Role of gap dynamics in the evolution of masting of trees

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ABSTRACT

Question: When should masting (the intermittent and synchronized reproduction of forest trees) evolve?

Mathematical models: The resource budget of each tree is traced. Trees need outcross pollen to produce fruits, and trees within an entire forest exchange pollen with each other (global pollen coupling). The forest is composed of a number of sites. Each site can lose its trees, after which it becomes a gap, available for recruitment from seeds.

Model analysis: We developed a new graphical method called the finite pairwise invasibility plot (fPIP), which shows whether a mutant phenotype has a fixation probability higher than the neutral case. We search for the evolutionary outcome in a finite population.

Conclusion: In the absence of seed predators, trees will evolve masting only if it improves their pollination efficiency. In addition, (1) empty sites (gaps) need to remain empty over multiple years, and (2) pollen limitation must be severe in non-mast years.

Keywords: finite pairwise invasibility plot, games in finite population, gap dynamics, masting, mast seeding.

INTRODUCTION

Masting is the intermittent reproduction of trees synchronized over long distances and is observed in many diverse forests (Kelly, 1994). In a mast year, many trees show high reproductive activity, which is followed by several non-mast years of no or low reproduction (Herrera *et al.*, 1998; Koening and Knops, 1998, 2000; Koening *et al.*, 1999). The variance in the reproductive activity of trees between years is great. It cannot be simply a result of environmental fluctuation in annual productivity (Tamura and Hiura, 1998).

Many studies on masting have focused on adaptive significance (Kelly and Sork, 2002). A popular hypothesis is the predator satiation theory – that is, seed predators starve during non-mast years, while they are unable to consume all seeds during mast years (Janzen, 1971; Silvertown, 1980; Nilsson and Wästljung, 1987; van Schaik *et al.*, 1993). An alternative hypothesis is pollination efficiency: in mast years trees receive a lot of outcross pollen, which may

improve fruiting success compared with reproduction in non-mast years (Nilsson and Wästljung, 1987; Smith *et al.*, 1990; van Schaik *et al.*, 1993; Shibata *et al.*, 1998; Kelly *et al.*, 2001; Rees *et al.*, 2002; Satake and Bjørnstad, 2004).

To explain the mechanisms responsible for the intermittent reproduction of trees, the resource budget model was proposed by Isagi *et al.* (1997), and has been analysed in detail by Satake and Iwasa (2000, 2002a, 2002b). The basic assumptions are as follows: Each tree accumulates resources every year from photosynthesis, and reproduces when the resource reserve exceeds a reproductive threshold. Depending on the resource investment required for flowering and fruiting, a single tree can show either constant reproduction over the years, or fluctuating reproduction with a chaotic time series (Satake and Iwasa, 2000). A key parameter in the control of fluctuation is the resource depletion coefficient k. When k is smaller than or equal to 1, each tree reproduces every year and no intermittent reproduction occurs. In contrast, when k is greater than 1, each tree reproduces intermittently. In this case, the level of reserves of each tree shows chaotic fluctuation, with a positive Lyapunov coefficient (Satake and Iwasa, 2000). This implies that trees with a very close energy reserve initially would become completely different after a relatively few years – highlighting the difficulty of maintaining synchronized reproduction of trees without additional processes. A shortage of outcross pollen may help to make trees synchronized, which Satake and Iwasa (2000) called 'pollen coupling'. Because the spatial range of pollen exchange is much shorter than a whole forest, the environmental fluctuation common to trees far from each other would also be important in making trees synchronized, called the 'Moran effect' (Satake and Iwasa, 2002a, 2002b). In a lattice structured population, a short-range interaction via pollen exchange (pollen coupling) combined with common environmental fluctuation synchronized over a long distance (Moran effect) is the most likely explanation for the synchronization of forest trees (Satake and Iwasa, 2002b).

None of the above theoretical studies of the resource budget model have discussed evolution of the resource depletion coefficient k. In the present paper, we discuss the evolution of this key parameter.

We consider N individuals that exchange their pollen with each other. We trace the level of resource reserve, flowering activity, and seeding success of each individual through time. When we think of the evolution of parameter k, we consider that a mutant with a different value k' invaded the population dominated by the resident phenotype with k. The mutant may go extinct or increase in number and finally take over the whole population. If the number of individuals N is not very large, there is considerable stochasticity in the process of invasion and replacement of mutants. Even a mutant that has on average a higher reproductive success than the resident goes extinct with a large probability, and a mutant less fit than the resident can take over in a finite population. The situation is the same as the game in a finite population (Nowak *et al.*, 2004), in which the advantage of a mutant over the resident is determined by whether its fixation probability is greater than that expected of a neutral mutant.

To address the evolution of k in a finite forest population model, we developed a new graphical method called the finite pairwise invasibility plot (fPIP). This method extends the pairwise invasibility plot (PIP) for an infinitely large population (Metz *et al.*, 1992; Kisdi and Meszéna, 1995; Geritz *et al.*, 1997, 1999) to a finite population.

We found that how gap sites are filled is very important in determining the evolution of masting. Masting cannot evolve if all the vacant sites created by disturbances in a year are filled within the same year. In contrast, masting can evolve if a significant proportion of

vacant sites created in a year remain unfilled over multiple years. Thus in the absence of seed predators, trees can evolve masting only through improving pollination efficiency.

MODEL

We assume that a forest is composed of N sites, each of which is either empty or filled by a single tree that might be immature or mature. To describe the condition of the i-th site, we introduce $\theta_i(t)$. If the i-th site is empty at the beginning of year t, $\theta_i(t) = 0$. If it is occupied by an immature tree, $\theta_i(t) = 1$. If it is occupied by a mature canopy tree, $\theta_i(t) = 2$.

Within each year, there are four phases: (1) In the growth phase, each tree photosynthesizes, and accumulates resources in its reserve (tree trunk). (2) This is followed by the reproduction phase, in which trees with sufficient resources make flowers and fruits. (3) In the death phase, a small proportion of trees are randomly killed by disturbances, leaving an empty site. Although a tree can die at any time of the year, we proceed as if all tree falls occur after the reproduction phase. (4) Finally, in the recruitment phase, each gap site is filled by an offspring started from a seed chosen at random. After some years in which this new individual remains immature, it reaches the canopy and starts reproduction. We explain each of these processes in detail below.

Resource budget model

We adopt the resource budget model to consider the dynamics of flowering and fruiting. The assumptions are as follows: A mature tree acquires annual net production P_S, and accumulates it in its trunk or branches. Let $S_i(t)$ be the amount of resource reserve of the individual of the i-th site at the beginning of year t. If $S_i(t) + P_S$ is below a threshold L_T, the tree devotes no resources to reproduction, instead saving all its resources for the following year. In contrast, if $S_i(t) + P_S$ exceeds L_T, the tree uses the excess amount $S_i(t) + P_S - L_T$ for flowering activity. The flowers produced are pollinated by outcross pollen, and then the plant sets fruits. The cost of fruit production following flower fertilization is determined by constant k_i, defined as the ratio of fruiting cost to flowering cost. After the reproduction phase, the resource reserve of the tree of the i-th site becomes:

$$S_i(t+1) = \begin{cases} S_i(t) + P_S & \text{if } S_i(t) + P_S \leq L_T \\ S_i(t) + P_S - (1 + P_i(t)k_i)(S_i(t) + P_S - L_T) & \text{otherwise} \end{cases}, \quad (1)$$

where $P_i(t)$ is pollination success and will be given below. In this model, if k_i is large, much of the tree's resources are depleted. Therefore, parameter k_i is called the resource depletion coefficient (Satake and Iwasa, 2000).

By introducing a non-dimensional variable $Y_i(t) = (S_i(t) + P_S - L_T)/P_S$, equation (1) becomes:

$$Y_i(t+1) = \begin{cases} Y_i(t) + 1 & \text{if } Y_i \leq 0 \\ -k_i P_i(t) Y_i(t) + 1 & \text{otherwise} \end{cases}, \quad (2a)$$

in which pollination efficiency $P_i(t)$ is given by

$$P_i(t) = \left[\frac{1}{N-1} \sum_{\substack{j \neq i \wedge \theta_j = 2}}^{N} [Y_j(t)]_+ \right]^{\beta}, \quad (2b)$$

where $[Y]_+ = Y$ if $Y > 0$, otherwise it is 0. $P_i(t)$ is between 0 and 1. Here the fruit production of a tree is constrained by the availability of outcross pollen – that is, by the flowering intensity of other individuals in the same forest ($j \neq i$) (Nilsson and Wästljung, 1987; Smith *et al.*, 1990). Parameter β in function $P_i(t)$ in equation (2b) is referred to as 'pollen coupling strength' (Satake and Iwasa, 2000). It determines the strength of this constraint and controls the dependence of fruit production on outcross pollen availability. A small β indicates that fruit production is almost independent of the reproductive activity of the other trees in the forest. In contrast, a large β implies a strong dependence of seed and fruit production on the reproductive activity of other individuals in the forest. If β is very large, a tree's resource reserve is depleted only when almost all trees flower.

According to Satake and Iwasa (2000), the dynamics of the globally coupled resource budget model (equation 2) are classified into several categories according to a combination of k and β. If the resource depletion coefficient k evolves to be significantly greater than 1 and if the coupling strength β is large compared with k, then synchronized and intermittent reproduction (masting) should be realized. In contrast, if k evolves to a value greater than 1 but β is not large compared with k, then each single tree shows intermittent reproduction but all the trees in the forest will not be synchronized, thus there will be no masting. Finally, if k evolves to a value close to 1, each tree will reproduce every year, showing no sign of masting.

Gap formation and gap filling

In a forest, only a very small fraction of seeds will survive to become canopy trees in the next generation. This is difficult under a dense canopy, because it is very dark on the forest floor. However, when a canopy tree dies, an empty site or 'gap' is created, where the local light availability is much improved. Hence for a seed to establish successfully, it must be lucky enough to be in a gap site, and also to win the race between competing seeds to fill that gap site.

To describe the regeneration of a forest, we consider a model similar to the Moran process (Moran, 1958). In the reproduction phase, each mature tree produces seeds. The number of seeds produced by a tree in any one year may reflect how much accumulated resources it invests and the availability of outcross pollen. To be specific, the seeds produced by a tree in the i-th site in a year is $\varphi_i(t) = k_i P_i(t)[Y_i(t)]_+$, if $\theta_i(t) = 2$. Therefore, the total number of seeds in the forest is

$$\varphi(t) = \sum_{\theta_i = 2} \varphi_i(t), \tag{3}$$

where the sum is calculated only for sites occupied by (mature) canopy trees.

In this section, we first analyse the case in which all vacant sites will be filled by the seeds produced in the same year. This is plausible given that some trees always produce seeds and the number of seeds produced by a tree is enormous. Under this simplifying assumption, the total number of trees N is kept constant, as for the Moran process.

At the beginning of a year, the number of trees is N. Since the mortality per year is δ, the number of newly formed vacant sites $F_{new}(t)$ follows a binomial distribution $B(N, \delta)$.

In the recruitment phase, each of these vacant sites is occupied by an offspring of the i-th tree with probability $\varphi_i(t)/\varphi(t)$. A new individual remains immature for τ years, during

which site i occupied by an immature tree satisfies $\theta_i(t) = 1$. After τ years, the individual reaches the canopy and starts reproduction, satisfying $\theta_i(t) = 2$.

Reproductive success is achieved either as a female (by producing fruit) or as a male (by being a pollen donor). For the simplest genetic system to be compatible with this picture, we assume that the trees are sexual but haploid. Plants undergo sexual reproduction, and a seed has two sets of genomes (diploid) derived from its parents. The zygote then experiences meiosis immediately, and the offspring trees from it will be haploid. For each genetic locus, an offspring inherits an allele either from its mother or father with a ratio of 50:50. For trees of a diploid genotype, the calculation becomes much more complex due to the genetic dominance of alleles, but the evolutionary process is very similar.

New mutants are generated with a small probability (0.01 per generation) by random mutation at reproduction. Mutants have a trait slightly different from the parent. The magnitude of difference from the parent $|k - k'|$ is 0.1. A novel mutant always starts from a single individual, and its descendents may increase or decrease during subsequent generations.

EVOLUTION OF THE RESOURCE DEPLETION COEFFICIENT, k

Since we have to trace the resource dynamics of each individual tree, the number of trees N is set at 100, which is plausible given that the spatial range of pollen exchange between trees is of the order of 100 m or less (Dow and Ashley 1998), and hence N is not very large.

Figure 1a shows the result of numerical simulation of the evolutionary process. The model starts with a monomorphic population at the beginning of the simulation. The mean k in the population starts at $k = 5$. Initially it becomes smaller with time, but later stabilizes at a certain value. This final value of mean k is the evolutionary outcome. Figure 1b shows as the evolutionary outcome the number of seeds produced in the forest over 50 years. Trees evolved to reproduce every year – masting could not evolve.

Finite pairwise invasibility plot

We describe a new graphical method to analyse the evolutionary game in a finite population. The reproductive success of each tree depends on the behaviour of other individuals in the population, and the situation is like the game in a finite population (Nowak *et al.*, 2004; Taylor *et al.*, 2004; Nowak, 2006). In such a situation, calculation of marginal fitness is no longer a good predictor of the evolutionary outcome, but instead we need to calculate the fixation probability of a mutant that appeared in the population dominated by the resident. Specifically, consider a population in which there is a single mutant with parameter k' and $N - 1$ resident individuals with parameter k. The run will end either with the extinction or with the fixation of the mutant. From a large number of replicates, we can calculate the fraction of runs with successful fixation. If the fraction of fixation runs exceeds that expected for the neutral case ($1/N$), we conclude that the mutant was favoured by natural selection (Taylor *et al.*, 2004). If the fixation rate was less than that expected for the neutral mutants, we conclude that the resident was favoured by natural selection. In between these two cases, we conclude that the mutant was neutral.

We ran these simulations for all possible combinations of the resident's k and the mutant's k', and marked the result on a two-dimensional square. The graph is a finite-population version of the pairwise invasibility plot, which we abbreviate as fPIP.
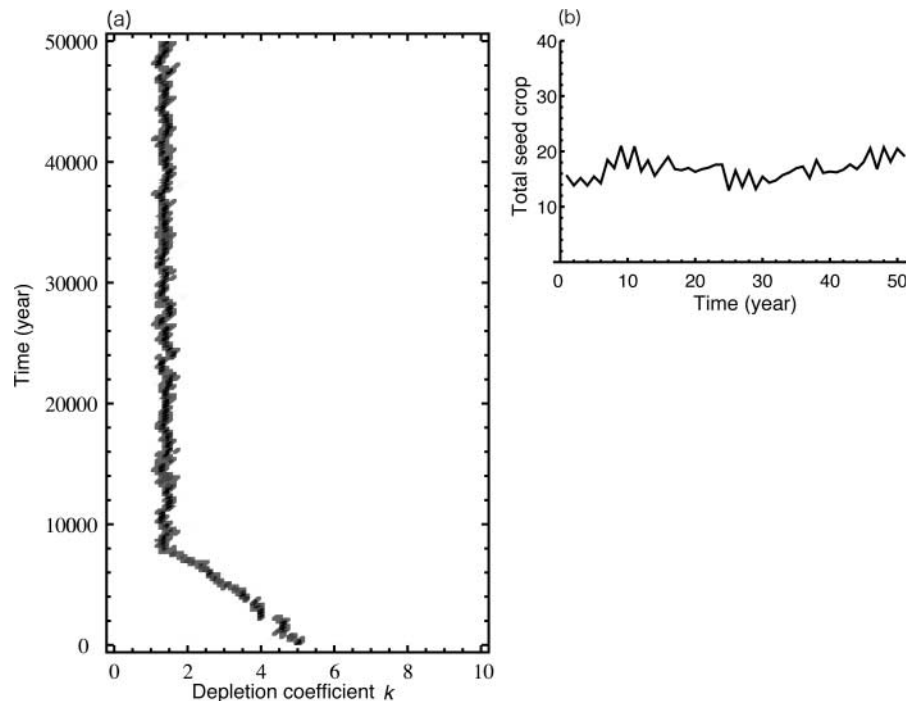
Fig. 1. (a) Evolutionary trajectory. Horizontal axis represents the resource depletion coefficient k that evolves. Vertical axis represents time. Population starting from $k = 5$ moved and finally reached the evolutionarily stable value of k. (b) Total seed production in the forest for final 50 years of the evolutionary end point of the trajectory in (a). Trees in the forest reproduce every year. Parameters are: $N = 100, \delta = 0.04, \tau = 10, \beta = 1.75$.

Figure 2 shows fPIPs with different values of the parameter β. In each panel, the horizontal axis is the resident's trait k, while the vertical axis is the mutant's trait k'. When the mutant had a fixation probability significantly higher than the neutral case, the corresponding site was shaded black. In contrast, when the mutant had a fixation probability significantly lower than the neutral case, the corresponding site was left white. No significant difference from the neutral expectation was shown in the grey area along the diagonal line, where the mutant's k is equal to the resident's k.

Using this graph, we can find evolutionary attractors to which the phenotype converges as a result of evolution. Since mutants are similar to the parent in phenotype, we can focus on the result near the diagonal line. If the area above the line is black and if the area below the line is white, the mutant with a greater phenotype has a higher fixation probability than the resident and the mutant with a smaller phenotype cannot invade. In such a case, we conclude that k should increase in evolution.

Figure 2h (as in Fig. 1) illustrates the case, starting from a population with k smaller than $k*$. Mutants with k' slightly larger than the resident's k have a fixation probability greater than that of the neutral case (indicated in black). They can invade and subsequently replace the resident. Similarly, a resident population with k greater than $k*$ is likely to be invaded and replaced by the mutants with smaller k more than by the mutants with the larger k.
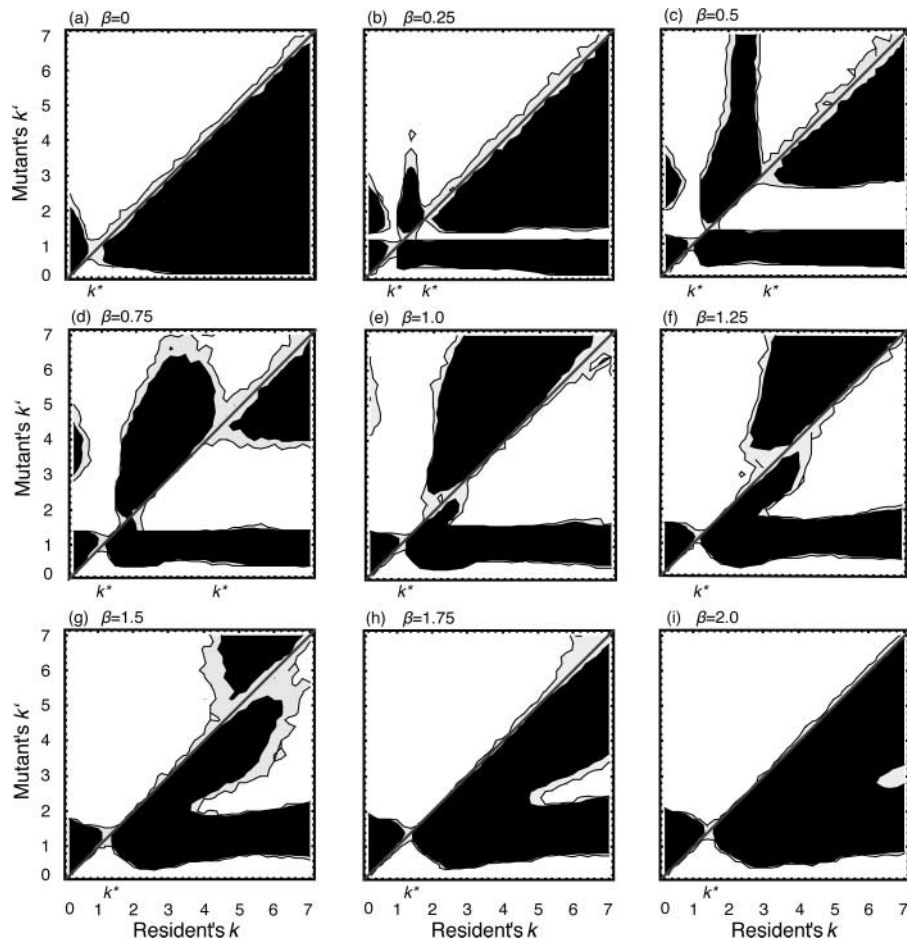
Fig. 2. Finite pairwise invasibility plots for different β. The vertical axis represents the mutant's resource depletion coefficient k', and the horizontal axis represents that of the resident's k, in the range $0 \le k \le 7$. In each panel, three regions are classified. The black region indicates that the mutant has a fixation probability significantly higher than the neutral expectation. The white region indicates that the mutant has a significantly low fixation probability. Grey means that the mutant has the same fixation probability as in the neutral case. Parameters are: $N = 100$, $\delta = 0.04$, $\tau = 10$. (a) $\beta = 0$, (b) $\beta = 0.25$, (c) $\beta = 0.5$, (d) $\beta = 0.75$, (e) $\beta = 1$, (f) $\beta = 1.25$, (g) $\beta = 1.5$, (h) $\beta = 1.75$, (i) $\beta = 2$.

Thus k^* is an evolutionary attractor because a population with different initial k will evolve gradually towards k^*. We expect that in the long run, k would approach k^*, although the stochasticity may sometimes cause the fixation of a mutant that is not favoured by natural selection.

Masting does not evolve

Figure 2 indicates that, when β is either very small ($\beta \approx 0$) or large ($\beta > 1.75$), there is only one evolutionary attractor satisfying $k^* \approx 1$. When β has an intermediate value, there are

two evolutionary attractors: One attractor is $k^* \approx 1$, corresponding to trees reproducing annually. The other attractor corresponds to trees showing intermittent reproduction but without synchronization [i.e. the desynchronized region in Satake and Iwasa (2000)]. We examined the model in detail for a wide range of β, and concluded that, irrespective of the choice of β, trees cannot evolve to the state in which they show intermittent and synchronized reproduction. The model always evolved either to annual reproduction (each tree reproduces every year) or to a desynchronized forest (each tree reproduces intermittently but not all trees are synchronized).

CARRY-OVER OF UNFILLED GAP SITES

The lack of masting evolution observed in the evolutionary simulations in the previous section is plausible if the assumption is met that all the gaps formed in a year are filled within the same year. Since δ is a constant, gaps are formed at the same rate between years, and hence the opportunity for successful recruitment is independent of the total seed crop in the forest. By joining masting, trees may be able to produce a large number of seeds owing to improved pollination efficiency. But the probability of recruitment success for a single seed is inversely proportional to the number of seeds produced in that year. In contrast, a few seeds that happen to be produced in non-mast years enjoy a high chance of becoming a canopy tree in the future. The benefit to a greater number of surviving seeds is cancelled by the intense competition among abundant surviving seeds in mast years. Hence the reproductive success of a tree would be improved by producing seeds every year, rather than entering into masting reproduction.

This intuitive argument suggests that masting may be favoured by natural selection if not all the gaps are filled in a year. Suppose that there are a considerable number of empty sites (or gaps) that remain unfilled for several years. The carry-over of unfilled sites would mitigate the competition among trees in a mast year. Then, the total reproductive success in a mast year with a big seed crop becomes greater than that in a non-mast year with a poor seed crop, providing some advantage to reproducing in mast years.

To examine this possibility, we consider the dynamics of the number of vacant sites. In the recruitment phase, the number of seeds that establish in a site is drawn from a Poisson distribution with mean $a\varphi(t)$, in which $\varphi(t)$ is the total seed crop and a is the gap-filling coefficient. A large a means that all the gaps created in a year by the death of canopy trees are filled within the same year, as was assumed in the last sections. In contrast, a small a means that there is considerable carry-over of unfilled gap sites that are produced in previous years. The probability of recruitment success is $1 - e^{-a\varphi(t)}$, which is the probability of one or more events of successful recruitment occurring. Then the probability that a seed produced by the i-th tree is established in a particular vacant site is $(\varphi_i(t)/\varphi(t))(1 - e^{-a\varphi(t)})$.

Let $F(t)$ be the number of vacant sites in the forest at the beginning of year t (i.e. the number of i satisfying $\theta_i(t) = 0$). Since the number of sites occupied by trees (including immature and mature ones) is $N - F(t)$, the number of newly formed vacant sites $F_{new}(t)$ follows a binominal distribution $B(N - F(t), \delta)$. The number of available gap sites in the recruitment phase is $F(t) + F_{new}(t)$. In the recruitment phase, some vacant sites are filled. But some vacant sites remain unfilled, and are carried over to the following year $F(t + 1)$.

Finite pairwise invasibility plot with carry-over of vacant sites

Figure 3 shows fPIPs for cases with different carry-over of unfilled gap sites. If *a* is large (Fig. 3a–c), all gap sites are filled even if seed production in the forest is small. The fPIPs in Fig. 3a–c are similar to those in Fig. 2 (corresponding to $a = \infty$). The resource depletion coefficient *k* always evolves to about 1. The tree with *k** reproduces every year. Since the number of available vacant sites is nearly constant (to be exact, following the binomial distribution with mean $N\delta$), the strategy of reproducing every year is advantageous.

   In contrast, in Fig. 3f, 3h, and 3i, *a* is smaller. We observe evolution towards mast seeding. In these cases, *k* evolves to a value significantly larger than 1. Since *k* is greater than 1 and β is relatively large, an intermittent and synchronized reproductive pattern is realized as a result of evolution. Hence masting can evolve when *a* is small and β is positive.
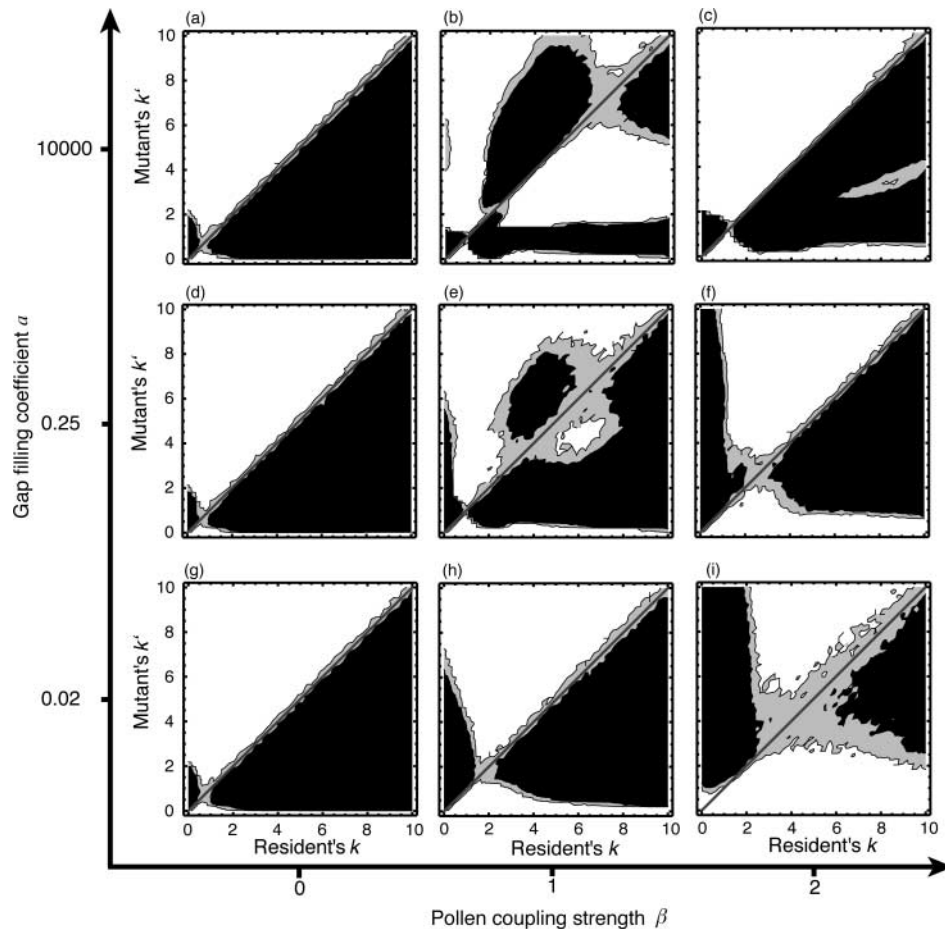

Fig. 3. Finite pairwise invasibility plots for different combinations of parameters *a* and β. In each panel, both axes are *k* from 0 to 10. Masting behaviour can evolve only if *a* is small and β is large, when the evolutionary attractor is significantly greater than 1. Parameters are: $N = 100$, $\delta = 0.04$, $\tau = 10$. (a) $a = 10{,}000$, $\beta = 0$, (b) $a = 10{,}000$, $\beta = 1$, (c) $a = 10{,}000$, $\beta = 2$, (d) $a = 0.25$, $\beta = 0$, (e) $a = 0.25$, $\beta = 1$, (f) $a = 0.25$, $\beta = 2$, (g) $a = 0.02$, $\beta = 0$, (h) $a = 0.02$, $\beta = 1$, (i) $a = 0.02$, $\beta = 2$.

For trees to achieve high reproductive success in mast years, a sufficient number of vacant sites must be available, which are supplied by the carry-over from several previous non-mast years, as is the case for small a. In Fig. 3i, the evolutionary attractor of k^* is an interval between 2 and 5. Within this interval of k, any pair of mutant and resident k's are neutral to each other. Hence the average phenotype in the population fluctuates due to random drift.

Figure 4a shows a direct simulation of the above situation. The simulation confirms the prediction. A population starting with $k = 1$ evolves towards an evolutionary attractor. Once the population reaches the evolutionary attractor, its phenotypic value of k fluctuates. A forest dominated by trees with k^* reproduces synchronously, the seed crops showing a chaotic time series (masting) (Fig. 4b).

We conclude that trees can evolve masting behaviour only through improving pollination efficiency if a considerable fraction of vacant sites created in a year remain unfilled for several years.
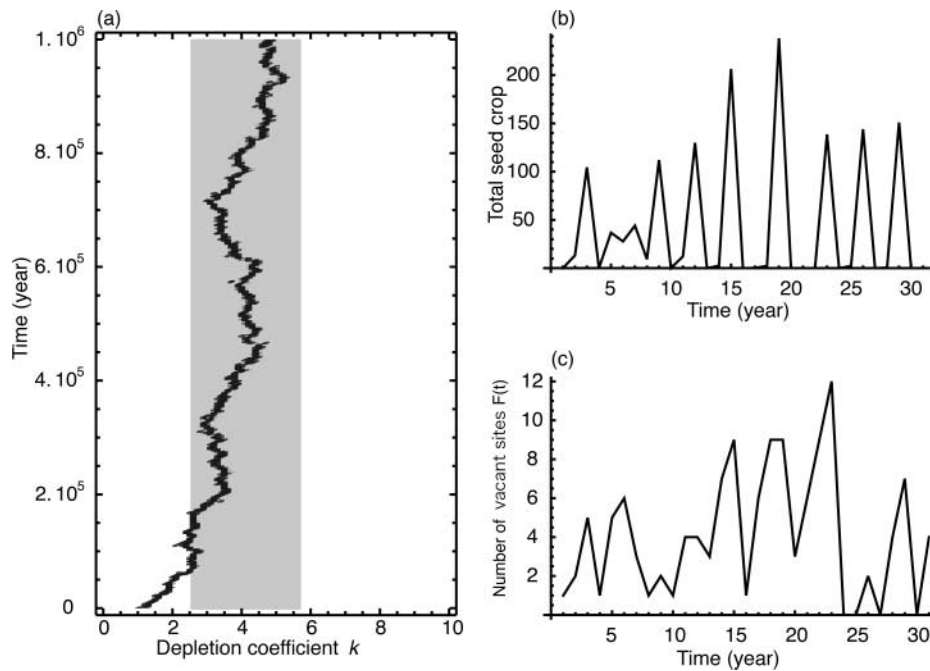

Fig. 4. (a) Evolutionary trajectory when the gap-filling coefficient a is small. The initial value is $k = 1$. The vertical axis represents time and the horizontal axis represents k. Once the population reaches the evolutionary attractor, k fluctuates within the evolutionary attractor, indicated by shading ($2.5 < k < 5.5$). This result corresponds to the fPIP in Fig. 2i. (b) Total seed crop in the forest for the last 30 years of the evolutionary end point of the trajectory in (a). Trees in the forest reproduce intermittently and synchronously. (c) The number of gaps at the beginning of year t, $F(t)$. The number of available free sites in the year t is the sum of $F(t)$ and newly created gaps $F_{new}(t)$. Vacant sites are carried over for several years. $F(t)$ is fluctuating. In years in which large amounts of seeds are produced synchronously, they can fill many vacant sites. This creates the reproductive advantage of masting. In the all panels, parameters are: $N = 100$, $\delta = 0.04$, $\tau = 10$, $a = 0.02$ and $\beta = 2$.

DISCUSSION

In the present paper, we examined the necessary evolutionary conditions for trees to show masting. We adopted the globally coupled map model for tree reproduction (Satake and Iwasa, 2000) and discussed the evolution of the resource depletion coefficient k of a tree, which regulates resource investment to fruit. The model considers pollination efficiency, which is regarded as a candidate mechanism for a tree entering into synchronized reproduction. We explicitly considered the dynamics of tree fall and recruitment (or gap dynamics), which are often neglected when arguing for the evolutionary advantage of masting. Our analysis demonstrated the importance of the recruitment dynamics in the evolution of masting – masting cannot evolve if all the gaps created in a year are filled within the same year, but can evolve if a considerable proportion of vacant sites formed by tree falls remain unfilled over multiple years. In addition, outcross pollen limitation needs to be sufficiently strong for the evolution of masting. Somewhat surprisingly, it can evolve without considering seed predators, which are supposed to provide the most important evolutionary benefit to masting.

To analyse the evolutionary game in a finite population, we developed the finite pairwise invasibility plot (fPIP). This graphical tool has been used previously by Kamo *et al.* (2007) and Proulx and Day (2001), but these authors did not discuss the statistical significance of the evolutionary advantage of mutants. Since stochasticitiy is unavoidable in the evolution of a finite population, an appropriate statistical test is needed to discuss the evolution properly.

If many trees in a forest show a very high reproductive success in a mast year, and there is almost no seed production over the following several years (Fig. 4b), the abundance of gap sites would be reduced after the mast year and increase slowly over subsequent non-mast years (Fig. 4c). Hence the recruitment success of a tree depends strongly on the availability of vacant sites, which is affected by the time series of the fruiting success of all the trees in the forest. In addition, as outcross pollen availability for a mutant is controlled by the flowering pattern of the resident, the temporal pattern of a mutant's seed production over the years would be determined by the behaviour of the resident trees in the forest in a complex manner.

The Moran process and lottery model have often been used for the dynamics or the evolution of sessile organisms (Chesson and Warner, 1981; Kisdi and Meszéna, 1995; Muko and Iwasa, 2000; Kisdi and Geritz, 2003; Schoolmaster, 2008; Higgins *et al.*, 2008), in which a vacant site produced by the death of an individual is filled immediately. Our results suggest that this assumption may not be always appropriate. The consideration of unoccupied space has been emphasized in the ecology of marine benthic species (Iwasa and Roughgarden, 1986; Roughgarden and Iwasa, 1986). When we consider the dynamics or evolution of sessile organisms, we should take account of the mechanisms by which vacant sites are created and filled.

The predator satiation theory (Janzen, 1971; Silvertown, 1980; Nilsson and Wästljung, 1987) is an important and plausible hypothesis for the evolutionary advantage of masting. There is plenty of experimental evidence supporting the advantage of seed survivorship (Kobro *et al.*, 2003). However, based on the results of the present paper, masting can evolve without seed predators.

In addition, masting cannot evolve if all the vacant sites are filled in the recruitment phase. Seeds produced in a mast year can enjoy high survivorship due to the predator satiation effect, but they face very intensive competition for vacant sites that are required for their

establishment. If the same number of vacant sites is available for recruitment in different years, the advantage of having many surviving seeds for a tree that enters into synchronized reproduction would be cancelled by the very intensive competition among seeds. We conjecture that masting is unlikely to evolve even in the presence of seed predators if all vacant sites are filled every year. However, it would be interesting theoretically to examine this conjecture in a model that considers seed predators, which may differ in dispersal ability, alternative food sources, and population growth potential.

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