Coexistence induced by pollen limitation in flowering-plant species

Reiichiro Ishii* and Masahiko Higashi

Centre for Ecological Research, Kyoto University, Kyoto 606-8502, Japan

We report a novel mechanism for species coexistence that does not invoke a trade-off relationship in the case of outbreeding flowering plants. Competition for pollination services may lead to interspecific segregation of the timing of flowering among plants. This, in turn, sets limits on the pollination services, which restrain the population growth of a competitively superior species, thereby allowing an inferior species to sustain its population in the habitat. This explains the often-observed tendency for interspecific differentiation in the timing of flowering between coexisting plants. It also predicts that the introduction of an efficient pollinator to a habitat may cause the extinction of competitively inferior plant species.

Keywords: plant coexistence without trade-off; competition for pollination; temporal interspecific segregation

1. INTRODUCTION

It has been suggested from the results of various field studies that competition for pollinators contributes to the reproductive efficiency and flowering phenology of outbreeding plants (Waser 1978a, 1983; Pleasants 1980; Campbell 1985; Campbell & Motten 1985; Ashton *et al.* 1988). Waser (1978a) and Campbell (1985) revealed that interspecific overlap in the timing of flowering in outbreeding plants causes a decrease in seed production, suggesting that interspecific competition for pollinators occurs only between plants that flower at the same time. Thus, the timing of flowering in outbreeding plants should be crucial to their reproductive success and population dynamics. Using a theoretical model that incorporates the effect of the numbers of flowering plants of two pollinator-sharing plant species, Levin & Anderson (1970) predicted the extinction of the minority species, but Waser (1978b), from the results of his simulations evaluating the effect of interspecific pollinator movements on plant reproduction, suggested that the two species may coexist if their flowering periods are separated.

To clarify when and how the coexistence of two pollinator-sharing plant species in a habitat may occur through the temporal separation of flowering, it is necessary to develop a population model that explicitly incorporates the temporal distributions of flowering in the two-species population because competition for pollinators is not a global phenomenon but a local one. Here, using a model for two outbreeding plant populations, each of which is composed of subsets with different flowering periods and on the assumption that competition for pollinators occurs between the subsets that flower at the same time, we examine the possibility of and conditions for coexistence of two plant species with different competitive abilities for resources (including space). We do not assume any trade-off relationships in their traits (such as the trade-off in competition versus dispersal or in resource competition versus pollinator attraction), which

are the commonly evoked mechanisms for species coexistence in a stable environment (Crawley & May 1987; Kohyama 1993; Tilman 1994; Tilman *et al.* 1994).

2. THE MODEL

Consider a habitat with populations of two species, n_1 and n_2 , of annual hermaphroditic outbreeding plants. Each population consists of sub-populations with different and non-overlapping flowering periods, $t=1, 2, \dots, m$ in year T : $n_k(T) = \sum_{t=1}^m n_{k,t}(T)$, where $k=1, 2$. Thus, we assume that a year is divided into m time slots and that a plant with trait t is in bloom during time slot t . We also assume that each individual plant has only one flower, for the simplicity of the model. Let p_t denote the pollination service supplied to the plants flowering in time slot t in any year. A pollination service is defined as a set of two visits by a pollinator to plants randomly chosen from the total, n_t , flowering plants, assuming no constancy (Levin & Anderson 1970); it is also assumed that pollen grains are not carried between any two flowers with different traits. The probability that a plant of species k flowering at time t in year T receives pollen, at least once, from another simultaneously flowering plant of the same species can be expressed as

$$P(n_t(T), n_{k,t}(T), p_t) = 1 - \left(1 - \frac{1}{n_t(T)} \frac{n_{k,t}(T) - 1}{n_t(T)}\right)^{p_t}, \quad (1)$$

where the term within the parentheses on the right represents the probability of failure to receive conspecific pollen in one pollination service. In equation (1), competition for pollination service is assumed to occur between all the flowering plants with the same t . We assume a random choice of flowers visited by a pollinator, implying that the populations of both plant species are distributed randomly in space and that neither plant species is more attractive than the other. Any relaxation of this assumption would introduce some asymmetry into the competition for pollinators between the two plant species, which we avoid because the main aim here is to examine the coexistence of two species competing for

*Author and address for correspondence: Department of Biological Sciences, Graduate School of Science, University of Tokyo, Tokyo 113-0033, Japan (ishii@ecol.biol.s.u-tokyo.ac.jp).

resources or space without invoking a trade-off mechanism, for example that an inferior resource competitor is superior in pollinator competition. Also, we assume that the two plant species are hermaphroditic. This assumption can be relaxed. For example, dioecious plants can be modelled by equation (1) if $(n_{k,t}(T) - 1)/n_t(T)$ is replaced by $(n_{k,t}(T)/2)/n_t(T)$, assuming a 1:1 sex ratio, which will change no qualitative features of the following theoretical results. The same holds for any case of other sexual system (Richards 1997) by a similar modification of equation (1). Provided that flowering time, t , is a heritable trait, the number of seedlings of species k with trait t can be expressed using a constant c_k (the number of seedlings that a pollinated flower produces) as: $c_k P(n_t(T), n_{k,t}(T), p_t) n_{k,t}(T)$.

Apart from the competition for pollination, competition for space or edaphic resources occurs between all seedlings in the habitat (irrespective of flowering time or species). We incorporate this into the model in the following way. Let N denote the maximum number of adult plants that the habitat can maintain and assume that all seedlings of any species with any trait compete for those N 'seats' (i.e. microsites). The population dynamics of species k with trait t can then be expressed as:

$$\begin{aligned} n_{k,t}(T+1) &= \frac{f_{k,t}(T) n_{k,t}(T)}{\sum_{i=1}^m (f_{1,t}(T) n_{1,t}(T) + f_{2,t}(T) n_{2,t}(T))} N \\ &= \frac{f_{k,t}(T)}{\sum_{i=1}^m [f_{1,t}(T) (n_{1,t}(T)/N) + f_{2,t}(T) (n_{2,t}(T)/N)]} n_{k,t}(T), \end{aligned} \quad (2)$$

where $f_{k,t}(T) = l_k c_k P(n_t(T), n_{k,t}(T), p_t) = r_k P(n_t(T), n_{k,t}(T), p_t)$ where l_k represents the relative survivability of a seedling to adult, and $r_k = l_k c_k$ is the relative competitive ability of species k . Let species 1 be the superior competitor, i.e. $r_2 < r_1$. Here, the r value is the only species-specific difference between the two species and no counterbalancing value is assumed. Note that in equation (2) the term $f_{k,t}(T)$ represents the relative fitness of a plant of species k with trait t in year T and, thus, the denominator $f(T) = \sum_{i=1}^m [f_{1,t}(T) (n_{1,t}(T)/N) + f_{2,t}(T) (n_{2,t}(T)/N)]$ is the mean fitness of the entire population. Summing both sides of equation (2) over k and t gives $\sum_{t=1}^m [n_{1,t}(T+1) + n_{2,t}(T+1)] = \sum_{t=1}^m n_t(T+1) = N$, implying that the populations in the habitat change in such a way that their total is always N .

3. RESULTS OF THE MODEL

(a) Sub-population densities at the steady state

We now show that, given a particular temporal (seasonal) distribution of pollination service in each year and the initial distributions of sub-populations of each plant species, the system governed by equation (2) converges on a stable steady state.

The pollination success of a plant depends on the availability of conspecific pollen and thus increases as the proportion of flowering individuals of the species in the population increases (equation (1)); interspecific

competition for pollinators enhances the majority advantage for each flowering period, as pointed out by Levin & Anderson (1970). This drives one species to monopolize each time slot at the steady state. The monopolizing species for each time slot is determined by the initial conditions. Eventually m sub-populations are monopolized by either species 1 or species 2. Letting $k(t)$ denote the species that monopolizes time slot t , we have $n_t^* = n_{k(t),t}^*$, where (and hereafter) the symbol $*$ indicates the value at the steady state ($T \rightarrow \infty$) (see Appendix A). Now, we can obtain the sub-population size of the single species in each time slot at the steady state in the following way. The per-capita fitness function, $\varphi_t(n_t)$, in a single-species-monopolized sub-population at time slot t, n_t , is found by substituting $k(t)$ for k and n_t for both $n_t(T)$ and $n_{k,t}(T)$ in $f_{k,t}(T) = r_k P(n_t(T), n_{k,t}(T), p_t)$ to give:

$$\varphi_t(n_t) = r_{k(t)} P(n_t, n_t, p_t). \quad (3)$$

Thus, we have m fitness functions for m periods; at the steady state each of them has the same fitness value (the mean fitness, f^*), and the following equation is satisfied for all t ($1 \leq t \leq m$):

$$\varphi_t(n_t^*) = r_{k(t)} P(n_t^*, n_t^*, p_t) = f^*. \quad (4)$$

Since $P(n_t, n_t, p_t)$ is a monotonically decreasing function of n_t (equation (1)), the steady-state size, n_t^* , of the sub-population of the monopolizing species in each flowering period, t , is given by the inverse function of f^* for given $r_{k(t)}$ and p_t . f^* is determined such that

$$\sum_{t=1}^m \varphi_t^{-1}(f^*) = N.$$

We now illustrate the process of determining f^* and all n_t^* using simplified examples, where species 1 and species 2 monopolize five and three periods, respectively ($m=8$) (figure 1a). Note that the fitness curves of species 1 (thick curves) are in relatively higher positions than those of species 2 (thin curves) and that among sub-populations monopolized by the same species, a function curve for a period with richer pollination service lies above that for a period with poorer pollination service, because $\varphi_t(n_t) = r_{k(t)} P(n_t, n_t, p_t)$ is an increasing function of $r_{k(t)}$ and p_t . The horizontal value (indicated by a dot on the horizontal, n_t , axis) of the intersection (open circle) of each fitness curve, φ_t , (depicted by each monotonically decreasing curve) with the horizontal line representing the overall mean fitness, f^* , at the steady state gives the value of n_t^* . If f^* moves down from r_1 to zero, the n_t^* values (and, thus, their sum) monotonically increase from zero to infinity. Hence, f^* can be uniquely determined such that the sum of the n_t^* values equals N . If a fitness curve, φ_t , does not cross the horizontal line f^* (as in the lower thin curves in figure 1a) then the species $k(t)$ that would monopolize flowering period t will not sustain the sub-population flowering during that period. Species $k(t)$ will therefore become a loser in the global competition between the sub-populations flowering in different periods.

If the sub-population size, n_t , of the monopolizing species for each flowering period, t , decreases or increases (indicated by the left and right open circles, respectively, in figure 1b) relative to its steady-state value, n_t^* , its fitness,

Figure 1. The relationship between the population size of one species monopolizing a sub-population, n_t , and the fitness of an individual plant in that sub-population, φ_t . (a) The procedure to obtain the sub-population sizes at the steady state ($m=8$ for visual simplicity). Thick and thin curves represent the fitness functions, φ_t , of sub-populations of species 1 and species 2, respectively. The maxima of the thick curves (φ at $n_t=2$) are mostly higher than those of the thin curves because of the assumption that $r_1 > r_2$. Fitness is a decreasing function of sub-population size, n_t , implying that fitness is decreased by the intraspecific competition for pollination service. (b) An illustration of the heuristic explanation for the stability of the steady state, n_t^* , under the simplified assumption that any flowering period is already monopolized by a single species. See §3(a) for an explanation.

φ_t will become greater or smaller than f^* and thus it will return to n_t^* (indicated by arrows 1 and 2, respectively, in figure 1b). This negative feedback, due to the negative density dependency of the fitness function, φ_t , for the monopolizing species in each flowering period, t , stabilizes the system and leads to the steady state. Our numerical simulations have confirmed the stability, although we cannot provide a mathematical proof of the stability of the steady state, beyond this heuristic explanation under the simplified assumption that any flowering period is monopolized by a single species.

(b) Condition for the coexistence of two species

Suppose now that species 1 has existed for a period of time in the habitat and has a population distributed mostly in the time slots with higher pollination service. Species 2 is immigrating to the habitat with a small population. To invade successfully, species 2 must first win the temporally local competition for pollination service in order to monopolize some time slots. This can be achieved more easily when the flowering periods of the invading population of species 2 are sufficiently different from those of the resident species 1 population. Assume now that species 2 fulfils this necessary condition for successful invasion, that is, that it wins the local competition in some flowering periods with a lower pollination service. By definition ($r_2 < r_1$), the maximum values of the fitness functions, φ_t , (the value at $n_t=2$, $\varphi_t(2)$) of species 2 are smaller than those of species 1. Therefore, species 1 sustains most (or all) of the sub-populations that win the local competition for pollination service and, thus, its overall population in the habitat. Species 2 may be unable to sustain any sub-populations and, thus, may fail

to establish in the habitat. The necessary and sufficient condition for species 2 to succeed and coexist with species 1 (that is, to sustain its overall population in the habitat by maintaining some sub-populations) is that the different sub-populations of species 1 cannot grow to occupy all the N microsites alone. Letting θ denote the greatest value of the maxima, $\varphi_t(2)$, of the fitness functions for species 2 (i.e. the highest point of the highest thin curve in figure 1a) that would monopolize period t if surviving, the condition for species 1 to occupy all N is $\sum_{k(t)=1} \varphi_t^{-1}(\theta) = N$. Therefore, the condition for species 2 to succeed in coexistence with species 1 can be derived (see Appendix B) as

$$\sum_{k(t)=1} \varphi_t^{-1}(\theta) = \sum_{k(t)=1} \frac{1 + \sqrt{-3 + 4(1 - \theta/r_1)}}{2(1 - (1 - \theta/r_1)^{1/p_1})} < N. \quad (5)$$

The left panel in figure 1a shows a case in which species 2 (thin curves) does not satisfy the condition given by equation (5) and fails to sustain its population in the habitat, while the right panel depicts a case in which species 2 satisfies the condition given by equation (5) and succeeds because the pollination service in the periods monopolized by species 1 (thick curves) is sufficiently poor (low).

The reverse case, in which the superior competitor, species 1, comes into a habitat already occupied by species 2, should be easier and thus the condition for successful invasion and coexistence is weaker than the condition given in equation (5). Therefore, the condition given in equation (5) represents the necessary and sufficient condition for the coexistence of the two species in the same habitat. From equation (5), it is predicted that

Figure 2. (a) The overlap of flowering periods of plants with similar traits. Horizontal bars denote the flowering periods of the plants. The filled circles (left ends) and the open circles (right ends) of the bars denote that the plant is in bloom at the left end of the bar but has already finished blooming at the right end of the bar. Therefore, only plants with neighbouring traits are in bloom at any time. (b) Two representative simulation results of the process of invasion of a small population of species 2 into the habitat ($N = 3000$, $m = 81$) already occupied by a population of species 1. The pollination service (grey dots) has a normal distribution with mean $\mu = 41$, s.d. $\sigma = 7$ and $p = \sum_{i=1}^m p_i = 1750$. (Top panel) The initial population size ($T = 0$) of species 1 (open circles) is $n_1(0) = 3000$ and its initial seasonal population distribution is a stationary distribution for the given distribution of pollination service. The invading population of species 2 (filled circles) is assumed to have a normal distribution with $n_2(0) = 1200$ and $\sigma = 4.7$. The mean value in the left panel is $\mu = 45$ and in the right panel is $\mu = 59$. (Bottom panel) The population distribution of species 2 reached at the steady state ($T = 50$). The population of species 2 is sustained in the right panel, while the invasion of species 2 fails and species 1 recovers its initial seasonal population distribution in the left panel.

the coexistence of the two species is more likely under the following circumstances:

- (i) larger capacity of the habitat, N ;
- (ii) more time slots won by the inferior species (fewer terms to sum in $\sum$ in equation (5));
- (iii) poorer pollination service in the time slots won by the superior species (lower p_i) and a richer service for those won by the inferior species (higher θ); and
- (iv) smaller difference in r -values between the two species (lower r_1 and/or higher θ).

More generally, we can consider any initial state and equation (5) still gives the necessary and sufficient condition for the coexistence of the two species with the general definition of θ . It indicates that, given the capacity of the habitat, poor pollination service (low p_i) limits the domination of the habitat by a single species because of intraspecific competition, particularly in relatively rich periods, allowing the other species (even when an inferior competitor) to sustain its population in the same habitat.

(c) Simulation results

To investigate the dynamics of the invading population of species 2 under more realistic conditions, we ran a simulation that incorporates pollen transport between flowering plants occupying sequential time slots. Here, we assume that the flowering period of a plant with trait τ covers two units of time, time slot τ and time slot $\tau + 1$. The first half, time slot τ , overlaps with the second half of the flowering period of a plant with trait $\tau - 1$, while the second half, time slot $\tau + 1$, overlaps with the first half of the flowering period of a plant with trait $\tau + 1$ (see figure 2a). For simplicity, an offspring of two plants with different traits is assumed to inherit the trait of one or other of its parents, with the same probability for each (i.e. haploid inheritance). The dynamics of each sub-population are governed by equation (2). We compared various situations with different temporal distributions, sizes of pollination service and sizes of the invading population of species 2 to observe their effect on two-species coexistence. Since the seasonal distribution of species 2 did not change after 30 generations, the distribution at $T = 50$ (bottom of figure 2b indicated by filled circles) can be regarded as the steady state.

Figure 2b depicts how the average timing of flowering of the invading population of species 2 affects the survival of species 2. Even if the conditions listed in §3(b) are favourable for coexistence, as long as the average time of flowering of the invading population is similar to that of the established population (left panel, figure 2b), none of its sub-populations can monopolize any time slot. On the other hand, if the average timing of flowering of species 2 is sufficiently different from that of the established species (a superior competitor) (right panel, figure 2b), some of the sub-populations can win the temporally local competition for pollination service and monopolize some flowering periods, and hence achieve stable coexistence.

Figure 3 shows how the frequency of pollination service affects the survival of species 2 after its invasion into the habitat occupied by species 1 once a steady state has been reached. The initial conditions of the two plant populations are identical to those illustrated in the right panel of figure 2b, except that the size of the invading population

Figure 3. The effect of the degree of pollination-service limitation on the survival of the inferior competitor, species 2. The initial conditions for both plant species are identical to those in the right panel of figure 2b. The horizontal axis represents the total pollination service supplied in the habitat ($p = 175\text{--}3150$), with a temporal distribution that is normally distributed with mean $\mu = 41$ and s.d. $\sigma = 7$. The vertical axis represents the size of the surviving population of species 2 50 generations after the invasion, $n_2(50)$. Four different invading-population sizes (open circles, $n_{2,0} = 300$; filled circles, $n_{2,0} = 600$; open diamonds, $n_{2,0} = 900$; and filled diamonds, $n_{2,0} = 1800$) are compared.

of species 2 differs between the cases represented by open circles ($n_{2,0} = 300$), filled circles ($n_{2,0} = 600$), open diamonds ($n_{2,0} = 900$) and filled diamonds ($n_{2,0} = 1800$). The figure indicates that severe pollen limitation (small value of p) and a larger invading population size of the inferior competitor (species 2) both enhance coexistence with the superior competitor (species 1).

4. DISCUSSION

The model presented here is applicable to annual plants without dormant seed banks, in a stable environment, that is, there is no 'storage effect' (Chesson 1985). However, as is evident from equation (2), numerical simulations show that the theoretical results also hold for perennial plants but with a slower convergence to the steady state resulting from the buffering effect. Also, although the inclusion of vegetative reproduction, which often occurs even in outbreeding perennial populations, in effect enhances the difference in competitive ability between the two species, the basic logic and theoretical results presented still hold.

In the model, we assume that the frequency of pollination service is fixed independently of the number of flowering individuals, in order to focus on the analysis of flowering-population dynamics. It has been reported that the frequency of pollination service is regulated by the number of flowers (e.g. Totland & Matthews 1998) but is also limited by the potential frequency of pollination service, that is, by the population size of pollinators and their activity, which are regulated by other environmental factors such as air temperature, light level and air velocity (Inouye & Pyke 1988; Herrera 1995; Vicens & Bosch 2000). If the potential pollination service is relatively large and the plant populations are relatively small, then the temporal flowering pattern regulates the number of

pollinator visits. On the other hand, in the opposite case, where the potential pollination service is relatively poor, the frequency of pollinator visits is primarily limited by the pollinators and hence also by abiotic seasonal factors (Inouye & Pyke 1988; Herrera 1995). Therefore, if the model incorporated the positive correlation between pollinator visits and flower numbers, coexistence would be more difficult in pollinator-rich conditions than the present study suggests, while it would make no difference in pollinator-poor conditions. Thus, the main qualitative prediction of this model, that coexistence occurs when pollination service is poor, would not change.

We do not fully understand the mode of inheritance of the timing of flowering; therefore, for simplicity, we employ a single-locus haploid genetic system for the inheritance of flowering traits in our simulation. Although the simulations presented here were run with a null mutation rate, we have confirmed in other numerical simulations that the times of flowering of the two populations shift only if the mutation rate is unrealistically high (larger than 5% per generation). Therefore, the incorporation of this variable (with realistic values) does not change our main conclusions regarding species coexistence.

In summary, by dividing plant populations into subpopulations with different flowering times, our model describes the dynamics of the timing of flowering of two plant species competing for a given seasonal distribution of pollinators and suggests that coexistence of the two plant species, even if they have different competitive abilities for static resources, can occur by temporal separation of their flowering times. Even a small population of an inferior species can invade a habitat dominated by a superior competitor if the inferior species can win the competition for pollination service during a sub-interval of the flowering season, by exceeding the superior competitor in the number of flowers open simultaneously, so as to eliminate the superior competitor from that time period. It can maintain its population if the frequency of pollination service in the sub-intervals won by the superior competitor is sufficiently low to force intraspecific competition between individuals of the superior species, suppressing their realized fitness to a level as low as that of the inferior species. This coexistence can occur in the following situation. Imagine a habitat where pollination service limits the growth of the resident population. Seeds of many alien species arrive and eventually, by chance alone, one alien species happens to become established. It exhibits strongly synchronous flowering that overlaps with one of the tails of the temporal flowering distribution of the resident species. This is sufficient for it to monopolize the pollinators for some sub-interval. Thus, temporally local competition for pollination service is sufficient to eliminate the resident species from this time period (temporal-niche contraction). The flowering season of the resident species is shortened as a consequence. We may observe this type of species coexistence as the result of rare chance incidents that lead to the successful establishment of an alien species from lots of trials, most of which have resulted in failure and left the resident population unchanged. Our model not only supports the idea that sympatric plants have interspecific

differences in their timings of flowering as the consequence of competition for pollinators (Waser 1978a, 1983; Pleasants 1980; Campbell 1985; Campbell & Motten 1985; Ashton *et al.* 1988), but also elucidates a feasible specific mechanism for interspecific differentiation of the timing of flowering. Also, it has been reported that many genera of alien plants in the British Isles flower in either an early or a late season of the year, which avoids overlap with the native plants (Crawley *et al.* 1996). These observations suggest that the pollen limitation-induced mechanism suggested here may be at work in nature for the sympatric coexistence of plant species.

It would be an interesting extension of the model to apply it to the case of multiple species. From our preliminary simulations, it is suggested that the coexistence of three or more plant species may occur by the same mechanism, although the order of invasion affects greatly how many plant species are able to coexist in a habitat (R. Ishii and M. Higashi, unpublished data).

The model predicts that, as well as the disturbance of abiotic components (e.g. soil erosion or soil pollution, reducing the N -value), disturbance to the pollinator abundance of a natural habitat (biotic components, e.g. the introduction of an efficient pollinator (Winston 1992), which increases the p -value) can cause the extinction of a competitively inferior species.

We thank N. Yamamura for valuable discussions throughout this study, M. J. Crawley and J. Lawton for their valuable comments offered in finalizing the manuscript and their hospitality during our stay at the Department of Biology, Imperial College and the Natural Environment Research Council Centre for Population Biology, UK. We also thank S. Schultz and N. Waser for their useful comments. This study was partly supported by grants from MESSC (Creative Research Programme: DIVER) and JSPS (a USA–UK–Japan Cooperative Research on the relationship between biodiversity and ecological complexity) to both authors and from the Sumitomo Foundation to R.I.

APPENDIX A

The equations for the pair of variables $n_{1,t}$ and $n_{2,t}$ for period t in equation (2) can be transformed into the following pair of equations with variables $n_{1,t}/n_t$ and n_t :

$$n_t(T+1) = \frac{f_t(T)}{f(T)} n_t(T) \quad (\text{A1a})$$

$$\frac{n_{1,t}(T+1)}{n_t(T+1)} = \frac{f_{1,t}(T)}{f(T)} \frac{n_{1,t}(T)}{n_t(T)}, \quad (\text{A1b})$$

where $f_t(T) = f_{1,t}(T)(n_{1,t}(T)/n_t(T)) + f_{2,t}(T)(n_{2,t}(T)/n_t(T))$. Equation (A1a) follows from summing the equations for $n_{1,t}$ and $n_{2,t}$, while equation (A1b) is derived by dividing the equation for $n_{1,t}$ by equation (A1a). At a steady state, equation (A1b) implies that:

$$\begin{aligned} \frac{f_{1,t}^* n_{1,t}^*}{f_t^* n_t^*} - \frac{n_{1,t}^*}{n_t^*} &= \frac{f_{1,t}^* - f_t^*}{f_t^*} \frac{n_{1,t}^*}{n_t^*} \\ &= \frac{f_{1,t}^* - f_{2,t}^*}{f_t^*} \left(1 - \frac{n_{1,t}^*}{n_t^*}\right) \frac{n_{1,t}^*}{n_t^*} = 0. \end{aligned} \quad (\text{A2})$$

Thus, we have $(n_{1,t}^*/n_t^*) = 0, 1$ and α/n_t^* , where $0 < \alpha/n_t^* < 1$ is the solution to the following equation:

$$\begin{aligned}
f_{1,t}^* - f_{2,t}^* &= r_1 \left[1 - \left(1 - \frac{1}{n_t^*} \left(\frac{n_{1,t}^*}{n_t^*} - \frac{1}{n_t^*} \right) \right)^{p_t} \right] \\
&\quad - r_2 \left[1 - \left(1 - \frac{1}{n_t^*} \left(\frac{n_{2,t}^*}{n_t^*} - \frac{1}{n_t^*} \right) \right)^{p_t} \right] \\
&= 0.
\end{aligned} \tag{A3}$$

The middle line of equation (A3) is a monotonically increasing function of $n_{1,t}^*/n_t^*$ and takes a negative value at $n_{1,t}^*/n_t^* = 0$ and a positive value at $n_{1,t}^*/n_t^* = 1$. This implies that equation (A3) has a unique solution $n_{1,t}^*/n_t^* = 0 < \alpha/n_t^* < 1$. It also implies (from equation (A2)) that the variable $n_{1,t}/n_t$ decreases below, and increases above, α/n_t^* . Therefore, there is no stable steady state where $0 < n_{1,t}^*/n_t^* < 1$. That is, at any stable steady state, $n_{1,t}^*/n_t^*$ is equal to either 0 or 1.

APPENDIX B

From equation (4), $\varphi_t(n_t^*)$ can be transformed by substituting equation (1) for $P(n_t^*, n_t^*, p_t)$ to give:

$$\varphi_t(n_t^*) = r_{k(t)} \left[1 - \left(1 - \frac{1}{n_t^*} \frac{n_{k(t),t}^* - 1}{n_t^*} \right)^{p_t} \right] = f^*. \tag{B1}$$

We can derive $\varphi_t^{-1}(f^*)$ by solving equation (B1) with respect to n_t^* as:

$$\varphi_t^{-1}(f^*) = \frac{1 + \sqrt{-3 + 4(1 - f^*/r_{k(t)})}}{2(1 - (1 - f^*/r_{k(t)})^{1/p_t})}. \tag{B2}$$

Thus, to obtain the sub-population of species 1, we substitute 1 for $k(t)$, and the total population of species 1 for $f^* = \theta$; $\sum_{k(t)=1} \varphi_t^{-1}(\theta)$ can be expressed as equation (5).

REFERENCES

- Ashton, P. S., Givnish, T. J. & Apanah, S. 1988 Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. *Am. Nat.* **132**, 44–66.
- Campbell, D. R. 1985 Pollinator sharing and seed set of *Stellaria pubera*: competition for pollination. *Ecology* **66**, 544–553.
- Campbell, D. R. & Motten, A. F. 1985 The mechanism of competition for pollination between two forest herbs. *Ecology* **66**, 554–563.
- Chesson, P. L. 1985 Coexistence of competitors in spatially and temporally varying environments: a look at the combined effect of different sorts of variability. *Theor. Popul. Biol.* **28**, 263–287.
- Crawley, M. J. & May, R. M. 1987 Population dynamics and plant community structure: competition between annuals and perennials. *J. Theor. Biol.* **125**, 475–490.
- Crawley, M. J., Harvey, P. H. & Purvis, A. 1996 Comparative ecology of the native and alien floras of the British Isles. *Phil. Trans. R. Soc. Lond.* **B351**, 1251–1259.
- Herrera, C. M. 1995 Floral biology, microclimate and pollination by ectothermic bees in an early-blooming herb. *Ecology* **76**, 218–228.
- Inouye, D. W. & Pyke, G. H. 1988 Pollination biology in the snowy mountains of Australia: comparisons with montane Colorado, USA. *Aust. J. Ecol.* **13**, 191–210.
- Kohyama, T. 1993 Size-structured tree populations in gap-dynamic forest—the forest architecture hypothesis for the stable coexistence of species. *J. Ecol.* **81**, 131–143.
- Levin, D. A. & Anderson, W. W. 1970 Competition for pollination between simultaneously flowering species. *Am. Nat.* **104**, 455–467.
- Pleasants, J. M. 1980 Competition for bumblebee pollinators in Rocky Mountain plant communities. *Ecology* **61**, 1446–1459.
- Richards, A. J. 1997 *Plant breeding systems*, 2nd edn. London: Allen & Unwin.
- Tilman, D. 1994 Competition and biodiversity in spatially structured habitats. *Ecology* **75**, 2–16.
- Tilman, D., May, R. M., Lehman, C. L. & Nowak, M. A. 1994 Habitat destruction and the extinction debt. *Nature* **371**, 65–66.
- Totland, O. & Matthews, I. 1998 Determinants of pollinator activity and flower preference in the early spring blooming *Crocus vernus*. *Acta Oecologica* **19**, 155–165.
- Vicens, N. & Bosch, J. 2000 Weather dependent pollinator activity in an apple orchard, with special reference to *Osmia cornuta* and *Apis mellifera* (Hymenoptera: Megachilidae and Apidae). *Environ. Entomol.* **29**, 413–420.
- Waser, N. M. 1978a Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology* **59**, 934–944.
- Waser, N. M. 1978b Interspecific pollen transfer and competition between co-occurring plant species. *Oecologia* **36**, 223–236.
- Waser, N. M. 1983 Competition for pollination and floral character differences among sympatric plant species: a review of evidence. In *Handbook of experimental pollination ecology* (ed. C. E. Jones & R. J. Little), pp. 277–293. New York: Van Nostrand Reinhold.
- Winston, M. L. 1992 *Killer bees: the Africanized honey bee in the Americas*. Cambridge, MA: Harvard University Press.

As this paper exceeds the maximum length normally permitted, the authors have agreed to contribute to production costs.