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# Adaptive foraging behaviour of individual pollinators and the coexistence of co-flowering plants

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Although pollinators can play a central role in determining the structure and stability of plant communities, little is known about how their adaptive foraging behaviours at the individual level, e.g. flower constancy, structure these interactions. Here, we construct a mathematical model that integrates individual adaptive foraging behaviour and population dynamics of a community consisting of two plant species and a pollinator species. We find that adaptive foraging at the individual level, as a complementary mechanism to adaptive foraging at the species level, can further enhance the coexistence of plant species through niche partitioning between conspecific pollinators. The stabilizing effect is stronger than that of unbiased generalists when there is also strong competition between plant species over other resources, but less so than that of multiple specialist species. This suggests that adaptive foraging in mutualistic interactions can have a very different impact on the plant community structure from that in predator–prey interactions. In addition, the adaptive behaviour of individual pollinators may cause a sharp regime shift for invading plant species. These results indicate the importance of integrating individual adaptive behaviour and population dynamics for the conservation of native plant communities.

## 1. Introduction

Are sympatric species that share a common mutualistic partner species able to coexist? In particular, an interesting question that has attracted both theoretical and experimental attention, but is still yet to be fully addressed, is how co-flowering plant species that share a common pool of pollinators are able to coexist [1,2]. This is more challenging than simple resource competition [3], because pollinator-mediated competition may inhibit the establishment of an initially rare plant species in a community owing to heterospecific pollen interference [4], as the rarer species receives a disproportionately smaller fraction of effective pollination from generalist pollinators. However, pollination niche overlap between plant species is often dynamic as individual pollinators may change their preferences and foraging behaviour, and partition their niches according to perceived resource availability, which is subject to but also shapes the community dynamics [5,6].

In pollination networks with a large number of common pollinator species relative to the plant species, niche partitioning among different pollinator species may be sufficient to maintain the coexistence of co-flowering species [7–11]. These studies take the individual foraging behaviours of the same pollinator species to be homogeneous, whereas different pollinator species have different preferences among them and visit the same plant species at different frequencies.

On the contrary, in pollination networks with limited common pollinator species, niche partitioning at the species level may be insufficient to maintain the plant species diversity, and it may be necessary to take niche partitioning among conspecific individuals into account. At the individual level, pollinators may partition the niche further among conspecific individuals as they may learn different foraging strategies, e.g. conspecific individuals often show flower constancy to one flower type or another, behaving like specialists, whereas others may switch frequently between flowers of different plant species, behaving like generalists [12]. Thus, a generalist species may consist of specialist

individuals. The pollination niche partitioning depends on the adaptive foraging at both species and individual levels, but the latter has so far received much less attention in studies of pollination networks.

Flower constancy of pollinators clearly benefits every visited co-flowering plant species as it leads to a high efficiency of pollen delivery. However, it is clearly not the direct cause for pollinators to adopt the foraging strategy; as Charles Darwin remarked, ‘That insects should visit the flowers of the same species for as long as they can is of great significance to the plant, as it favours cross fertilization of distinct individuals of the same species; but no one will suppose that insects act in this manner for the good of the plant [13, p. 419]’. For most pollinators, flower constancy is not a fixed trait but a plastic foraging strategy [14]. In general, there is a trade-off in foraging efficiency between maintaining flower constancy and frequently switching plant species. Different hypotheses have been proposed concerning the biological mechanisms underpinning the trade-off, including the interference hypothesis, which assumes a limited memory of flower handling [13], the search image hypothesis and others [15–17]. These hypotheses are not mutually exclusive.

It is clear that the foraging strategies of individual pollinators affect the population dynamics, and the latter also have an impact on the development of the former. However, almost all previous studies have dealt with the two mechanisms separately, using two different types of models. One group addresses how individual pollinators try to optimize their foraging strategies in a static plant community [18,19]. The other investigates the stability of a plant community, assuming that the pollinators use fixed foraging strategies [10,11,20]. Thus, it is necessary to consider the population–behaviour interaction in a complete feedback loop in order to understand the coexistence of co-flowering plant species that share a common pollinator species.

While adaptive foraging behaviour has been incorporated in many studies of population dynamics of predator–prey systems [21,22], to the best of our knowledge, the only published study that has explicitly incorporated pollinator adaptive foraging and plant community dynamics is the recent work by Valdovinos *et al.* [23]. Their simulation results based on an empirical pollination network (with 64 plant species and 100 pollinator species) indicate that adaptive foraging at the species level enhances biodiversity and community stability, although it is yet to be addressed whether this conclusion generalizes to pollination networks with different demographic or structural characteristics. Further, they focus on the adaptive change of relative foraging preference only at the species level by assuming homogeneous populations, without considering within-species variation of individual foraging strategies.

To investigate the potential impact of adaptive individual foraging on the coexistence of plant species, in this article we construct a mathematical model of a very simple pollination network with two co-flowering plant species sharing a common pollinator species. We integrate a pollinator-focused model [19] and a plant-focused model [10], and perform numerical analyses to test the stability of the plant community. (i) We show that adaptive foraging of individual pollinators, on top of adaptive foraging at the species level, may lead to niche partitioning between conspecific individuals and further enhance the coexistence of plant species, especially when the number of pollinator species is relatively small. (ii) There is a strong founder effect when the initial

total plant density is low, as the pollinators would abandon the rare species. Consequently, adaptive foraging pollinators may also destabilize the coexistence of plant species against population density fluctuations, compared with strict specialists, or even generalists in certain situations. (iii) This also indicates that a plant species which relies on animal-associated pollination must overcome a pollination barrier to invade a local community. Only if the immigration rate is sufficiently high, can the invading plants accumulate and start to reproduce locally by attracting pollinators, after which they can rapidly grow to and sustain a high-density local population, resulting in a sharp regime shift.

## 2. Methods

We model a simple pollination network with two co-flowering plant species (enumerated as 1 and 2) and a shared pollinator species, and analyse the interaction between two mechanisms, namely the adaptive foraging behaviour of individual pollinators and the population dynamics of plants and pollinators. The pollinators can frequently change their foraging strategies and reach a behavioural equilibrium quickly, whereas the plant population dynamics occur much more slowly across seasons (figure 1).

For the sake of simplicity, the two plant species are assumed to be spatially well mixed in the community, and they produce rewards at the same rate. Denote by  $P$  the total plant density, and by  $P_1$  and  $P_2$  the densities of plant species 1 and 2, respectively, so that  $P = P_1 + P_2$ . Let  $p_i = P_i/P$  be the fraction of plant species  $i$ . Assume that plant species 2 is the relatively rarer species so that  $p_2 \leq p_1$ .

The pollinators adopt their foraging strategies to optimize their individual energy intake rates. Each individual can show flower constancy to plant species 1 (strategy  $S_1$ ) or to plant species 2 (strategy  $S_2$ ), or it can behave as a generalist (strategy  $S_3$ ). Let  $A_1$ ,  $A_2$  and  $A_3$  be the densities of pollinators adopting the three foraging strategies, respectively, with  $A = A_1 + A_2 + A_3$ . The descriptions of all the variables and the parameters used in this model are summarized in the electronic supplementary material, tables S1 and S2. The default values of most parameters are the same as in Kunin & Iwasa’s model [19], which was based on previous empirical studies.

### (a) Adaptive foraging model

We adopt Kunin & Iwasa’s model [19] to analyse how the plant community structure determines the adaptive foraging strategies of individual pollinators.

Denote by  $F_i$  the mean reward obtained per visit by adopting foraging strategy  $i$  ( $i = 1, 2, 3$ ), and  $F_3 = p_1 F_1 + p_2 F_2$ . Denote by  $T$  the mean travel time between successive flowers for a generalist pollinator. When the plant density is spatially homogeneous, we simply use  $T = 1/(s\sqrt{P})$ , where  $s$  is a constant standing for the flying speed. The time to collect the reward from a flower is assumed to be proportional to the amount of reward offered. A pollinator also has to spend a constant minimum time  $c$  to handle a flower, regardless of its reward. The generalist strategy incurs a penalty on the foraging efficiency, assumed to be of the form  $\beta = b(p_1 p_2^\alpha + p_1^\alpha p_2)$ , which represents the extra handling or searching time that a generalist requires. The penalty is maximized when the two plant species have equal density in the community.

Let  $V_j$  be the rate of flower visits of a pollinator with foraging strategy  $j$  ( $j = 1, 2, 3$ ):

$$V_1 = \frac{1}{T/p_1 + aF_1 + c}, \quad (2.1a)$$

$$V_2 = \frac{1}{T/p_2 + aF_2 + c} \quad (2.1b)$$

$$\text{and } V_3 = \frac{1}{T + aF_3 + \beta + c}, \quad (2.1c)$$

where  $a$  is the time required to collect a unit amount of floral reward, and  $c$  is the minimum handling time per flower.

Denote by  $R_i$  the rate at which pollinators visit a plant of species  $i$ . The amount of reward that a flower supplies to a visiting pollinator increases with the time interval between consecutive visits at the rate  $g$  when the reward remaining in the flower is low, and saturates to a maximum asymptotic value  $f_{\max}$  as  $R_i \rightarrow 0$ . Then,  $F_i$  can be written as a function of  $R_i$ :

$$F_i = \frac{f_{\max}}{1 + R_i f_{\max}/g}. \quad (2.2)$$

Apparently, the total number of visits received by plants of species  $i$  must be equal to the total number of visits to them made by the pollinators, including both specialists and generalists. Thus, we have the equations ( $i = 1, 2$ ):

$$R_i P_i = A_i V_i + A_3 V_3 p_i. \quad (2.3)$$

Here, we assume that the energetic costs per unit time for flight and flower handling are equal, designated by  $E$ , so that the average energy intake rate  $\phi_i$  of pollinators with foraging strategy  $i$  ( $i = 1, 2, 3$ ) can be simply written as

$$\phi_i = V_i F_i - E. \quad (2.4)$$

Pollinators tend to adopt more profitable strategies by individual or social learning [14,24]. For example, learning dynamics of a strategy can be governed by a replicator equation:

$$\frac{dA_i}{dt} = LA_i(\phi_i - \bar{\phi}), \quad (2.5)$$

where  $\bar{\phi} = \frac{A_1 \phi_1 + A_2 \phi_2 + A_3 \phi_3}{A}$  is the mean energy intake rate of all pollinators, and  $L$  is the learning rate.

## (b) Population dynamics model

We assume that the production of seeds is pollen limited, and the pollinator-associated seed production rate  $Q_i$  of plant species  $i$  is proportional to the rate of received conspecific pollen delivery contributed by both specialists and generalists:

$$Q_i = z \left( \frac{A_i V_i}{P_i} + \frac{(1 - (1 - p_i)^B) A_3 V_3}{P} \right). \quad (2.6)$$

The efficiency of pollination by a generalist pollinator (the second component in the parentheses on the right-hand side) is limited by the pollen carry-over rate,  $B$ , which is the number of flowers that the pollen from a visited flower can effectively reach. For example,  $B = 1$  if a pollinator can only deliver the pollen to the next visited flower (strong heterospecific pollen interference), and  $B = \infty$  if a pollinator can carry the pollen forever, i.e. until it is delivered to a conspecific flower (no heterospecific pollen interference). Plants may also reproduce without pollinators, either by selfing (if self-compatible) or vegetative reproduction, at a low rate  $Q_0$ .

The population dynamics in the local community are described, similarly to Benadi *et al.*'s model [10], by

$$\Delta P_i = [P_i(Q_i + Q_0) + M] \left( 1 - \frac{P_i + \gamma P_j}{H} \right) - \mu P_i \quad (2.7a)$$

$$\text{and } A = \frac{P}{r}, \quad (2.7b)$$

where  $M$  is the migration rate from other patches,  $H$  is the habitat capacity for plants, constrained by the availability of resources and  $\mu$  is the plant mortality rate. The two plant species may use resources differently, and  $\gamma$  measures the overlap of the resource niches:  $\gamma = 1$  if they use resources in exactly the same

way, so that the interspecific competition is as strong as intraspecific competition;  $\gamma = 0$  if they use completely different resources, so that there is no interspecific competition. We assume that the recruited pollinator density is simply proportional to the total local plant density, with a constant plant–pollinator ratio  $r$ . As our model focuses on the dynamics in a local patch, and pollinators can easily move between patches and change their spatial distribution, the density of pollinators in a patch is determined by the recruitment instead of local reproduction.

For comparison, besides the scenario modelled above (scenario (i)), we also consider scenarios with pollinators consisting of only unbiased generalists (scenario (ii)), only homogeneous adaptive foragers (a pollinator may accept a plant species with a probability between 0 and 1, and all individuals share the same adaptive preference, scenario (iii)), and only strict specialists (two species, scenario (iv)). In the last scenario, the density of each pollinator species is proportional to the density of the associated plant species with the same plant–pollinator ratio  $r$ .

We also analyse a particular situation when a new plant species is introduced into an established community with a constant immigration rate and encounters a pollination barrier as the local pollinators do not visit the rare species. Owing to the Allee effect, the local community is initially a sink patch for the new species, and whether it can overcome the barrier and establish a local stable population depends on the accumulated density at the immigration–death equilibrium [25].

## (c) Analysis

While the boundary conditions between different strategy combinations at the behavioural equilibrium can be found analytically [19], we do not derive analytical solutions for the population dynamics, owing to the complexity of the coupled system. Instead, we analyse the stability of the plant community numerically with different initial conditions, using code written in PYTHON v. 2.7. Each run ends when an equilibrium state is reached.

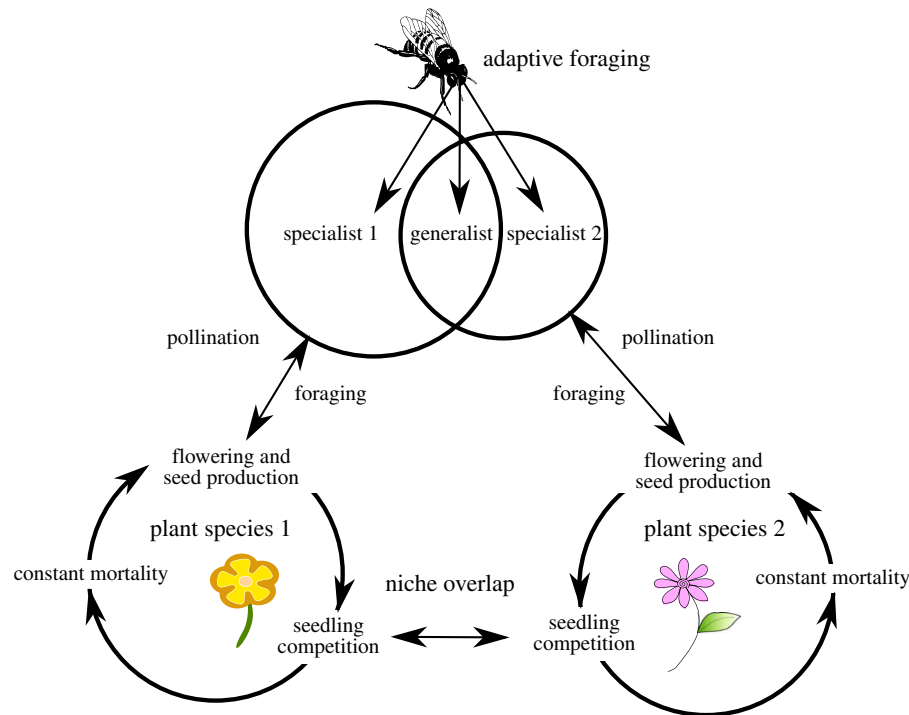
## 3. Results

### (a) Adaptive foraging at the individual level

The profitability of each foraging strategy decreases as more individuals adopt it, reducing the expected reward per visit. As pollinator individuals learn to adopt more profitable strategies, the energy intake rates of any coexisting foraging strategies at a behavioural equilibrium, when no individual can independently find a more profitable strategy, must be equal. In other words, according to equation (2.5),  $\phi_i = \phi_j$  if foraging strategies  $i$  and  $j$  coexist stably. The fraction of each foraging strategy at the behavioural equilibrium depends on the current total plant density, pollinator density and the composition of the plant community. As shown in Kunin & Iwasa's analysis [19], for our behavioural model, only four combinations of foraging strategies are feasible at the behavioural equilibrium; namely  $S_3$ ,  $S_1 + S_3$ ,  $S_1$  and  $S_1 + S_2$  (figure 2), where '+' represents the coexistence of strategies, and the boundaries between any two combinations can be derived analytically by equating  $\phi_i$  and  $\phi_j$  ( $i, j = 1, 2, 3$ ). For any given community composition, only one evolutionarily stable state exists, which can be verified by checking the stability of equation (2.5) (see the electronic supplementary material).

Using constant plant–pollinator ratios  $r = 1000$  (figure 2a) and  $r = 10\,000$  (figure 2b), we show the feasible combinations of adaptive foraging strategies at the behavioural equilibrium.





**Figure 1.** Structure of the model that couples adaptive foraging by individual pollinators and plant population dynamics. (Online version in colour.)

Our approach generates results significantly different from the model with constant pollinator densities [19, fig. 1].

When the total flower density is very low, the generalist ( $S_3$ ) is the single best strategy. Generalists and common-plant specialists can coexist given a medium total plant density ( $S_1 + S_3$ ). Both specialist strategies coexist when the total plant density is high and the fraction of the rarer plant species is not too low ( $S_1 + S_2$ ). The monomorphic equilibrium of common-plant specialists ( $S_1$ ) may exist only when the plant–pollinator ratio is high (figure 2*b*). If we lower the penalty on the foraging efficiency of generalists by increasing  $\alpha$  from 1 to 4, then the range of plant densities producing the equilibrium where only the generalist strategy is stable expands, and that without generalists shrinks (see the electronic supplementary material, figure S1).

### (b) Stability of plant species coexistence

A system with two plant species that share pollinators is often bistable. One stable equilibrium is completely dominated by the initially common species, and the rare species is excluded if the reproduction rate is low in the absence of animal-associated pollination and continuous immigration. At the other equilibrium, two species coexist stably. As the two plant species in our model have exactly the same growth function, and the rarer one has a competitive advantage in resource use, the negative density dependence leads to an even species composition if the two can coexist at the equilibrium. The stability of coexistence is measured by the size of the basin of attraction, or say, the persistence against temporary disturbances on the fraction of each species and on the total plant density.

The stability of plant species coexistence is sensitive to the overlap of resource niches (interspecific competition) and the plant–pollinator ratio. Coexistence is more stable with a lower plant–pollinator ratio ( $r = 1000$ ), i.e. more pollinators per plant (figure 3*a* versus 3*b*), as the competition over the

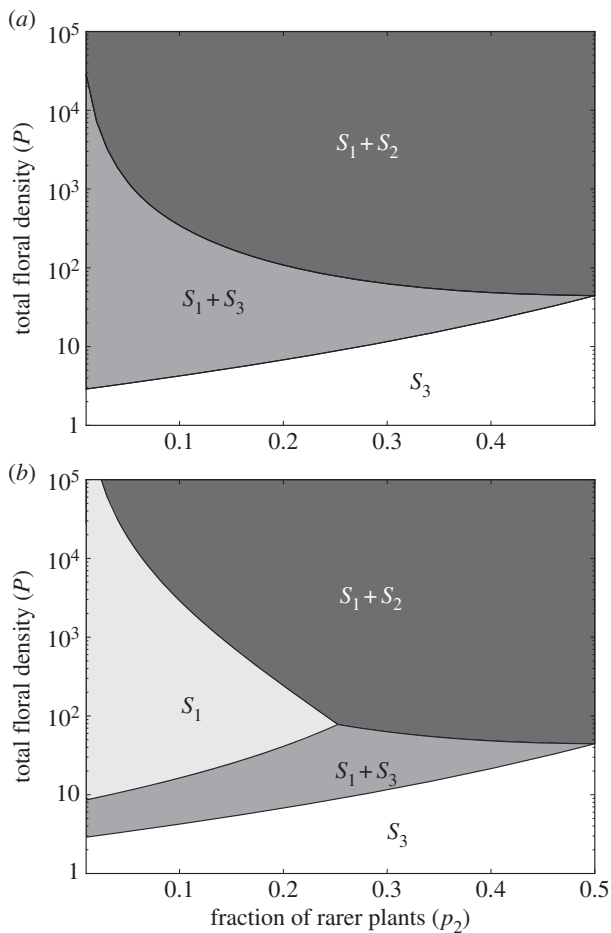
more common plants between pollinators is stronger, and they are thus less likely to abandon the rarer plants. Interestingly, the stability of coexistence is sensitive to the overlap of resource niches only if the plant–pollinator ratio is high ( $r = 10\,000$ ; figure 3*b*). This suggests that the effects of niche overlap and plant–pollinator ratio are complementary, and one's effect appears to be stronger if the other is constrained.

Plant species with similar flowers may lower the penalty on the foraging efficiency of generalists and encourage more pollinators to adopt the generalist strategy. The result with  $\alpha = 4$  shows that a lower penalty on generalists has little effect on the stability of plant species coexistence if the resource niche overlap of the two plant species is low ( $\gamma = 0.2$ ), but it clearly reduces the stability when the overlap is greater than 0.5 (see the electronic supplementary material, figure S2*a*). Therefore, all else being equal, plant species with distinct flower types are more likely to coexist.

We also tested the stability of plant species coexistence with different pollen carry-over rates,  $B$ . Apparently, this only matters with pollen transmission by generalists; if generalists can carry pollen for a longer time and thus deliver conspecific pollen more efficiently ( $B = 4$  versus  $B = 1$ ), then it is easier for the two plant species to coexist when the total plant density is low (see the electronic supplementary material, figure S2*b*).

### (c) Comparison between scenarios with different types of pollinators

To illustrate the effects of adaptive individual foraging on the coexistence of plant species, we make a comparison between our model (scenario (i)) and the other three scenarios ((ii), (iii) and (iv)) with different types of pollinators as described in §2*b*, assessing the plant community stability under different scenarios.



**Figure 2.** Adaptive foraging strategies at the behavioural equilibrium, as functions of plant species proportion and total plant density, given the constant plant–pollinator ratio: (a)  $r = 1000$ ; (b)  $r = 10\,000$ . The foraging penalty on generalists is high ( $\alpha = 1$ ). The white colour ( $S_3$ ) marks the area where the generalist strategy is the single best strategy. The light grey colour ( $S_1$ ) marks the monomorphic equilibrium of common-plant specialists. The medium grey colour ( $S_1 + S_3$ ) marks the area where generalists and common-plant specialists coexist. The dark grey colour ( $S_1 + S_2$ ) marks the area where both specialist strategies coexist. All the other situations are unstable. Note that the monomorphic equilibrium of common-plant specialists ( $S_1$ ) does not exist when the plant–pollinator ratio is low (a).

First, the result of our numerical analysis shows that plant species are less likely to coexist with unbiased generalist pollinators (scenario (ii)) than with a heterogeneous adaptive foraging species (scenario (i)) if their resource niches overlap substantially. But the coexistence can also be more stable in scenario (ii) if the resource uses overlap very little (figure 3c). This is because the generalist pollinators do not abandon the rare plant species, and the rare species has a strong advantage in interspecific competition owing to negative density dependence.

Second, if foraging preference changes continuously and remains homogeneous among individual pollinators, as is assumed in the models with adaptive foraging at the species level [23], then the pollinators are actually using mixed strategies, corresponding to the different pure strategies used in scenario (i). Therefore, whenever different pure strategies coexist in scenario (i) (figure 2), they should always behave as generalists with a biased preference towards the more common plant species in scenario (iii), as the average profitability from visiting the more common

species is always higher. Consequently, the rarer plant species is less likely to persist with homogeneous adaptive pollinators (scenario (iii)) than with heterogeneous adaptive pollinators (scenario (i)) or with unbiased generalist pollinators (scenario (ii)).

Third, when two pollinator species that specialize on different plant species are included in the model (scenario (iv)), the stability of plant species coexistence is enhanced (figure 3d), because the pollinators do not change their foraging preferences and never abandon the rare species even when the total plant density is low. The enhancement is even stronger if the resource niche overlap of the plant species is low.

To sum up the comparison, the stability of plant species coexistence in each scenario can be ranked as  $iii < ii < i < iv$  if their resource niches overlap substantially, otherwise,  $iii < i < ii < iv$ .

#### (d) Allee effect and regime shift

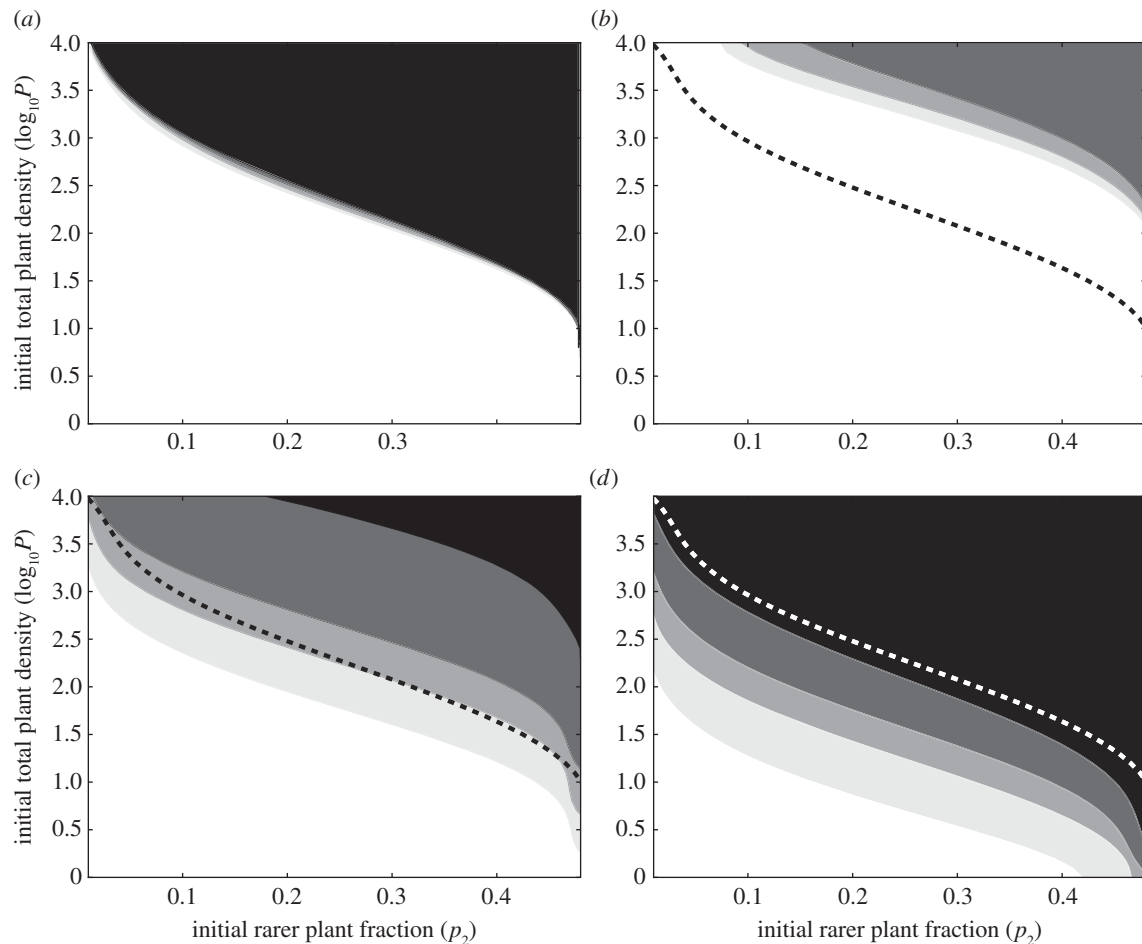
Here, we focus only on the case of a true sink patch with  $Q_0 = 0$ , so that the growth of the invading plant population depends either on pollinator-associated reproduction or immigration. It is clear that the invading plant species can sustain a local population more easily if it can reproduce without pollinator visitation ( $Q_0 > 0$ ), by self-fertilization or vegetative reproduction.

With a low immigration rate  $M$ , the density of the invading species at the equilibrium,  $P_2^*$ , is approximately a linearly increasing function of  $M$ , and  $P_2^* \ll P_1^* \approx H$ . We can make the approximation:  $P_2^* \approx (1 - \gamma)M/\mu$ . If the immigration rate is above a threshold, then the invading plants can accumulate to a density that is sufficiently high to trigger a switch of the pollinator foraging strategy and some local pollinators become attracted. Once the invaders are able to reproduce locally with sufficient pollination, they start to grow at a much faster rate before reaching the new equilibrium in which the two species coexist stably with equal densities (figure 4a). The new equilibrium is independent of the immigration rate, and as expected, the less the resource niches overlap, the easier it is to reach the regime shift (figure 4b).

## 4. Discussion

In most natural plant communities, multiple plant species coexist and share common pollinators, and this has inspired studies on how animal-associated pollination has shaped the plant diversity. However, studies that incorporate the interaction of the adaptive foraging behaviour of pollinators and the plant community dynamics have been very limited until recently [23,26,27], and it is still unclear how heterogeneous adaptive foraging strategies, e.g. different types of flower constancy among conspecific individual pollinators, may influence the coexistence of plant species. To bridge the gap, in this study, we combine two types of plant–pollinator models [10,19] and integrate adaptive foraging behaviour of individual pollinators and plant community dynamics. The result of our numerical analysis indicates that the coexistence of plant species may be further enhanced through niche partitioning between conspecific individual pollinators.

The mechanism that drives niche partitioning between conspecific individuals is similar to that leading to niche partitioning between species. Once the assumption of behavioural homogeneity within species is relaxed, conspecific



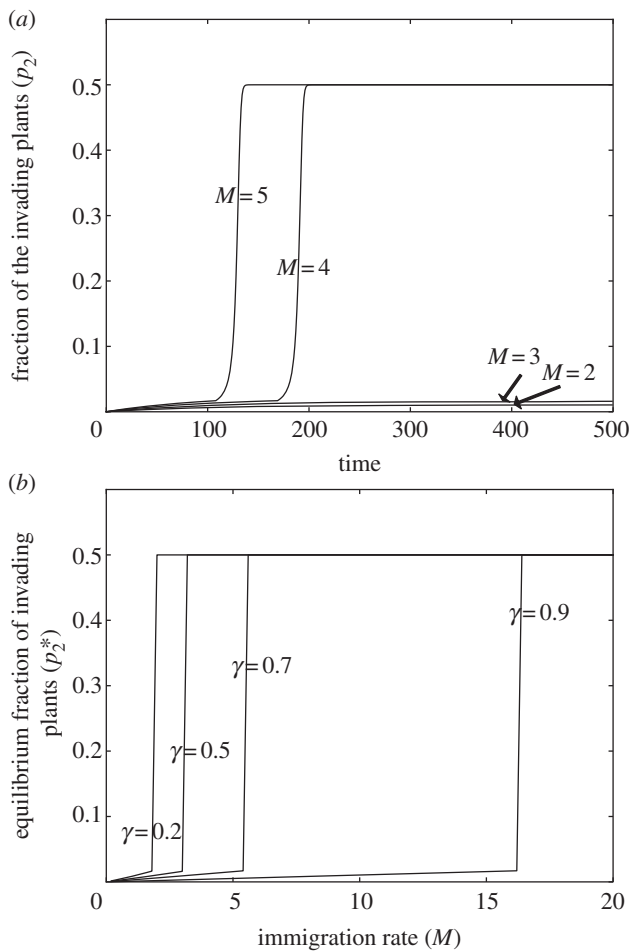
**Figure 3.** The coexistence of the two plant species depends on the initial total plant density and the proportion of each species. The white colour marks the region where the initially common species excludes the rare species. Above the lower boundaries of the light grey, medium grey, dark grey and black regions, coexistence is stable for  $\gamma \leq 0.2$ ,  $\gamma \leq 0.5$ ,  $\gamma \leq 0.7$  and  $\gamma \leq 0.9$ , respectively. (a) The benchmark model, where pollinators adopt adaptive foraging strategies at the behavioural equilibrium, given the parameters  $r = 1000$ ,  $\alpha = 1$ ,  $B = 1$ ,  $Q = 0.01$ ,  $M = 0$ . The dashed lines in all the other figures (b–d) represent the bistable boundary of this benchmark model. (b) The plant species coexistence is less stable if the plant–pollinator ratio is higher ( $r = 10\,000$ ). (c) If pollinators are unbiased generalists, the two plant species are less likely to coexist, and they can coexist only if the resource uses overlap very little. (d) If pollinators are two species of strict specialists, the two plant species are more likely to coexist.

individual pollinators may adopt different foraging strategies if the number of plant species exceeds that of pollinator species and the intraspecific competition is sufficiently strong. The effect is equivalent to adding more pollinator species in the pollination network. As a result, the adaptive foraging behaviour at the individual level can be an important complementary force, in addition to the niche partitioning between species, which maintains the biodiversity in plant communities, especially when the biodiversity of common pollinators is relatively low.

However, we find that adaptive foraging of pollinators does not always enhance the stability of plant species coexistence, in contrast to the previous study [23]. This is because they focus on the stability against species removals, whereas we focus on stability against population density fluctuations. Adaptive foraging at either the species or individual level may sometimes destabilize the plant coexistence, because pollinators may abandon a rare-plant species, hindering its recovery and accelerating its extinction. This is exactly the reverse of the effect of adaptive foraging in predator–prey interactions, where if predators abandon a rare prey species, then its recovery is easier [28,29].

At the behavioural equilibrium, it is clear that some pollinators may specialize on the rarer plant only when the rarer

plant density is sufficiently high, which is more likely if the total plant density is high. On the one hand, this is because the travelling cost between the rarer plants must be sufficiently low to encourage some pollinators to abandon the more common but less rewarding plant species. In general, the rarer plant species is more sensitive to plant density change, because the more common species is already dense, and the marginal change of its density is smaller. On the other hand, as the local pollinator density is assumed to be proportional to the total plant density, and owing to the reduced travelling cost, each plant on average receives more pollinator visits when the plant density is higher, an effect that is even stronger with a low plant–pollinator ratio. Consequently, the initially more common plant species becomes less rewarding as the plant density increases, and it may become more profitable for some pollinators to switch to the rarer species if it is not too rare. Therefore, the coexistence of the two plant species is more stable in a denser community. However, any dense community must grow from an initially sparse community, in which the initially common plant species has a strong founder advantage in the pollination competition. Furthermore, the adaptive foraging behaviours of individual pollinators also lead to a greater variety of transient states, depending on the initial state of a plant community [30].



**Figure 4.** A plant species can stably invade a local community only if the immigration rate is sufficiently high to overcome the pollination barrier. (a) Given  $\gamma = 0.5$ , the invading plants cannot establish a stable local population when the immigration rate is low ( $M = 2$  and  $M = 3$ ) and the persistence of a local population can be only maintained by seed immigration from other patches; by contrast, when the immigration rate is sufficiently high ( $M = 4$  and  $M = 5$ ), the invading species can accumulate up to a critical density, which triggers a sharp regime shift by attracting pollinators and reproducing locally. (b) The fraction of the invading plants at the equilibrium ( $p_2^*$ ) is a discontinuous function of the immigration rate ( $M$ ).

Our results show that the stability of plant species coexistence is sensitive to the recruitment rate of pollinators, as the adaptive foraging strategies depend on the strength of competition between individual pollinators [14]. This is consistent with the idea of biological markets, in which the supply–demand ratio regulates the structure of mutualistic interactions [31,32]. Coexistence is less likely when pollinators are relatively rarer, because it is more profitable to specialize on the common plant species. This result suggests that declining pollinator populations such as in honeybees [33] and bumblebees [34], whose declines have become a global problem, may not only reduce total plant productivity, but also destabilize plant communities and cause a loss of biodiversity.

Plant species with similar flower types may lower the penalty on the foraging efficiency of generalists, as it would be easier for the latter to search and handle the flowers of different species. Thus, more pollinators will tend to adopt the generalist strategy. The subsequent effect on the stability of plant coexistence is, however, less straightforward. This is because, while generalists benefit the rare species more than the common-plant specialists, they provide less efficient

pollination to the rare species than rare plant specialists. Our numerical analysis shows that more generalists actually reduces the stability of plant species coexistence, and the effect is strong when the interspecific resource competition is strong. This suggests that the marginal benefit from extra generalists cannot often offset the marginal cost to the rarer species of reducing specialists. This effect may help explain the widely observed phenomenon of ‘pollination syndromes’, namely that co-flowering plants tend to present different floral traits [35].

To overcome the pollination barrier and the advantage of the founding plant species, an invading species must have a sufficiently high immigration rate or reproduction rate without pollinators, to sustain a local population at the early stage when pollinators ignore it. If the accumulation of the invading population can reach a threshold that stimulates a foraging strategy switch by some pollinators, then a sharp regime shift in the plant community can occur and the invading species can rapidly grow to a high density owing to the boost of animal-associated pollination. Thereafter, the two plant species can coexist stably. In addition, further work is needed to study how the adaptive behaviour of pollinators may drive the evolution of self-fertilization [36] and seed dispersal [37] in plants that affect the colonization of newly appearing plant species.

In general, ecological change in natural communities often co-occurs with adaptive changes in organisms, including adaptive behaviour, developmental plasticity and gene frequency change. Without incorporating the relevant adaptive change, predictions of ecological models are likely to suffer from inaccuracy, particularly for long-term change [38]. Depending on the interacting species and the nature of the interaction, the behavioural trait may be continuous or discrete, and the adaptive change may be faster (behaviourally) or slower (evolutionarily) than ecological dynamics. Consequently, different approximation approaches are needed to model interactions between adaptive behaviour and ecological dynamics in different systems, and generalization from any specific type of model must be done with caution. For example, quantitative genetic models have been widely used to describe the gradual evolution of continuous behavioural traits in a population [39], whereas game theoretical models are often used to study discrete decision-making by animal individuals, which result in instantaneous equilibria relative to ecological dynamics [21]. The different time-courses of these behavioural models may lead to different population dynamics [40]. For interactions between pollinators and flowering plants, it is appropriate to consider the adaptive foraging behaviour as an instantaneous equilibrium, because pollinators learn and switch foraging strategies much faster than the reproduction of plants [6].

In this article, we have focused only on a very simple system with two plant species and one pollinator species. But this approach can be expanded into a model of a larger and more realistic pollination network. All the equations in the behavioural model should hold but with the numbers of plant and pollinator species expanded to be larger. The population dynamics need to be expanded in a similar way [11]. Furthermore, consistent with the idea of adaptive resource responses in predator–prey interactions, it is plausible that plant floral traits also evolve in mutualistic interactions with pollinators on an evolutionary timescale. Our previous work with a model of one plant species and



one pollinator species has shown that the evolution of floral reward depends on the phenotypic variance among plant individuals, which drives the evolution or development of choosiness of pollinators [32]. Therefore, phenotypic plasticity of plants should also be included for the ecological, and evolutionary dynamics of a pollination network to be more fully understood.

In conclusion, we find that the adaptive foraging behaviour of individual pollinators may further enhance the coexistence of plant species through niche partitioning between conspecific pollinators, in addition to niche partitioning between species. But the stabilizing effect against population density fluctuations is still less effective than that of multiple specialist species. This suggests that the

adaptive behaviour in mutualistic interactions can have a different impact on community structure from that in predator–prey interactions. In addition, the adaptive foraging of individual pollinators may cause a sharp regime shift for the invading plant species. These results suggest that adaptive foraging at the individual level could be an important complementary mechanism to adaptive foraging at the species level in shaping the structure of pollination networks, with implications for conservation of native plant communities as well as the management of invasive plant species.

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