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SYNCHRONIZED REPRODUCTION OF TREES CAUSED BY POLLEN EXCHANGE: MODELED AS COUPLED CHAOS SYSTEMS

REPRODUCCION SINCRONIZADA DE ARBOLES CAUSADA POR INTERCAMBIO DE POLEN: MODELAJE CON SISTEMAS CAOTICOS ACOPLADOS

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ABSTRACT

Trees in mature forests often show intermittent reproduction. Intensive flowering and seed production occur only once in several years, often synchronized over a long distance. We study a coupled map model for the dynamics of energy reserve of individuals, and show that trees become synchronized in reproduction when their fruit production is limited by the availability of outcross pollen. Without pollen limitation, the trees show independent chaotic fluctuation. With global pollen coupling, trees show various degree of reproductive synchronization. Lyapunov exponents are calculated analytically for perfectly synchronized forests, demonstrating that synchronized reproduction of trees can occur only if trees flower at low (but positive) levels in a significant fraction of years, resulting in small fruit sets due to the shortage of outcross pollen. We then study a coupled map lattice with local pollen exchange. Dynamic spatial covariance shows that a strong synchronization over the whole forest can develop from rather short range pollen exchange. We also discuss the reproductive synchronization between different species who share common pollinators.

RESUMEN

Los árboles de los bosques maduros se reproducen frecuentemente de manera intermitente. La floración intensiva y la producción de semillas ocurren solo una vez en muchos años y frecuentemente están sincronizadas en grandes distancias. Nosotros estudiamos la dinámica de la reserva de energía en individuos con un modelo de mapa acoplado, encontrando que los árboles sincronizan su reproducción cuando su producción de frutos es limitada por la disponibilidad de polen proveniente de otras plantas. Cuando no hay limitación de polen, los árboles muestran fluctuaciones caóticas independientes. Cuando hay acoplamiento global de producción de polen, los árboles muestran un grado variable de sincronización reproductiva. Los exponentes de Lyapunov se calculan analíticamente para bosques perfectamente sincronizados, demostrando que la reproducción sincronizada de los árboles puede ocurrir solamente si éstos florean a niveles bajos (pero positivos) en una fracción significativa de años, resultando en producciones pequeñas de frutos debido a la escasez de polen proveniente de otras plantas. Se estudia entonces un modelo de rejilla de mapa acoplado ("coupled map lattice") con intercambio de polen. La dinámica de la covarianza espacial muestra que, aun con una gama de valores bastante bajos de intercambio de polen, se puede producir una sincronización alta en todo el bosque. También discutimos la sincronización reproductiva entre diferentes especies que comparten los mismos polinizadores.

Key words: synchronized reproduction, masting, globally coupled map, Lyapunov exponents, coupled map lattice; pollen coupling of trees; dynamic spatial covariance.

Palabras clave: reproducción sincronizada, masting, mapa globalmente acoplado, exponentes Lyapunov, mapa lattice acoplado, polen acoplado de árboles, covarianza dinámica espacial

Introduction

Many forest trees reproduce intermittently, rather than at a constant rate. A mast year of high reproductive activity is followed by several years of no or low reproduction. However the interval between mast years is not fixed and rather irregular (Kelly, 1994, Silvertown, 1980). Most studies of masting focus on the adaptive significance. The variance between years in reproductive output due to masting is very large and cannot be simply the outcome of the environmental fluctuation in annual productivity.

Most ecological studies on masting focus on their adaptive significance. A popular hypothesis is based on the predator satiation—seeds might be more likely to escape predation in mast years than in non-mast years (Janzen, 1971; Silvertown, 1980; Koenig *et al.*, 1994, Kelly and Sullivan, 1997). An additional adaptive function is an improved pollination efficiency in mast years (Shibata *et al.*, 1998).

However these hypotheses on the evolutionary advantages of masting explain neither the mechanism causing masting nor how the adjustment of timing of reproduction over different individuals is achieved. Isagi *et al.* (1997) proposed a very simple mechanistic model that considers the resource budget of each tree. Assumptions are: a tree gains a constant energy income every year from their photosynthetic activity, and that the tree may not reproduce while the energy reserve level is below a threshold. Once the energy reserve exceeds the threshold, the tree flowers and may have ovules fertilized by outcrossed pollen. The investment to seeds and fruits produced from these ovules subsequently depletes the energy reserve of the tree. Depending on the degree of energy depletion, a single tree can show either constant reproduction over years, or fluctuating reproduction with a chaotic time series. If the seed and fruit production of a tree is limited by the availability of outcrossed pollen supplied by other trees in the same forest, different tree individuals are coupled by pollen supply and show a synchronized reproductive pattern without an environmental cue (Isagi *et al.*, 1997).

We analyzed Isagi *et al.*'s model in detail (Satake and Iwasa, 2000) and also extended the model to local pollen coupling to answer whether short range coupling by pollen exchange can achieve the synchronization over a very long distance (Satake and Iwasa, 2001).

Trees with sufficient pollen availability. Consider the energy budget of an individual tree. From photosynthesis, a mature tree gains net production P_s each year, and accumulates it in the trunk or branches. Let $S(t)$ be the amount of energy reserve in the beginning of year t. If sum $S(t) + P_s$ is below a critical level L_T the tree does not reproduce and saves all the energy reserve for the following year. In contrast if the sum exceeds L_T, the tree uses energy for flowering. Satake and Iwasa (2000) assumed that the energy expenditure for flowering is proportional to the excess, $a(S(t)+P_s-L_T)$, in which a is a positive constant (Isagi *et al.* (1997) assumed a=1). Flowering plants may be pollinated and set seeds and fruits. If the cost for fruits is proportional to the cost of flowers, it is expressed as $R_c a(S(t)+P_s-L_T)$, in which R_c is the ratio of fruiting cost to flowering cost. After the reproduction, the energy reserve of the tree falls.

$$S(t+1)=\begin{cases} S(t)+P_S & \text{if } S(t)+P_S \le L_T \\ S(t)+P_S-a(R_c+1)(S(t)+P_S-L_T) & \text{if } S(t)+P_S > L_T \end{cases} \quad \textbf{(1)}$$

By introducing a non-dimensionalized variable $Y(t) = (S(t) + P_s - L_T)/P_s$, Eq. (1) becomes:

$$Y(t+1)=\begin{cases} Y(t)+1 & \text{if } Y(t)\le 0 \\ -kY(t)+1 & \text{if } Y(t)>0 \end{cases}, \quad \textbf{(2)}$$

in which $k = a(R_c+1)-1$. The parameter k is depletion coefficient that indicates the resource depletion after a reproductive year divided by the excess energy reserve before the year. From Eq. (2), $Y(t) \le 1$ holds. $Y(t)$ is positive if and only if the tree invests some to reproductive activity in year t.

Dynamics (2) include only one parameter k. Other parameters such as the annual productivity P_s or the critical level of reproduction L_T do not affect the essential features of the dynamics if k remains the same. Figures 1 illustrates trajectories for three different values of k. As shown in Fig. 1A, when k is less than 1 ($0<k<1$), $Y(t)$ quickly converges to the stable equilibrium $1/(k+1)$. Then

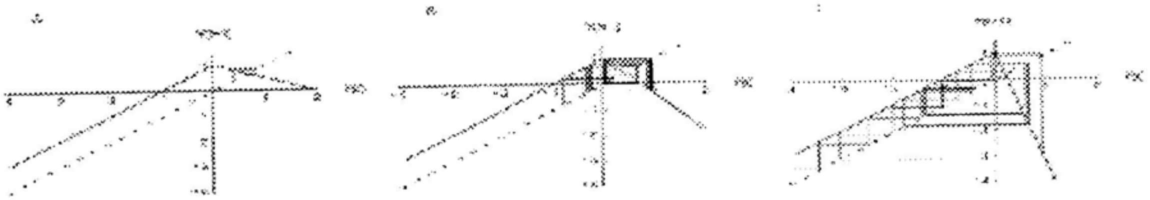

Figure 1. Return map and the trajectory of a tree without pollen limitation. (A) $k = 0.5$, stable equilibrium. (B) $k = 1.4$, chaotic fluctuation. (C) $k = 4.3$, chaotic fluctuation with longer intervals between mast years. Source: Satake and Iwasa (2000).

the tree reproduces every year at a constant rate. In contrast when k is greater than 1, $Y(t)$ keeps fluctuating with a chaotic time series (Figs. 1B and 1C).

Figure 2A illustrates a bifurcation diagram of Eq. (2). The horizontal axis is the depletion coefficient k. The long term trajectory of $Y(t)$ after transients is plotted, and it fills an interval: $-k + 1 \leq Y \leq 1$ for $k > 1$. Negative values of $Y(t)$ with $k > 1$ imply non-reproductive years. As the depletion coefficient k increases, a longer interval between nonproductive years is needed for the energy reserves to recover the reproductive threshold. Satake and Iwasa (2000) calculated the long-term average distribution of $Y(t)$.

Lyapunov exponent. Chaotic behavior exhibits a sensitive dependence on the initial condition. The difference between two trajectories starting from slightly different initial conditions increases with time, and the two trajectories become entirely different after many years. We can distinguish chaotic behavior from equilibria or stable periodic cycles by the Lyapunov exponents (Wolf *et al.*, 1985; Ruelle, 1989), which is the long-term average of the exponential rate of divergence of nearby trajectories, in which the average is calculated along a trajectory. If Lyapunov exponent l is negative, the trajectory converges to either an equilibrium or a stable periodic cycle. If l is positive, the trajectories tend to deviate from each other, and wander around indefinitely without converging to any periodic cycle. Hence the system is chaotic.

For the model given by Eq. (2), the Lyapunov exponent is positive for $k > 1$. This implies that small initial differences in energy reserves between individuals increase with time, and that the perfect synchronization cannot be maintained without additional process to make trees synchronized.

Coupling of trees through pollen availability. Fruiting efficiency may depend on the flowering activity of the other trees in the same forest because pollination efficiency changes with the number of flowering plants (Nilsson and Wästljung, 1987; Smith *et al.*, 1990). Consider a tree that flowers in a year in which only a small fraction of other trees flower. The tree fails to produce many fruits because of pollen limitation, and it will not experience a heavy resource depletion. It will continue to flower in the following years, until the year comes in which many other trees in the forest also flower at a high blooming intensity. Then they all experience a large fruit set and resource depletion, which gives a mechanism to make different individuals synchronized in the face of chaotic tendency of each individual.

Consider a forest including N individuals with index i ($i = 1, 2, .., N$). To model the pollen limitation of reproduction, we replace k in Eq. (2) by $kP_i(t)$. $P_i(t)$ is a factor smaller or equal to 1, and it indicates pollen availability for the ith tree. Then the non-dimensionalized energy reserve of the ith tree is:

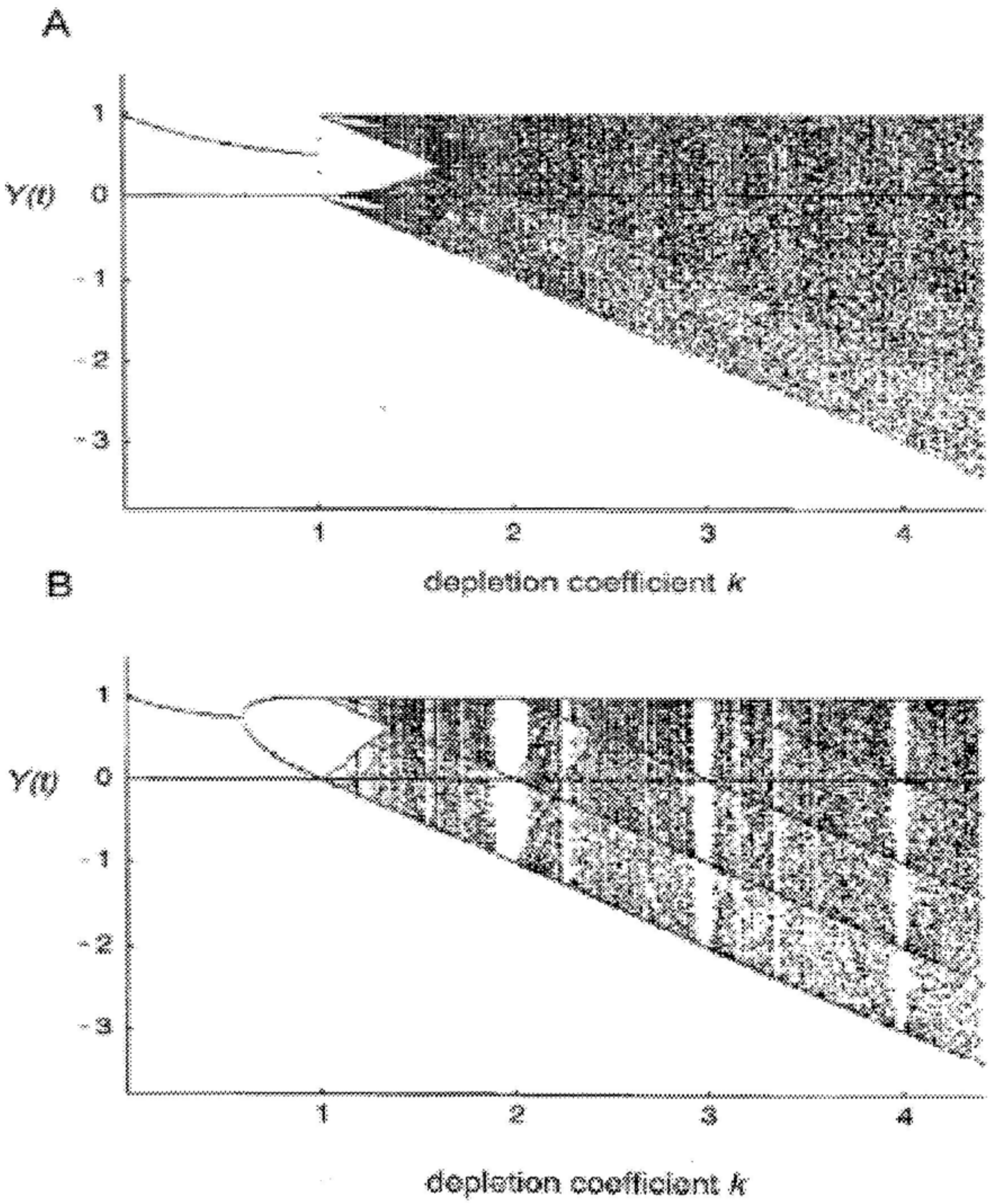

Figure 2. Bifurcation diagram of a single tree. Horizontal axis is depletion coefficient k, and the vertical axis is $Y(t)$ for many time units t. (A) A single tree without pollen limitation. (B) A tree in a globally coupled forests. Parameters are $\beta = 2$; $N = 100$. Source: Satake and Iwasa (2000).

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

in which $P_i(t)$ is given by

$$P_i(t)=\left(\frac{1}{N-1}\sum_{j\neq i}\left[Y_j(t)\right]_+\right)^{\beta}, \qquad \textbf{(3b)}$$

where $[Y]_+=Y$ if $Y>0$; $[Y]_+=0$ if $Y\le 0$. $P_i(t)=1$ holds when all the other trees reproduce at full intensity ($Y_j(t)=1$ for all $j \neq 1$). The smallness of $P_i(t)$ indicates the strength of pollen limitation in seed and fruit production. Parameter β in Eq. (3b) controls the dependence of fruit production on outcross pollen availability. If β is close to zero, fruit production is almost independent of the reproductive activity of the other trees. Small β corresponds to either a high pollination efficiency or a high density of trees because a small fraction of flowering in the rest of the forest is sufficient to achieve a good fruiting success. In contrast, a large β implies a strong dependence of seed and fruit production on the reproductive activity of other trees in the forest. Hence β indicates coupling strength.

Eq. (3) is an example of coupled nonlinear dynamics in which each element in isolation has chaotic dynamics. It exhibits diverse dynamical behaviors that are qualitatively similar to coupled logistic maps (e.g. Kaneko, 1990; Hastings, 1993)

The model includes only two parameters k and β. Figure 3 is a phase diagram, in which the horizontal and vertical axes are k and β, respectively. Five phases are classified:

[1] Annual reproduction: If the depletion coefficient k is less than one, all the mature trees in the forest reproduce every year.

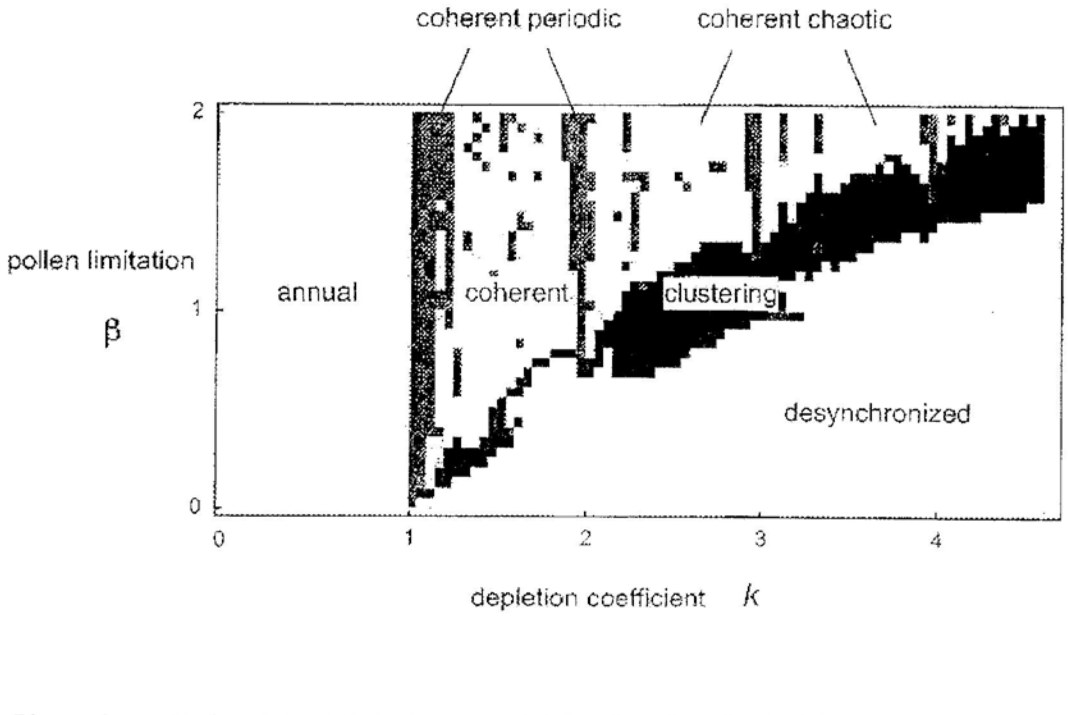

Figure 3. Phase plane. Horizontal axis is depletion coefficient k, and vertical axis is coupling strength β. We classified five regions, as explained in the text. For each run, we calculated effective number of clusters based on $NC = 1/\sum_i p_i^2$, in which p_i is the fraction of trees belonging to the ith cluster. The region with $k>1$ is classified according to the average of NC for 100 replicates: desynchronized phase ($N-1<\overline{NC}\le N$), coherent phase ($1\le \overline{NC}<2$), and clustering phase ($2\le \overline{NC}\le N-1$). Total number of individuals was $N=100$. Source: Satake and Iwasa (2000).

[2] Desynchronized phase: If the depletion coefficient k is sufficiently large compared to the coupling strength β, any two trees in the forest reproduce in a different way and there is no synchronous reproduction. The amount of pollen produced in the forest is constant because there are always some trees that reproduce, but each individual tree shows intermittent reproduction.

[3] and [4] Coherent phases: If the coupling β is large compared to the depletion coefficient k, all the trees in the forest show synchronized and fluctuating reproduction. Depending on the nature of the time series of seed crop, we further classify into [3] a coherent chaotic phase and [4] a coherent periodic phase.

[5] Clustering phase: Between the desynchronized phase and the coherent phase, there is a region in which clustering phenomena are observed. Typically trees are separated into several clusters, with trees of the same cluster reproducing in a synchronized manner.

In Fig. 3, the desynchronized, coherent, and clustering phases are distinguished by the average effective number of clusters (see caption to Fig. 3).

Periodic reproduction of coupled trees

In this section, we focus on the coherent phase in which all the trees are perfectly synchronized. Periodic reproduction when parameter k is close to an integer can be seen from bifurcation diagram in Fig. 2B. If k is close to an integer n, the system shows a stable periodic reproduction that is close to a cycle with period of $n+1$. The trajectory of period $n+1$ consists of a mast year in which all the trees in the forest reproduce nearly at the maximum strength, followed by n years of no or very small reproduction. The exact period of the cycle may be multiple of $n+1$, but their trajectory is numerically close to the one with period $n+1$ (Satake and Iwasa, 2000).

Stability of synchronized reproduction implies imperfect masting

In the coherent phase, all the trees are perfectly synchronized and have the same energy reserve levels. Along such a trajectory, the Jacobi matrix is diagonal because of the symmetry between trees, and all the Lyapunov exponents are calculated (Satake and Iwasa 2000). The whole system has N Lyapunov exponents. The largest exponent λ_1 is related to the fluctuation of the total energy reserve summed over the trees

$$\sum_i Y_i$$

The other N-1 exponents are related to the difference of energy reserve between trees, and they have a common value λ_2. For a coherent trajectory to be locally stable, small differences in energy reserve between individuals should decrease with time, and hence λ_2 needs to be negative. This condition gives the following inequality if the number of trees N is large:

$$\prod_{\substack{t \text{ s.t.} \\ Y(t)>0}} kP(t) < 1, \tag{4}$$

where the product is calculated for t with $Y(t)>0$ along the trajectory, i.e. only for those years in which trees reproduce. Since all the trees have the same Y_i, we dropped the suffix i. $P(t)$ is the pollen availability ($P(t)=Y(t)^{\beta}$), which is 1 when all the trees reproduce at full intensity, and it is less than 1 if pollen availability is limited. k is larger than 1 since we consider a forest consisting trees that show intermittent reproduction ($k>1$). For Japanese beeches k is estimated to be close to 5 (Isagi *et al.* 1997). If $P(t)$ is always close to 1, Eq. (4) cannot be satisfied. Equation (4) is satisfied only if the trajectory includes sufficiently many years in which trees reproduce ($Y(t)>0$), but pollen availability $P(t)$ is clearly smaller than 1 ($0<P(t)<<1$). In those years, trees engage in some flowering but cannot set many fruits because of limited outcross pollen availability. A stable coherent trajectory must include a significant fraction of imperfect mast years.

Satake and Iwasa (2000) analyzed the distribution of energy reserve level in a desynchronized forest.

Local pollen coupling

Pollen dispersal range, measured using genetic markers (Cruzan 1998), is fairly long (>500m, Hamrick and Loveless, 1989; and about 75m, Dow and Ashley, 1998). However the reproductive activity of trees show synchronization over a very long distance (>100 km) (Koenig *et al.*, 1999), which is much greater than the spatial range for direct interaction between trees. Because of this difference in spatial scale, the observed long-distance synchronization has been regarded as a simple outcome of environmental forcing caused by climatic fluctuation that are experienced commonly by trees located distantly. Satake and Iwasa (2002) asked whether the local interaction of trees is able to create the reproductive synchronization of a much longer spatial scale.

We consider a forest composed of a number of trees arranged on lattice points of a two-dimensional square grid. Trees are indexed by $\mathbf{x}=(x_1,x_2)$, in which x_1 and x_2 are integers ($x_1,x_2=1,2,...L$). Each tree accumulates photo-synthate, reproduces, and experiences subsequent depletion of stored resources in a way proposed by Isagi *et al.* (1997).

$Y_{\mathbf{x}}(t)$ is nondimensionalized storage for a tree at $\mathbf{x}$. Eq. (3a) holds if index i is replaced by $\mathbf{x}$. The pollen availability for a tree is determined by the average flowering intensity of its neighbors:

$$P_{\mathbf{x}}(t)=\left(\frac{1}{z}\sum_{\mathbf{y}\in U_{\mathbf{x}}}\left[Y_{\mathbf{y}}(t)\right]_+\right)^{\beta}, \qquad \textbf{(5)}$$

where $[Y]_+=Y$ if $Y>0$; $[Y]_+=0$ if $Y\leq 0$. $U_{\mathbf{x}}$ stands for the set of neighboring trees that are pollen donors for the focal tree at $\mathbf{x}$, and z is the number of trees in $U_{\mathbf{x}}$. Satake and Iwasa (2002) chose $U_{\mathbf{x}}$ as a circle centered around the focal tree with radius D. Two flowering trees located at $\mathbf{x}=(x_1,x_2)$ and $\mathbf{y}=(y_1,y_2)$ can exchange pollen only if

$$\left|x_1-y_1\right|^2+\left|x_2-y_2\right|^2\leq D^2$$

The model given by Eqs. (3a) and (5) is an example of "coupled map lattices" (abbreviated as CMLs), which have been studied in theoretical physics (Kaneko 1989) and in population ecology (Hassell *et al.*, 1991; Hastings, 1993; Bascompte and Solé, 1998; Blasius *et al.*, 1999). A CML is a system of many elements, each engaging discrete-time state transitions and interacting with neighbors in a simple manner. CMLs were adopted for forest gap dynamics in tropical seasonal forest (Sole and Manrubia, 1995), and also for the global pattern formation of forests generated by simple local interaction between trees exemplified by modeling wave-regeneration (Sato and Iwasa, 1993; Iwasa *et al.*, 1991; Jeltsch and Wissel, 1994; Satake *et al.*, 1998; Yokozawa *et al.*, 1998).

Synchronization and spatio-temporal patterns

To analyze the spatio-temporal pattern of reproductive activity of trees, we consider the fruit production activity (or seed crop size) of a tree at $\mathbf{x}$ in year t, denoted by:

$$\varphi_{\mathbf{x}}(t)=kP_{\mathbf{x}}(t)\left[Y_{\mathbf{x}}(t)\right]_+$$

Between-year and Within-year Variances

We first consider two indexes for the variations of seed crop size $\varphi_{\mathbf{x}}(t)$. Suppose that we have a data set of the seed crop size for N trees in a forest recorded for a period of T years. Let $\varphi_{\mathbf{x}}(t)$ be the seed crop size produced by a tree located at $\mathbf{x}=(x_1,x_2)$ in year t ($t=1,2,...,T$). The mean seed crop of all the trees in the forest in year t is denoted by $\overline{\varphi}(t)$, and its average over the years is denoted by $\overline{\overline{\varphi}}$. The between-year variance V_{by} is the magnitude of fluctuation of the mean seed crop $\overline{\varphi}(t)$ over the years, and the within-year variance V_{wy} is the variance of seed crop size between trees in a single year, and then averaged over the years:

$$V_{by}=\frac{1}{T}\sum_{t=1}^{T}\left(\overline{\varphi}(t)-\overline{\overline{\varphi}}\right)^2, \qquad \textbf{(6a)}$$

$$V_{wy}=\frac{1}{T}\sum_{t=1}^{T}\frac{1}{N}\sum_{\mathbf{x}}\left(\varphi_{\mathbf{x}}(t)-\overline{\varphi}(t)\right)^2. \qquad \textbf{(6b)}$$

In a forest with trees strongly synchronized in reproduction, the year-to-year fluctuation of the reproductive level is large(the within-year variance V_{wy} is small but the between-year variance V_{by} is large) (Koenig *et al.*, 1994). In contrast, in a desynchronized forest, the mean reproductive level of the forest does not change between years, and the forest always includes some trees producing a large number of acorns and others producing little, with their fractions unchanged (the within-year variance V_{wy} is large but the between-year variance V_{by} is small).

In the computer simulations, we started from a random initial condition, ran the model for 20,000 years, and then sampled the data $\{\varphi_x(t)\}$ (for details see Satake and Iwasa, 2002). The lattice was of 100x100, and the periodic boundary condition was adopted to remove the effect of margins. We first examine the case in which each tree has only four neighbors (Neuman neighborhood).

Figure 4 illustrates the density-plot of the ratio of between-year variance to the total variance $V_{by}/(V_{by}+V_{wy})$, an index of global synchrony, for various parameter sets (k,β) (Satake and Iwasa, 2002). If depletion coefficient k is smaller than 2, the model with nearest neighbor pollen exchange can show a strong synchronization, as indicated by the dark area in Fig. 4. This implies that a strong synchronization of tree reproduction over the whole forest can be produced by a short range interaction.

The effect of the coupling strength β is rather weak. Even if coupling strength β increases, synchronization over the whole forest does not occur if k is larger than 2. This result makes a clear contrast to the model of global pollen exchange, illustrated in Fig. 3.

Bifurcation Diagram

Fig. 5 illustrates the bifurcation diagram. The vertical axis represents the mean reproductive activity of the forest, denoted by $\overline{\varphi}(t)$ showing the results after the transients. The diagram shows a clear difference in behavior between $1<k<2$ and $k>2$. For k smaller than 2, $\overline{\varphi}(t)$ visits two sets of values. The forest in a year is either at a high reproductive level or at a low reproductive level, alternately, showing strong synchrony (Fig. 4). If k is larger than 2, $\overline{\varphi}(t)$ centered around a single value (Fig. 5), which implies that the mean reproductive activity does not change between years. In such a desynchronized forest, the fraction of trees which bloom, the mean pollen availability, the total number of seeds produced in the forest are almost constant.

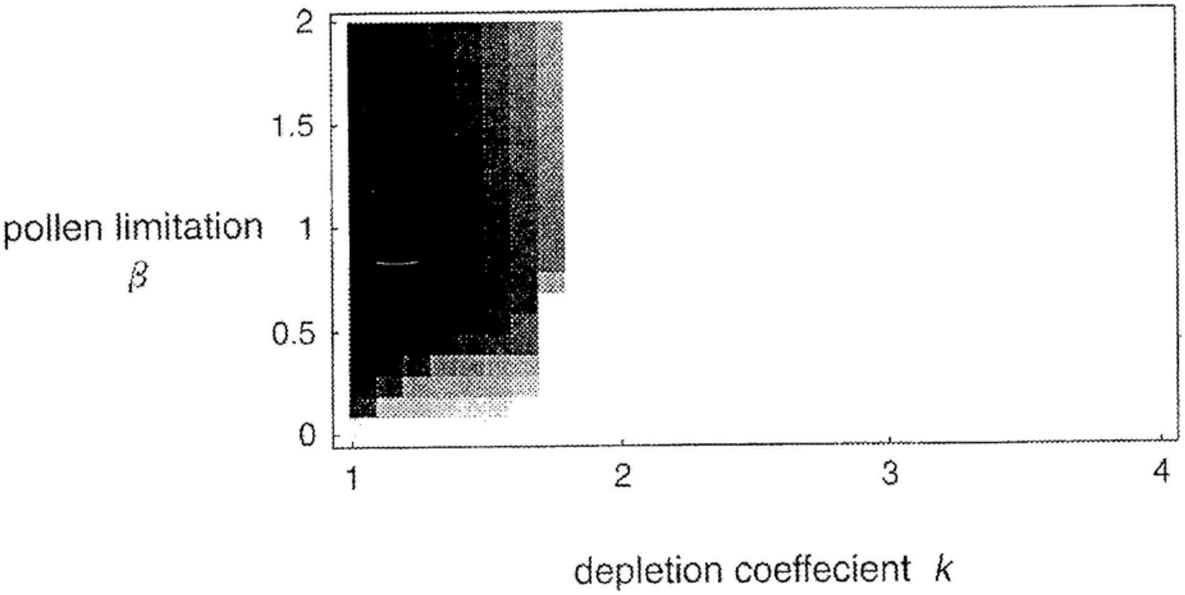

Figure 4. Phase diagram of the ratio V_{by}/V_{total}, indicated by the density plot where dark squares indicate a large index of global synchrony V_{by}/V_{total}. Horizontal axis is for depletion coefficient k, vertical axis is for coupling strength β. We consider pure local coupling (D=1). The number of years sampled is T=100. Source: Satake and Iwasa (2002).

Dynamic Spatial Covariances

A commonly used statistic for spatio-temporal dynamics in population ecology is the spatial covariance $\hat{C}(d)$ (Ranta *et al.*, 1998; Bjørnstad *et al.*, 1999; Koenig *et al.*, 1999). It indicates the degree of synchronization between two sampled trees as a function of their distance. It gives both the magnitude and the spatial scale of synchrony over which trees show positive reproductive correlation. We first consider a pair of points, **x** and **y** on the lattice and calculate the cross-covariance of two time series of seed crop at these locations:

$\{\varphi_{\mathrm{x}}(t)\}_{t=1}^{T}$ and $\{\varphi_{\mathrm{y}}(t)\}_{t=1}^{T}$, defined as follows:

$$C(\mathbf{x},\mathbf{y}) = \frac{1}{T}\sum_{t=1}^{T}\left(\varphi_{\mathrm{x}}(t)-\hat{\varphi}_{\mathrm{x}}\right)\left(\varphi_{\mathrm{y}}(t)-\hat{\varphi}_{\mathrm{y}}\right), \tag{7a}$$

where $\hat{\varphi}_{\mathrm{x}}$ is the mean seed crop of a tree located at **x** over T years. Then we calculate the average of two point covariance $C(\mathbf{x},\mathbf{y})$ for those pairs with distance equal to d:

$$\hat{C}(d) = \frac{1}{P(d)}\sum_{|\mathrm{x}-\mathrm{y}|=d} C(\mathbf{x},\mathbf{y}), \tag{7b}$$

where the sum is calculated over all the pairs of sites separated by distance d, and $P(d)$ is the number of those pairs. Satake and Iwasa (2002) called $\hat{C}(d)$ "the dynamic spatial covariance".

Dynamic spatial covariance $\hat{C}(d)$ decreases with distance d (Fig. 6), and it becomes equal to the variance in the average over the forest V_{by}. If k is less than 2, V_{by} is large and the dynamic spatial covariance $\hat{C}(d)$ remains high even for large d (Fig. 6A). This implies that the synchrony between two isolated trees is realized even if their distance is large. In contrast, for k larger than 2, V_{by} is very small, and $\hat{C}(d)$ becomes close to zero for large d (Fig. 6B). In such a case, two trees separated beyond several times longer than the interaction distance are not correlated in their reproductive activity.

Extended Range of Pollen Dispersal

Even when a strong global synchrony occurs, the synchronization between individuals in the forest is not perfect. There remains some spatial variation of $\varphi_{\mathrm{x}}(t)$ between individuals. The spatial pattern is not uniform but has a characteristic heterogeneity, as illustrated in Fig. 7. This makes a sharp contrast with the globally coupled model, in which all the trees in the same forest have exactly the same $\varphi_{\mathrm{x}}(t)$ for a wide range of parameters (Satake and Iwasa, 2000). This local spatial heterogeneity causes spatial covariance $\hat{C}(d)$ for small d larger than the covariance between randomly chosen individuals $\hat{C}(\infty) = V_{by}$, which implies that close neighbors tend to behave similarly.

We also examined the cases in which pollen dispersal range D is greater than 1 (Satake and Iwasa, 2002). The availability of outcross pollen for a tree now depends on the neighbors more than four. The overall spatial patterns look quite similar, and the condition in which synchronization occurs remain the same, but the spatial scale of the pattern is larger and becomes more coarse grained as D increases. When the pollen availability of a tree is a mixture of local pollen (depending on the flowering intensity of neighbors) and the global pollen (the average over the entire forest). As the contribution of globally dispersed pollen increases, the parameter range for synchronization becomes broader. Even for k larger than 2, global synchronization occurs if coupling constant b is correspondingly large.

DISCUSSION

We analyzed in detail coupled map models for pollen-coupled trees first proposed by Isagi *et al.* (1997), in which the dynamics of the energy reserve of each tree are explicitly considered. When coupling is global, depending on the strength of coupling by pollen limitation relative to the magnitude of energy reserve depletion after reproduction, the whole forest may show diverse dynamic behaviors, such as perfectly synchronized periodic reproduction, synchronized reproduction with a chaotic time series, clustering phenomena, and chaotic reproduction without synchronization.

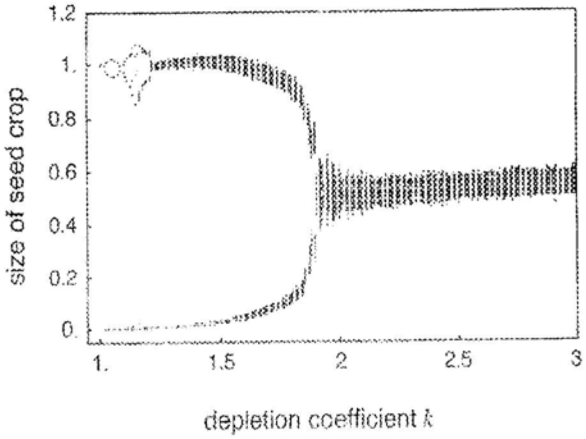

Figure 5. Bifurcation diagram. Starting from a random initial condition, we ran the model for 20,000 years, and then plotted 250 iterations in this graph. Horizontal axis is depletion coefficient k. The pollen dispersal range is: (A) D = 1; (B) D = 5; and (C) D = 10. Coupling strength is β = 1.6. Source: Satake and Iwasa (2002).

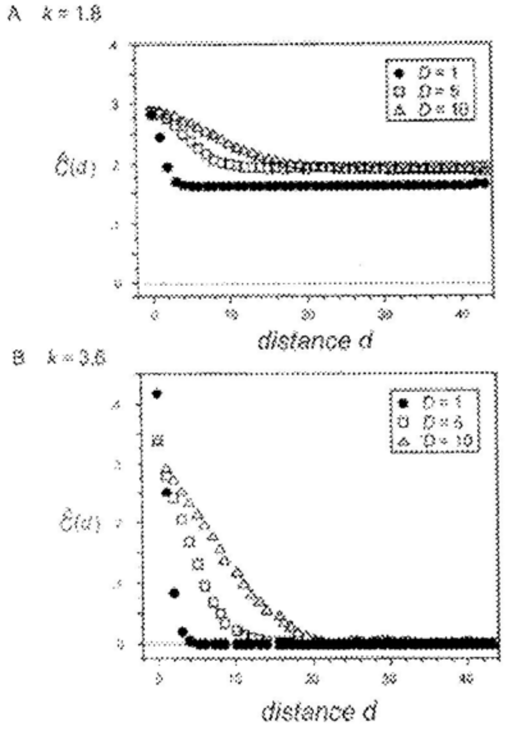

Figure 6. Dynamic spatial covariance $\hat{C}(d)$ of seed output of trees. Results for different neighborhood sizes, indicated in the graph, are shown (D = 1, 5, and 10). Depletion coefficient is: (A) k = 1.8, and (B) k = 3.6. Coupling strength is β = 1.6. Source: Satake and Iwasa (2002).

Figure 7. The spatial patterns generated by the model. The density plot is for seed output of individual trees, $\varphi_x(t)$. Dark squares are for high seed crops. Open squares are trees without seed crop ($\varphi_x(t) = 0$). Neighborhood size is D = 1. Parameters are: k = 3.6, and β = 1.6. Source: Satake and Iwasa (2002).

In masting, many trees reproduce synchronously but the synchrony is often not perfect (Sharp and Sprague, 1967; Koenig *et al.*, 1994). Even for synchronized reproduction, the time series of mast years is not perfectly periodic (Sork *et al.*, 1993; Koenig *et al.*, 1994). These are regarded as deviations from ideally synchronized periodic reproduction caused by external environmental fluctuations (Sork *et al.*, 1993) or by individual variability in production rate (Yamauchi, 1996). The pollen-coupled tree model proposes an alternative view — each tree has an inherent tendency to fluctuate chaotically, and the synchronization and periodicity are secondary characteristics formed through pollen-coupling.

In the coherent phase, the coupling strength is large compared to the depletion coefficient, and the reproduction of all the trees are synchronized (Fig. 6). Stability analysis based on Lyapunov exponents revealed that the time series of reproductive activity must include sufficiently many years in which trees reproduce but at a low level (Satake and Iwasa, 2000). This prediction is consistent with the observation that the distinction between mast years and non-mast years is not clear-cut (Kelly, 1994; Herrera *et al.*, 1998).

The local coupling model demonstrated that the pollen exchange between trees over short distances (about 20 to 50 meters) can create reproduction synchronized over the whole forest (10 to 100 km). However, the condition for the long-range synchronization of the local pollen coupling model is different from the global coupling model. First, in the model with local pollen coupling, a strong long-range synchronization occurs only for k smaller than 2 and the time series of mean reproductive activity of the whole forest is close to a cycle of period 2 (Fig. 6A). Second, a large coupling strength β cannot promote the synchronization very much (Fig. 4). Third, for any set of parameters, the locally coupled model always generates nonuniform spatial patterns (Fig. 7).

The currently accepted explanation for the synchronization of trees in masting over a long distance is based on the common climatic fluctuation experienced by different individuals, often special climatic conditions (e.g. a very cold winter) that triggers reproduction of different individuals is suspected as responsible. The present study proposes an alternative hypothesis for the mechanism of synchronization. Synchronization of reproduction between individuals over a very long distance can be created as a spontaneous outcome of short range pollen-coupling.

Modification of our model to incorporate an aspect of the environment as a cue to synchronize the reproduction can easily be achieved by assuming that the reproductive threshold L_T may depend on climatic conditions. According to the preliminary results (A. Satake, H. Tanaka and Y. Iwasa, MS in preparation), the effect of common environment can create the positive correlation between trees, but in the absence of pollen coupling, the effect is not very strong because underlying chaotic dynamics constantly work to make the forest desynchronized.

In tropical rain forests, trees of different species sometimes show synchronized reproduction (Momose *et al.*, 1996; Sakai *et al.*, 1999), but within each year different species reproduce in a staggered manner (Ashton *et al.*, 1988). Synchronization of different species is often explained by assuming that these species happen to adopt a common environmental cue (such as a low temperature) to achieve synchronization within each species (T. Kohyama, personal comm.). Reproductive synchrony between different animal-pollinated species, reported among tropical rain forest can be explained if they share the common pollinators, because an intensive flowering of a tree enhances the availability of pollinators for the other species by supplying the reward (Satake and Iwasa, 2000). Here again the study of tropical ecosystems, especially on the interaction of trees with various fauna, including pollinators, seed dispersers, herbivores, as well as pathogen vectors, will be one of the research foci of spatio-temporal pattern formation in ecology. Professor Jesus Alberto Leon is one of the founders of the modern evolutionary ecology. Many of his theoretical works on life history evolution, resource allocation, population/community dynamics and coevolution constitute an indispensable part of our current understanding of how tropical ecosystems and biological communities work. We believe that theoretical and experimental studies by Professor Leon and his colleagues in Venezuela will continue to play a key role in ecology and evolution over the centuries.

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