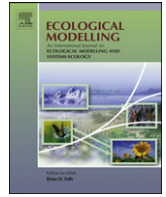




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The influence of habitat autocorrelation on plants and their seed-eating pollinators

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ABSTRACT

Model systems for studying mutualism costs and benefits include the many species of plants that rely on seed-eating pollinators for their reproduction. Empirical studies of these interactions show that mutualism costs and benefits can vary greatly within populations. Here we investigate the role of plant habitat autocorrelation on mutualism properties when mutualist dispersal is limited. We build a spatially explicit individual-based model of an obligate mutualism that includes a plant and its obligate seed-eating pollinator. We also model exploiters of this mutualism, which do not pollinate, but compete with pollinators for pollinated plant ovules in which to develop. We test how the autocorrelation of habitable plant environment affects pollinator production, seed production, pollinator visitation to plants, and the persistence of exploiters at different dispersal distances and rates of exploitation. We find that positive habitat autocorrelation increases the mean number of pollinator visits to plants. More frequent pollinator visitation to plants increases the probability that a random plant will be pollinated, but also the probability of pollinator oviposition into plant ovules at the cost of a developing seed. This process leads to spatial variation in the production of pollinators versus seeds. For a given scale of habitat autocorrelation, the turnover of this variation decreases when pollinator dispersal distance is high. Exploiters of the mutualism dramatically lower the number of pollinator visits per flower, which decreases pollinator production, seed production, and mutualist densities. Exploiters persist with mutualists when the mean number of pollinator visits per plant is neither too low, nor too high. When the mean number of pollinator visits a plant receives is too low, overexploitation and the extinction of both mutualists and exploiters follows; a high mean number of pollinator visits results in the competitive exclusion of exploiters by pollinators. Because the autocorrelation of habitat strongly affects the number of pollinator visits per flower, our results show that habitat autocorrelation can influence key mutualism properties and the susceptibility of mutualisms to exploitation.

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1. Introduction

A mutualism is a type of interspecific interaction in which two or more species exploit one another for mutual gain. Model mutualisms include obligate plant–pollinator interactions in which pollinators consume seeds as a resource during development. Interactions among plants and their seed-eating pollinators are among the most well-studied of mutualisms partly because the costs and benefits associated with these mutualisms can be measured with straightforward estimates of seed and pollinator production (Bronstein, 2001). Such estimates of mutualism properties have been assessed in many empirical systems, including the well-studied interactions between yuccas and their pollinating and seed-eating moths (e.g., Keeley et al., 1984, 1986; Addicott, 1986),

figs and their associated wasps (e.g., Bronstein, 1988; Herre and West, 1997), senita cacti and their moth pollinators (e.g., Holland and Fleming, 1999), and globe flowers and the flies that pollinate them (e.g., Pellmyr, 1989; Després et al., 2007). Bronstein (2001) notes that many studies of these interactions find great variation in fitness costs and benefits at the population level (e.g., Keeley et al., 1984, 1986; Addicott, 1986; Pellmyr, 1989), and emphasizes the importance of understanding this variation for predicting the strength and nature of plant–pollinator interactions, and the evolution of mutualism properties. Focusing on the Florida Strangling Fig (*Ficus aurea*) and its pollinating wasp (*Pegoscopus mexicanus*), Bronstein (2001) observed variation in fig morphology and the number of pollinators arriving to figs to be driving much variation in mutualism costs and benefits. Here we focus on pollinator dispersal to receptive plants, how the spatial distribution of plant habitat affects pollinator and seed production, the density of plants and pollinators, and the susceptibility of the mutualism to exploitation.

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Mutualisms are often associated with one or more exploiter species that use resources from one mutualist without providing anything in return. In model systems of mutualisms with seed-eating pollinators, these exploiters do not pollinate and typically feed off of developing seeds after pollination occurs. Such exploiters are thus obligately dependent upon both mutualists and compete with pollinators for access to developing plant seeds. The obligate and species-specific nature of this three-way interaction facilitates modeling the community (Wilson et al., 2003). Because many exploiter species in these systems can only oviposit into flowers that have been pollinated, they can directly affect the production of seeds, but not the production of pollinators. In contrast, pollinators can directly affect the production of both seeds and exploiters. To reproduce, pollinators must first disperse to plants with ovulating flowers, and exploiters must disperse to flowers that have ovulated and been pollinated. The movement of both pollinators and exploiters on a landscape is thus expected to strongly influence the population dynamics of these species and the susceptibility of plant–pollinator mutualisms to exploitation.

The effects of dispersal on interspecific interactions can be explored with spatially explicit models. In these models, a spatially explicit, environmentally uniform landscape often facilitates community coexistence and can sometimes reveal interesting spatial dynamics (e.g., Holmes et al., 1994; Wilson et al., 1995, 1993; Wilson and Hassell, 1997). When the assumption of environmental uniformity on a landscape is violated, community dynamics can change dramatically. By adding landscape-level environmental heterogeneity to a host–parasitoid model, Singh et al. (2004) show that even slight deviations from landscape uniformity can break spatio-temporal population synchrony. In mutualistic interactions, landscape heterogeneity has been shown to affect population dynamics and community coexistence, sometimes in counter-intuitive ways. For example, Amarasekare (2004) found that dispersal of mutualists between habitat patches can facilitate coexistence by maintaining sink populations of mutualists, but if dispersal becomes too high between patches, source growth rates can decrease from Allee effects and lead to the regional extinction of both mutualists. The sensitivity to changes in dispersal is even greater for obligate mutualisms (Amarasekare, 2004). Hence, the movement of pollinators on a landscape is likely to influence mutualism properties, including the interactions between plants, pollinators, and their exploiters. The frequency at which mutualists visit plants and exclude exploiters may be affected by demographic properties of individuals, but also by the distribution of habitat on a landscape, which is usually positively spatially autocorrelated (Lennon, 2000). For example, the tropical understory plant *Cordia nodosa* hosts and provides food for ant species, which in turn defend the tree from herbivory (Davidson and Mckey, 1993). For ants of the genus *Azteca*, this interaction is mutualistic, but for a species of *Allomerus* ants, which castrate their *C. nodosa* host, the interaction is parasitic. In this system, ants face a trade-off between fecundity and their ability to colonize hosts; foundresses of *Azteca* are better at colonization, but colonies of *Allomerus* are more than twice as fecund (Yu et al., 2001). In locations wherein host plants are more dense, *Allomerus* is relatively more abundant than *Azteca* (Yu et al., 2001). Yu et al. (2001) conclude that both habitat heterogeneity and the spatial arrangement of habitat influences coexistence in these ant–plant systems.

The effects of individual movement have been explored in models of plants, their obligate seed-eating pollinators, and seed-eating exploiters on a uniform landscape of habitat (Bronstein et al., 2003; Wilson et al., 2003). Here we extend the obligate plant–pollinator–exploiter model community of Wilson et al. (2003) with the addition of habitat heterogeneity and habitat arrangement by dividing a landscape into areas in which plants are able to inhabit and areas that they cannot inhabit at varying levels

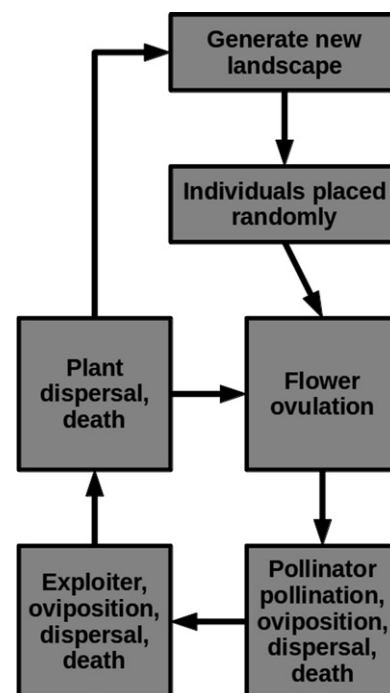


Fig. 1. Interactions among plants, obligate pollinators, and obligate exploiters for a single set of parameter values.

of habitat autocorrelation. Uninhabitable landscape in our model might include areas already inhabited by plants of other species or areas in which the abiotic conditions are too poor to permit plant establishment or flower ovulation. Our model addresses how landscape heterogeneity and autocorrelation affect plant and pollinator density, pollinator production, seed production, and mutualism susceptibility to exploitation.

2. Model

2.1. The plant–pollinator community

Like previous models of obligate mutualisms in the presence of obligate exploiters (e.g., Bronstein et al., 2003; Morris et al., 2003; Wilson et al., 2003), we use time increments of a single discrete season over which the interactions between plants, pollinators, and exploiters occur. The modeled order of interactions among plants, pollinators, and exploiters reflects the biological order of their interactions, and the discrete nature of the model is reflected in the seasonality of plant reproduction (Fig. 1; Wilson et al., 2003). Our model builds off those of Morris et al. (2003) and Wilson et al. (2003), which describe the change in the density of plants (P), pollinators (M), and exploiters (E) over a season (t). Within a season, a smaller window of time (τ) exists for pollinators and exploiters to visit plants at a rate of η and ε , respectively, before individuals of each species (i) are lost to background mortality with a probability of δ_i . The demographic parameter values we use are identical to those of Wilson et al. (2003, Table 1).

We use a torus landscape with multiple square cells to construct a spatially explicit individual-based model (IBM) of this community. In our model, individuals occupy a single cell, and cells can be empty or contain individuals of one or more species. Only one plant can occupy a particular cell, but any number of pollinators and exploiters can occupy the same cell. In a single season of the model, each plant on the landscape occupies a single cell and produces one flower that ovulates with a probability of θ .

Pollinators disperse from their natal cell to new cells, some of which contain ovulating flowers. During dispersal, a pollinator moves to a random cell within a Euclidean distance of Δ_M cells in any direction of its previously occupied cell. If the cell at which it arrives is empty, it moves to another random cell within Δ_M cells of the last. If the cell at which it arrives is occupied by a plant with an ovulating flower, it will pollinate the flower and oviposit into the flower with a probability of γ . A pollinated flower is still a potential resource for pollinator oviposition, but a flower with a developing pollinator cannot become a seed. The dispersal of a pollinator is exhausted when the pollinator has moved $\text{Poisson}(\eta\tau)$ times, which leads to variation in both visitation and dispersal distance per season among individual pollinators. After dispersal, the pollinator will die with a probability of δ_M . Pollinators that do not die remain in the cells they last visited until the following season, when all developing pollinators will mature.

After pollinator dispersal, exploiters disperse from their natal cells to a random cell within a Euclidean distance of Δ_E cells in any direction of their previously occupied cell. If after dispersing an exploiter does not arrive on a plant cell with a flower that has been pollinated, it will move to another cell. If an exploiter arrives on a plant cell with a flower that has been pollinated, but does not already contain a developing pollinator or exploiter, the exploiter will oviposit into the flower. The dispersal of an exploiter is exhausted when the exploiter has moved $\text{Poisson}(\varepsilon\tau)$ times, and the exploiter will die with a probability of δ_E at the end of the season. Like pollinators, exploiters that do not die remain in the cells they last visited. Newly developing exploiters will be mature in the following season.

After pollinators and exploiters have dispersed, flowers that were pollinated but not used for oviposition develop into seeds that disperse to a random cell within Δ_P cells in Euclidean distance of their mother plant. If a seed lands in a cell that is not habitable,

or is already occupied by another plant, the seed will die. If the seed lands in a habitable cell that is unoccupied, it will immediately develop into a new plant that can ovulate in the following season. After all seeds have dispersed, new and old plants die with a probability of δ_P .

2.2. The landscape

We model the community on a 128×128 torus landscape, which has cyclical boundary conditions whereby opposing edges of the landscape are effectively joined together. The advantage of this approach is that there are no edge effects because all cells on the landscape are spatially equivalent (Comins et al., 1992). The landscape is divided into cells that are habitable for plants, and cells that plants cannot use. To construct habitable cells that are autocorrelated on the landscape, we generate real values in cells that are spatially autocorrelated using a power spectrum function. This process generates varying levels of autocorrelation using different degrees of stochastic noise, which are often described by the color of their spectra (Lennon, 2000). The spectra have a simple relationship between their density (S) and frequency (f ; Voss, 1988) such that:

$$S_f \propto f^{-\beta} \quad (1)$$

This relationship allows us to vary the level of spatial autocorrelation of values on the landscape with a single parameter (β). We use β values that range from 0 (random habitat placement) to 6 (high habitat autocorrelation; see Fig. 2 for examples).

Following Yearsley (2005), to produce a square landscape, we start with a 128×128 matrix (U) in which every column (u) is an identical vector of frequencies. For a 128×128 landscape, values for these frequencies increase linearly from zero to 0.5, then decrease until the last vector element is equal to the second vector element such that $u = [0.0000000, 0.0078125, 0.015625 \dots 0.5000000,$

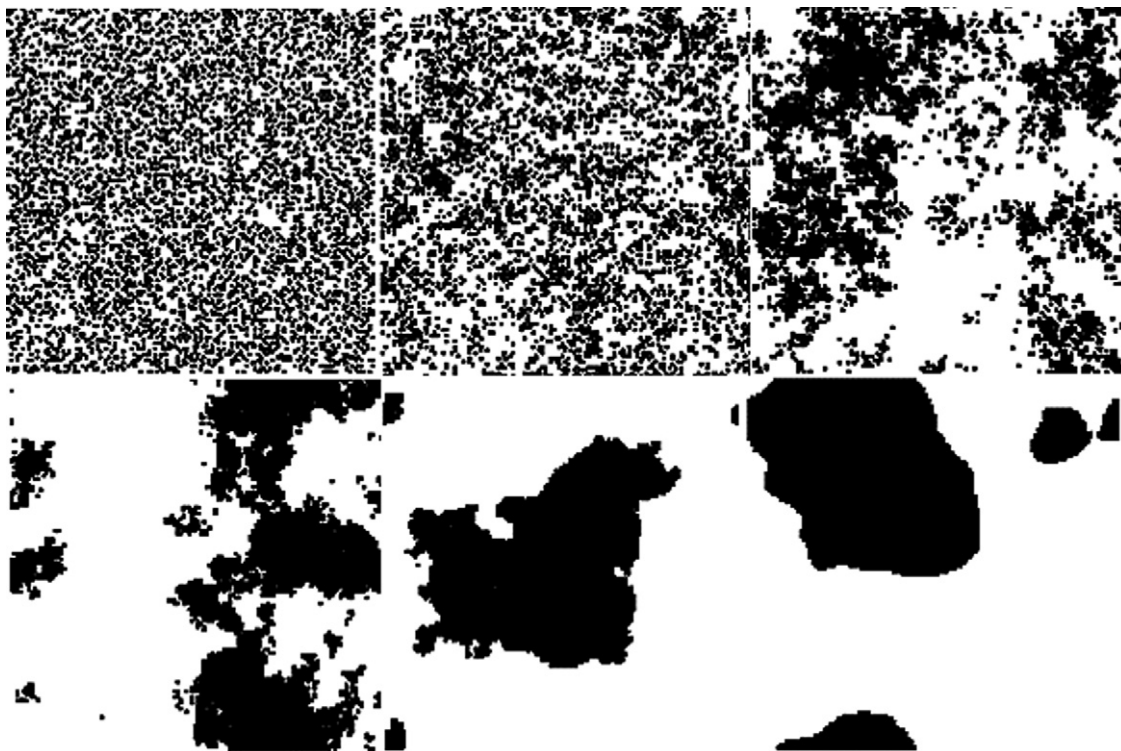


Fig. 2. Different levels of habitat autocorrelation on a landscape constructed with a power spectrum function. Autocorrelation varies with different values of β . The values of β shown range from a random landscape to a highly autocorrelated landscape ($\beta = 0$, upper left; $\beta = 1$, upper middle; $\beta = 2$, upper right; $\beta = 3$, lower left; $\beta = 4$, lower middle; $\beta = 5$, bottom right).

0.4921875, 0.4843750 ... 0.0078125] (see Yearsley, 2005). A matrix of spectrum densities is then generated by

$$S_f = (U^2 + V^2)^{-\beta/2}, \quad (2)$$

wherein V is the transpose of U . Infinite values are set to zero, and a 128×128 matrix (Φ) of random phase shifts (elements are random uniform numbers from zero to one) is generated. To get a matrix of autocorrelated values, we take the real components of an inverse fast Fourier transformation on M , which is calculated as follows:

$$M = S_f^{1/2} (\cos(2\pi\Phi) + i \sin(2\pi\Phi)). \quad (3)$$

The transformation on M produces a 128×128 matrix of autocorrelated real values, the errors of which are normally distributed. To model a torus landscape with autocorrelated habitat, we select the 30% of cells on the matrix that have the highest values and model them as habitable cells for plants (Fig. 2). The remaining cells are modeled as not habitable.

2.3. Verification of IBM accuracy

Wilson et al. (2003) model a single season of plant, pollinator, and exploiter interactions with the following equations:

$$\begin{aligned} \frac{\Delta P}{\Delta t} = & \theta P [1 - e^{-(1-\gamma)\eta\tau M}] (e^{-\gamma\eta\tau M}) (e^{-\varepsilon\tau E}) \\ & \times [1 - (1 - \delta_P \Delta t)P] - \delta_P P \end{aligned} \quad (4)$$

$$\frac{\Delta M}{\Delta t} = \theta P [1 - e^{-\gamma\eta\tau M}] - \delta_M M \quad (5)$$

$$\frac{\Delta E}{\Delta t} = \theta P [1 - e^{-(1-\gamma)\eta\tau M}] (e^{-\gamma\eta\tau M}) (1 - e^{-\varepsilon\tau E}) - \delta_E E. \quad (6)$$

To ensure that our IBM was functioning properly, we used the demographic parameter values found in Wilson et al. (2003, Table 1; C code available upon request), set $\theta = 0.3$, and allowed species in our IBM to disperse without limitation over a homogeneous 128×128 landscape (all cells are habitable). We then compared the population dynamics of our IBM to those of the numerical simulations of Eqs. (4)–(6). In the absence of dispersal limitations, only stochasticity should engender a difference between the numerical model (Morris et al., 2003) and our IBM. We compared the simulated equations to our IBM with unlimited dispersal at three different exploiter cell inspection rates. At low exploiter cell inspection ($\varepsilon = 15$), populations are stable. When exploiter cell inspection rate is increased ($\varepsilon = 20$), populations in both the numerical model and the IBM begin to cycle (Wilson et al., 2003); stochastic effects occasionally result in extinction in the IBM when cycling occurs. When exploiter cell inspection rate is high ($\varepsilon = 25$), all three species become extinct. We interpret this as strong evidence that the population dynamics of our IBM accurately reflect those of the equations in Wilson et al. (2003) and Morris et al. (2003).

2.4. Habitat autocorrelation and mutualism properties

We test the effect of habitat autocorrelation (β) on properties of the plant–pollinator mutualism at all combinations of short ($\Delta_i = 2$) and long ($\Delta_i = 10$) distance dispersal for each mutualist. We select these distances for short and long dispersal to be identical to those modeled by Wilson et al. (2003). For each combination of mutualist dispersal distances, we run simulations in the absence of exploiters and in the presence of exploiters with simulations of short and long distance exploiter dispersal. We examine values of β ranging from 0 (random habitat placement) to 6 (highly autocorrelated habitat) increasing by increments of 0.5. Other parameters

Table 1

Default parameter values for an individual-based model of plant, pollinator, and exploiter interactions on a spatially explicit landscape.

Parameter	Description	Default value
Δ_P	Plant (seed) dispersal distance	2
Δ_M	Mutualist pollinator dispersal distance	2
Δ_E	Exploiter dispersal distance	2
δ_P	Plant mortality probability	0.02
δ_M	Mutualist pollinator mortality probability	0.2
δ_E	Exploiter mortality probability	0.2
γ	Mutualist pollinator oviposition probability	0.5
η	Mutualist pollinator cell inspection rate	6
ε	Exploiter cell inspection rate	15
θ	Plant ovulation probability	1.0

are set to default values (Table 1), and individuals are randomly placed in all simulations with initial population densities of $P = 0.3$, $M = 0.19$, and $E = 0.05$. In a single season, the maximum distance a random short dispersing pollinator moves from its initial location is 3.6 cells, while the maximum distance a random long dispersing pollinator moves is 15.7 cells. For any given habitable cell on the landscape, the density of habitable cells within a 3.6 or 15.7 cell radius increases with β , but this increase is slower and peaks more quickly for the 15.7 cell radius associated with long distance pollinator dispersal (Fig. 3). We simulate plants and pollinators on the landscape for 1000 seasons, which allow populations to reach stationarity, before calculating the densities of plants, pollinators, and exploiters. On season 1000, we also calculate mean pollinator and seed production per plant, and the mean number of pollinator visits plants received. Data collection is repeated for 100 unique landscapes at each level of habitat autocorrelation.

2.5. Habitat autocorrelation and community coexistence

To estimate the effect of habitat autocorrelation on community coexistence and the spatial dynamics of interacting species, we simulate different habitat autocorrelations (β), dispersal values (Δ_i), and exploiter cell inspection rates (ε). Like tests of mutualism properties, we use values of β ranging from 0 to 6 by increments of 0.5 at different combinations of short and long distance dispersal in different species, and we examine three levels of exploiter cell inspection rate. These three levels include low ($\varepsilon = 15$), medium

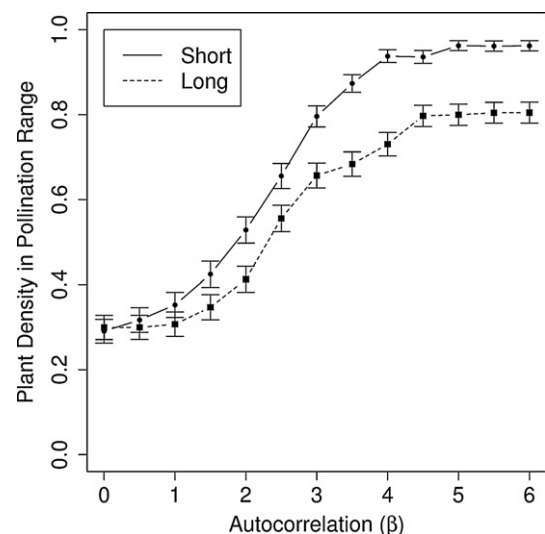


Fig. 3. For a random habitable cell, the density of habitable cells on a landscape within the radius of maximum dispersal for an average short (ca 3.6 cells) and long (ca 15.7 cells) distance dispersing pollinator as a function of habitat autocorrelation values (β). Error bars reflect 95% confidence intervals around the means.

($\varepsilon=20$), and high ($\varepsilon=25$) cell inspection rate as used in Wilson et al. (2003). Other parameters are set to default values (Table 1). To test for community coexistence at different parameter combinations, individuals are randomly placed on the landscape at starting densities of $P=0.3$, $M=0.19$, and $E=0.05$; coexistence results were found to be robust to different starting densities. One thousand seasons are run for each simulation, and extinction events are recorded in each of 100 simulations for each parameter combination. For each parameter combination, we also record the spatial and spatio-temporal dynamics of individuals. To examine the spatial distributions of plants, pollinators, and exploiters, the positions of individuals are recorded after 500 seasons of a simulation. We examine the spatio-temporal dynamics of individuals with the “space-time” (XT) images used in Bronstein et al. (2003) and Wilson et al. (2003); we sample a single transect row from the 128×128 landscape at every season (Supplemental material S1).

2.6. Model sensitivity to θ , γ , and η

To determine how the results of our model depend on the seasonal probability of flower ovulation (θ), the probability that a pollinator oviposits after pollinating (γ), and pollinator cell inspection rate (η), we vary each of these parameters to assess how variation in θ (0.7–1.0), γ (0.3–0.7), and η (4–8) affect species densities, pollinator production, seed production, pollinator visits received by plants, and community coexistence. In all of these simulations, parameters not varied are set to their default values (1), and all species have short distance dispersal.

3. Results

The 100 replicate simulations resulted in means with very low standard errors for all parameter combinations used. Error bars showing a 95% range around each point would not be clearly distinguishable from the points in the figures, so we omit them in presenting our results. An example of the consistency of these results for the mean number of pollinator visits per flower can be found in the Supplemental material (S2).

3.1. Habitat autocorrelation, species densities, and mutualism properties

All simulations of plant–pollinator interactions in the absence of exploiters resulted in long-term coexistence of mutualists. In the absence of exploiters, the relationship between habitat autocorrelation and the density of plants and pollinators differed depending on the dispersal abilities of the mutualists. For all combinations of long and short mutualist dispersal, the increase in habitat autocorrelation led to an increase in the mean number of times that a random plant was visited by a pollinator in a season (Fig. 4c). This increase in pollinator visits per flower was caused by the aggregation of pollinators in areas of the landscape containing habitable cells for plants. When these habitable cells were autocorrelated, plant distribution was likewise autocorrelated. Pollinators, which initially emerge from plants used for oviposition, have a higher likelihood of visiting cells in the vicinity of their natal plant – especially if these pollinators disperse short distances. If the spatial distribution of plants is autocorrelated, nearby cells are more likely to be habitable and contain plants, so the number of pollinator visits per flower increases with increasing habitat autocorrelation, most dramatically when pollinators have short distance dispersal (Fig. 4c). The increase in pollinator visits per flower reduces the probability that a plant goes unpollinated, but it also increases the probability of pollinator oviposition due to the likelihood of repeated pollinator visits. And in the absence of exploiters, mean pollinator production per plant increased (Fig. 4b), and mean seed production per plant

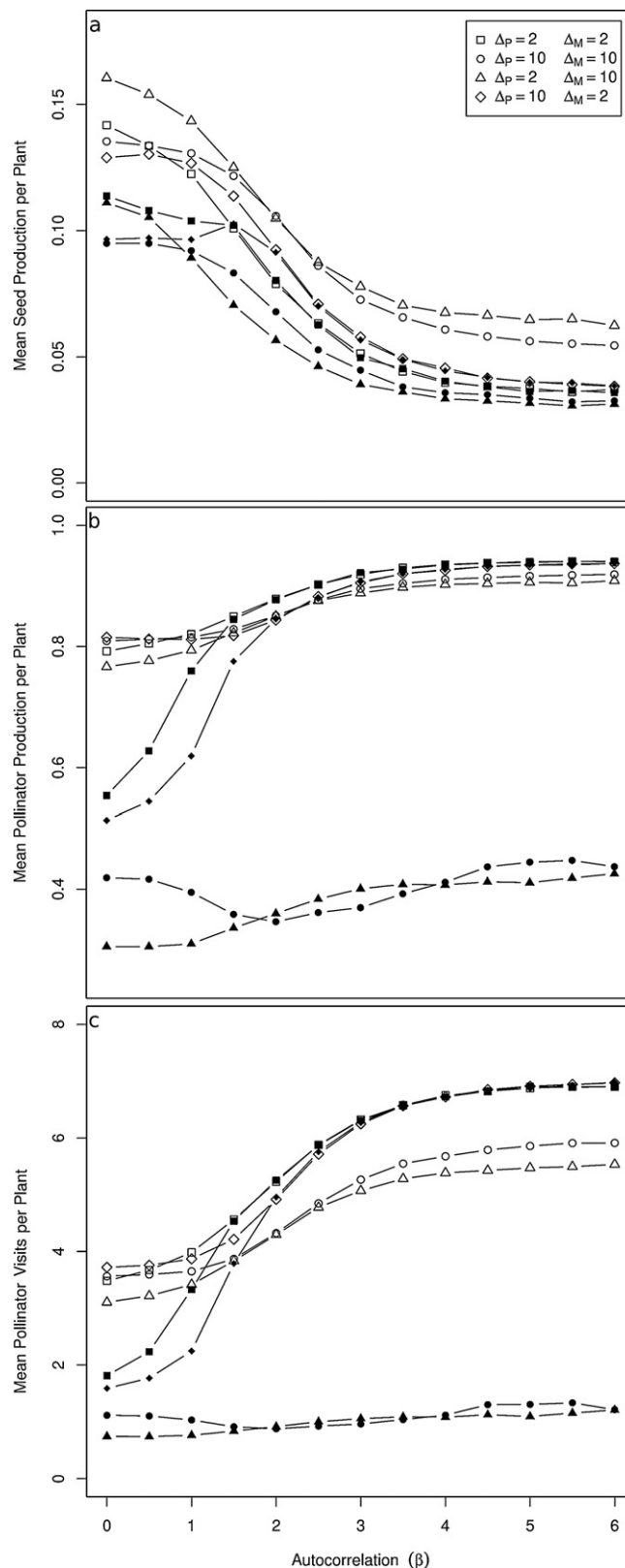


Fig. 4. Mean seed production, pollinator production, and pollinator visits per plant as habitat autocorrelation increases. Unfilled symbols show simulations with different combinations of high (10) and low (2) plant dispersal Δ_P and pollinator dispersal Δ_M in the absence of exploiters. Simulations with exploiters included (always with low dispersal) are shown with filled symbols.

decreased (Fig. 4a), as habitat became more autocorrelated. This increase in pollinator production and decrease in seed production was strongest at low pollinator dispersal, leading to a decrease in plant density (and, in turn, pollinator density) at higher levels of habitat autocorrelation (Fig. 5a) as plants became less likely to produce seeds. The mean number of visits pollinators made to plants at high habitat autocorrelation was lower when pollinators had long distance dispersal, and plant density did not decrease at higher levels of habitat autocorrelation as a result of increased pollinator oviposition probability, which was balanced by the decreased likelihood of plants going unpollinated.

When exploiters of the mutualism were included in simulations of plant–pollinator interactions and able to avoid extinction for 1000 seasons, mutualist density, seed production, pollinator production, and the mean number of pollinator visits per flower declined at all levels of habitat autocorrelation. The nature of the effect of exploiters on these species densities and mutualism properties was not different for short versus long distance exploiter dispersal, but long dispersing exploiters were more likely to go extinct than short dispersing exploiters because short dispersing exploiters were more likely to search cells near their natal plant; when habitat was autocorrelated, these nearby cells were more likely than distant cells to be receptive to exploitation. For simplicity, we focus on the effects of exploiters only when dispersal is short. In these simulations, the extinction of exploiters occurred only when pollinator dispersal was short and the level of autocorrelation was higher than $\beta = 2$. When exploiter extinction occurred, plant and pollinator densities after 1000 seasons in these simulations were generally the same as in simulations without the inclusion of exploiters (Fig. 5a and b), as was seed production, pollinator production, and flower visitation rate (Fig. 4). When exploiters persisted, plant density was only ca 1/2 of what it was in the absence of exploiters, and the density of pollinators dropped to ca 1/5 of its density in exploiters' absence; this was consistent across all levels of habitat autocorrelation (Fig. 5). Because exploiters oviposit after pollinators in each season, exploiters can only directly affect the production of seeds by using flowers that have been pollinated, but not used by pollinators for oviposition. As such, the decrease in seed production caused by exploiters led to a subsequent decrease in plant density. When plant density was reduced by exploiters, fewer pollinators were produced, and the mean number of pollinator visits per flower dropped dramatically (Fig. 4c). For example, in the absence of exploiters, when plant seeds had short distance dispersal and pollinators long distance dispersal, the mean number of pollinator visits per flower rose from a mean of 3.1 pollinators per season at the lowest level of habitat autocorrelation (more randomly scattered habitat) to 5.5 pollinators per season at the highest level of habitat autocorrelation. But when exploiters were included in these simulations, the mean number of pollinator visits per flower ranged only between 0.74 and 1.2 pollinators per season.

3.2. Habitat autocorrelation and community coexistence

We recorded the proportion of long term coexistence of plants, pollinators, and exploiters using the same dispersal combinations as in Wilson et al. (2003) for multiple levels of exploiter cell inspection rate. Long term coexistence of mutualists and exploiters was greatly affected by the level of habitat autocorrelation (β) at different relative species dispersals (Δ_i) and exploiter cell inspection rates (ε ; Fig. 6). In all simulations, as expected (Wilson et al., 2003), exploiters were the first species to become extinct when extinction occurred. Sometimes this extinction occurred because exploiters were competitively excluded by pollinators. This happened at higher β values in which pollinators were more aggregated (Supplementary material S1) and the mean number of pollinator visits per flower was higher (Fig. 4c) resulting in higher pollinator

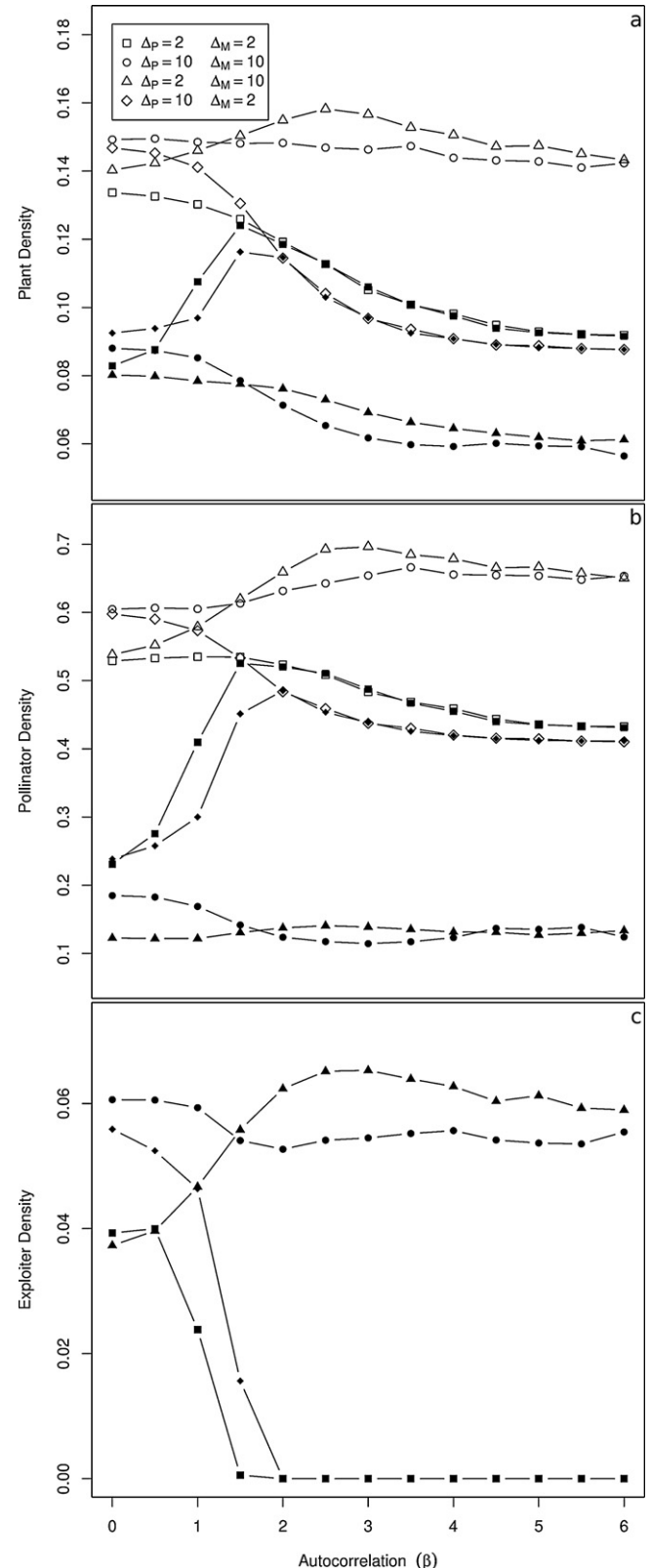


Fig. 5. Mean plant, pollinator, and exploiter density as habitat autocorrelation increases. Unfilled symbols show simulations with different combinations of high (10) and low (2) plant dispersal Δ_P and pollinator dispersal Δ_M in the absence of exploiters. Simulations with exploiters included (low dispersal) are shown with filled symbols.

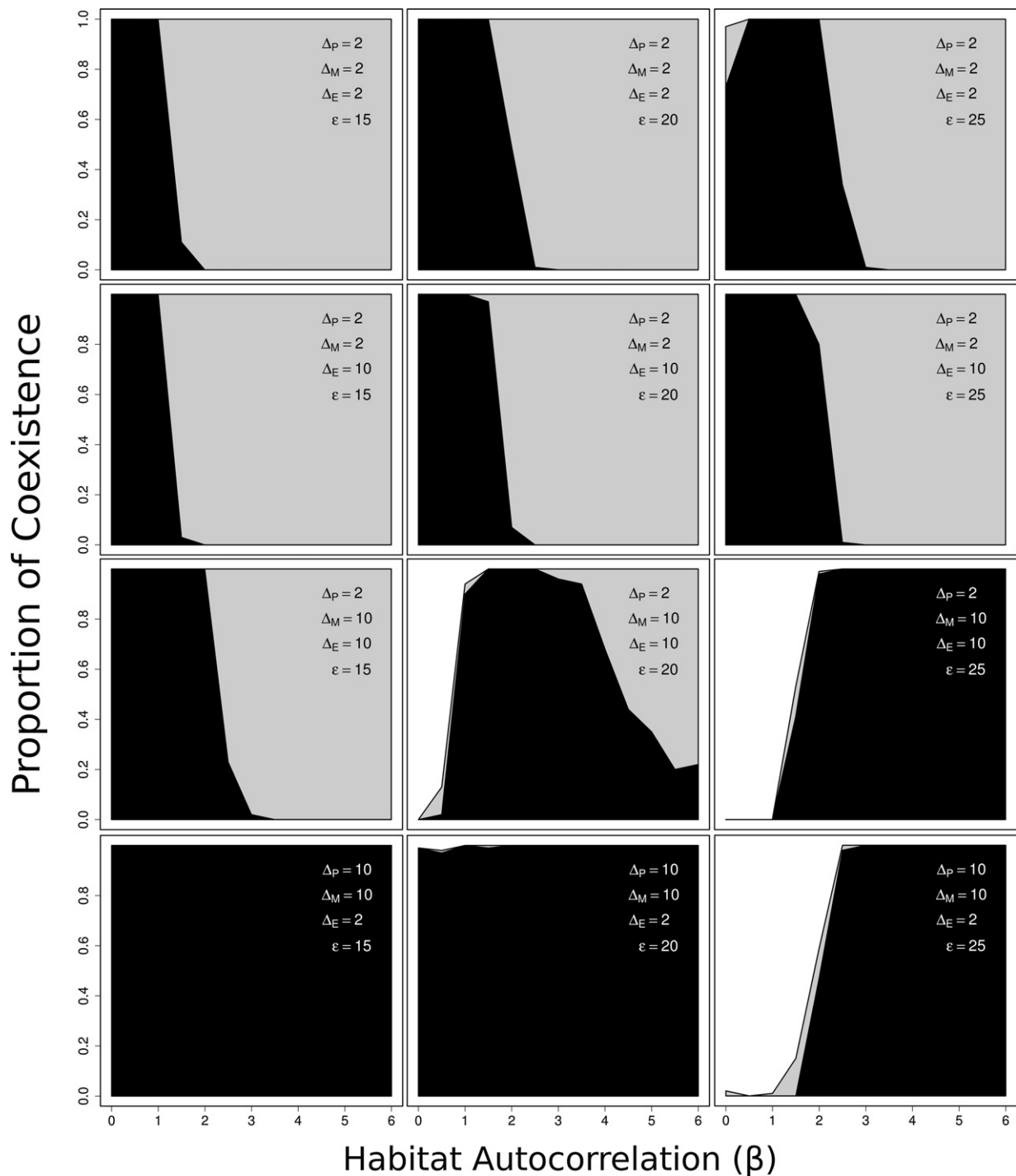


Fig. 6. Results of different dispersal and exploiter cell inspection rates at different levels of habitat autocorrelation on community coexistence. Rows show different dispersal combinations in plants, pollinators, and exploiters. Columns show simulations of different levels of exploiter cell inspection rates. The x-axis of each graph within the figure shows habitat autocorrelation ranging from no autocorrelation ($\beta=0$) to high autocorrelation ($\beta=6$). The y-axis of each graph shows the proportion of simulations that lead to one of three results: long-term coexistence of mutualists and exploiters (black), extinction of only the exploiter (gray), and extinction of all three species (white).

oviposition per plant (Fig. 7). When the probability of pollinator oviposition increased, fewer pollinated flowers were available for exploiters to use (Fig. 7c). The mean number of pollinator visits per flower was also affected by the dispersal distance of pollinators; long distance dispersal lowered the number of flower visits, and subsequently pollination, when habitat was autocorrelated because pollinators were less likely to visit nearby cells on the landscape. This resulted in the persistence of exploiters at higher values of β when pollinators dispersed longer distances (Fig. 5c).

As expected, increasing ϵ lowered the probability of exploiters being competitively excluded by pollinators; when exploiters were able to visit more cells in a season, pollinated plants available for exploiter oviposition were more likely to be used.

In some simulations, the extinction of exploiters was quickly followed by the extinction of both mutualists (Fig. 6). The extinction of the entire community occurred when the mean number of pollinator visits per flower was low, and exploiter cell inspection rates were high. Fewer pollinator visits to flowers decreased

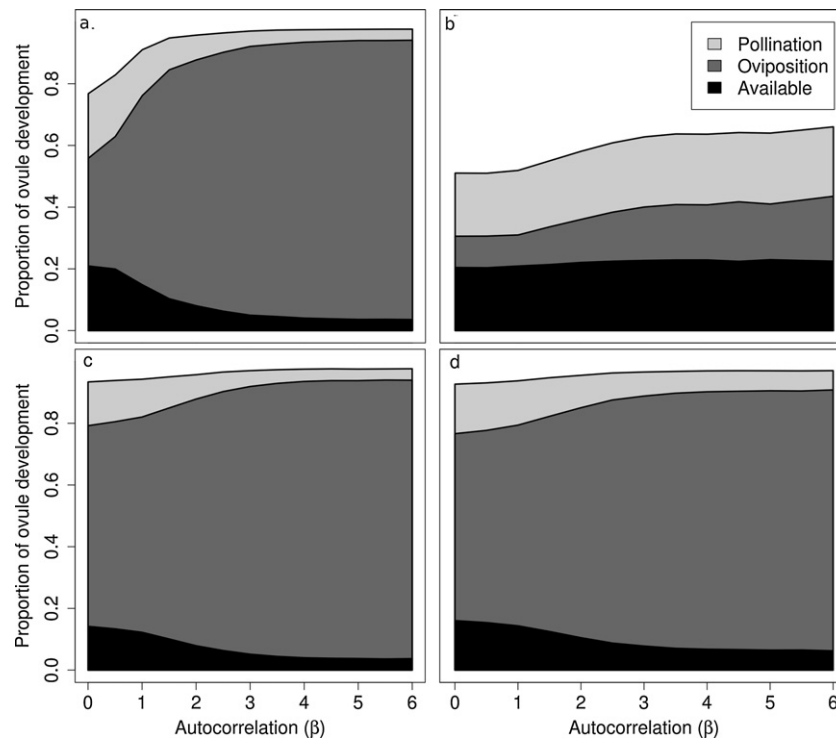


Fig. 7. Proportion of plant ovules pollinated (light gray), used for oviposition by pollinators (dark gray), and remain available for either seed or exploiter development (black). Ovule proportions are shown at different levels of habitat autocorrelation with short (A) and long (B) distance pollinator dispersal in the presence of short dispersing exploiters, and with short (C) and long (D) distance pollinator dispersal in the absence of exploiters. Simulations in A consistently resulted in early exploiter extinction for values of $\beta \geq 2$.

the probability of plants experiencing pollinator oviposition, increasing the proportion of pollinated plants available to exploiters. When exploiter cell inspection rates were high enough to take advantage of the high proportion of available pollinated flowers in these communities, seed production was also lowered, and the densities of both mutualists and exploiters fell until all three species became extinct.

3.3. Sensitivity to θ , γ , and η

Decreasing the probability of plant ovulation (θ) did not affect the mean number of seeds a plant produced (Fig. 8a) and consistently decreased the mean number of pollinators produced (Fig. 8d) and pollinator visits per plant (Fig. 8g). At all values of θ , seed production decreased with increasing habitat autocorrelation, and pollinator production and pollinator visits per flower increased with habitat autocorrelation. Exploiters were always competitively excluded by pollinators when $\beta \geq 2$.

Increasing the probability of pollinator oviposition (γ) decreased seed production (Fig. 8b), especially at low habitat autocorrelation, in which the mean number of pollinator visits a flower received was low (Fig. 8h). The increase in seed production that resulted from more pollinator visits without oviposition at low γ values was less dramatic at high habitat autocorrelation in which pollinator visits were more frequent; pollinator production increased slightly with increasing β (Fig. 8e), and was affected little by differences in γ . Interestingly, low pollinator oviposition ultimately resulted in higher pollinator densities – the increase in seed production at lower pollinator oviposition led to a higher density of plants for pollinators to use as a resource for oviposition. Low pollinator oviposition also made exploiter persistence more likely, and resulted in exploiters driving all three species to extinction at low levels of pollinator oviposition and habitat autocorrelation.

Increasing the number of cells pollinators were able to visit in a season led to a predictable decrease in seed production (Fig. 8c) as the mean number of times a plant was visited by a pollinator increased (Fig. 8i). Plant visitation by pollinators increased with increasing habitat autocorrelation, which resulted in lower seed production and higher pollinator production as β increased. Competitive exclusion of exploiters by pollinators occurred at all but the lowest value of $\eta = 4$ in which coexistence was possible when $\beta < 3$. When $\eta = 4$ and $\beta = 0$, exploitation led to the extinction of all three species.

4. Discussion

Positive autocorrelation is observed in most spatial data in ecology (Legendre and Fortin, 1989; Lennon, 2000). This positive spatial autocorrelation influences key mutualism properties in our simulated plant and seed-eating pollinator community. Here we show that the autocorrelation of habitat can affect mutualistic interactions in ways that may be counterintuitive. For example, low habitat autocorrelation can reduce the ability of pollinators to find new plants. And while this leaves some plants without any reproductive output for one season, the reduction in pollinator search efficiency can also lead to a net gain in the probability that a plant will produce a seed by lowering the effective rate of pollinator oviposition. The implications of these results may be relevant to studies of seed-eating mutualisms, wherein much focus has been devoted to understanding how long-term stability is maintained when mutualist partners experience asymmetric fitness benefits from pollinator and seed production (e.g., Bronstein, 2001; Holland et al., 2002). Fitness costs and benefits are often determined by the measure of seed production in these systems. Because measurement of seed production is straightforward and easy to interpret comparatively among systems, seed-eating mutualisms have been recognized as the centerpiece of our understanding of the costs

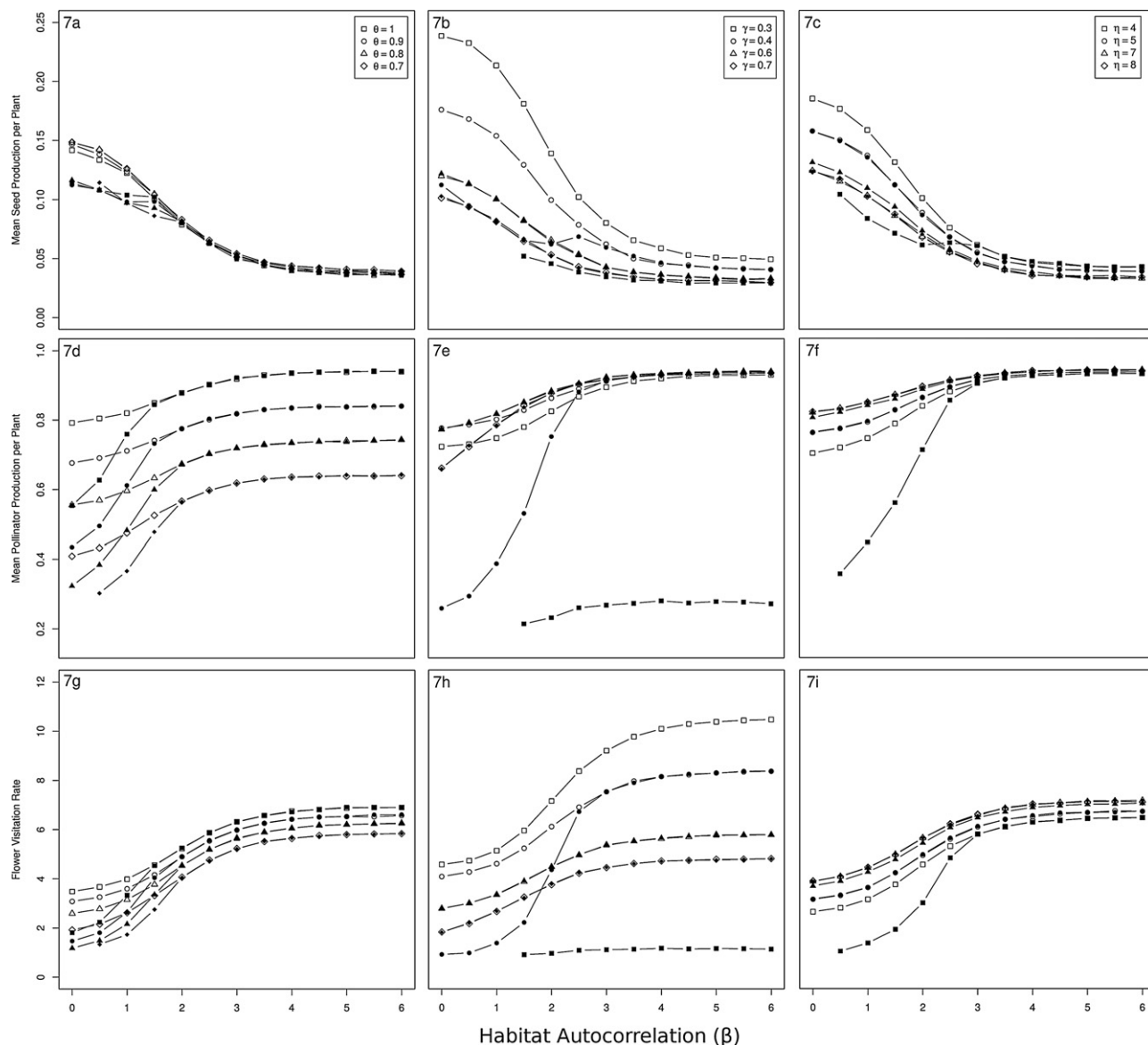


Fig. 8. Effect of habitat autocorrelation on mean seed production, pollinator production, and flower visitation per plant at different values of flower ovulation probability (θ ; a, d, and g), pollinator oviposition probability (γ ; b, e, and h), and pollinator cell inspection rate (η ; c, f, and i). Unfilled symbols show simulations in the absence of exploiters; simulations with exploiters are shown with filled symbols.

associated with mutualism (Bronstein, 2001). The proportion of flowers that develop into seeds can vary greatly in plant populations associated with seed-eating pollinators (e.g., Addicott, 1986; Pellmyr, 1989). We suggest that the autocorrelation of habitat may play an influential role in determining seed and pollinator production, thus affecting the costs and benefits of mutualism for both plant and pollinator.

In the absence of habitat autocorrelation ($\beta = 0$), the general pattern of patchy plant distribution in the presence of relatively long distance exploiter dispersal that Wilson et al. (2003) observed on a uniform landscape was also observed in our model (Supplemental material S1). This result shows that the spatial dynamics of interacting mutualists and exploiters are robust to habitat heterogeneity. This robustness to non-uniform habitat is an important result that reinforces the applicability of previous plant–pollinator–exploiter models in light of more realistic landscape properties (e.g., Wilson et al., 2003; Morris et al., 2003; Bronstein et al., 2003). The emergence of patchiness with landscape non-uniformity is attributable to the same processes that occur on a uniform landscape as in

Wilson et al. (2003). As plants disperse short distances to new areas of unoccupied habitat, exploiters with long distance dispersal are able to rapidly invade and block the expansion of mutualists. That this general spatial distribution pattern of mutualists and exploiters persists in the presence of habitat heterogeneity is different than spatial patterns observed in some other community models. For example, Hassell et al. (1991) and Comins et al. (1992) modeled a uniform landscape with spatially explicit subpopulations of hosts and parasitoids connected by diffusive dispersal; they found emergent spatial patterns such as spiral waves or crystal lattices, but only a small amount of environmental heterogeneity is needed to destroy the spatio-temporal synchrony upon which these results depend (Singh et al., 2004; Hirzel et al., 2007). The resilience of spatio-temporal processes to habitat heterogeneity in our plant–pollinator–exploiter model reaffirm the prediction of spatial patchiness in mutualisms that include a relatively long dispersing species of exploiter.

The autocorrelation of plant habitat strongly affects the susceptibility of the mutualism to exploitation. Because exploiters

oviposit into flowers that pollinators have visited and pollinated, but not used for oviposition, the persistence of exploiters depends on the number of pollinator visits that plants receive in a season. Pollinator visitation increases with habitat autocorrelation, especially when pollinator dispersal distance is low and pollinators are more likely to visit nearby cells on the landscape. When pollinators visit more flowers, more plants are both pollinated and used for pollinator oviposition. When the number of pollinator visits per flower is high, exploiters competing for pollinated flowers are competitively excluded. When the number of pollinator visits per flower is lower, in contrast, we find an increase in the mean number of flowers pollinated but not used for pollinator oviposition. In the absence of exploiters, this results in lower pollinator production and higher seed production, but when exploiters are present, the high proportion of pollinated flowers makes the mutualism more susceptible to exploitation. Our observations are consistent with previous models of mutualisms that include an exploiter species. In an analytical model of a plant and seed-eating pollinator, Morris et al. (2003) found high pollinator densities to lower seed production, leading to a feedback loop that ultimately prevents pollinators from over-exploiting plant resources, which would otherwise cause the extinction of both mutualists. Upon including exploiters, which compete with pollinators for access to plant resources, coexistence is possible as long as the birthrate of pollinators lies between two extremes relative to the birthrate of exploiters. When pollinator birthrate is too high, it becomes more difficult for exploiters to achieve positive growth and persist in the community. In contrast, when pollinator birthrate is low, exploiters can increase to high densities and drive both mutualists (and themselves, in turn) to extinction. Our results show that these dynamics are sensitive to habitat heterogeneity and the spatial arrangement of habitat on a landscape. When high habitat autocorrelation leads to the aggregation of plants, the number of pollinator visits per flower increases (Fig. 4c). The increase in pollinator visits per flower and subsequent increase in pollinator production is enough for habitat autocorrelation alone to lead to the competitive exclusion of exploiters for many demographic values (Fig. 6). In turn, when exploitation is sufficiently high to lead to the extinction of all three species at low habitat autocorrelations, higher levels of habitat autocorrelation increase the number of pollinator visits per flower and reduce exploitation rates, leading to long-term coexistence.

We noticed another pattern of plant spatio-temporal patchiness in simulations with positive habitat autocorrelation that either did not include exploiters, or in which exploiters were competitively excluded by pollinators very early in the simulations. As with pollinator production, seed production, and global mutualist densities, this spatio-temporal patchiness was driven by the mean number of pollinators plants received during a season. As the mean number of pollinator visits increased, the probability of seeds being produced in areas wherein pollinators were most aggregated became vanishingly small, and plants in these areas were much more likely to produce pollinators instead of seeds. At high habitat autocorrelation, the centers of large habitat patches were areas in which the mean pollinator visits per flower were especially high. As a result, pollinator production was higher in these regions, leading to spatial segregation in plants that produced pollinators versus plants that produced seeds. Large habitat patches often contained subpatches in which plants were sparse or entirely absent because no nearby plants were producing seeds. In simulations with high habitat autocorrelation, plant distribution was most dense toward the outer edges of large habitat patches because pollinator visits around edges were less frequent than visits to patch centers, which received pollinators from every direction. This resulted in localized variability in seed and pollinator production among plants, with pollinator production being more likely in regions wherein plants and pollinators aggregated, and seed production being more likely

in regions wherein pollinator dispersal limitation led to low mean numbers of pollinator visits. Predictably, as pollinator dispersal distance increased, the scale of this variability increased too. Relatively long distance pollinator dispersal resulted in lower turnover of pollinator versus seed production on the landscape (Supplemental material S1). When dispersal is unlimited, all cells are effectively spatially equivalent, and no turnover occurs. In sum, our model shows how the autocorrelation of habitat combined with limited dispersal leads to spatial variation in pollinator visits to plants and ultimately the costs and benefits of mutualistic interactions. This relationship is likely to be further complicated in real world plant–pollinator mutualisms. In our model, plants produce a single ovule, which is sufficiently pollinated by the arrival of a single pollinator. For empirical systems in which plants rely on seed-eating pollinators, multiple ovules exist on a single plant, and multiple visits from pollinators may result in increased pollination in addition to an increase in seed predation. For example, in the mutualism between the perennial herb *Trollius europaeus* and its pollinating and seed-eating *Chiastocheta* flies, repeated pollinator visits lead to increasing, but diminishing, pollination efficacy (Pellmyr, 1989). And because pollinator larvae in this mutualism feed on multiple developing seeds, plants with especially frequent pollinator visits suffer a net reproductive loss (Pellmyr, 1989).

Empirical studies of other seed-eating mutualisms suggest that spatial dynamics are important to consider when interpreting ecological patterns. In a study of *Tegeticula yuccasella*, the seed-eating pollinator of *Yucca filamentosa*, dispersal was observed to be highly leptokurtic – much pollination was observed on the same plant from which pollinators developed (Marr et al., 2000). Rarely, pollinators were observed dispersing as far as 50 m, but the average distance for pollen transfer was 4.66 m. The distribution of pollinator dispersal in our model was similarly leptokurtic. Cell inspection for a pollinator with short distance dispersal was on average a distance of ca 2.7 cells away from the cell at which it began at the start of a season (ca 11.8 cells away for pollinators with long distance dispersal). If we consider each cell of our model to represent an area of roughly 2 × 2 m, our model predicts significant, spatially correlated, variation in pollinator and seed production at the within population level of *Y. filamentosa*. In a study of eight species of *Yucca*, Addicott (1986) observed high variation in seed and pollinator production within populations. Addicott suggested the mean number of pollinator visits could be influential in explaining this variation, but did not explicitly consider the spatial autocorrelation of plants within a population. Addicott (1986) further suggested the high variation observed in seed production to be evidence against the hypothesis that there is strong regulation of yucca–yucca moth interaction. Here we show that this need not be the case; both strong population regulation and high variation in pollinator and seed production are expected when habitat is autocorrelated (Supplemental material S1). Given the high pollinator and seed production variation observed in similar systems, such as those of figs and their pollinating wasps (e.g., Bronstein and Hossaert-McKey, 1996) or globeflowers and their pollinating flies (e.g., Després et al., 2007), our results may be useful for interpreting ecological patterns in these communities. In the context of mutualistic interactions between plants and their seed eating pollinators, spatial variation in pollinator and seed production may also be relevant given that pollinators represent the male fitness of plants, while seeds represent female plant fitness. It would be interesting to consider the influence of habitat autocorrelation and pollinator visits per flower on the mating strategies of seed plants. Because pollinator production in our model was very high relative to seed production in the centers of large habitat patches, plants in these regions producing seeds may be expected to have especially high fitness due to the high probability of successful pollination and seed establishment. In contrast, the more common pollinator producing

plants in these regions would be expected to have especially low fitness due to the lower mean reproductive success caused by intense competition among local pollinators for access to ovules.

Our model shows the potential complexities involved in understanding the ecological dynamics of even simple three species communities. In a classic plant–pollinator mutualism that includes an exploiter species, relatively small changes in the spatial autocorrelation of habitat may cause substantial changes in community dynamics. Further, Jones et al. (2009) suggest that environmental heterogeneity may influence coevolutionary dynamics in such systems, and that metapopulations of mutualists and exploiters may be evolutionarily stabilized if populations differ in their evolutionary stages. While the impact of environmental autocorrelation on ecological processes is still not fully understood (Schiegg, 2003), empirical studies show that it can have important effects on population dynamics (e.g., González-megías et al., 2005; Schooley and Branch, 2007; Trenham et al., 2001). We suggest that environmental autocorrelation may similarly influence the ecology and evolution of model communities of mutualists that include seed-eating exploiters.

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Appendix A. Supplementary Data

Supplementary data associated with this article can be found, in the online version, at doi:<http://dx.doi.org/10.1016/j.ecolmodel.2012.12.019>.

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