Evolutionary Ecology Research, 2007, **9**: 987–1004

Evolutionarily stable dispersal with pattern formation in a mutualist–antagonist system

Curtis A. Smith* and William G. Wilson

University Program in Ecology and Department of Biology, Duke University, Durham, NC 27708, USA

ABSTRACT

Question: How does the evolution of dispersal distance affect the persistence, distribution, and population dynamics of a mutualist–antagonist system capable of endogenous pattern formation?

Modelling approach: We let dispersal distance evolve within an individual-based model involving an obligate plant–pollinating seed parasite pair and a parasitoid that preys upon pollinator larvae. The model incorporates demographic parameters for ovule production, pollinator oviposition, pollinator and parasitoid visitation rates, in addition to background mortality probabilities for each of the three species. A corresponding non-spatial mathematical model verifies our representation of the interspecific dynamics.

Key assumptions: Individuals move over a homogeneous underlying environment with dispersal distances drawn from probability distribution kernels. Each species is subject to density-dependent reproduction. Pollinators and parasitoids make multiple visits per time step that are Poisson distributed.

Conclusions: Dependent on demographic parameter values, there is a spectrum of outcomes, including: (1) runaway selection for increased dispersal distance resulting in homogeneous distributions of all three species; (2) an evolutionarily stable state with pattern formation and metapopulation-like dynamics; and (3) rapid extinction of one or more species. Interestingly, a weak relaxation of the obligacy between the plants and the pollinators erodes the evolutionarily stable state with pattern formation. We argue that this dependence upon and sensitivity to obligacy may explain the lack of empirical observations of endogenous pattern formation in nature.

Keywords: disperse, evolutionarily stable state, heterogeneity, host–parasitoid, individual-based simulation, mathematical model, metapopulation dynamics, obligate mutualism, patches.

INTRODUCTION

Mutualistic interactions between species are very common (Boucher *et al.*, 1982) with most organisms either directly or indirectly involved in mutualisms (Herre *et al.*, 1999). Although most mutualisms are facultative, some are obligate, including the interactions between various species of yucca plants and yucca moths, whereby a single species of yucca plant completely

---

* Author to whom all correspondence should be addressed. e-mail: ecosmith@gmail.com

relies upon the pollination services of a single species of yucca moth, which in turn produce larvae that require the plant's seeds for food (Pellmyr, 2003). Several species of figs and fig wasps have similar obligate relationships (Wiebes, 1979). A particularly interesting question concerns how mutualisms persist in the presence of antagonists (Yu, 2001; Yu *et al.*, 2001; Morris *et al.*, 2003). For example, yucca–yucca moth mutualisms are confronted with a variety of antagonists that include numerous parasitoids of the yucca moth (Force and Thompson, 1984) and several non-pollinating seed parasites that prey upon the yucca seeds without providing pollination services in return (Addicott, 1996; Pellmyr *et al.*, 1996; Marr *et al.*, 2001). Fig and fig wasp mutualisms encounter similar sets of antagonists (West and Herre, 1994; West *et al.*, 1996).

Recent theoretical work by Morris and colleagues (2003) addressed the issue of co-existence among an obligate plant–pollinating seed parasite pair and an antagonist when the antagonist is a non-pollinating seed parasite. They showed that there was a wide region of parameter space in which all three species could co-exist despite the presence of the cheating antagonist. Wilson *et al.* (2003) put the same system in a spatial context, while Bronstein *et al.* (2003) created a spatial model of the same mutualistic interaction in the presence of a florivore. Each of the spatial models demonstrated that stable patches form when antagonist dispersal distances are relatively larger than the dispersal distances of the plants and pollinators despite an underlying homogeneous environment. Furthermore, the stable patches permit co-existence among all three species for parameter values that produce extinctions of one or more of the species when interactions are mixed homogeneously. Clearly, dispersal can be an important driver in the distribution and persistence of species in mutualist–antagonist communities.

Given this importance, we investigate the dynamics and ecological ramifications that result when dispersal distance evolves within a mutualist–antagonist model. We base the model on an obligate plant–pollinator pair and an obligate parasitoid that preys upon pollinator larvae, much like the yucca plant–yucca moth mutualism with one of the numerous yucca moth parasitoids (Force and Thompson, 1984). We show that the model is capable of endogenous pattern formation and we specifically address the following topics: (1) How does the persistence and distribution of each species change throughout demographic parameter space when dispersal distance is under selection? (2) Does pattern formation emerge and persist when dispersal distance evolves? (3) How does the degree of obligacy between the plant–pollinator pair affect the distribution and persistence of each species when dispersal distance is under selection?

We demonstrate that, included within a spectrum of outcomes, there exists an evolutionarily stable state characterized by endogenously generated metapopulation dynamics and pattern formation with each species distributed among patches of varying sizes. In addition, we show that a minimal decrease in obligacy between the plants and the pollinators erodes the evolutionarily stable state with pattern formation. We discuss how our research pertains to various conservation-related issues, and why, in general, there is a lack of empirical observations of pattern-forming systems.

METHODS

We base our model conceptually on the interactions involving an obligate plant–pollinating seed parasite pair and a parasitoid that preys upon the larvae of the pollinator. As will be seen in the Results section, compared with spatial models in which the antagonist is instead a non-pollinating seed parasite (Wilson *et al.*, 2003) or a florivore (Bronstein *et al.*, 2003), our parasitoid model generates qualitatively similar results regarding co-existence and stable pattern formation when we fix dispersal distance appropriately. We extend this previous work by considering the simultaneous evolution of dispersal distance in all three species.

Individual-based simulation

Our main investigative approach involves a spatial simulation model that incorporates the stochasticity associated with the random events that individuals experience. Space is represented by a ‘one-dimensional’ periodic lattice with 20×2000 cells. Modelling dispersal using a one-dimensional lattice represents the simulation analog of a partial differential equation model in one-spatial dimension, and it allows for easy visualization of species distributions with space–time plots. Furthermore, a one-dimensional lattice allows for efficient investigations at large spatial scales without straining computer resources at similar scales on two-dimensional landscapes. The dispersal distances of plant seeds, pollinators (i.e. ‘mutualists’), and parasitoids (i.e. ‘antagonists’) are taken from uniform dispersal kernels with means of zero and maximum distances given by D_P, D_M, and D_A respectively. Qualitatively similar results occur when we draw deviates from Gaussian or Laplacian dispersal kernels with the corresponding means and standard deviations. The magnitude and sign of a random deviate dictates the distance and direction respectively that an individual moves in the longer dimension. A random number between 1 and 20 then specifies the individual’s new location in the shorter dimension. The landscape thickness of 20 cells decreases the demographic stochasticity that would otherwise rapidly drive one or more of the species to extinction. We also performed simulations on small two-dimensional lattices (500×500 cells) generating qualitatively similar results (Supplementary Information, Fig. S1; www.evolutionary-ecology.com/data/2051supplement.pdf), and we have no reason to believe that our conclusions would not hold on larger two-dimensional landscapes.

Each cell can contain at most one plant, with no limit on the numbers of pollinators or parasitoids per cell. The simulation begins with individuals of each species randomly distributed throughout the landscape. During a time step, each plant has probability θ of producing a single ovule requiring pollination to develop into a seed. If a pollinator visits a plant with an ovule, it pollinates the ovule with probability 1, at which point the ovule becomes a seed. Each seed can then either disperse or the pollinator oviposits with probability γ, thereby consuming the seed and producing a single larva. If a parasitoid lands in a cell with a pollinator larva, it produces an offspring that consumes its prey with probability 1. The number of visits a pollinator and parasitoid makes per time step is assumed to be Poisson distributed with means β and ε, respectively. Competition and survival among pollinator (or parasitoid) larvae is such that the first offspring produced within a cell is also the only larva produced in that cell. Plants, too, are subject to density-dependent recruitment in the sense that the simulation kills a seed that disperses to a location already occupied by a plant. Offspring of all three species inherit the dispersal kernel of their mother, where the kernel’s maximum distance (henceforth referred to as ‘dispersal distance’) is subject to mutation. The probability of mutation is zero for time $t < 5000$ and 0.01 for time $t \geq 5000$, which provides enough time for transient dynamics to give way to a stable state before selection on dispersal distance begins. The simulation determines the magnitude and direction of mutation by drawing a deviate from a normal distribution with a mean of zero and standard deviation of 0.2. Mutated dispersal distances

Table 1. Parameter descriptions and their default values for the model

Parameter	Description	Value
θ	ovule production probability per time step	0.3
β	mean number of mutualist/pollinator visits per time step	6
γ	mutualist/pollinator oviposition probability per visit	0.5
ε	mean number of antagonist/parasitoid visits per time step	15
δ_P	probability of plant death per time step	0.02
δ_M	probability of mutualist/pollinator death per time step	0.2
δ_A	probability of antagonist/parasitoid death per time step	0.2
D_P	seed dispersal distance	varied
D_M	mutualist/pollinator dispersal distance	varied
D_A	antagonist/parasitoid dispersal distance	varied
—	lattice size	20 × 2000

that are negative are set to zero, which we contend does not introduce any biases (e.g. the mean dispersal distance for each of the three species remained at least 24 standard deviations greater than zero throughout the simulation run depicted in Figure 1a). Lastly, the background mortality probabilities are δ_P, δ_M, and δ_A for plant, mutualist, and antagonist respectively. Table 1 lists the default parameter values used, chosen to be biologically reasonable and comparable to the values used by Wilson *et al.* (2003) and Bronstein *et al.* (2003) in their mutualist–antagonist models. We also present results from parameter sweeps that test the sensitivity to changes in our default values. Although unlikely in nature, we assumed no trade-offs between dispersal and any of the demographic parameters. The implementation order in the simulation is as follows:

1. Plants make ovules.
2. Pollinators move about the landscape pollinating and ovipositing.
3. Parasitoids move about the landscape producing offspring that prey on pollinator larvae.
4. Individuals die subject to background mortality.
5. New individuals disperse and grow (e.g. seeds disperse and become plants).

In terms of modelling movement on the lattice, the deviates drawn from each dispersal kernel are real numbers (i.e. not necessarily integer). However, since plant locations are discrete (due to the explicit density-dependence of one plant per cell), each plant and seed only has integer coordinates associated with it (obtained by rounding after dispersal). However, when pollinators and parasitoids disperse, they have continuous (i.e. real) coordinates associated with them, which are rounded for the purposes of determining interactions with plants. For example, if an individual pollinator is at position (2.0, 2.6) and it disperses 1.7 units to the right, its new continuous coordinates would be (2.0, 4.3). Before dispersing, the pollinator has the opportunity to interact with the plant (if any) at location (2, 3), while after dispersal it interacts with the plant (if any) at location (2, 4). We modelled the movement and interactions of parasitoids similarly.

Non-spatial mathematical model

The following set of equations corresponds to the rules specified in the computer simulation:

$$\mathrm{d}P/\mathrm{d}t = \theta P(1 - \mathrm{e}^{-(1-\gamma)\beta M})(\mathrm{e}^{-\gamma\beta M})(1 - P) - \delta_{\mathbf{P}}P \tag{1}$$

$$\mathrm{d}M/\mathrm{d}t = \theta P(1 - \mathrm{e}^{-\gamma\beta M})(\mathrm{e}^{-\varepsilon A}) - \delta_{\mathbf{M}}M \tag{2}$$

$$\mathrm{d}A/\mathrm{d}t = \theta P(1 - \mathrm{e}^{-\gamma\beta M})(1 - \mathrm{e}^{-\varepsilon A}) - \delta_{\mathbf{A}}A \tag{3}$$

The first term in the plant equation consists of four factors. From left to right, the first factor (θP) represents ovule production. Since pollinator and parasitoid visits are assumed to be Poisson distributed, the second factor represents the probability that an ovule experiences at least one pollination-only visit by a pollinator over the behavioural time scale on which visits are made, which is infinitesimally small compared with population dynamical time scales (see Wilson *et al.*, 2003). Similar reasoning generates the third factor, which is the probability of no oviposition visits by pollinators. The fourth factor in the first term represents density-dependence among plants. Finally, the last term in the plant equation takes into account background death. One should read the corresponding terms in the pollinator and parasitoid equations similarly. As was the case in Wilson *et al.* (2003), there is excellent agreement between results generated from numerical solutions to the mathematical model and those from a version of the simulation with global dispersal (Supplementary Information, Fig. S2; www.evolutionary-ecology.com/data/2051supplement.pdf). Although we provide no mathematical representation of dispersal with evolution, the above agreement provides assurance that the simulation accurately captures the interspecific dynamics associated with the mathematical model.

In the absence of the antagonist, Wilson *et al.* (2003) showed that the obligate mutualism is subject to an Allee effect (i.e. both species will go extinct at sufficiently low densities). From equation (1), it is clear that plant growth ($\mathrm{d}P/\mathrm{d}t$) becomes negative with sufficiently high pollinator densities, thereby preventing unbounded population growth. This stabilization is consistent with the mode of regulation argued to be prevalent in pollinating seed parasite mutualisms (Holland and DeAngelis, 2001; Holland *et al.*, 2002).

RESULTS

In a typical simulation run with initial dispersal distances of $D_{\mathbf{P}} = D_{\mathbf{M}} = 10$ and $D_{\mathbf{A}} = 15$, spatial instabilities lead quickly to a patchy landscape that would otherwise remain stable were it not for evolution (Figure 1a). After selection begins, there is a continuous decrease in mean dispersal distances among each of the three species until the system achieves a steady state after which mean dispersal distances remain relatively unchanged. The mean dispersal distances for pollinators and parasitoids decrease much more quickly than for plants, which have a ten-fold longer life span. The parasitoids evolve to a state in which persistence is only possible as a metapopulation. We use the term ‘metapopulation’ to describe a collection of parasitoid sub-populations that persist as a result of local extinction and recolonization events in endogenously generated temporally dynamic patches of plants/pollinators. For example, when only the parasitoids go locally extinct, plant/pollinator patches grow unimpeded, and occasionally merge, until recolonization by parasitoids causes large patches to either shrink in size or split into numerous smaller patches (Figure 1a).

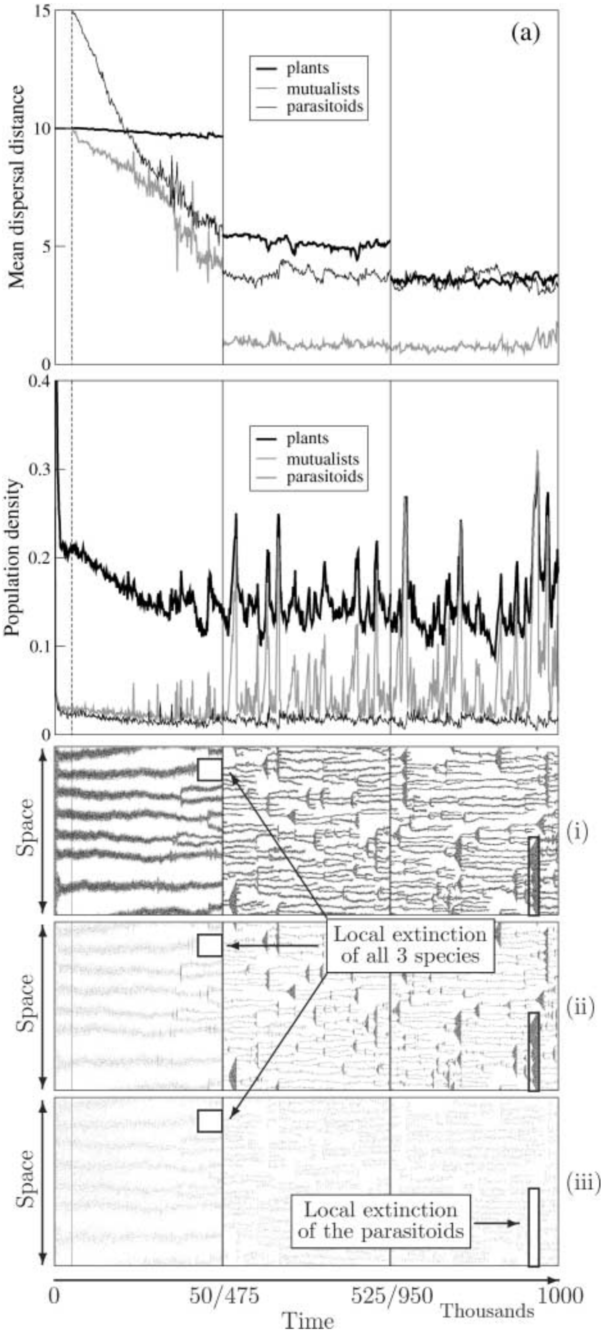
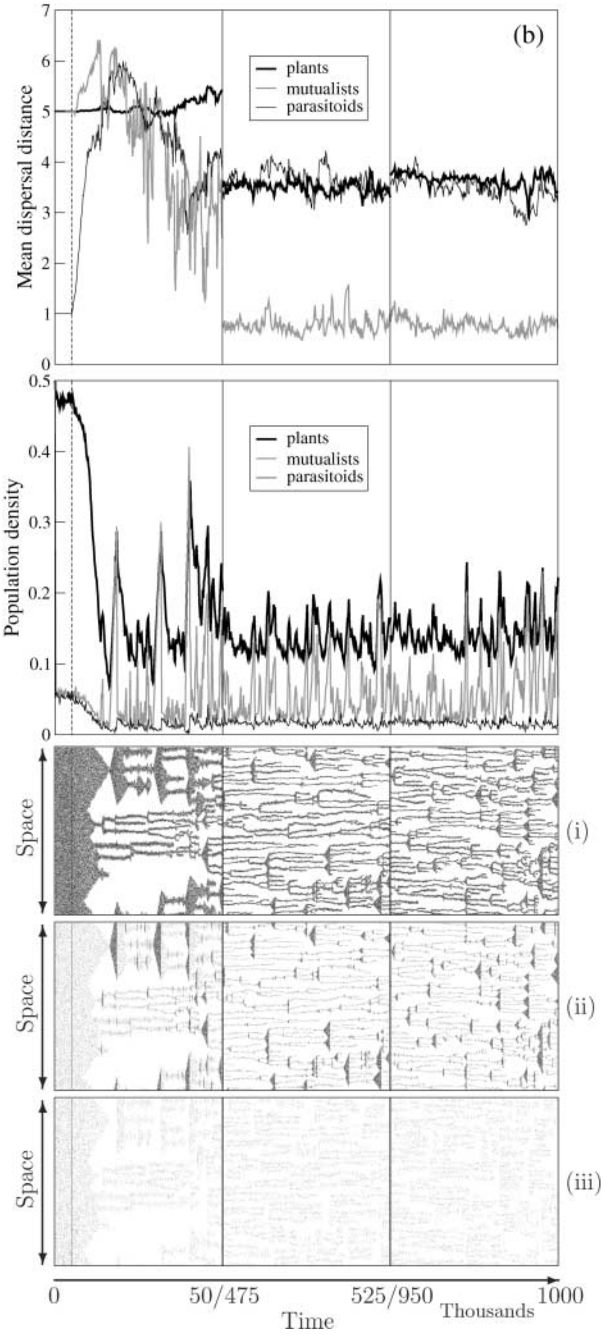


Fig. 1. Results from two simulation runs in which selection on dispersal distance leads to an evolutionarily stable state characterized by metapopulation dynamics. From top to bottom, panel (a) depicts the mean dispersal distances, population densities, and space–time plots (i = plants, ii = mutualists/pollinators, iii = antagonists/parasitoids) for a typical simulation where $D_P = D_M = 10$ and $D_A = 15$ initially. Panel (b) depicts the same information for a simulation where



$D_P = D_M = 5$ and $D_A = 1$ initially. Local extinctions of one or more species are evident in each run (e.g. see the boxed and labelled regions of panel a). Each of the panels shows the first, middle, and last 50,000 time step intervals in simulations run for 1 million time steps. Evolution began at $t = 5000$. The space–time plots depict every other cell along the first row of the lattice for every 50th time step.

The system can also achieve a similar evolutionary state when the initial dispersal distance of the parasitoids is less than the dispersal distances of the plants and pollinators. In a typical simulation run with initial dispersal distances of $D_P = D_M = 5$ and $D_A = 1$, each of the three species would remain homogeneously distributed were it not for evolution (see the first 5000 time steps of the simulation depicted in Figure 1b). However, after selection begins, there is a continuous increase in mean dispersal distances among each of the three species until the mean dispersal distance of the parasitoids surpasses that of the pollinators, at which point patchy species distributions erupt and the system evolves to the steady state described above (compare the last 50,000 time steps depicted in Figure 1a and Figure 1b).

To better gauge the extent of initial dispersal distances that result in the evolutionary state characterized by metapopulation dynamics, we ran simulations with the eight combinations of initial dispersal distances that arise when individuals for the three species start with a dispersal distance of either 1 or 20. On sufficiently sized landscapes, so as not to limit the scale of dispersal, all cases bar two result in the evolutionary state characterized by metapopulation dynamics. One exception occurs when $D_P = D_M = 20$ and $D_A = 1$ initially, in which case a simulation run on a $20 \times 50{,}000$ lattice over 2 million time steps results in runaway selection for increased dispersal distances, with the mean dispersal distance of the parasitoids never surpassing that of the pollinators. Homogeneous species distributions result. However, when either the default mutation rate or the magnitude of mutation is increased modestly by a factor of 2, a sufficient amount of variation among the dispersal distances of individuals eventually leads to an eruption of patchiness with $D_A > D_M$, and the dispersal distances subsequently evolving to the levels depicted in Figure 1. The other exception occurs when $D_P = D_M = D_A = 1$ initially. In this case, the parasitoids go globally extinct after over-exploiting their prey, which share the same dispersal distance. However, if evolution is allowed to begin at time $t = 0$ (instead of $t = 5000$), then sufficient variation among the dispersal distances of the parasitoids allows them to persist, with the system eventually resulting in the evolutionary state characterized by metapopulation dynamics.

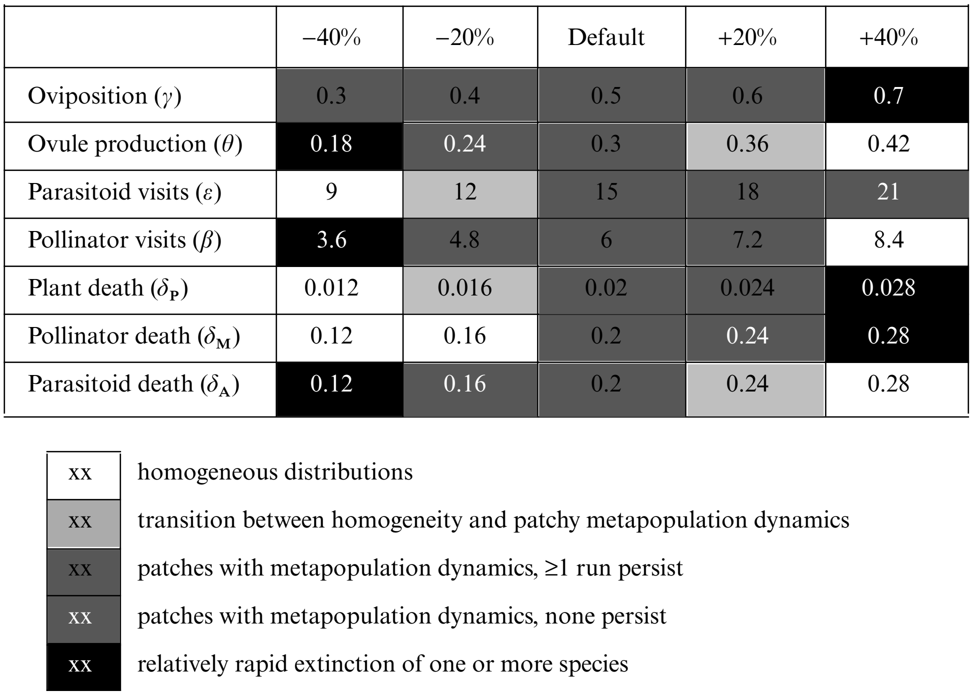
To further test the robustness of our results, we ran simulations in which initial dispersal distances were randomly assigned to each individual from within the interval $[0, 2D]$, where D was much greater than the steady-state dispersal distances. As expected, those individuals with dispersal distances close to the steady-state distances quickly dominate the landscape, with selection on dispersal distance further driving the system to the evolutionary state characterized by metapopulation dynamics. Our results are also robust to at least three shapes of dispersal kernels: uniform, Gaussian, and Laplacian (data not shown).

An alternative final evolutionary state for the system is the global extinction of parasitoids. Since metapopulation dynamics among parasitoids characterizes the previously described steady state, the long-term persistence of parasitoids is highly dependent upon landscape size. For example, in simulation runs on a 20×2000 lattice with $D_P = D_M = 6$ and $D_A = 8$ initially, the parasitoids went globally extinct before $t = 500{,}000$ in 11 of 100 simulation runs, whereas on a 20×1000 lattice, the parasitoids went globally extinct in 96 of 100 simulation runs. The landscape needs to be large enough to contain an adequate number of parasitoid patches to act as sources for recolonization events when local extinctions occur.

The steady state characterized by metapopulation dynamics is also evolutionarily stable to perturbations of dispersal distance. We ran four simulations for each of the eight various combinations of perturbations where, at time $t = 500{,}000$, the dispersal distances for all the individuals in a species were either increased (or decreased) by 20%. Initial dispersal distances were set to $D_P = D_M = 6$ and $D_A = 8$, and to remove the potentially confounding effect of an insufficiently sized lattice, we ran the perturbation experiments on lattices that were 20 × 8000 cells. In all 32 simulation runs, metapopulation dynamics quickly emerged and persisted despite the perturbations.

Although it was not feasible to run exhaustive sweeps of the demographic parameters (e.g. ovule production, death probabilities, visitation rates, oviposition probability), we ran simulations allowing dispersal distance to evolve while using the default parameter values in Table 1 and varying each parameter one at a time by ±20% and ±40%. For example, as we varied the probability of death for plants, the spatial dynamics shifted from homogeneous species distributions when $\delta_P = 0.012$ to a transitional state between homogeneity and patchy distributions of metapopulations when $\delta_P = 0.016$, to persistence with patchy distributions and metapopulation dynamics at the default value of $\delta_P = 0.020$, with similar dynamics and decreased persistence when $\delta_P = 0.024$, and finally to rapid extinction of the parasitoid when $\delta_P = 0.028$ (see Table 2 and Figure 2). It is important to note that if we allow more than one parameter to vary at a time, the evolutionarily stable state characterized by metapopulation dynamics prevails in a much larger region of parameter space than that depicted in Table 2. For example, there is no need to assume a large asymmetry of life spans between the plants and their pollinating seed parasites, since qualitatively similar results to those depicted in Figure 1 occur when $\delta_P = 0.045$ (an increase of 125% from the

Table 2. Characterization of simulation results from demographic parameter sweeps in which each parameter was varied one at a time by ±20% and ±40%, while the default values from Table 1 were used for the remaining parameters



	−40%	−20%	Default	+20%	+40%
Oviposition (γ)	0.3	0.4	0.5	0.6	0.7
Ovule production (θ)	0.18	0.24	0.3	0.36	0.42
Parasitoid visits (ε)	9	12	15	18	21
Pollinator visits (β)	3.6	4.8	6	7.2	8.4
Plant death (δ_P)	0.012	0.016	0.02	0.024	0.028
Pollinator death (δ_M)	0.12	0.16	0.2	0.24	0.28
Parasitoid death (δ_A)	0.12	0.16	0.2	0.24	0.28

xx	homogeneous distributions
xx	transition between homogeneity and patchy metapopulation dynamics
xx	patches with metapopulation dynamics, ≥1 run persist
xx	patches with metapopulation dynamics, none persist
xx	relatively rapid extinction of one or more species

Note: Initial dispersal distances were $D_P = D_M = 10$ and $D_A = 15$. We interpreted the results from a sample of three simulation runs for each parameter combination.

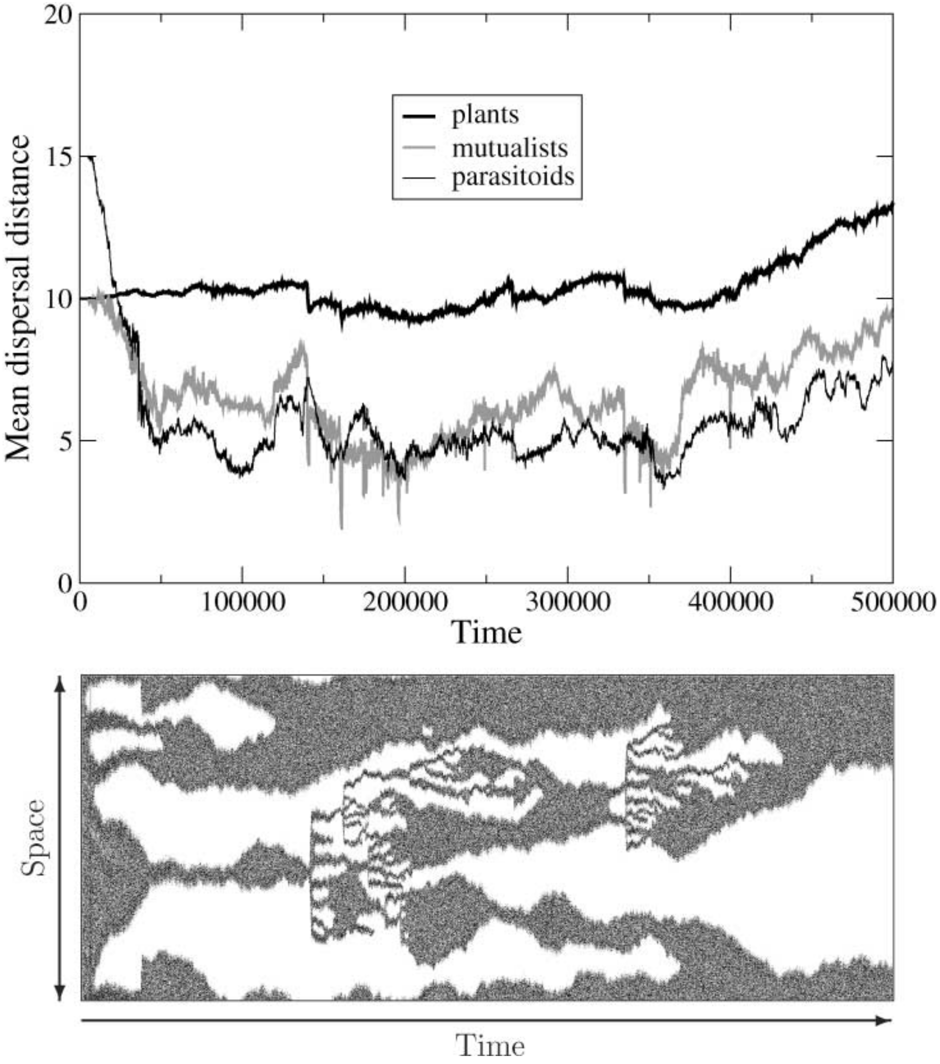
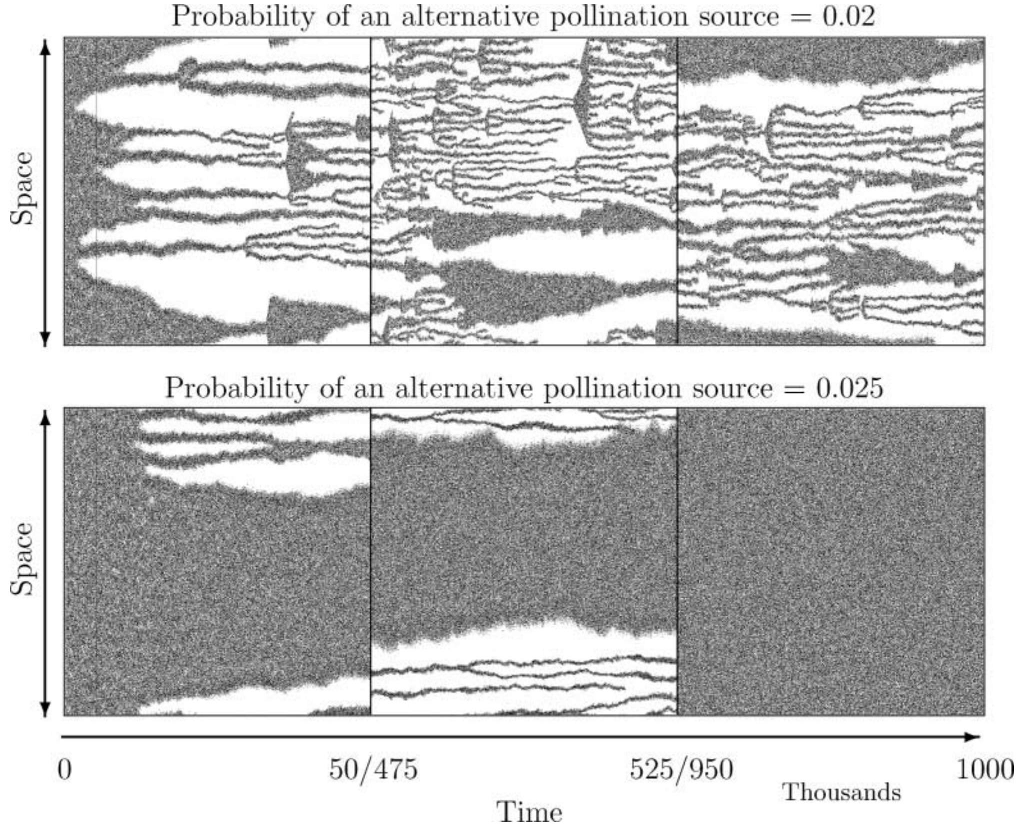


Fig. 2. Mean dispersal distances and a space–time plot of plants from a simulation run demonstrating that a reduction in plant mortality homogenizes the spatial distributions associated with the heterogeneous evolutionarily stable state. When plant mortality $\delta_P = 0.016$ (depicted here), the dynamics are associated with the transition between homogeneous distributions when $\delta_P = 0.012$ (data not shown) and patchy metapopulation dynamics when $\delta_P = 0.020$ (see Fig. 1). The remaining parameters have default values (see Table 1). Evolution began at $t = 5000$ with initial dispersal distances of $D_P = D_M = 10$ and $D_A = 15$. The space–time plot depicts every other cell along the first row of the lattice for every 200th time step.

default value) and $\delta_M = 0.09$ (a decrease of 55% from the default value), which corresponds to a relatively small two-fold difference in life spans.

For this particular system, whether the evolutionarily stable state with pattern formation and metapopulation dynamics emerges is dependent upon the degree of obligacy between the plants and their pollinators. We ran simulations in which ovules that were unfertilized by



Probability of an alternative pollination source = 0.02

Probability of an alternative pollination source = 0.025

Fig. 3. Space–time plots of plants demonstrating that as the likelihood of having an alternative pollination source increases, there is homogenization of the spatial distributions associated with the heterogeneous evolutionarily stable state. The alternative pollination probability is 0.02 (top) versus 0.025 (bottom) versus 0.0 in Fig. 1. Evolution began at $t = 5000$ with initial dispersal distances of $D_P = D_M = 6$ and $D_A = 8$. Each space–time plot shows the first, middle, and last 50,000 time step intervals in simulations run for 1 million time steps. The space–time plots depict every other cell along the first row of the lattice for every 50th time step.

mutualists had a fixed probability of having an alternative pollination source. With a fixed alternative pollination probability of 0.02, selection on dispersal distance leads to patchy metapopulation dynamics with a tendency towards homogeneity. Increasing the alternative pollination probability to 0.025 eventually results in homogeneous distributions (Figure 3). As expected, there tends to be selection for decreased dispersal distances with heterogeneous species distributions, and selection for increased dispersal distances with homogeneous species distributions (data not shown). Qualitatively similar results occur when the pollinating seed parasites have a fixed probability of finding alternative hosts.

DISCUSSION

Dispersal distance strongly influences the distribution and abundance of species. Recent theoretical work includes analyses of mutualist–antagonist systems based upon an obligate plant–pollinating seed parasite pair where the antagonist is either a non-pollinating seed parasite (Wilson *et al.*, 2003) or a florivore (Bronstein *et al.*, 2003). Each of these works showed that for parameter values that lead to extinction in a non-spatial model (i.e. with global dispersal), there is co-existence among all three species when the dispersal distance of the antagonist is greater than that of the plant–pollinator pair, which results in the formation of extraordinarily stable patchy distributions. Since dispersal distance affects both the co-existence and the distribution of species, it is therefore only natural to investigate the effects on system dynamics when dispersal distance is under selection.

In this paper, we allowed dispersal distance to evolve within a mutualist–antagonist system, where the mutualism involves an obligate relationship between a plant and a pollinating seed parasite with an antagonist/parasitoid that preys on pollinator larvae. We have shown that there is a spectrum of outcomes, including: (1) runaway selection for increased dispersal distance with homogeneous distributions of all three species; (2) an evolutionarily stable state characterized by endogenously generated metapopulation dynamics with emergent patches of varying sizes; and (3) rapid extinction of one or more species. Within the region of demographic parameter space capable of producing the second outcome listed above, there are dispersal distances that result in stable homogeneous distributions of all three species in the absence of selection. However, in the presence of selection, patterns emerge that ultimately drive the system to the evolutionarily stable state characterized by metapopulation dynamics (Figure 1b). Therefore, not only is the system capable of producing patterns, selection yields dispersal distances that result in pattern formation. As was the case for Wilson *et al.* (2003) and Bronstein *et al.* (2003), exceptionally stable patches form when the antagonist dispersal distance exceeds that of the plants and pollinators, and co-existence is assured with fixed dispersal distances. However, when we allow the dispersal distance of each species to evolve, the presence of these patches subsequently selects for dispersal distances that put one or more of the species at risk of global extinction on insufficiently sized landscapes. Thus, our work provides yet another example of how evolution can result in dynamics that put species on the edge of extinction (see also Rand *et al.*, 1995; Richards *et al.*, 1999). We have also shown that the likelihood that metapopulation dynamics and pattern formation emerge and persist varies directly with the degree of obligacy between the plants and their pollinators. When dispersal distance evolves, even extremely small levels of non-obligate interactions eventually cause the evolutionary state characterized by metapopulation dynamics and patchy distributions to erode into a spatially homogeneous community (Figure 3).

Pattern-forming mechanism and its implications

Since pollinators and parasitoids each make multiple visits during a time step, we will use the phrase ‘realized dispersal distance’ to represent the actual distance travelled by these two species (which we derived using simulated experiments of random walks). Our interpretation of these results requires a partial understanding of a mechanism for pattern formation reminiscent of a Turing instability (Turing, 1952), whereby one of the necessary conditions for endogenous patches of pollinators to form is that their realized dispersal distance (or diffusion rate) be less than that of the parasitoids (Figure 4). In this way, parasitoids disperse too far to quell the growth of pollinators within the patch, while a disproportionately high level of parasitoids just outside the patch helps sustain the heterogeneity by inhibiting patch growth (Edelstein-Keshet, 1988). Consequently, with patchy

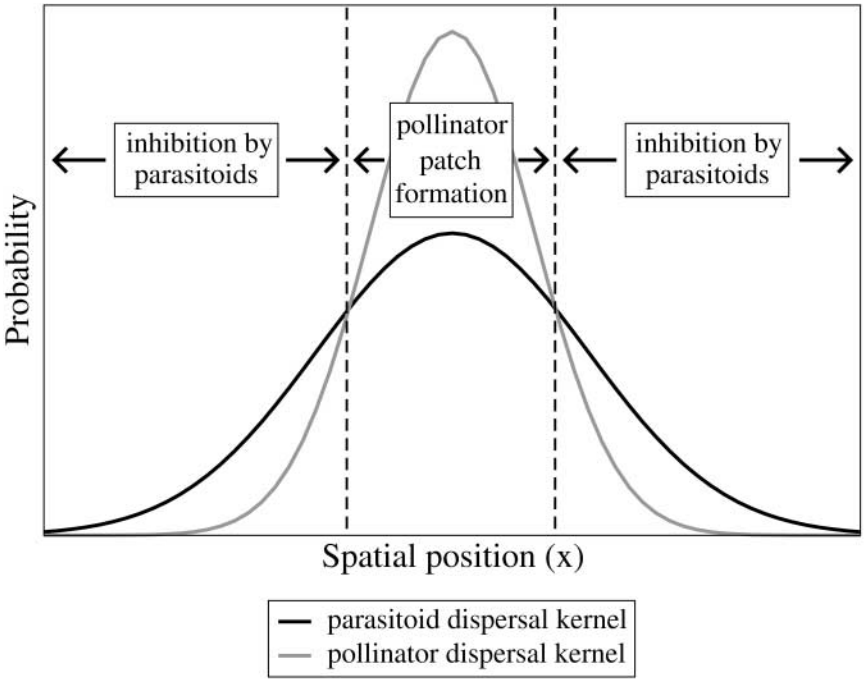


Fig. 4. A mechanism for pattern formation in which patches of pollinators form when parasitoids disperse comparatively further than the pollinators. Long dispersing parasitoids are unable to suppress resource-limited pollinators within the patch. However, strong suppression of the pollinators by parasitoids just outside the patch inhibits patch growth, thereby sustaining heterogeneity.

species distributions, there is selection for the realized dispersal distances among pollinators to remain less than that of parasitoids, since it is disadvantageous to export offspring into the ‘halo’ of parasitoids surrounding patches. However, there is also selection among pollinators for non-zero dispersal distances due to competition with kin (Hamilton and May, 1977). Adult pollinators with dispersal distances of zero are unable to search for oviposition sites, and even if they have the opportunity to oviposit in their present location, their offspring will likely inherit a dispersal distance of zero, at which point mother and offspring occupy the same cell and are in direct competition with one another. Similarly, plants with intermediate dispersal distances are favoured since there is selection against those individuals that disperse their seeds outside of the patches where pollinators are sparse and simultaneous selection against those individuals with extremely small dispersal distances since they must compete heavily with kin for colonization sites. For the parasitoids, there is selection against realized dispersal distances greater than the realized dispersal distances of pollinators since it is disadvantageous for parasitoids to export offspring to areas outside of patches where pollinators are sparse. However, there is also selection for the realized dispersal distances of parasitoids to remain greater than those of pollinators. Strains of parasitoids with realized dispersal distances similar to the pollinators go extinct because over-exploitation of the resource results in the local extinction of one or more of the species (Figure 1a).

To substantiate further the pattern-forming mechanism described above, we conducted simulations allowing the dispersal distances of only one of the species to evolve while the dispersal distances of the other two species remained fixed (data not shown). For example, realized dispersal distances of parasitoids always evolved to levels just greater than the realized dispersal distance of pollinators, resulting in metapopulation dynamics regardless of whether initial dispersal distances produce homogeneous or patchy species distributions. When the mean realized dispersal distance of the parasitoids is much greater than that of the pollinators, patchy distributions prevail and there is strong selection for decreased dispersal distance among parasitoids. However, when the mean realized dispersal distance of the parasitoids is much less than that of the pollinators, all three species are homogeneously distributed initially. Then there is selection for increased dispersal distance among parasitoids until their mean realized dispersal distance catches up to the realized dispersal distance of the pollinators, resulting in rapid over-exploitation until either parasitoids suffer global extinction on insufficiently sized landscapes or patches and metapopulation dynamics emerge on sufficiently large landscapes. Simulation runs in which the dispersal distance of plants or pollinators evolves alone also produced results consistent with the pattern-forming mechanism and our interpretation thereof, including selection for intermediate dispersal distances in the presence of patchy distributions.

The pattern-forming mechanism described above also helps with our interpretation as to why a weak relaxation of the obligacy between the plant–pollinator pair erodes the evolutionarily stable state characterized by metapopulation dynamics. The obligacy apparently prevents the pollinators from escaping the halo of parasitoids surrounding each patch since the chances of also finding a plant outside of a patch are very low. However, if the plants have an alternative pollination source, or if the pollinators have alternative hosts, then the likelihood that pollinators can persist outside of a patch increases significantly (Figure 3).

Lack of empirical observations for pattern formation

The pattern-forming mechanism described in the previous section provides empiricists with several hypotheses to test. For example, Figure 4 and previous theoretical work by Wilson *et al.* (1999) imply that parasitoids should have higher realized dispersal distances than pollinators and that one should find relatively higher parasitoid-to-pollinator ratios with higher rates of parasitism in the periphery of each plant–pollinator patch. However, empirical observations in support of these predictions are lacking. The strongest support comes from studies involving the western tussock moth (a defoliator) and its parasitoids. Since adult female tussock moths are flightless, this particular system satisfies the condition that the parasitoids disperse further than the hosts. Furthermore, by placing tussock moth eggs and larvae along a transect extending away from the edge of a tussock moth patch, Brodmann *et al.* (1997) found increased parasitism rates in the area surrounding the outbreak. Additional support comes from Maron and Harrison (1997), who showed that the parasitism near the edge of a tussock moth outbreak is strong enough to inhibit the growth of nearby incipient outbreaks while outbreaks further away were able to increase, thereby sustaining patchy moth distributions.

Despite the limited evidence from the tussock moth example, why is there an overall lack of empirical observations of the previously described pattern-forming mechanism? While the effects of selection on dispersal distance within the tussock moth system is best left for future work, our results here clearly demonstrate that even if a system is capable of endogenous pattern formation, selection on dispersal distance can eliminate all patchiness. For example, in our model, selection on dispersal distance drives the system to a pattern-forming distribution, which is then susceptible to extinction on insufficiently sized landscapes. Furthermore, the likelihood that patterns emerge and persist is extremely sensitive to, and varies directly with, the degree of obligacy between the plants and the pollinators (Figure 3). It is therefore interesting to note that even some of the oft-quoted yucca–yucca moth mutualisms involve species that only facultatively depend on one another. For instance, some species of yucca plants have multiple pollinators (Pellmyr, 1999, 2003), whereas some yucca moths have multiple hosts (Pellmyr, 2003). Exceptions to obligacy are also found in some fig–fig wasp mutualisms (Michaloud *et al.*, 1985, 1996; Kerdelhue *et al.*, 1999). Variance within a species can also decrease the levels of obligacy with at least one example of a plant–pollinating seed parasite mutualism that is obligate in some geographic locations and facultative in others (Despres *et al.*, 2002). Since obligate mutualisms may be the exception and not the rule (Howe, 1984), our results may help explain why observations of pattern-forming systems are rare. In the quest for empirical evidence of endogenous pattern formation, perhaps we need to focus our efforts on fully obligate multi-species mutualisms.

Ecological and conservation-related implications

As depicted in Figure 1, there are at least two additional important ecological ramifications based on this study. First, our results may provide a mechanism by which landscapes with patches of varying sizes can evolve simply as a result of interspecific dynamics and selection on dispersal distance, without any assumptions of underlying environmental structure. Second, the growth and subsequent splitting of plant–pollinator patches that occurs as a consequence of the local extinction and eventual re-establishment of parasitoids provides a potential mechanism for the recolonization of areas long void of each species.

The evolution of dispersal distance is an emerging and increasingly important issue in ecology as habitats become more fragmented. If certain systems only persist naturally as metapopulations, our research could be relevant to conservation-related efforts, including the design of reserves large enough to contain an adequate number of patches to act as sources for recolonization events when local extinctions occur. If conservation biologists wish to design reserves to sustain species threatened by fragmentation, it is imperative that they have a firm understanding of the distances travelled by the species in question and how natural selection acts on those distances (Thomas *et al.*, 1998; Hill *et al.*, 1999; Thomas, 2000). Sustainability may depend directly on the dispersal distance of the target species, while the configuration of a reserve may actually affect the level and direction of selection on dispersal distance. For example, Botsford *et al.* (2001) constructed a model demonstrating that marine reserves that are either too small and/or distributed improperly could result in selection for shorter dispersal distances among larvae.

Related research, shortcomings, and future work

We are aware of only one other study pertaining to the evolution of dispersal distance in a multi-species pattern-forming system. Savill and Hogeweg (1998) studied a predator–prey model in which selection on dispersal distance drove the predators to extinction under certain conditions, as was the case for the parasitoids in our system. However, their results were a direct consequence of boundary conditions, which varied from absorbing to fully reflecting. Unlike our study, in which we demonstrate selection for intermediate dispersal distances, Savill and Hogeweg (1998) found that there is selection for increased dispersal distance as waves of predators track travelling waves of prey until, depending on the boundary conditions, either a loss of spatial patterning drives the predators extinct or the prey speciate and the system persists.

Although our model incorporates many of the characteristics of a mutualist–antagonist system, we have not yet considered several important realistic features. For example, an interesting question is whether the evolutionary state characterized by metapopulation dynamics would result with simultaneous selection on various other parameters (e.g. ovule production), perhaps through the incorporation of trade-offs. In addition, we assumed an underlying homogeneous and unchanging environment in our model, whereas there may be even stronger selection towards the extinction of antagonists/predators when the underlying landscape is heterogeneous/fragmented or dynamic. Long-term persistence of antagonist metapopulations may depend upon the spatial autocorrelation of disturbances (Johst and Drechsler, 2003; Kallimanis *et al.*, 2005). Furthermore, patchy disturbances tend to select for longer dispersal distances (Kallimanis *et al.*, 2006). Thus, future studies should address the evolution of dispersal distance on spatially heterogeneous and dynamic landscapes. Another important realistic feature is the cost of dispersal, which influences selection on the shape of dispersal kernels (Rousset and Gandon, 2002). Future studies should also consider incorporating dispersal costs, either in terms of explicitly defined functions of distance or, alternatively, in the form of a trade-off with reproduction, which is what Hughes *et al.* (2003) observed in the speckled wood butterfly. Johst and Brandl (1999) showed that dispersal may be favoured in juveniles even when dispersing juveniles have no special social, genetic or dispersal cost advantages over dispersing adults. Perhaps future work should include stage-structured models.

Since selection on dispersal distance may generate situations in which there is evolution for species to teeter on extinction, it is imperative that further research goals include determining the conditions necessary for these dynamics to occur. For example, does selection on dispersal distance in other mutualist–antagonist systems also lead to the emergence of pattern formation with metapopulation dynamics? More generally, does the evolution of dispersal distance in all pattern-forming systems generate similar results and, if not, what features of a system predispose it towards these dynamics? Are endogenously generated patches in other mutualist–antagonist pattern-forming models similarly sensitive to the degree of obligacy between the mutualists? The next step would be to consider various two-species pattern-forming models, potentially including the Rosenzweig-MacArthur model (Rosenzweig and MacArthur, 1963; Wilson, 1998) and numerous activator–inhibitor type models (e.g. Levin and Segel, 1976), and to look at the evolution of dispersal distance in other mutualist–antagonist models.

The research presented here provides several empirical predictions for an obligate mutualist–antagonist system similar to the one modelled here (e.g. yucca plant–yucca moth system in the presence of a yucca moth parasitoid). The list of predictions includes:

1. Within persistent plant–pollinator patches, the realized dispersal distance (i.e. the dispersal distance after taking into account visitation rate) of the parasitoids should remain greater than the realized dispersal distance of the pollinators.
2. An endogenously produced pattern should most likely emerge when the mutualism between the plants and the pollinators is obligate.

3. Plant–pollinator patches that grow unimpeded should be devoid of parasitoids.
4. Plant–pollinator patches that either shrink or split into numerous smaller patches should have parasitoids present.

Of course, the most difficult aspect of any empirically based research along these lines would be devising creative ways for quantifying the important measures for each of the species involved – especially dispersal distance. We hope that the work presented here will encourage others to address these challenging problems.

ACKNOWLEDGEMENTS

We thank William Kunin for his numerous valuable comments and suggestions, all of which greatly improved the manuscript. We also thank Judie Bronstein, Sebastien Lion, Bill Morris, and members of the Wilson and Morris labs at Duke University for their intellectual input and helpful comments.

REFERENCES

Addicott, J.F. 1996. Cheaters in yucca/moth mutualism. *Nature*, **380**: 114–115.

Botsford, L.W., Hastings, A. and Gaines, S.D. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol. Lett.*, **4**: 144–150.

Boucher, D.H., James, S. and Keeler, K.H. 1982. The ecology of mutualism. *Annu. Rev. Ecol. Syst.*, **13**: 315–347.

Brodmann, P.A., Wilcox, C.V. and Harrison, S. 1997. Mobile parasitoids may restrict the spatial spread of an insect outbreak. *J. Anim. Ecol.*, **66**: 65–72.

Bronstein, J.L., Wilson, W.G. and Morris, W.E. 2003. Ecological dynamics of mutualist/antagonist communities. *Am. Nat.*, **162**: S24–S39.

Despres, L., Pettex, E., Plaisance, V. and Pompanon, F. 2002. Speciation in the globeflower fly *Chiastocheta* spp. (Diptera: Anthomyiidae) in relation to host plant species, biogeography, and morphology. *Mol. Phylogenet. Evol.*, **22**: 258–268.

Edelstein-Keshet, L. 1988. *Mathematical Models in Biology*. Boston, MA: McGraw-Hill.

Force, D.C. and Thompson, M.L. 1984. Parasitoids of the immature stages of several southwestern yucca moths. *Southw. Natural.*, **29**: 45–56.

Hamilton, W.D. and May, R.M. 1977. Dispersal in stable habitats. *Nature*, **269**: 578–581.

Herre, E.A., Knowlton, N., Mueller, U.G. and Rehner, S.A. 1999. The evolution of mutualisms: exploring the paths between conflict and cooperation. *Trends Ecol. Evol.*, **14**: 49–53.

Hill, J.K., Thomas, C.D. and Lewis, O.T. 1999. Flight morphology in fragmented populations of a rare British butterfly, *Hesperia comma*. *Biol. Conserv.*, **87**: 277–283.

Holland, J.N. and DeAngelis, D.L. 2001. Population dynamics and the ecological stability of obligate pollination mutualisms. *Oecologia*, **126**: 575–586.

Holland, J.N., DeAngelis, D.L. and Bronstein, J.L. 2002. Population dynamics and mutualism: functional responses of benefits and costs. *Am. Nat.*, **159**: 231–244.

Howe, H.F. 1984. Constraints on the evolution of mutualisms. *Am. Nat.*, **123**: 764–777.

Hughes, C.L., Hill, J.K. and Dytham, C. 2003. Evolutionary trade-offs between reproduction and dispersal in populations at expanding range boundaries. *Proc. R. Soc. Lond. B*, **270**: S147–S150.

Johst, K. and Brandl, R. 1999. Natal versus breeding dispersal: evolution in a model system. *Evol. Ecol. Res.*, **1**: 911–921.

Johst, K. and Drechsler, M. 2003. Are spatially correlated or uncorrelated disturbance regimes better for the survival of species? *Oikos*, **103**: 449–456.

Kallimanis, A.S., Kunin, W.E., Halley, J.M. and Sgardelis, S.P. 2005. Metapopulation extinction risk under spatially autocorrelated disturbance. *Conserv. Biol.*, **19**: 534–546.

Kallimanis, A.S., Kunin, W.E., Halley, J.M. and Sgardelis, S.P. 2006. Patchy disturbance favors longer dispersal distance. *Evol. Ecol. Res.*, **8**: 529–541.

Kerdelhue, C., Le Clainche, I. and Rasplus, J.Y. 1999. Molecular phylogeny of the *Ceratosolen* species pollinating *Ficus* of the subgenus *Sycomorus sensu stricto*: biogeographical history and origins of the species-specificity breakdown cases. *Mol. Phylogenet. Evol.*, **11**: 401–414.

Levin, S.A. and Segel, L.A. 1976. Hypothesis for origin of planktonic patchiness. *Nature*, **259**: 659.

Maron, J.L. and Harrison, S. 1997. Spatial pattern formation in an insect host–parasitoid system. *Science*, **278**: 1619–1621.

Marr, D.L., Brock, M.T. and Pellmyr, O. 2001. Coexistence of mutualists and antagonists: exploring the impact of cheaters on the yucca–yucca moth mutualism. *Oecologia*, **128**: 454–463.

Michaloud, G., Carriere, S. and Kobbi, M. 1996. Exceptions to the one : one relationship between African fig trees and their fig wasp pollinators: possible evolutionary scenarios. *J. Biogeogr.*, **23**: 513–520.

Michaloud, G., Michaloud-Pelletier, S., Wiebes, J.T. and Berg, C.C. 1985. The co-occurrence of two pollinating species of fig wasp and one species of fig. *Proc. K. Ned. Akad. Wet., C*, **88**: 93–119.

Morris, W.F., Bronstein, J.L. and Wilson, W.G. 2003. Three-way coexistence in obligate mutualist–exploiter interactions: the potential role of competition. *Am. Nat.*, **161**: 860–875.

Pellmyr, O. 1999. Systematic revision of the yucca moths in the *Tegeticula yuccasella* complex (Lepidoptera: Prodoxidae) north of Mexico. *Syst. Entomol.*, **24**: 243–271.

Pellmyr, O. 2003. Yuccas, yucca moths, and coevolution: a review. *Ann. Missouri Bot. Gard.*, **90**: 35–55.

Pellmyr, O., LeebensMack, J. and Huth, C.J. 1996. Non-mutualistic yucca moths and their evolutionary consequences. *Nature*, **380**: 155–156.

Rand, D.A., Keeling, M. and Wilson, H.B. 1995. Invasion, stability and evolution to criticality in spatially extended, artificial host–pathogen ecologies. *Proc. R. Soc. Lond. B*, **259**: 55–63.

Richards, S.A., Wilson, W.G. and Socolar, J.E.S. 1999. Selection for intermediate mortality and reproduction rates in a spatially structured population. *Proc. R. Soc. Lond. B*, **266**: 2383–2388.

Rosenzweig, M.L. and MacArthur, R.H. 1963. Graphical representation and stability conditions of predator–prey interactions. *Am. Nat.*, **97**: 209–223.

Rousset, F. and Gandon, S. 2002. Evolution of the distribution of dispersal distance under distance-dependent cost of dispersal. *J. Evol. Biol.*, **15**: 515–523.

Savill, N.J. and Hogeweg, P. 1998. Spatially induced speciation prevents extinction: the evolution of dispersal distance in oscillatory predator–prey models. *Proc. R. Soc. Lond. B*, **265**: 25–32.

Thomas, C.D. 2000. Dispersal and extinction in fragmented landscapes. *Proc. R. Soc. Lond. B*, **267**: 139–145.

Thomas, C.D., Hill, J.K. and Lewis, O.T. 1998. Evolutionary consequences of habitat fragmentation in a localized butterfly. *J. Anim. Ecol.*, **67**: 485–497.

Turing, A.M. 1952. The chemical basis of morphogenesis. *Phil. Trans. R. Soc. Lond. B*, **237**: 37–72.

West, S.A. and Herre, E.A. 1994. The ecology of the New World fig-parasitizing wasps *Idarnes* and implications for the evolution of the fig–pollinator mutualism. *Proc. R. Soc. Lond. B*, **258**: 67–72.

West, S.A., Herre, E.A., Windsor, D.M. and Green, P.R.S. 1996. The ecology and evolution of the New World non-pollinating fig wasp communities. *J. Biogeogr.*, **23**: 447–458.

Wiebes, J.T. 1979. Co-evolution of figs and their insect pollinators. *Annu. Rev. Ecol. Syst.*, **10**: 1–12.

Wilson, W.G. 1998. Resolving discrepancies between deterministic population models and individual-based simulations. *Am. Nat.*, **151**: 116–134.

Wilson, W.G., Harrison, S.P., Hastings, A. and McCann, K. 1999. Exploring stable pattern formation in models of tussock moth populations. *J. Anim. Ecol.*, **68**: 94–107.

Wilson, W.G., Morris, W.F. and Bronstein, J.L. 2003. Coexistence of mutualists and exploiters on spatial landscapes. *Ecol. Monogr.*, **73**: 397–413.

Yu, D.W. 2001. Parasites of mutualisms. *Biol. J. Linn. Soc.*, **72**: 529–546.

Yu, D.W., Wilson, H.B. and Pierce, N.E. 2001. An empirical model of species coexistence in a spatially structured environment. *Ecology*, **82**: 1761–1771.