants within a forest may produce seeds annually or intermittently in time and synchronously or asynchronously across space. This range of dynamical behavior is captured by the pollen coupled tree model (eqns. (1)-(3); Isagi 1997; Satake and Iwasa 2000, 2002a, 2002b). The effect of mast seeding on dynamics and invasibility of specialist consumers was explored by examining the population dynamics of seed predators in a bottom-up fashion (eqns. (4)-(6)). When plants produce seeds intermittently, persistence and invasion of the predator is most critically dependent on the degree of synchrony of seed set. The predator population can only persist through dispersal to adjacent host plants in a forest showing weak synchrony because there is then some fraction of asynchronously reproducing plants within the dispersal range of the predators. In contrast, extinction of seed predators is likely when intermittent reproduction is highly synchronized among different plants (Fig. 2). Spatial synchrony in seed production with intermittence creates negative time lag-1 auto-correlation and cross-correlation in seeding, which most effectively reduce invasibility of the seed predators (eqn. 8). This means that "classic" mast seeding, exhibiting seed set that is negatively correlated in time but positively correlated across space, is a good strategy to reduce seed loss to seed predators. In addition, analysis of invasion criterion suggest that spatial synchrony at local spatial scales may further reduce losses by preventing invasion of seed predators (Fig. 4).

The spatial scale at which synchrony in seed production reduces seed losses to seed predators depends on the mobility of the predators (Kelly and Sork 2002). Insect predators considered in this chapter may disperse over relatively short distances. Birds or mammals in contrast may be highly mobile (Curran and Leighton 2000). In order to satiate such predators so as to reduce seed losses, larger spatial scales of reproductive synchrony must be maintained. The analysis of approximate invasion criteria given in equations 7 and 8 applies also to highly mobile specialist consumers because the formulations can be written for arbitrary neighborhood sizes (not restricted to nearest neighbor dispersal).

The community consequences of masting are only known for selected case studies. Mice and squirrels, for instance, experience enhanced survival and rapid population growth in years of oak mast. Such population may conversely crash to low levels in years of little acorn because of a shortage of food resources (Wolff 1996; McShea 2000). Masting has also been shown to have cascading effects through food webs and ecological communities, in systems ranging from outbreaks of gypsy moth in oak forests to human risk of Lyme exposure (Ostfeld *et al.* 1996; Ostfeld and Keesing 2000). Such studies on the trophic cascades following variable masting may provide key insights into invasion as a community process (Shea and Chesson 2002).

In this chapter, we focus on the dynamics of a single seed predator species on a single masting resource. In the future it will be of interest to consider invasibility to additional seed predators (and possibly exotic species). When exotic seed predators are introduced into a plant population that show masting, a potential strategy the predator may employ to cope with variable resource availability may be an extended diapause. Kelly *et al.* (2000) and McKone *et al.* (2001) demonstrated that plant populations suffering seed predation by the predators who have extended diapause may need to show extremely high levels of mast seeding. This demonstration has been recently supported by a theoretical study of Satake and Bjørnstad 2004. Therefore, how pre-existing masting might mitigate the impact of invading predators is dependent on the level both of pre-existing masting of plant population and the extended diapause of invader. When the resident seed predator persists on a masting resource, the competitive intensity between the resident and invading species will fluctuate due to spatiotemporal variability in resource availability. Invasion success of an exotic species may be enhanced when the resident population is satiated through large seed crops because unconsumed resources may result in a competitive release. This increase in invasibility may occur through temporal competitive release, or spatially through the formation of competition-free spatial clusters. Invasibility of exotic seed predators is determined by the interwined interaction between temporal process and spatial pattern illustrating the complex community consequences of masting.

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