



On Mutualists and Exploiters: Plant–insect Coevolution in Pollinating Seed–parasite Systems

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We investigate the coevolution of time of flowering and time of pollinator emergence in an obligate association between a plant and an insect that both pollinates and parasitizes flowers. Numerical analysis shows that the system in general evolves towards a time of flowering different from the time favoured by the abiotic environment. The equilibrium towards which the system evolves is a local fitness maximum (an ESS) with respect to mutational variation in flowering time but, for the insect, it can be a local fitness minimum at which selection on mutational variation in the time of insect emergence is disruptive. A consequence of evolutionary convergence to a fitness minimum is that pollinators having an earlier phenology can coexist with pollinators having a later phenology. Since late emerging insects are more likely to encounter and oviposit within previously pollinated flowers, their effect on the plant is more exploitative, leading them to function as cheaters within the system. Thus, in the long term, pollinators and exploiters are likely to be found in stable coexistence in pollinating seed–parasite systems.

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1. Introduction

Considerable attention has been paid in recent years to the timing of critical life history stages (e.g. Ims, 1990; Gilbert, 1990; Ollerton & Lack, 1992; Fox, 1992; Tuljapurkar & Istock, 1993). Beyond its demographic significance, phenological timing strongly influences the outcome of the biotic interactions that an organism is likely to experience. Phenologies influence the likelihood that prey will be able to avoid predators (Ohkawara *et al.*, 1997), predators will be able to locate prey (Hunter, 1990), hosts will be able to

resist diseases (Parker, 1991; Marr, 1997), mimics will coincide with models (Brodie, 1981), competitors will be able to avoid each other (Stone *et al.*, 1998), and mutualists will be able to find each other (Addicott *et al.*, 1990).

The degree to which interspecific interactions have acted as important selective forces on phenologies is, however, much less clear. Behavioural plasticity permits many animal species to make adaptive phenological adjustments (Fleming, 1992); in these cases, behaviour rather than phenology *per se* is the target of selection. In other cases, it seems probable that an evolutionary shift in phenology has taken place in one organism that has increased its ability to coincide with or to avoid another (Myers, 1979; Juenger &

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Bergelson, 1998). It is also plausible that phenologies of interacting species might undergo coevolution. Coevolved phenologies would appear especially likely in obligate mutualisms, in which each of two partner species can only survive and/or reproduce if it successfully locates the other.

Here, we focus on coevolution of the well-known obligate 'pollinating seed-parasite' mutualisms. In these mutualisms, insects not only pollinate flowers but also lay eggs in them, leading to a delicate balance between the beneficial effects of pollination and the deleterious effects of seed parasitism by the offspring. The two most thoroughly studied cases involve figs and fig wasps (Anstett *et al.*, 1997) and *Yucca* and yucca moths (Pellmyr & Leebens-Mack, 2000). Lesser-known interactions of the same type take place between globeflowers (*Trollius* species) and *Chiastocheta* flies (Pellmyr, 1992) and between senita cactus (*Lophocereus schottii*) and the senita moth (*Upiga virescens*) (Holland & Fleming, 1999).

Coevolutionary processes that might affect phenological patterns are surprisingly complex in pollinating seed-parasite mutualisms, in part because insects that differ slightly in phenology are likely to differ in the degree to which they deliver benefits to the plant (Addicott *et al.*, 1990). Individuals that arrive relatively late have a high probability of depositing their eggs into flowers already sufficiently pollinated; this behaviour adds to the cost but not to the benefit of their host plants. Furthermore, all of the well-studied obligate pollinating seed-parasite interactions are inflicted with seed parasitism by close relatives of the mutualists that arrive late in the flowering or early in the fruiting period and that confer no pollination service whatsoever (Pellmyr, 1989; Compton *et al.*, 1994; Pellmyr *et al.*, 1996; West *et al.* 1996; Desprès & Jaeger, 1999). Diverse arguments have been raised in recent years that exploiters like these must be deterred or else mutualisms will not be able to persist evolutionarily (Axelrod & Hamilton, 1981; Bull & Rice, 1991; Pellmyr *et al.*, 1996; Bronstein, 2001).

In Section 2, we describe a formal model for analysing the coevolution of flowering phenology and emergence time of pollinating seed parasites. Numerical analysis of the model in Section 3

shows the existence of an evolutionary attractor at which flowering phenology is at a local fitness maximum with respect to variation in flowering time (i.e. an evolutionary stable strategy, ESS), but at which the insect emergence time can have a peculiar property of being at a local fitness minimum at which selection is disruptive. In the neighbourhood of a fitness minimum, an early and late insect phenology can coexist, individuals with the early phenology acting more in the role of pollinators and those with a late phenology acting more as pure seed parasites; the latter are referred to as exploiters below (Bronstein, 2001). In other words, coexistence of mutualists and exploiters is a natural outcome of the evolutionary process modelled here.

2. Model

2.1. BACKGROUND

We consider a specialist pollination system comprising a population of (1) flowering plants and (2) insect pollinators, the association being obligate for both species. The environment is seasonal with a limited period suitable for flowering. The insect both pollinates and lays eggs in the flowers; the larvae eat and destroy some of the developing seeds, pupate away from the plant after feeding, and emerge as adults the following year. Seeds that escape parasitism and other causes of mortality become mature plants by the start of the next season.

Each plant and insect has a phenological trait that evolves, these traits being the time s_1 at which the rate of flowering is greatest in the plant, and the time s_2 of (synchronous) emergence of the adult insect (Fig. 1). Trait values that pre-dominate in the system at any one time are written as $s = (s_1, s_2)$, and these values evolve over the course of time through mutation and natural selection generated by the interaction. Abiotic conditions are optimal for flowering in the middle of the flowering season; plant phenotypes synchronized to this time produce flowers at the greatest rate and, all other things (including pollination and parasitism rate) being equal, would be most successful in reproduction. The rate of flower production decreases as plant population density increases, and this eventually curtails

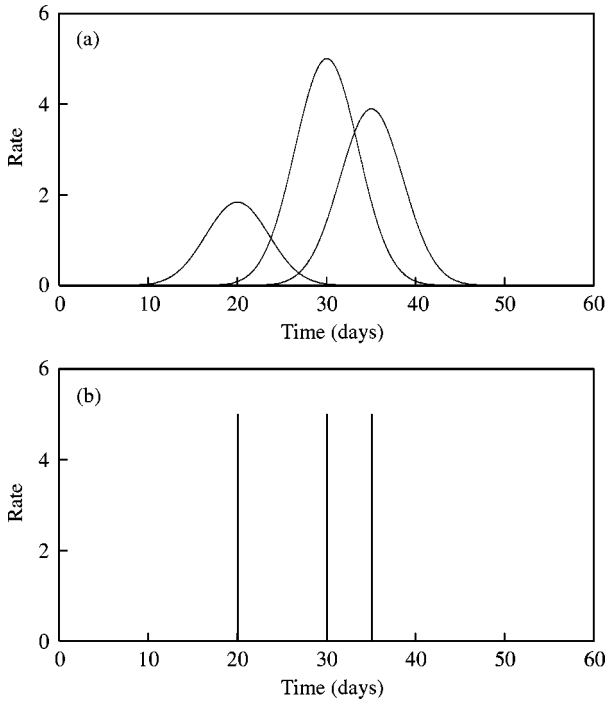


FIG. 1. Phenotypic traits. (a) Shows the rate of ovule production by three phenotypes with contrasting flowering times; the trait s_1 is the mid point of the curve. (b) Shows pulses of emergence of pollinators with three contrasting times of emergence s_2 .

growth of the plant population. Precise definitions of s_1 and s_2 are given in Appendix A.

The model makes use of three nested time-scales to describe how the proximate ecological interactions within flowering seasons feed through to long-term evolution of the phenologies. (1) The shortest time-scale covers the period of flowering within a season for a given pair of trait values s and pair of population densities $x = (x_1, x_2)$. The term x_1 is the density of adult plants and x_2 is the density of insect pupae, the census time being just before the start of the flowering season. At the end of flowering, some new density of seeds and pupae is present. (2) The intermediate time-scale tracks the abundance of plants and insects from one year to the next until an equilibrium density is reached for a given pair of phenotypes s . (3) The longest time-scale describes evolution of s due to rare mutations in the phenology of flowering and emergence of adult insects; this process can be thought of as a sequence of trait substitutions caused by successful mutants spreading to

fixation. Adaptive dynamics (Dieckmann & Law, 1996; Metz *et al.*, 1996) provides an appropriate formal framework for dealing with these nested time-scales, as explained below.

2.2. TIME-SCALE 1: WITHIN-SEASON POLLINATION AND PARASITISM

Pollination takes place in continuous time, and applies to a population with a given pair of trait values s and of population densities x . There are four state variables that change during pollination (Fig. 2), these being the densities of: (1) unfertilized ovules (ξ_1^-), (2) adult insects (ξ_2^-), (3) fertilized, unparasitized ovules (ξ_1^+), and (4) fertilized, parasitized ovules (ξ_2^+), denoted by the vector $\xi = (\xi_1^-, \xi_2^-, \xi_1^+, \xi_2^+)$. At the end of the flowering season, each fertilized, unparasitized ovule becomes a seed, and each fertilized, parasitized ovule becomes an insect pupa. For simplicity flowers are thought of as containing one ovule, although there may be multiple flowers per plant.

The dynamics of pollination are described by the following system of differential equations:

$$\begin{aligned} \frac{d\xi_1^-}{d\tau} = f_1^-(s_1, x_1, x, \tau, \xi) = & \underbrace{B_1(s_1, x_1, x, \tau)}_{(a)} \\ & - \underbrace{d_1 \xi_1^-}_{(b)} - \underbrace{e \xi_1^- \xi_2^-}_{(c)}, \end{aligned} \quad (1a)$$

$$\frac{d\xi_2^-}{d\tau} = f_2^-(s_2, x_2, \tau, \xi) = \underbrace{B_2(s_2, x_2, \tau)}_{(a)} - \underbrace{d_2 \xi_2^-}_{(b)}, \quad (1b)$$

$$\frac{d\xi_1^+}{d\tau} = f_1^+(\xi) = \underbrace{e(1-q) \xi_1^- \xi_2^-}_{(c)} - \underbrace{e q \xi_1^+ \xi_2^-}_{(d)}, \quad (1c)$$

$$\begin{aligned} \frac{d\xi_2^+}{d\tau} = f_2^+(\xi) = & \underbrace{e q \xi_1^- \xi_2^-}_{(c)} + \underbrace{e q \xi_1^+ \xi_2^-}_{(d)} \\ & - \underbrace{e q (q_{11} - q_{22}) \xi_2^+ \xi_2^-}_{(e)} \end{aligned} \quad (1d)$$

with fluxes as illustrated in Fig. 2 and explained below. Terms (a) in eqns (1) are the rates of flower and insect emergence, depending on phenotype, population density and time τ within the season

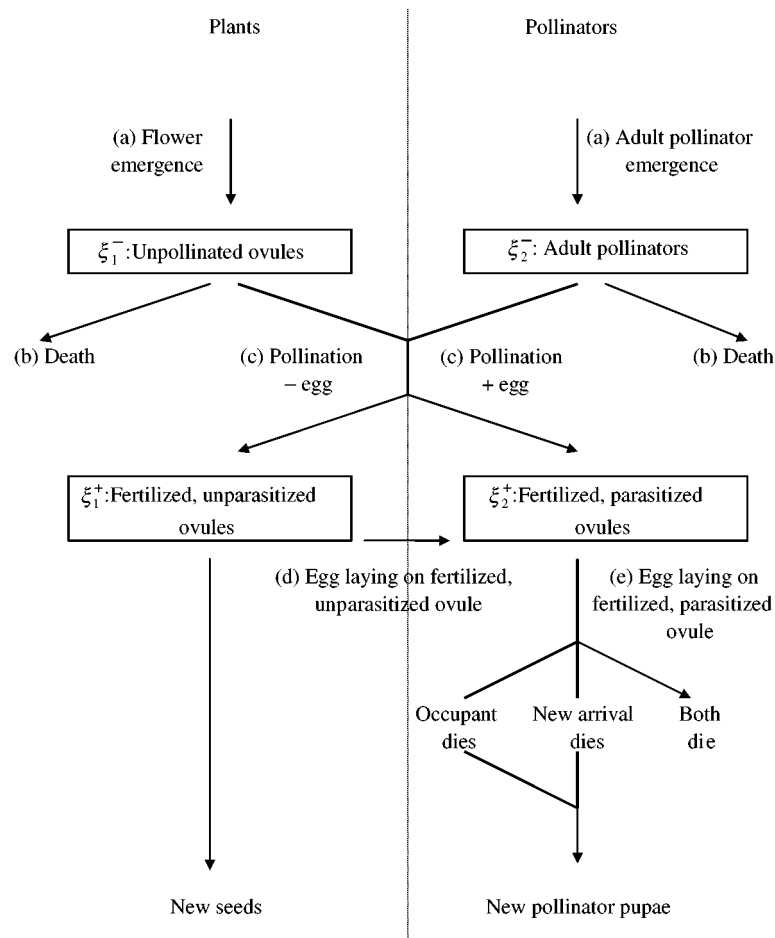


FIG. 2. Events during pollination. Terms in boxes are state variables in eqns (1); letters refer to components of flux in eqns (1).

as described in Appendix A, eqns (A.3) and (A.4). Terms (b) describe the loss due to the intrinsic death rate d_1 , d_2 of unfertilized flowers and adult insects, respectively. Terms (c) deal with encounters between adult insects and flowers leading to pollen deposition with a rate constant e . The ovule is fertilized without an egg being laid with probability $1 - q$, and fertilized with egg laying (i.e. parasitized) with probability q . Insects do not discriminate between unpollinated, pollinated, and parasitized ovules; terms (d) describe the flux caused by visits to ovules previously pollinated, but still unparasitized, that result in egg laying (i.e. parasitism).

The last term (e) in eqns (1) describes the effect of laying a further egg in an ovule already pollinated and parasitized, leading to competition among larvae within an ovule. There are four outcomes of the interaction; these occur with

probabilities q_{11} that both die, q_{12} that the occupant lives and the new arrival dies, q_{21} that the occupant dies and the new arrival lives, and q_{22} that both live, these probabilities summing to one. Of these probabilities, only q_{11} and q_{22} are associated with net change in the density of larvae and appear in eqns (1); q_{12} and q_{21} are needed below for dealing with competition between resident and mutant phenotypes (see Appendix A). For simplicity, it is assumed that $q_{22} = 0$, so that at the end of flowering there is never more than one larva per ovule. Ovules are damaged by parasitism and do not develop into seeds, even though there may be no surviving larvae following larval competition.

Integration of eqns (1) over the flowering season gives the density of new seeds and pupae generated by pollination and parasitism, which then contribute to the densities x in the following

year. The per capita production of new adult plants $b_1(s_1, s, x)$ surviving at the next census is found from the density of new seeds, after dividing by the density of adult plants before flowering and adjusting for mortality prior to the next census. The per capita production of pupae $b_2(s_2, s, x)$ surviving at the next census is found similarly. The extra arguments s_1, s_2 in these per capita birth functions distinguish the trait value of offspring from that of the resident population, and are needed below to deal with invasion by mutants with trait values differing from those of the residents.

2.3. TIME-SCALE 2: POPULATION DYNAMICS

Population dynamics take place in discrete time, and apply to the plant and insect populations with trait values s , the populations being censused once a year just before the start of the flowering season. The following recurrence relations give the population densities x'_i at the next census as functions of their values x_i at the present census:

$$x'_1 = x_1 [p_1 + b_1(s_1, s, x)] \quad (\text{plants}), \quad (2a)$$

$$x'_2 = x_2 b_2(s_2, s, x), \quad (\text{insects}), \quad (2b)$$

where p_1 is the proportion of adult plants that survive from one census to the next, and b_i is the per capita production of new individuals from the pollination dynamics, as described above. (It is assumed that adult insects all die after egg laying.)

After a sufficiently long period of time has elapsed, the population densities reach an asymptotic state. This could easily be extinction of both species; persistence requires both that pollination without parasitism is great enough to maintain the plant population and, at the same time, that pollination with parasitism is great enough to maintain the insect population. Despite this delicate balance, there is a range of parameter values that permits persistence of the species. For simplicity, the parameter values are set here such that the asymptotic state is a feasible equilibrium; the equilibrium is fully determined by the trait values s , and is written as the vector $\hat{x}(s)$.

The growth ratio of a plant of phenotype s_1 (respectively, an insect of phenotype s_2) from one year to the next, in a system with resident phenotypes s at equilibrium densities, is written as $f_1(s_1, s)$ (respectively, $f_2(s_2, s)$), the first argument being the trait value of the individual and the second being the trait values of the resident system. (The extra arguments s_1, s_2 in the growth ratios are needed to deal with invasion by mutants with trait values differing from those of the residents below.) The growth ratios at equilibrium are:

$$f_1(s_1, s) = p_1 + \hat{b}_1(s_1, s) = 1 \quad (\text{plants}), \quad (3a)$$

$$f_2(s_2, s) = \hat{b}_2(s_2, s) = 1 \quad (\text{insects}), \quad (3b)$$

where $\hat{b}_i(s_i, s)$ is the number of surviving offspring at the next census produced by an individual of species i in a community at equilibrium population densities.

2.4. TIME-SCALE 3: EVOLUTIONARY DYNAMICS

Evolution is envisaged as a stochastic sequence of trait substitutions in which mutations arise at random and, if advantageous, stand some chance of going to fixation, thereby replacing resident phenotypes (Metz *et al.*, 1992; Dieckmann & Law, 1996). Mutations are assumed to occur infrequently enough for the population densities to reach equilibrium between mutation events; this assumption has the effect of separating the ecological and evolutionary time-scales.

The probability of survival of a plant mutant s'_1 (similarly an insect mutant s'_2) depends on how quickly it increases when it first arises in the system with resident phenotypes s , given by the growth ratio

$$f_1(s'_1, s) = p_1 + \hat{b}_1(s'_1, s) \quad \text{for a plant mutant}, \quad (4a)$$

$$f_2(s'_2, s) = \hat{b}_2(s'_2, s) \quad \text{for an insect mutant}, \quad (4b)$$

the *per capita* production of mutant offspring being obtained by numerical integration of eqns (A.5) and (A.6) over the flowering season. If the growth ratio of a mutant is less than one, then the mutant is certain to go to extinction; if the ratio is

greater than one, the mutant may invade the resident system.

With a measure of initial increase of a mutant in place, a stochastic mutation-selection process can be constructed, as described in Appendix A, giving the probability per unit (evolutionary) time of the trait substitution from s_1 to s'_1 (similarly from s_2 to s'_2). The derivation assumes that there is a one to one mapping from genotype to phenotype, that the resident population is large, and that a mutant surviving initial stages of growth eventually replaces the resident trait. The last of these assumptions is known to be true for a mutant with a small enough effect on the phenotype, as long as the system is not close to a bifurcation point of population dynamics or an equilibrium point of evolution (Jacob & Metz, pers. comm.); this covers the early evolution of the plant/insect system, but there is an important case in which the assumption does not hold close to the equilibrium point of evolution, as described later.

The generic features of the mutation-selection process are easiest to understand as a deterministic approximation for the average of many stochastic trait-substitution sequences, a model of adaptive dynamics (Dieckmann & Law, 1996):

$$\frac{ds_1}{dt} = \underbrace{\frac{\gamma \mu_1 \sigma_1^2 \hat{x}_1(s)}{2p_1 + \hat{b}_1(s_1, s)}}_{(a)} \underbrace{\frac{\partial}{\partial s'_1} f_1(s'_1, s)|_{s'_1=s_1}}_{(b)} \quad (5a)$$

$$\frac{ds_2}{dt} = \underbrace{\frac{\gamma \mu_2 \sigma_2^2 \hat{x}_2(s)}{\hat{b}_2(s_2, s)}}_{(a)} \underbrace{\frac{\partial}{\partial s'_2} f_2(s'_2, s)|_{s'_2=s_2}}_{(b)} \quad (5b)$$

for the plant and insect phenotypes, respectively [eqns (A.11)]. Part (a) of these equations holds information about the mutation process and can be thought of as scaling the rate of evolution, with parameters μ_i being the proportion of births that are mutants, σ_i^2 being the variance of the mutation distribution, and γ defining the area occupied by the species and time unit of evolution (area yr^{-1}). Part (b), the selection derivative, carries information about the ecological interaction $f_i(s'_i, s)$, and determines the selection acting on the phenology of the plant and pollinator. Together, eqns (5) describe the adaptive dynam-

ics of the pollination system, showing quantitatively how the emergence times of flowers and adult insects change on the evolutionary time-scale through natural selection generated by the ecological interactions.

3. Results

3.1. DYNAMICS ON THREE TIME-SCALES

Linking the time-scales of pollination, population dynamics and evolution is unfamiliar, and we therefore illustrate the idea by means of a numerical example in Fig. 3. Within-season pollination dynamics obtained by integrating eqns (1) are shown in Fig. 3a for fixed phenotypic values s and densities x , giving the density of new seeds and pupae at the end of the season. A sudden change occurs near day 38 due to the emergence of adult insects that then start to pollinate and parasitize flowers.

The pollination dynamics in Fig. 3a determine the single step from year 3 to 4 on the intermediate time-scale of population dynamics (Fig. 3b). Repeating the within-season processes over and over again gives the time course of population densities (the phenotypes s are still held constant), leading eventually to an equilibrium point $\hat{x}(s)$ at which the populations have positive densities.

The equilibrium densities $\hat{x}(s)$ in Fig. 3b, together with the current trait values s , describe the state in year 10000 on the long time-scale of evolution (Fig. 3c). This state affects the probability per unit time of a trait substitution, and hence the adaptive dynamics. Repeating the computations at the lower levels of nesting over and over again enables stochastic trait-substitution sequences (dashed lines in Fig. 3c) and the average of many stochastic realizations given by the adaptive dynamics (smooth continuous lines in Fig. 3c) to be computed. A gradual change in the phenotype of both species takes place, nonmonotonic in this instance for the insect, leading to a peak rate of flowering on day 35 and adult insect emergence on day 42. The plant phenotype that would lead to the greatest number of flowers in this example has peak flowering on day 30, but the asymptotic value differs from this because it is also influenced by evolution of the insect.

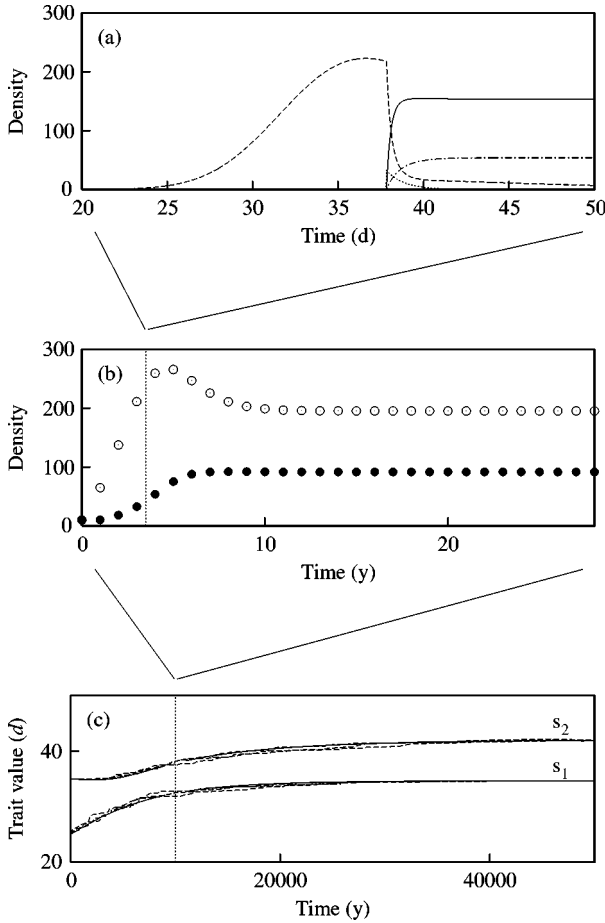


FIG. 3. Dynamics on three time-scales. (a) Shortest time-scale of pollination with $x = (211, 33.6)$, $s = (32.4, 37.8)$, showing densities over the course of the flowering season of: (i) unfertilized ovules (dashed line), (ii) adult pollinators (dotted line), (iii) fertilized, unparasitized ovules that become seeds (continuous line), (iv) parasitized ovules that become insect pupae (dash-dot line). (b) Intermediate time-scale of population dynamics with $s = (32.4, 37.8)$, showing the density of adult plants (open circles) and the density of pupae (solid circles); the vertical dotted line marks the time at which the pollination is computed in (a). (c) Longest time-scale of phenotypic evolution of flowering time (s_1) and time of emergence of adult insects (s_2); dashed lines are three realizations of the stochastic mutation/selection process, continuous lines are deterministic approximations; the vertical dotted line marks the time at which the population densities are computed in (b). Parameter values: $\hat{\tau} = 30$ d, $\hat{\sigma} = 10$ d, $\hat{\beta} = 5$ d $^{-1}$, $\alpha = 0.1$, $\sigma = 5$ d, $\delta\tau = 0.01$ d, $d_1 = 0.1$ d $^{-1}$, $d_2 = 1.0$ d $^{-1}$, $e = 0.1$ d $^{-1}$, $q = 0.1$ d $^{-1}$, $q_{11} = 0.8$, $q_{12} = 0.1$, $q_{21} = 0.1$, $q_{22} = 0$, $p_1 = 0.5$, $\gamma = 100$ area units y^{-1} , $\mu_1 = \mu_2 = 10^{-2}$, $\sigma_1 = \sigma_2 = 10^{-1}$ d.

3.2. PHASE SPACE OF PHENOTYPIC EVOLUTION

A clearer overall picture of how the plant-insect system evolves is gained from examining the phenotype space comprising the resident trait values of the populations (Fig. 4). Coevolution of

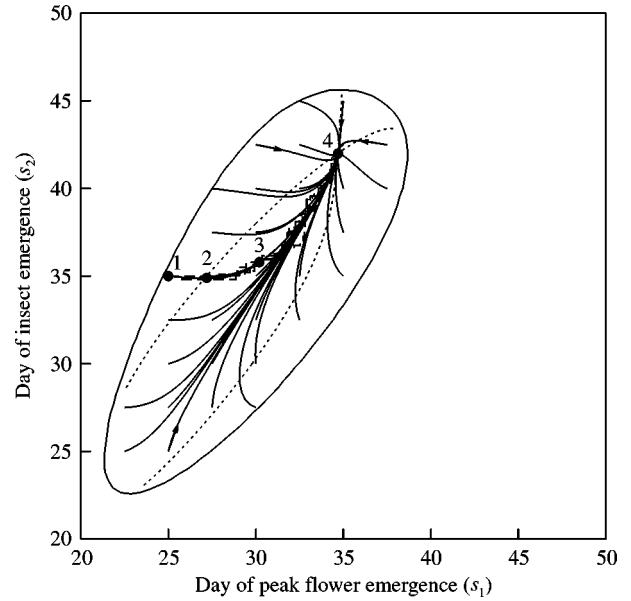


FIG. 4. Example of a phenotype space of plant and insect phenology. Every point inside the oval region is a combination of phenotypic values of plant and insect that permits persistence of the species on the time-scale of population dynamics; outside the oval region the species die out. Inner evolutionary isoclines are shown as dotted lines across the region of persistence. The evolutionary attractor at the intersection of the inner isoclines is shown as the solid circle labelled 4. Evolutionary paths are shown as continuous lines; all paths converge on the solid circle (4). Paths starting from point (1) correspond to the stochastic solutions (dashed lines) and deterministic solution (continuous line) in Fig. 3c. Points (1), (2), (3) and (4) indicate where $f_1(s'_1, s)$, $f_2(s'_2, s)$ are computed in Fig. 5. Parameter values are as shown in Fig. 3.

plant and insect phenologies can be thought of as paths in this space. For instance, the three stochastic trait substitution sequences from Fig. 3c are the dashed lines starting at point (1), moving in small steps across the phenotype space towards point (4); the smooth continuous line from point (1) to (4) is the corresponding path given by the model of adaptive dynamics in Fig. 3c.

3.2.1. Region of Persistence

The plant-insect system can only persist for a subset of phenotypic values in some region around the line $s_1 = s_2$, shown as the oval region in Fig. 4. This is because there must be some synchrony in the time of emergence of flowers and adult insects: insects that emerge at a time when there are no flowers will lay no eggs and carry out no pollination before they die, and both

species will consequently go to extinction. How wide the region around the line depends on the longevity of unpollinated flowers and adult insects. A low intrinsic death rate of flowers extends the region, allowing persistence of the species further above the diagonal line, because more unpollinated flowers remain until emergence of the insects. In a similar way, a low intrinsic death rate of adult insects extends the region of persistence further below the diagonal line, because more insects remain until flowers appear. The example in Fig. 4 is a case in which the mortality rate of unpollinated flowers is low and the mortality rate of adult insects is high, so most of the region of persistence lies above the diagonal line. A further constraint on persistence is the length of the flowering season itself; plant populations with phenologies that are either too early or too late do not produce enough flowers to keep the plant and insect species in existence. This sets a lower and upper limit to the time of flowering allowing the system to persist, irrespective of the phenology of the insect; in the case of Fig. 4, persistence is only possible in the range day $21 < s_1 < 39$.

3.2.2. Inner Evolutionary Isoclines

The region of persistence is divided into different sectors by inner evolutionary isoclines of each species, lines on which the selection derivatives in eqns (5) vanish. Broadly, resident plant phenotypes with early flowering are replaced by mutants with later flowering, and resident plant phenotypes with late flowering are replaced by mutants with earlier flowering; the plants' inner evolutionary isocline defines the boundary between these two regions. A similar argument applies to the inner evolutionary isocline of the insects. In addition, the isoclines depend to some extent on the phenotypic state of the other species, it being disadvantageous to have a phenology too different from the other species.

3.2.3. Paths of Evolution

In qualitative terms, the direction of evolution is determined by the inner evolutionary isoclines as described above. Within those qualitative constraints, variations in the direction of the paths of evolution depend on the detailed shape of the

mutant growth ratios [eqns (4)]. To illustrate this, Fig. 5 shows the shape of the two functions $f_1(s'_1, s)$, $f_2(s'_2, s)$ with respect to mutant trait values s'_1 , s'_2 in the immediate neighbourhood of the current resident trait values s , at four points along one of the paths in Fig. 4. Point (1) is characterized by a strong advantage for plant mutants with later flowering (Fig. 5a) and a smaller advantage for insect mutants with earlier emergence (Fig. 5b), so the evolutionary path moves to the right and slightly downwards. Point (2), which lies on the insect's inner isocline, still has selection for later flowering (Fig. 5c), but no selection on insect emergence time (Fig. 5d), and the path of evolution therefore moves horizontally across the isocline. (There is disruptive selection as the path crosses the insect's isocline, and the insect population could become polymorphic, but such polymorphism is transitory because evolution in the plant soon moves the system away from the isocline and selection becomes directional again.) At point (3), there is selection of a similar strength for plant mutants with later flowering (Fig. 5e) and for insect mutants with later emergence (Fig. 5f), so the path moves up and to the right. Eventually, at point (4) evolution has brought the phenotypes close to the intersection of the isoclines where plant fitness is at a maximum (Fig. 5g) and insect fitness is at a minimum (Fig. 5h).

The paths in Fig. 4 thus give a broad picture as to how the plant–insect system evolves as the species interact. In this example, the paths point away from the boundary of persistence. Exceptions to this are rare in the parameter sets we have investigated, suggesting that a pollinating seed–parasite mutualism that persists on an ecological time-scale is likely to continue to exist after evolution has taken place, rather than evolving to extinction.

3.3. COEXISTENCE OF MUTUALISTS AND EXPLOITERS

3.3.1. Evolutionary Equilibrium

The parameter sets we have investigated typically contain one evolutionary equilibrium (at the intersection of the inner evolutionary isoclines), and this acts as an attractor, as the example in Fig. 4 illustrates. This example has a flowering time at the evolutionary equilibrium

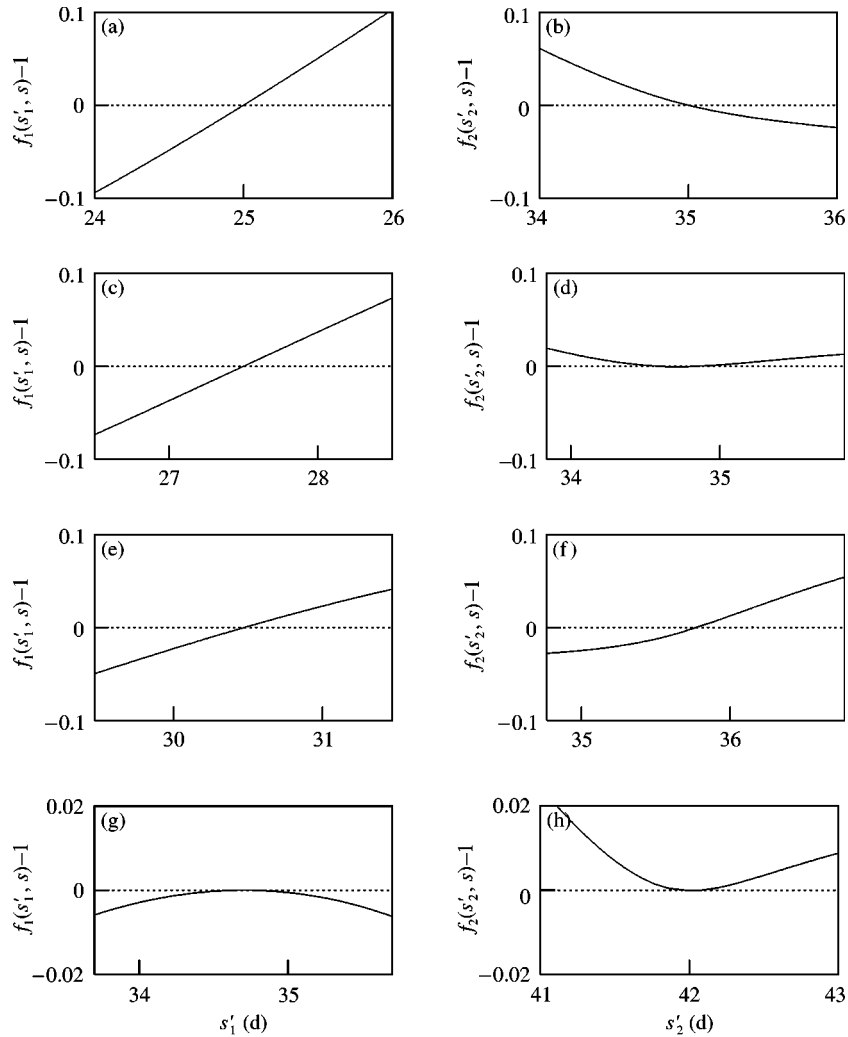


FIG. 5. Functions $f_1(s'_1, s)$, $f_2(s'_2, s)$, showing the growth ratio of mutant plants s'_1 and insects s'_2 , respectively, in the neighbourhood of the resident phenotypes s . The functions are computed at four points along the numbered path in Fig. 4. Resident trait values are given by the intersections of the lines with $f_1(s'_1, s), f_2(s'_2, s) = 1$. (a) Growth ratio of mutant plants at point (1); (b) growth ratio of mutant insects at point (1); (c) growth ratio of mutant plants at point (2); (d) growth ratio of mutant insects at point (2); (e) growth ratio of mutant plants at point (3); (f) growth ratio of mutant insects at point (3); (g) growth ratio of mutant plants at point (4); (h) growth ratio of mutant insects at point (4). Parameter values are as shown in Fig. 3.

later than that which would give the greatest number of flowers. The reason for this is that plant mutants with late flowering are pollinated, yet less parasitized than earlier-flowering resident phenotypes. Later-flowering mutants therefore invade and replace earlier-flowering residents (although ongoing evolution of delayed flowering is eventually halted by reduced flowering late in the season). But the location of the equilibrium depends on the ecological details of the system. For instance, if pre-emption of a flower by a larva gives this larva an advantage over later-develop-

ing larvae, insect mutants with earlier adult emergence replace later-emerging residents. This lowers the insects' isocline, and shifts the equilibrium to an earlier phenology for insects; the plant's isocline is unchanged because it is independent of the parameters of larval competition.

3.3.2. Fitness Maxima and Minima

In our numerical tests, the flowering phenology of the plants at the equilibrium point corresponds to a local fitness maximum with respect

to mutant trait values (e.g. Fig. 5g). In other words, the equilibrium phenotypic value is an ESS, and resists invasion by mutants causing small deviations in flowering time. However, the emergence time of the insects at the equilibrium point can have the peculiar feature of being at a fitness minimum, i.e., a point at which there is disruptive selection such that it is invisable by all mutants causing small deviations in emergence time (e.g. Fig. 5h). Although not biologically intuitive, in mathematical terms this outcome is possible because the condition for convergence to an equilibrium point is different from the condition for the equilibrium to be a local maximum with respect to changes in mutant phenotype (Taylor, 1989; Geritz *et al.*, 1998).

Our numerical results in some cases show disruptive selection along the full length of the insect's inner isocline. We have also found that, if there is a competitive advantage to the larva already occupying a flower when a further egg is laid (i.e. $q_{12} > q_{21}$), part of the insect's inner evolutionary isocline can be a local fitness minimum and part a local maximum. In these circumstances, the evolutionary equilibrium may be a fitness minimum or a fitness maximum for the insect, depending on where the inner isocline of the plant intersects with the insect's isocline.

3.3.3. Coexistence of Early- and Late-emerging Insects

A consequence of disruptive selection acting on the insects is that evolution does not come to a halt at the equilibrium of the monomorphic model of adaptive dynamics. But evolution cannot now be approximated by a monomorphic dynamical system given in eqns (5) because coexistence of an earlier and later phenology occurs. We explain what happens next to the insects by means of a pairwise invasibility plot (Geritz *et al.*, 1998), with resident s_2 and mutant s'_2 phenotypes as axes (Fig. 6).

The pairwise invasibility plot partitions the space s_2, s'_2 into combinations of trait values where the insect mutant can invade, and where it cannot. First, note the dashed diagonal line along which $s_2 = s'_2$; this line forms a boundary of the region allowing invasion, because the growth ratio of the mutant is the same as the resident's on

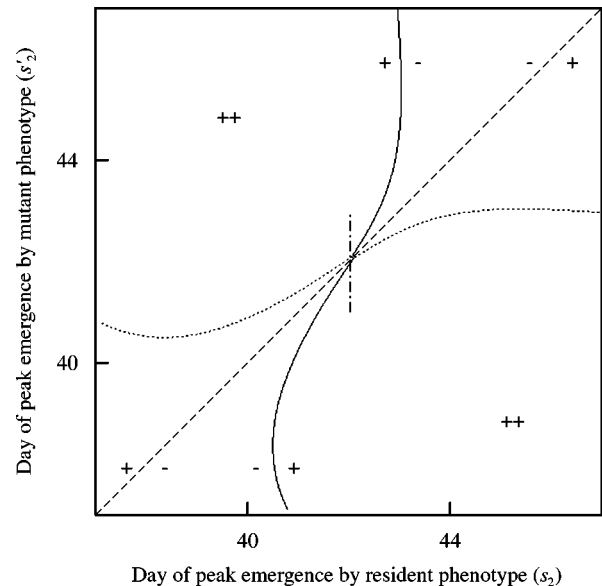


FIG. 6. Pairwise invasibility plot for adult insect emergence in the neighbourhood of the equilibrium point of Fig. 4. The dashed and continuous lines are lines on which $f_2(s'_2, s) = 1$; on the side of these lines labelled '+' mutants can invade; on the side labelled '-' they cannot invade. The dotted line marks the boundary of the region in which s_2 can invade s'_2 , giving regions labelled '++' in the upper-left and lower-right comprising values of s_2 and s'_2 with reciprocal invasibility. The vertical dash-dot line corresponds to the section of $f_2(s'_2, s)$ plotted in Fig. 5h. Parameter values are as shown in Fig. 3.

the diagonal. Second, note the continuous line marking the other boundary of the invasion region. Together, these two lines divide the space into four sectors, the top-left and bottom-right ones being combinations of s_2, s'_2 that permit invasion by the mutant and the other two sectors being combinations that prevent it. Third, note that the equilibrium (emergence on day 42) is at the intersection of these two lines, and that mutants with trait values both greater and less than day 42 (vertically above and below the equilibrium), can invade. The vertical dash-dot line is equivalent to the horizontal axis in Fig. 5h, and invasion by mutants above and below the equilibrium corresponds to mutant fitness being at a minimum on day 42. Fourth, note the dotted line in Fig. 6, obtained by rotating the continuous line around the diagonal. This line shows the boundary of the region in which s_2 can invade s'_2 , in effect turning the phenotype that was previously the mutant into the resident.

From the pairwise invasibility plot (Fig. 6), it can be seen that there is a region labelled '++' at the top left and bottom right of the plot allowing reciprocal invasibility. In other words, for combinations of s_2 , s'_2 in this region, if s'_2 is rare, it invades s_2 and, if s_2 is rare, it invades s'_2 . The insect population thus evolves beyond the equilibrium to a state in which both an early- and a late-emerging phenotype coexist, a phenomenon known as evolutionary branching (Geritz *et al.*, 1998). The later-emerging insects lay a greater proportion of eggs in flowers already pollinated and act more as pure exploiters than as mutualists. The earlier-emerging insects carry out more pollination as they move between flowers, and are more beneficial to the plants than the later-emerging insects. Evidently, a natural consequence of the insects' evolution towards a point at which selection is disruptive is to cause a system to develop in which both pollinators and exploiters coexist.

4. Discussion

The phenological evolution described above is driven by an interplay of potentially conflicting selective pressures generated within species, between species, and by the physical environment. Taken at face value, one might expect flowering phenology to evolve until it matches the time most favoured by the physical environment, and the emergence of adult insects to follow suit. But plant mutants that flower late relative to the resident may gain some advantage by still being pollinated and, at the same time, by being less parasitized than the resident; other things being equal, this causes the evolutionary equilibrium to shift to later flowering. Also, insect mutants with early emergence could gain an advantage by pre-emptive parasitism of flowers, causing the evolutionary equilibrium to shift to an earlier time of emergence. On top of this, mutants with phenologies offset too much from the other species are clearly disadvantageous, because they simply fail to locate mutualists.

Overall, our results suggest that there is no reason to expect evolution of a very close match of phenologies, or a close match between the phenologies and the physical environment. Poor matching of phenologies has been noted repeat-

edly in mutualisms (e.g. Ollerton & Lack, 1992; Herrera, 1998), even in relatively specific ones (Tepedino & Stanton, 1980; Zimmerman *et al.*, 1989; Addicott *et al.*, 1990), but this has been attributed to various forces that might constrain close coordination from evolving. Such forces include phylogenetic constraints (Wright & Calderon, 1995), constraints imposed by the abiotic environment (Addicott *et al.*, 1990; Herrera, 1998), temporally and spatially variable selection (Domínguez & Dirzo, 1995), and contrasting selection pressures on phenology from mutualists and antagonists (Brody, 1997). The results described here suggest, in addition, that poor matching could be a direct consequence of adaptive evolution of the mutualists themselves.

Our results show that evolutionary paths can move towards a point at which there is disruptive selection on the insect, enabling a phenotype with early (pollinating) phenology to coexist stably with a phenotype that has a later (exploitative) phenology. [Ferdy *et al.* (pers. comm.), have also observed this phenomenon in modelling the adaptive dynamics of the *Trollius/Chiastocheta* system.] Pollinating seed-parasite mutualisms are in fact heavily afflicted by exploitation from species closely related to the mutualists (Pellmyr, 1989; Compton *et al.*, 1991, 1994; Pellmyr *et al.*, 1996; West *et al.*, 1996; Després & Jaeger, 1999). Most of these exploiters appear late during their host plant's flowering season, consistent with this model; they contribute little or nothing in the way of pollination, but add substantially to the cost of seed predation.

If evolution moves the insect phenotype towards a point with disruptive selection, there are at least three scenarios for subsequent evolution. First, in view of the diploid sexual genetic system of the insects involved in most pollinator/seed-parasite interactions, the insect population could simply remain near this point in a polymorphic state for phenology. Second, there could be sympatric speciation. This is because heterozygous individuals have intermediate phenotypes and their fitness would be lower than that of homozygotes; genes for assortative mating could be selected under these conditions; the temporal separation of insects with early and late phenologies would itself help to promote this. In effect, evolution towards a point with disruptive

selection creates conditions under which sympatric speciation is possible (Dieckmann & Doebeli, 1999; Doebeli & Dieckmann, 2000), in this case facilitated by allochronic isolation (e.g., Wood & Guttman, 1982). Third, the invading phenotype could be another species with similar ecology but somewhat different phenology, rather than a mutant of the same species. In this case, evolution can be thought of as changing the pollinating seed–parasite system until it reaches a state at which the pollinator species can coexist with a species that acts as a pure exploiter of the interaction. The second and third scenarios both permit subsequent evolutionary divergence between the early- and late-emerging phenologies. A more abstract analysis suggests that an early/late divergence could be the first in a sequence of branching points, leading eventually to coexistence of several species with different phenologies (Ferrière *et al.*, unpublished manuscript).

The origin of exploitation in the *Trollius* and *Yucca* systems may represent, respectively, the second and third evolutionary scenarios presented above. Recent phylogenetic studies suggest that, in both cases, exploiter species diverged from resident pollinators at least one million years ago (Pellmyr & Leebens-Mack, 1999; Després & Jaeger, 1999). For *Trollius*, it is possible that a resident pollinator itself diverged into pollinator and exploiter species. Després & Jaeger (1999) argue that the sole western European species, *Trollius europaeus*, was first colonized by a *Chiastocheta* fly ancestral to the species that now confers the highest net benefits to the plant. Subsequent branching events led to what is now group of *Chiastocheta* sister species that appear in a temporal sequence during the flowering period and that range from strongly mutualistic (the one that visits earliest in the season) to weakly mutualistic to purely parasitic (the one that visits latest in the season, ovipositing into young fruits rather than flowers). Although Després & Jaeger (1999) invoke a series of allopatric speciation events leading to this species complex, the sympatric speciation scenario we develop above also seems reasonable.

In contrast to the *Trollius* system, pollinators and exploiters associated with a given *Yucca* species are not sister species. In this case, it is

probable that coexisting pollinators and exploiters originated via separate invasions onto the same host plant. Some *Yucca* species have two pollinators, a phenomenon Pellmyr and colleagues suggest originated via a host shift by one of the moths (Pellmyr *et al.*, 1996; Pellmyr & Leebens-Mack, 2000). If the host shift resulted in one species with a relatively early phenology and one with a relatively late phenology, the conditions would be in place for a divergence of strategies. Note that by this process, the resident mutualist might feasibly end up as the exploiter, if the invading species was the one with the earlier phenology.

The existence of exploitation, both in pollinating seed–parasite mutualisms and more generally, has initiated much discussion about mechanisms by which it might be punished, the assumption being that without some mechanism of deterrence, the mutualism would be fated to go to extinction (e.g. Axelrod & Hamilton, 1981; Bull & Rice, 1991; Pellmyr & Huth, 1994; Pellmyr *et al.*, 1996). However, mechanisms that effectively deter the activities of exploiters have proven elusive (Bronstein, 2001). Results presented here instead imply that coexistence of pollinator and exploiter insects can be evolutionarily stable. Furthermore, exploitation readily arises within these mutualisms.

Our coevolutionary model was developed as a schematic representation of an obligate mutualism between plants and pollinating seed parasites living in a seasonal environment. However, some of the assumptions could be altered to address specific biological issues, with small modifications to the formal framework.

For instance, there is strong evidence for environmental stochasticity in flowering phenology from year to year (Jackson, 1966; Rathcke & Lacey, 1985; Addicott *et al.*, 1990). The onset of yucca flowering, for example, commonly varies among years from one to several days, sometimes resulting in a near-miss with yucca-moth emergence time (Addicott *et al.*, 1990; J. L. Bronstein, unpublished data). Yucca flowering is delayed or even absent in cool and/or dry years (Smith & Ludwig, 1978; Laslei & Ludwig, 1985; J. L. Bronstein, unpublished data). The effects of such stochasticity on coevolution of phenologies could be investigated by making the time of maximum

flowering and of adult insect emergence random variables.

Multiple parasitism of flowers could be dealt with, for the most part, by introducing further ecological parameters into eqns (1) of the pollination dynamics, although such parameters would increase the model's complexity without changing the basic results, at least for moderate parameter values. Competition among more than two larvae within flowers, which is not covered in the rather simple model of pairwise interactions presented here, could have more fundamental effects on the paths of phenological evolution predicted from models. Plants could themselves manipulate larval competition. For instance, Ferdy *et al.* (pers. comm.) argue that the closed globe formed by the overlapping sepals of the *Trollius* flower increases the chance of survival of insect eggs; these authors use an adaptive-dynamics model to show that this intensifies competition among larvae, with the effect of selecting for lower clutch size in early-emerging *Chiastocheta* species.

If larval competition were strong, as it appears to be in most pollinating seed-parasite systems (Pellmyr & Huth, 1994; Jaeger, 1998; Wilson & Addicott, 1998; Marr *et al.*, 2001), one might expect insect visitors to discriminate among flowers, as it would clearly be advantageous not to lay eggs in flowers already parasitized. Evidence for discrimination on the part of the insects and plants is currently rather limited in pollinating seed-parasite systems (Pellmyr & Huth, 1994; Addicott & Tyre, 1995; Wilson & Addicott, 1998; Johannsen & Loeschke, 1996; Huth & Pellmyr, 1997, 1999; Addicott & Bao, 1999; Holland & Fleming, 1999). Discrimination has the effect of giving early-emerging mutant insects a greater advantage, shifting the insect's inner evolutionary isocline towards earlier emergence. Remarkably, the advantage for early insect emergence could be strong enough to remain in place even when close to the boundary of persistence, in which case evolution would eventually lead to extinction of the plant/insect system (unpublished data). The existence of an evolutionary path to extinction is in keeping with a more abstract model of evolution of mutualistic investment (Ferrière *et al.*, unpublished manuscript), which shows that, under certain biologically

reasonable circumstances, extinction is a likely outcome of coevolution of mutualists.

A number of more technical assumptions underpinning the model of adaptive dynamics should also be noted. Most important is the separation of time-scales of population dynamics and of evolution, or equivalently, the assumption that the rate of evolution is limited by the rarity of advantageous mutations. This is a great simplification of real systems, but means that evolution can be modelled as a relatively tractable monomorphic trait-substitution sequence. It is important to understand, though, that even if evolution is mutation-limited, the monomorphic model becomes inappropriate in the neighbourhood of the evolutionary equilibrium, because more than one insect phenotype can persist near the fitness minimum. We have used the model here to show broadly the evolutionary paths towards evolutionary attractors, and stress that evolution close to the attractor requires other methods of investigation. We also stress that, because the model contains fourteen ecological parameters, our numerical tests could only cover a small part of parameter space; further exploration could uncover other classes of evolutionary dynamics.

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APPENDIX A

This appendix gives formal details of the model on which the results in the text are based. The traits that evolve in the plant and insect are defined; the *per capita* production of offspring by mutant plants and insects is obtained from the pollination dynamics; a stochastic mutation–selection process is defined, from which a dynamical system for evolution of the traits can be derived following the methods of Dieckmann & Law (1996).

A.1. PLANT TRAIT s_1

The evolutionary variable s_1 determines the time within the flowering season at which an individual is flowering at its greatest rate. There are two constraints on how large this rate is. The first is the physical environment, there being an optimal time $\hat{\tau}$ for flowering, such that phenotypes with s_1 closest to $\hat{\tau}$ have the greatest rate. The following Gaussian function $\beta(s_1)$ is used to define the flowering season

$$\beta(s_1) = \hat{\beta} \exp[-(s_1 - \hat{\tau})^2/\hat{\sigma}^2], \quad (\text{A.1})$$

where $\hat{\sigma}$ scales the length of the flowering season, and $\hat{\beta}$ is the maximum rate of flowering by a plant with peak flowering at $\hat{\tau}$. The second constraint is that the maximum rate of flowering goes down as the density x_1 of adult plants goes up. To put this density dependence in place, we define the function as

$$\beta_1(s_1, x) = \beta(s_1)/(1 + \alpha x_1), \quad (\text{A.2})$$

α scaling the effect of population density on flowering. Given these two constraints, we write the rate of flowering by phenotype s_1 $B_1(s_1, x_1, x, \tau)$ as a Gaussian function of time τ :

$$B_1(s_1, x_1, x, \tau) = x_1 \beta_1(s_1, x) \exp[-(\tau - s_1)^2/\sigma^2], \quad (\text{A.3})$$

where σ^2 measures the spread of flowering across the season by a single phenotype. The function contains the two arguments x_1, x because the density of mutants has to be distinguished from the density of residents below.

A.2. INSECT TRAIT s_2

The evolutionary variable s_2 determines the time within the flowering season at which adult insects emerge. Emergence occurs as a pulse over a short period of time $\delta\tau$, and the total rate $B_2(s_2, x_2, \tau)$ at which adult insects emerge defined by

$$B_2(s_2, x_2, \tau) = \begin{cases} x_2/\delta\tau & \text{for } s_2 \leq \tau < s_2 + \delta\tau, \\ 0 & \text{otherwise,} \end{cases} \quad (\text{A.4})$$

where x_2 is the density of insect pupae.

A.3. POLLINATION DYNAMICS OF PLANTS WITH MUTANT PHENOTYPE s'_1

The pollination dynamics of a mutant s'_1 in the plant population, at low density in a resident system at equilibrium, are given by the equations

$$\frac{d\xi_1'^-}{d\tau} = B_1(s'_1, x'_1, x, \tau) - d_1 \xi_1'^- - e \xi_1'^- \xi_2'^-, \quad (\text{A.5a})$$

$$\frac{d\xi_1'^+}{d\tau} = e(1 - q) \xi_1'^- \xi_2'^- - eq \xi_1'^+ \xi_2'^-, \quad (\text{A.5b})$$

where $\xi_1'^-$ is the density of mutant unfertilized ovules and $\xi_1'^+$ is the density of mutant, fertilized, unparasitized ovules. These dynamics are coupled to eqns (1) for the pollination dynamics of the resident phenotypes

$$\frac{d\xi_1^-}{d\tau} = f_1^-(s_1, \hat{x}_1, x, \tau, \xi) \quad (\text{A.5c})$$

$$\frac{d\xi_2^-}{d\tau} = f_2^-(s_2, \hat{x}_2, \tau, \xi), \quad (\text{A.5d})$$

$$\frac{d\xi_1^+}{d\tau} = f_1^+(\xi), \quad (\text{A.5e})$$

$$\frac{d\xi_2^+}{d\tau} = f_2^+(\xi) + eq \xi_1'^- \xi_2'^- + eq \xi_1'^+ \xi_2'^-, \quad (\text{A.5f})$$

By solving eqns (A.5), it is possible to determine the number $\hat{b}_1(s'_1, s)$ of offspring of a mutant plant with trait value s'_1 , for a resident community at equilibrium \hat{x} with trait values s .

A.4. POLLINATION DYNAMICS OF POLLINATORS WITH MUTANT PHENOTYPE s'_2

The pollination dynamics of a mutant s'_2 in the pollinator population, at low density in a resident system equilibrium, are given by the equations

$$\frac{d\xi_2'^-}{d\tau} = B_2(s'_2, x'_2, \tau) - d_2 \xi_2'^-, \quad (\text{A.6a})$$

$$\begin{aligned} \frac{d\xi_2'^+}{d\tau} = & eq \xi_1'^- \xi_2'^- + eq \xi_1'^+ \xi_2'^- \\ & + \underbrace{eq(q_{12} + q_{22}) \xi_2'^+ \xi_2'^-}_a \\ & - \underbrace{eq(q_{11} + q_{12}) \xi_2'^+ \xi_2'^-}_a, \end{aligned} \quad (\text{A.6b})$$

where $\xi_2'^-$ is the density of mutant adult pollinators and $\xi_2'^+$ is the density of fertilized ovules parasitized by mutant larvae. These dynamics are coupled to eqns (1) for the pollination dynamics of the resident phenotypes

$$\frac{d\xi_1^-}{d\tau} = f_1^-(s_1, \hat{x}_1, x, \tau, \xi) - e \xi_1 \xi_2', \quad (\text{A.6c})$$

$$\frac{d\xi_2^-}{d\tau} = f_2^-(s_2, \hat{x}_2, \tau, \xi), \quad (\text{A.6d})$$

$$\frac{d\xi_1^+}{d\tau} = f_1^+(\xi) + e(1 - q) \xi_1'^- \xi_2'^- - eq \xi_1'^+ \xi_2'^-, \quad (\text{A.6e})$$

$$\begin{aligned} \frac{d\xi_2^+}{d\tau} = & f_2^+(\xi) - \underbrace{eq(q_{11} + q_{12}) \xi_2'^+ \xi_2'^-}_a \\ & + \underbrace{eq(q_{12} + q_{22}) \xi_2'^+ \xi_2'^-}_a. \end{aligned} \quad (\text{A.6f})$$

Term (a) in eqns (A.6) deal with the effect of laying a further egg in an ovule already parasitized, leading to interchange between the resident and mutant pollinator phenotype. By solving eqns (A.6), it is possible to determine the number $\hat{b}_2(s'_2, s)$ of offspring of a mutant insect with trait value s'_2 , for a resident community at equilibrium \hat{x} with trait values s .

A.5. STOCHASTIC PROCESS FOR MUTATION AND SELECTION

The stochastic process has phenotypic values as states, and a transition probability per unit (evolutionary) time $w_i(s'_i, s)$ for transition $s_i \rightarrow s'_i$ in species i in a system with phenotypes s . Two statistically independent events contribute to $w_i(s'_i, s)$: the probability per unit time $M_i(s'_i, s)$ of

a mutation s'_i , and the probability $S_i(s'_i, s)$ that the mutant escapes extinction when rare, giving

$$w_i(s'_i, s) = M_i(s'_i, s) \cdot S_i(s'_i, s). \quad (\text{A.7})$$

It is known that, in a population that tends to an equilibrium density not close to a bifurcation point for population dynamics, and not close to an evolutionary fixed point, a mutant which has a sufficiently small effect on the phenotype and which escapes extinction when rare, goes to fixation (Jacob & Metz, pers. comm.).

The contribution of mutation to $w_i(s'_i, s)$ is determined by (a) the probability per unit time of a mutation, and (b) the probability density of the mutation having value s'_i , i.e.

$$M_i(s'_i, s) = \underbrace{\gamma \mu_i \hat{b}_i(s_i, s) \hat{x}_i(s)}_{(a)} \underbrace{M_i(s'_i - s_i)}_{(b)}. \quad (\text{A.8})$$

Here μ_i is the constant probability that a new-born individual of species i is a mutant. The parameter γ , with units area yr^{-1} , (1) scales from population density to population size by multiplying by area, and (2) defines the time unit for evolution. The term $M_i(s'_i - s_i)$ is a probability density function for a mutation s'_i , assumed to be symmetric around the current phenotypic value, dependent only on the difference between them, and with variance σ_i^2 .

A mutation first occurs in a single individual, and stands some chance of going to extinction, even if it has an advantage over the resident trait value. Two independent random variables contribute to the risk of extinction: Y , the number of offspring an individual gives birth to, and Z , survival of the individual itself. It is assumed that Y has a Poisson distribution with mean $\hat{b}_i(s'_i, s)$,

and that Z takes value 0 with probability $1 - p_i$ and value 1 with probability p_i . Starting with 1 individual at census 0, the number present at the next census is a random variable $X = Y + Z$, with probability generating function

$$F_X(z) = (1 - p_i + p_i z) \exp[(z - 1) \hat{b}_i(s'_i, s)], \quad (\text{A.9})$$

the probability of ultimate extinction being the smallest non-negative root of $F_X(z) = z$ (Athreya & Ney, 1972: 7). To solve $F_X(z) = z$ for a mutant of small effect on the phenotype, it is appropriate to consider a Taylor expansion around $z = 1$, giving a probability of ultimate survival

$$S_i(s'_i, s) = \begin{cases} \frac{f_i(s'_i, s) - 1}{[p_i + 0.5 \hat{b}_i(s'_i, s)] \hat{b}_i(s'_i, s)} & \text{for } p_i + \hat{b}_i(s'_i, s) > 1, \\ 0 & \text{otherwise.} \end{cases} \quad (\text{A.10})$$

With eqns (A.8) and (A.10) in place, the transition rates of the stochastic process are fully specified.

A.6. DETERMINISTIC APPROXIMATION

Using eqns (A.7), (A.8) and (A.10), and carrying out a Taylor expansion for small deviations s'_i around s_i , gives the deterministic path

$$\frac{ds_i}{dt} = \frac{\gamma \mu_i \sigma_i^2 \hat{x}_i(s)}{2p_i + \hat{b}_i(s_i, s)} \frac{\partial}{\partial s'_i} f(s'_i, s)|_{s'_i=s_i} \quad \text{for } i = 1, 2 \quad (\text{A.11})$$

(Dieckmann & Law, 1996). These equations describe the adaptive dynamics of the pollination system.