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Habitat conversion, extinction thresholds, and pollination services in agroecosystems

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Abstract. Parallel declines of wild pollinators and pollinator-dependent plants have raised alarms over the loss of pollination services in agroecosystems. A spatially explicit approach is needed to develop specific recommendations regarding the design of agricultural landscapes to sustain wild pollinator communities and the services they provide. I modeled pollination services in agroecosystems using a pair of models: a stochastic individual-based simulation model of wild pollinators, pollinator-dependent plants, and crop pollination; and a set of coupled difference equations designed to capture the nonspatial component of the simulation model. Five spatially explicit models of habitat conversion to crops were simulated, and results for pollination services were compared. Mean-field behavior of the simulation model was in good agreement with analysis of the difference equations. A major feature of the models was the presence of a cusp leading to loss of stability and extinction of pollinators and pollinator-dependent plants beyond a critical amount of habitat loss. The addition of pollen obtained from crop visitation caused a breakdown of the cusp preventing extinction of pollinators, but not of wild pollinator-dependent plants. Spatially restricted foraging and dispersal also altered model outcomes relative to mean-field predictions, in some cases causing extinction under parameter settings that would otherwise lead to persistence. Different patterns of habitat conversion to crops resulted in different levels of pollination services. Most interesting was the finding that optimal pollination services occurred when the size of remnant habitat patches was equal to half the mean foraging and dispersal distance of pollinators and the spacing between remnant patches was equal to the mean foraging and dispersal distance. Conservation of wild pollinators and pollinator-dependent plants in agroecosystems requires careful attention to thresholds in habitat conversion and spatial pattern and scale of remnant habitats. Maximization of pollination services was generally incompatible with conservation of wild pollinator-dependent plants. My prediction is that pollination services will be maximized by providing islands of nesting habitat where interisland distance matches mean foraging distances of wild pollinators.

Key words: agroecosystems; Allee effect; conservation; difference equations; ecosystem services; habitat conversion; habitat fragmentation; landscape model; mutualism; pollination services.

INTRODUCTION

Human alteration of landscapes for food production affects ecosystems worldwide and is possibly the largest single component of global change (Matson et al. 1997, Vitousek et al. 1997, Tilman et al. 2001). The resultant agroecosystems are often highly fragmented with areas of intensive cultivation interspersed among remnant patches of original habitat. The close juxtaposition of semi-natural remnants to intensively managed lands creates a strong opportunity for "spill over" effects where ecological interactions extend across habitat boundaries to affect ecosystem function in adjacent patches (Rand et al. 2006). In a recent synthesis, Kremen et al. (2007) evoked the phrase "Mobile Agent-Based Ecosystem Services" (MABES) to describe situations in which animal vectors propagate ecological functions across habitat boundaries. Here "services" refers to the subset of these interactions that directly or indirectly affect human welfare. A multitude of services can be imagined ranging from animal seed dispersal to predatory control of pest species (Kremen and Ostfeld 2005). Among these, pollination services hold particular importance. More than one-third of global agricultural output depends on animal pollinators (Klein et al. 2007). The value of wild-pollinated agricultural products may range as high as U.S.$3 billion per year within the United States (Losey and Vaughan 2006), and as high as $127 billion per year worldwide (Costanza et al. 1997).

There is growing concern over the large-scale conversion of landscapes to agricultural and other human land uses and its impact on pollinator communities (Kearns et al. 1998, Klein et al. 2003, Tscharntke et al. 2005, Biesmeijer et al. 2006, Cane et al. 2006, Pauw 2007, Steffan-Dewenter and Westphal 2008). Pollen supplementation experiments indicate many natural plant

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communities experience pollen limitation (Cunningham 2000, Donaldson et al. 2002, Ashman et al. 2004, Aguilar et al. 2006, Wagenius et al. 2007). Pollen limitation is likely to be even more severe in agroecosystems because crops are often grown in large blocks inhospitable to nesting of wild pollinators. In such cases, the large travel distances required to reach crops in the interior of fields may discourage visitation (Cresswell et al. 2000, Priess et al. 2007). Pollen limitation has the potential to affect not only crop production, but also wild pollinator-dependent plants in remnant habitat fragments (Aizen and Feinsinger 1994, Matsumura and Washitani 2000). The conservation implications of pollen limitation have led to calls to determine exact thresholds of habitat conversion leading to plant and pollinator extinctions (Ashman et al. 2004).

Domesticated bee pollinators have long been used to enhance pollination services to crops, a practice that can offset losses of wild pollinators. However, reliance on a pollinator monoculture carries strong risks. Populations of managed and feral honey bees for example have recently experienced strong declines across North America (Allen-Wardell et al. 1998) increasing costs to farmers (Kevan and Phillips 2001). The low genetic diversity of domestic pollinators may expose them to high risk of epidemic disease and there is evidence to suggest that a long history of episodic declines in domestic pollinators may be due to pathogen outbreaks (Wilson and Manapace 1979*a*, *b*, Cox-Foster et al. 2007, Pettis et al. 2007, Stokstad 2007, Winfree et al. 2007). The developing view of unfavorable economics of domesticated pollinators, along with biodiversity concerns, has focused attention of the problem of restoring wild pollinators to agroecosystems (Kremen et al. 2002, Pywell et al. 2005, Morandin and Winston 2006, Winfree et al. 2007). Enhancement of wild pollination services must have a strong spatial component because of the combined actions of metapopulation dynamics and spillover effects. Hence there is a need to consider in detail the consequences of different patterns and scales of habitat conversion in a spatially explicit individual-based context in order to better understand the impacts of land management decisions on wild pollinators and pollinator-dependent plants (Brosi et al. 2008).

I consider models of MABES in agroecosystems and specifically focus on how patterns of habitat conversion relate to the persistence of wild pollinators and pollinator-dependent plants in a fragmented landscape. I also model the spillover of pollinators into cultivated areas and evaluate the pollination services provided under different scenarios of habitat conversion. Reasonable models of pollination in agroecosystems can be arbitrarily complex. Additional complexity, however, carries considerable costs in terms of data requirements and difficulty of interpretation and generalization. I intentionally chose a highly simplified modeling framework as being most productive in setting a formal basis for understanding landscape aspects of pollination services. The framework permits both stochastic simulations and equivalent deterministic mathematical representations providing a form of cross validation, yet can be extended to explore more complex scenarios as needed.

Materials and Methods

My results are based on a pair of models: one a detailed individual-based simulation and the other composed of a set of coupled difference equations. The models update the total density of plant populations (P), pollinator populations (N), and of seeds in a seed bank (S). As the emphasis of the modeling was on spatial aspects of habitat conversion, details of reproductive life histories were omitted (the only constraint being contact between a plant and a pollinator). Hence one can equivalently assume P and N represent single generalist populations or guilds of ecologically equivalent species. (Generalizations of the model to complex communities are considered in *Discussion*.) The difference equations were constructed to capture the mean-field behavior of the simulation model, as occurs when starting and ending points of individual movements are spatially independent. The framework follows closely the yucca-moth model of Wilson et al. (2003), but departs in significant aspects as described below. I first describe the details of the individual-based model and then derive the mean-field equations.

Simulation model

Plant–pollinator dynamics were simulated on an artificial landscape composed of a grid of cells. A fraction Λ of these cells could be occupied by individual plants; the remaining portion of the landscape was assumed empty or occupied by crop plants. As in Wilson et al. (2003), I recorded all population measurements in terms of individuals per landscape grid cell. Plants were restricted to no more than one individual per cell, whereas density of seeds and pollinators could grow as long as recruitment exceeded mortality (see Eqs. 2–4). Pollinators were assumed to be central-place foragers and visit a fixed number of sites per season. Pollinator density was equated to the density of nest sites, which could without loss of generality represent a solitary foraging female or a nest with one or more reproductive females and accessory foragers. It was further assumed that the density of male pollinators was never limiting in pollinator reproduction and that male pollinators contributed nothing to pollination. Newly emerged reproductive females could establish new sites after dispersal away from the natal site. The scheme most closely approximates the ecology of bee pollinators although it may capture certain aspects of other pollinator systems.

Simulations were run in one of two modes, either "mean field" or "spatial." When run in mean field mode, individuals moved randomly without regard to distance or direction such that a foraging or dispersing

TABLE 1. Parameter descriptions.

Parameter	Description	Default value
θ	seed production probability	1
ϕ	flower visits per nest per season	100
τ	portion of season flowers are available	0.5
γ	germination fraction	0.5
δ_S	seed mortality	0.1
α	seedling survivorship	1
δ_P	plant death rate	0.2
λ	nest production probability from plant visit	0.2
ν	nest production probability from crop visit	0.2
δ_N	nest death rate	0.5

individual could visit any cell in the landscape with equal probability independent of the individual's current location. When run in spatial mode, movement direction was drawn uniformly on the circle, and movement distance X was drawn from the negative exponential:

$$P_{\vartheta}(X = x) = \vartheta e^{-\vartheta x} \tag{1}$$

where $1/\vartheta$ is the mean dispersal distance. To simplify the modeling, I always used the same function for both foraging and dispersal (i.e., dispersal ϑ = foraging ϑ). The negative exponential was chosen based on results of field studies showing exponential decline of pollinator visits with increasing distances (Ricketts et al. 2008). Periodic boundary conditions were imposed such that movement beyond the edge of the grid wrapped around to the opposing side.

To simplify linkage of the simulation model to the difference-equations, a seasonal cycle was defined with events (pollination, recruitment, mortality, and so forth) occurring in discrete phases. The following events occurred during each simulation time step:

1) Flowering and pollination. Each plant flowers with probability θ after which pollination occurs. Each nest generates $\beta\tau$ cell visits within the flowering period τ. Pollination occurs on the first pollinator visit.

2) Seed and larvae production. Each pollinated plant produces a single seed. Each pollinator making a first visit to a flower causes the production of a new larval "queen" with probability λ (if a wild plant was visited) and ν (if a crop plant was visited). Subsequent pollinator visits have no effect on either plants or pollinators.

3) Seed, plant, nest mortality. Background mortality is assessed on each of the stocks at rates δ_S, δ_P, and δ_N, respectively.

4) Seed dispersal and germination. Seeds are displaced in random directions with distances governed by Eq. 1. Those landing in the fraction Λ of the landscape suitable for growth germinate at rate γ. For any habitat cell not currently occupied by an adult and receiving one or more germination events, a single seedling recruits to the adult population with probability α.

5) Nest recruitment. Larval "queens" disperse according to Eq. 1 (using the same value of ϑ as was used in step 4). Those landing in the fraction Ω of the landscape suitable for growth establish a new nest site.

6) Populations censused. Densities of seeds, plants, and pollinator nests are recorded along with information on crop pollination.

Notice that termination of the time step occurs at the beginning of the simulated growing season, just after recruitment, rather than at the end of the season. This choice simplified the derivation of the mean-field equations.

Mean-field equations

I constructed a deterministic mean-field model as a benchmark for comparison to the individual-based simulations. The model updates stocks (of seeds S, plants P, and pollinator nests N) over a seasonal time step Δt by computing frequencies of different events related to recruitment and mortality. The frequency of independent events can be computed as the probability of an event multiplied by the number of trials. If the locations of events are chosen at random, the probability of m events occurring within a cell is given by the Poisson distribution $p(m; x) = (x^m e^{-x})/m!$ where x is the number of events per cell. The probability of one or more events is then $p(m > 0; x) = 1 - e^{-x}$. With these preliminaries, I define the deterministic, mean-field system:

$$\frac{\Delta S}{\Delta t} = \theta P\left(1 - e^{-\phi\tau N}\right) - \gamma(1 - \delta_S \Delta t)S - \delta_S S \tag{2}$$

$$\frac{\Delta P}{\Delta t} = \alpha\left[1 - e^{-\gamma(1-\delta_S\Delta t)S}\right]\left[\Lambda - (1 - \delta_P \Delta t)P\right] - \delta_P P \tag{3}$$

$$\frac{\Delta N}{\Delta t} = \Omega[\lambda P + \nu(1 - \Lambda)]\left(1 - e^{-\beta\tau N}\right) - \delta_N N \tag{4}$$

where Λ is the proportion of the landscape available to plants and Ω is the fraction of the landscape suitable for pollinator nesting. Definitions and default values of other parameters are provided in Table 1. Terms in Eqs. 2–4 compute frequencies of events per unit area (again scaled to the area occupied by a single plant). For example, the first term in Eq. 2 computes the number of seeds recruited per unit area over the period Δt. Frequency of flowers per unit area is given by θP. The probability of one or more visits to these flowers is given by $1 - e^{-\phi\tau N}$ where per area visitation rate is computed as the number of pollinator visits per nest per time (ϕ) multiplied by the time period over which pollination occurs (τ) multiplied by the number of nests per unit area (N). Frequencies of other events were computed analogously.

The deterministic model is still relatively complex with 12 parameters. Model complexity can be substantially reduced through judicious rescaling of time and state variables. Making the substitutions $t' = t\delta_P$, $S' = \gamma(1 - \delta_P \Delta t)S$, $P' = (1 - \delta_P \Delta t)P$, and $N' = \phi\tau N$ yields (after dropping primes) the eight-parameter model:

TABLE 2. Scaled model parameters.

Parameter	Description	Default value
$\varphi = \dfrac{\theta\gamma(1-\delta_S\Delta t)}{\delta_P(1-\delta_P\Delta t)}$	seed production	2.8125
$\rho = \dfrac{\gamma(1-\delta_S\Delta t)+\delta_S}{\delta_P}$	seed germination and mortality	2.75
$\xi = \dfrac{\alpha(1-\delta_P\Delta t)}{\delta_P}$	seedling survival	4
$\mu = \dfrac{\lambda\phi\tau}{\delta_P(1-\delta_P\Delta t)}$	nest production	62.5
$\varepsilon = \dfrac{\nu\phi\tau}{\delta_P}$	nest production from crop visitation	50
$\omega = \dfrac{\delta_N}{\delta_P}$	nest mortality	2.5

Note: Variables are defined in Table 1.

$$\frac{\Delta S}{\Delta t} = \varphi P(1-e^{-N}) - \rho S \tag{5}$$

$$\frac{\Delta P}{\Delta t} = \xi\left(1-e^{-S}\right)(\Lambda - P) - P \tag{6}$$

$$\frac{\Delta N}{\Delta t} = \Omega[\mu P + \varepsilon(1-\Lambda)]\left(1-e^{-N}\right) - \omega N \tag{7}$$

where the aggregated parameters are defined in Table 2. In the rescaled model, S is equivalent to the density of germination events, P is the post-mortality plant density, and N is the density of pollinator visits. It may be noted that the equilibrium solution to Eqs. 5–7 can be collapsed into a single expression only involving nest density. While the collapsed form is convenient for numerical analysis, it involves a large number of hyperexponential expressions that yield little additional insight and is thus omitted from further discussion. As the model cannot be solved in closed form, equilibrium solutions were obtained numerically using standard methods (Brent 1973). Numerical iteration of the mean-field equations closely matched simulation results obtained from the discrete stochastic model (Fig. A1).

Simulated landscapes

Five separate models were used to simulate habitat conversion (Fig. 1). In the island model, patches of original habitat are evenly distributed across a matrix of converted habitat. The moat model does just the opposite creating islands of converted habitat surrounded by a moat-like strip of unconverted habitat. Two wavelet-based models were constructed based on the

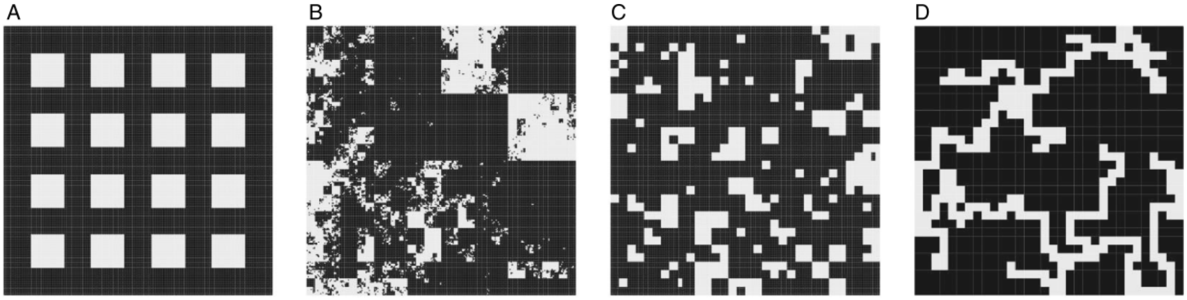

FIG. 1. Landscape models. Lighter cells represent unconverted habitat; black areas have undergone habitat conversion. In each model, 75% of the area is converted. Grid sizes are 256 × 256 cells: (A) 4 × 4 "island" landscape, (B) wavelet-synthesized fractional-Brownian landscape with scaling exponent $\beta = 1.5$, (C) wavelet-synthesized Gaussian landscape with correlation length $\sigma = 32$ grid cells, and (D) spanning-tree landscape with eight-cell "nugget."

method described in Keitt (2000). The first is the β-wavelet model where variance scales as

$$\mathrm{Var}(w; f) \propto f^{-\beta}$$

and w are wavelet coefficients and f is frequency or the inverse scale of analysis. The β-wavelet model ranges between random white noise ($\beta = 0$) to strongly clustered ($\beta = 3$). Intermediate values ($1 \leq \beta \leq 2$) yield so-called fractal landscapes where cluster sizes vary from a minimum approaching a single grid cell to a maximum approaching the size of the entire grid. The parameter β can thus be thought of as a condensation measure that determines the extent of fragmentation for a particular value of Λ. The second wavelet model is the Gaussian-wavelet model:

$$\mathrm{Var}(w; \sigma) \propto e^{-2\sigma^2 f^2}$$

where σ determines the characteristic patch size. Unlike the β-wavelet model, the distribution of patch sizes in the Gaussian-wavelet landscapes are strongly modal rather than hierarchical. The "spanning tree" model derives from graph theory and is described in more detail in Keitt (2003). In this model, the nugget parameter defines the minimum feature width. Cells in a nugget must be either converted or unconverted and cannot be further subdivided. The spanning-tree method connects all nuggets in the grid by (1) growing a minimum spanning tree while breaking nearest-neighbor ties randomly, and then (2) pruning leaves randomly until the desired extent of habitat conversion is reached. The resulting habitat remnant spans much of the grid yet remains fully connected. This is a useful contrast to the other stochastic landscape models where habitat loss and fragmentation covary.

Model simulations

Simulation runs involved choosing parameters, setting initial conditions and iterating the model until no change was detectable in average numbers of seeds, plants and nests between successive 50-step intervals. In all simulations, a grid size of 256 × 256 was used to ensure results were not unduly biased by finite-size effects. Initial placements of seeds, plant, and nests were uniform random. Pollination services were measured as the density of crop plants receiving one or more visits during a simulated season (one step) averaged over the final 50 steps of a simulation run. Note that density was measured relative to the entire simulated landscape. Hence if 10% of the landscape was in crops and all crop plants received pollinator visits, then pollination services over the entire landscape was recorded as 10%. Pollination services measured in this way are directly related to potential crop yield accumulated over the entire landscape.

In order to determine properties of landscapes that resulted in the greatest pollination services (see Fig. 6 and Appendix C: Fig. C1), I ran a series of simulations for each of the landscape models described above. For a given landscape model, I then varied the amount of habitat conversion (x-axis in Fig. 6 and Appendix C: Fig. C1) and the degree of fragmentation or clustering (y-axis in Fig. 6 and Appendix C: Fig. C1). At each level of habitat conversion and fragmentation, I ran 10 replicate simulations each with a different random landscape drawn from the appropriate model (described in *Materials and methods: Simulated landscapes*) and with random initial placement of seeds, plants, and pollinators. Maximum pollination services was then determined by recording those parameter values (amount of habitat conversion and fragmentation) that resulted in the greatest pollination services averaged over the 10 replicate simulation runs. In Fig. 6 and Appendix C: Fig. C1, the parameter combination that resulted in the greatest pollination services for a given landscape model is indicated by a square symbol. In addition, I added contour lines to aid in visualizing pollination services over the full range of landscape parameters simulated. To do this, I fitted a thin-plate spline surface to the results using the "Tps" function from the "fields" package in R (R Development Core Team 2008) and subsequently generated height contours for plotting.

RESULTS

Persistence of pollinators and wild plants under habitat loss

Qualitative dynamics and stability were further probed via isocline analysis of the deterministic system (Fig. 2). Plant density dependence combined with increasing pollination failure at very low plant densities generated bistable dynamics with upper and lower stable points separated by an unstable (saddle-point) node. Trajectories simulated in the phase plane (dotted lines) confirmed this observation. For the parameters considered here, the unstable extinction threshold occurred at very low plant and pollinator densities. With habitat loss, the extinction threshold was much higher. At 50% habitat conversion (Fig. 2B), both the upper stable solution and the unstable point occur at relatively high seed, plant and pollinator densities and are relatively close together. In this situation, even small disturbances could potentially push the system below the unstable point leading to extinction. The effect of habitat conversion was far less severe when pollinators were allowed to nest in the converted habitat ($\Omega = 1$, gray line in Fig. 2B). The bistable pattern was however maintained. Simulated trajectories show attraction to stable points and repulsion from the unstable node. With 40% habitat conversion (Fig. 2C), the isoclines completely separate indicating a cusp catastrophe. Once the stable and unstable nodes meet, the single remaining solution is zero density for both populations. Nesting in converted habitat averted the catastrophe, but it is clear that further habitat reduction would eventually destabilize this scenario as well.

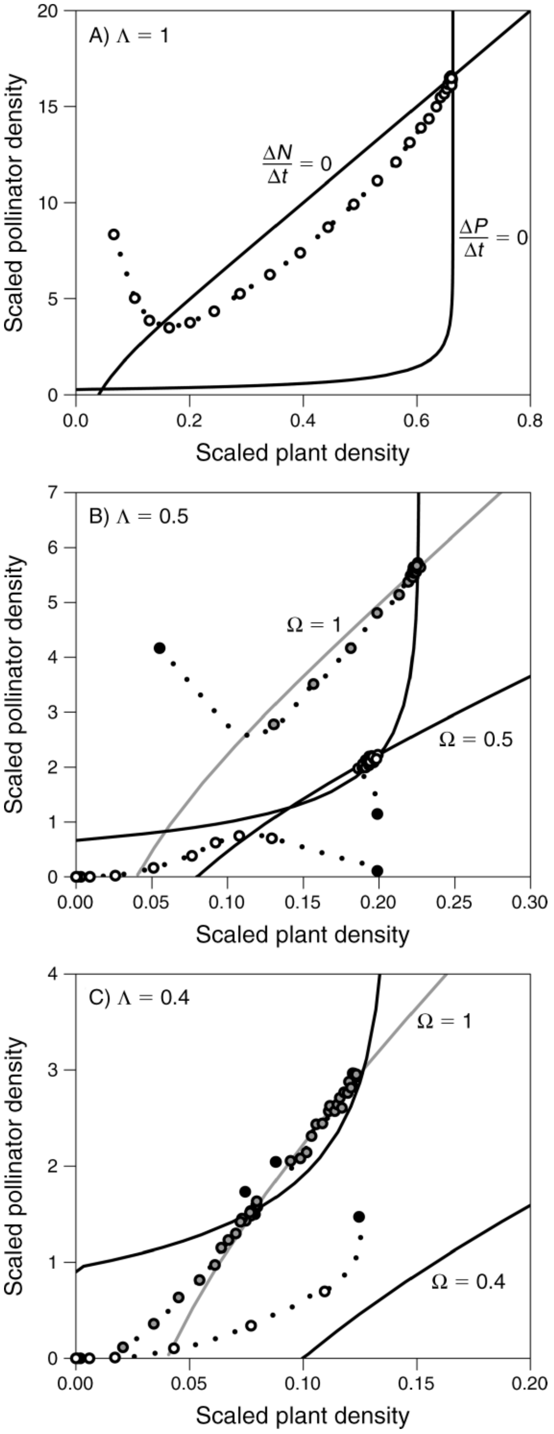

FIG. 2. Pollinator and plant isoclines projected onto the surface of the seed bank isocline. Overlays show simulation results. Solid circles show initial conditions. The dotted lines show subsequent trajectories. Open circles correspond to pollinator nesting constrained to unconverted habitat. Gray isoclines and circles give results where pollinators can nest anywhere. Lambda (Λ) is the fraction of the landscape that remains as wild, unconverted habitat; $\Delta P/\Delta t$ and $\Delta N/\Delta t$ are seasonal growth increments of plant and pollinator populations; Ω is the proportion of the landscape suitable for pollinator nesting. (A) No habitat conversion; (B) 50% habitat conversion; (C) 60% habitat conversion. Circles are shown only every five simulation steps in panels (B) and (C) so as not to obscure the trajectory. The diagrams are for default parameter values with no crop pollen (nest production from crop visitation $\varepsilon = 0$).

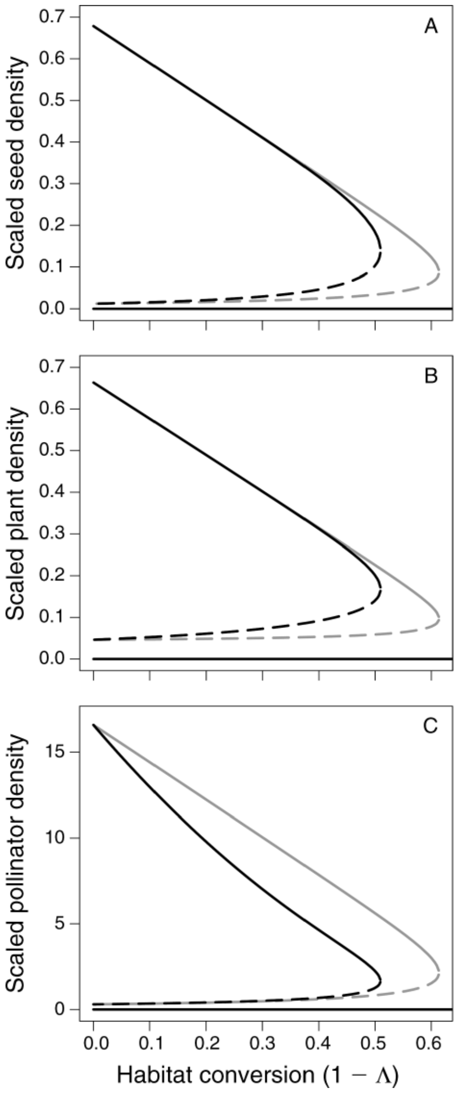

FIG. 3. Bifurcation diagrams showing cusps at critical value of habitat conversion. The gray lines show results where pollinators were allowed to nest in the converted landscape. The diagrams are for default parameter values with no crop pollen ($\varepsilon = 0$).

A more global view of model dynamics is provided by constructing a bifurcation plot showing the pattern of stable and unstable solution as model parameters are varied. Bifurcation plots of the plant-pollinator model reiterate the cusp dynamics at a critical level (moving left to right) of habitat conversion (Fig. 3). The cusp occurs where the unstable branch (dashed lines) meets the stable branch (solid lines) eliminating any non-zero solution. Sensitivity of the threshold to changes in individual parameters is shown in Appendix B: Fig. B1. The general conclusions of the sensitivity analysis are that the plant–pollinator system was more robust to habitat loss when reproductive rates were higher and less robust to habitat loss when mortality related parameters were increased. Position of the cusp was more sensitive to plant and seed related parameters (ϕ, ξ, ρ) and less so to parameters governing nest density (μ, ω).

Fig. 4 compares spatial and mean-field simulations. In this scenario (50% habitat loss), plant and pollinators survived in the mean-field case, but went extinct in the spatial simulation. Notice however the timescale over which extinction occurred: nearly 600 seasons pass before the collapse. The extended transient behavior of the system is a combined result of positive feedback and spatially localized interactions. As shown in Fig. 4B, large voids opened in the spatial simulations. Because of positive feedback between plants and pollinators, these voids grew slowly until consuming the entire landscape. The slow progression to collapse has important implications for conservation as indicators of instability may only appear after a long period has passed after habitat conversion.

The influence of crop pollen on pollinator and wild-plant persistence

When pollinators forage for crop pollen in addition to wild-plant sources, the model dynamics were considerably different (Fig. 5). Under this scenario, as habitat is converted to croplands, the pollinator receives a guaranteed pollen source that is not itself dependent on the pollinator for reproduction. As a result, pollinator populations may be sustained at low wild-plant density or even after wild-plant populations have gone extinct. At moderate extents of habitat conversion, the increased density of pollinators (owing to crop foraging) can cause a breakdown of the bistable pattern, leaving behind a pair of saddle-point nodes (Fig. 5A and shaded regions in Fig. 5B, C). In the bistable condition, zero density is locally stable for both species. Interestingly, with intermediate habitat conversion to crops, the zero-density solution for wild plants becomes conditionally stable. Once the pollinator has successfully colonized (surviving on crop pollen), the wild plants can subsequently also invade because they have a preestablished source of pollination. Simulation results bear this out (dashed trajectory Fig. 5A).

With further habitat conversion, wild plants go extinct (Fig. 5B). Pollinator nesting in the converted habitat has only a small effect on wild-plant persistence (gray lines in Fig. 5B). Loss of wild pollen sources and nesting habitat has a negative impact on pollinators reducing density by roughly half the preconversion density ($\Omega = \Lambda$, Fig. 5C). Pollinators were able to persist on crop pollen until ultimately, loss of nesting habitat drives them extinct. When nesting was allowed in converted habitat (gray lines), pollinators showed little effect of habitat conversion until the point of wild-plant extinction, and then increased in density as more crop area was added.

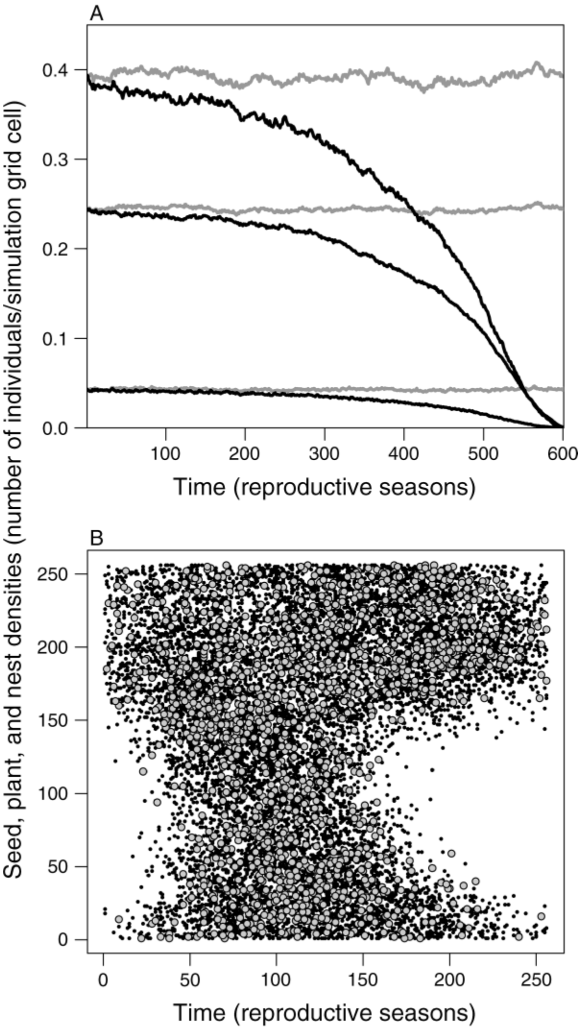

FIG. 4. Comparison of nonspatial (random visitation) and spatial dynamics ($\vartheta = 0.1$). Habitat conversion was set at 50%. Location of converted cells was chosen at random. Pollinator nesting was not allowed in the converted habitat. (A) Time series of spatial (black lines) and nonspatial (gray lines) dynamics. The upper, middle, and lower trajectories are seed, plant, and pollinator densities, respectively. (B) Snapshot of spatial configuration with localized movement at around 400 time steps; units are cell location out of 256 × 256 cells. Parameters were set at their default values as specified in Table 2.

The influence of habitat geometry on pollination services

Alternative patterns of habitat conversion to crops had significant effects on pollination services. In the case of the Gaussian-wavelet landscape model (Fig. 6), increasing average patch size generally had a positive effect on plant and nest densities. Uncorrelated landscapes (i.e., small σ) produced results close to the mean-field predictions whereas longer range autocorrelation (larger patch sizes) boosted plant and nest densities because of reduced fragmentation. Small values of σ resulted in near-mean-field behavior because the resultant fragment sizes were considerably smaller than the 16 cell-width dispersal and foraging distances leading to a more-or-less random pattern of cultivated and uncultivated fragments within the foraging and dispersal range of the pollinators. Note that it is unnecessary to vary both dispersal distance and patch size as it is their ratio that matters, so one can be held constant while the other varies. For completeness, additional simulations were run with much longer and much shorter dispersal and foraging distances (results not shown). For a fixed landscape pattern, longer-range dispersal tended to push the results more toward the mean-field limit whereas shorter-rage dispersal tended to exacerbate fragmentation effects as well as limit the number of flowers accessible to pollinators.

Pollination services varied considerably with changes in amount of habitat conversion and landscape autocorrelation (Fig. 6C). Several interesting results were found. First, creating large, uninterrupted crop fields diminished pollination services by a significant amount despite having a positive effect on the density of pollinators. This result was repeated across all simulations and all landscape models. Although pollinators did better in these landscapes, spillover into crops occurred less frequently resulting in less crop pollination overall. Second, as one would expect, total density of pollination services increased with increasing conversion of the landscape to crops. In the Gaussian-wavelet model, maximum pollination services occurred at approximately 90% habitat conversion, resulting in 83% of the landscape producing harvestable crop. Another interesting result was the apparent matching of the scale of habitat fragmentation and mean foraging and dispersal distance. The greatest pollination services occurred when the autocorrelation parameter (σ) was set to 16 cell widths, the same value as the mean foraging and dispersal distances used in the simulations. Further analysis of the Gaussian-wavelet landscapes with $\sigma = 16$ revealed that this value produced patches roughly eight cells across and separated by approximately 16 cell widths. Some variation in patch sizes and separation did occur owing to random variation. This result nonetheless suggests a general pattern of matching foraging and dispersal distances to mean inter-patch distances. Simulations using four additional landscapes (see Fig. 1) generally agreed with results from the island landscape (see Appendix C).

DISCUSSION

Landscape pattern and scale of fragmentation clearly have a large potential to influence pollination services in agroecosystems (Fig. 6 and Appendix C: Fig. C1). The principal mechanism at work is a tension between maximizing spill-over of pollinators into crop areas and providing sufficiently large and interconnected blocks of nesting habitat. The models presented here

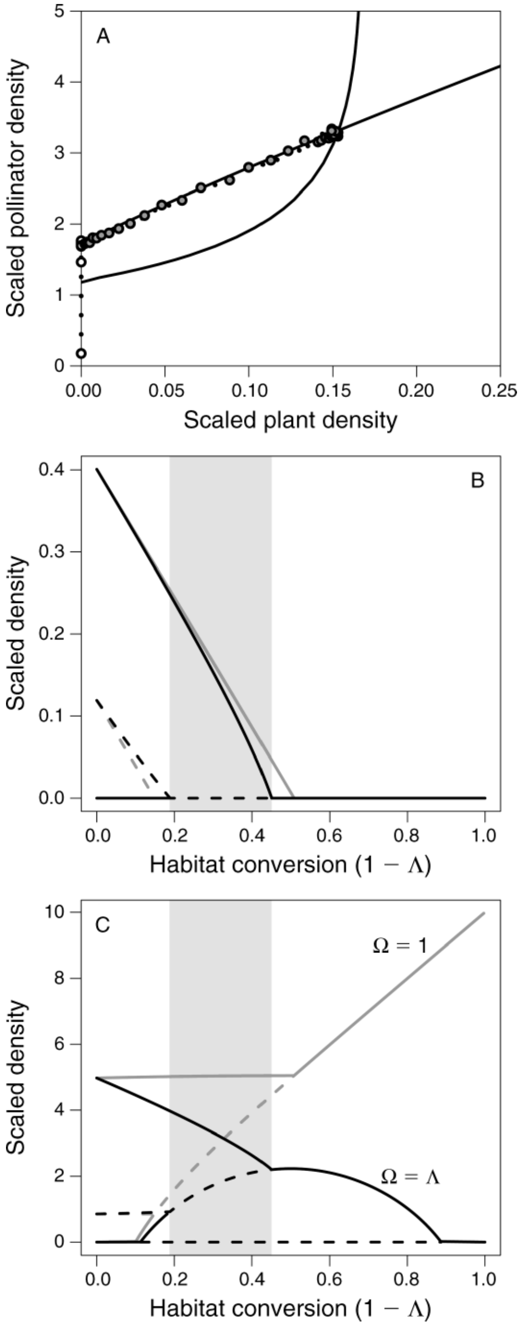

FIG. 5. Isoclines and bifurcation plots with crop pollination. (A) Pollinator and plant isoclines projected onto the surface of the seed bank isocline. Two trajectories are shown: open circles mark points along the trajectory after introduction of pollinators, but prior to reintroduction of wild plants; gray circles mark points along the trajectory after reintroduction of wild plants. (B) Plant bifurcation plot. Gray lines give results when pollinators nest in the crop. The light-gray region indicates where the plant can invade subsequent to the pollinator. Bistable dynamics occur to the left of the light-gray shaded region. (C) Pollinator bifurcation plot. In the light-gray shaded region, stability of solutions depends on whether the plant has colonized or not. All parameters are at default values.

establish a theoretical basis for understanding the dynamics of pollinators, pollinator-dependent plants, and pollination services in fragmented landscapes. A significant feature of the models is the presence of a cusp at a critical level of habitat conversion beyond which pollinator and pollinator-dependent plant populations are expected to collapse (see also Amarasekare 2004). While this result may seem obscure from the management perspective, understanding the potential consequences of the nonlinear dynamics governing the collapse is of critical importance (Scheffer and Carpenter 2003). The key lesson is that as habitat is converted, the domain over which the plant–pollinator system remains intact is reduced. As a result, even small disturbances may shift the balance toward collapse of wild plants and pollinators in remaining fragments. Providing nesting habitat in converted areas delays, but does not eliminate this effect unless the converted habitat also provides a sustained pollen source.

The implication of a reduced domain of stability is that a shift from a sustainable pollinator guild to an extinction trajectory could occur with little warning. The reason is that system dynamics tend to be very slow near isoclines (Hastings 2004). If a plant–pollinator mutualism is pushed only slightly past the unstable equilibrium such that it is now attracted to the zero-density solution, it may take a very long time to actually reach extinction. This is because the rate of repulsion away from the unstable solution varies exponentially with distance in the phase space (Seydel 1988). Near the unstable solution deaths will only slightly outnumber births and the system may respond so slowly that the decline in density goes unnoticed. Simulation results bear this out (e.g., Fig. 2C). The effect is exaggerated with localized spatial interactions (Fig. 4). Local regions of high plant and pollinator densities will tend to persist for many generations even when the system is globally moving toward extinction. Under monitoring scenarios, two observations would be indicative of a slide toward eventual extinction: an acceleration in the rate of decline as the plant and pollinator populations uncouple and gradually expanding voids absent of both plant and pollinator.

Flowering crops may present a significant resource to attendant pollinator guilds (Westphal et al. 2003). Pollen supply from crops while not immediately dependent on pollinators, can influence pollinator abundances and pollinator interactions with wild plants. An interesting scenario occurs in the region where the extent of habitat conversion to crops is sufficient to allow pollinators to persist solely on crop pollen, but is not yet extensive enough to cause extinction of wild plants (shaded region in Fig. 5). In this case, crops may act as "apparent mutualists" (or perhaps apparent commensalists) with wild plants by increasing pollinator density and indirectly wild plant recruitment. The net effect is a breakdown of the Allee effect: as long as pollinators are present, wild plants can colonize regardless of their

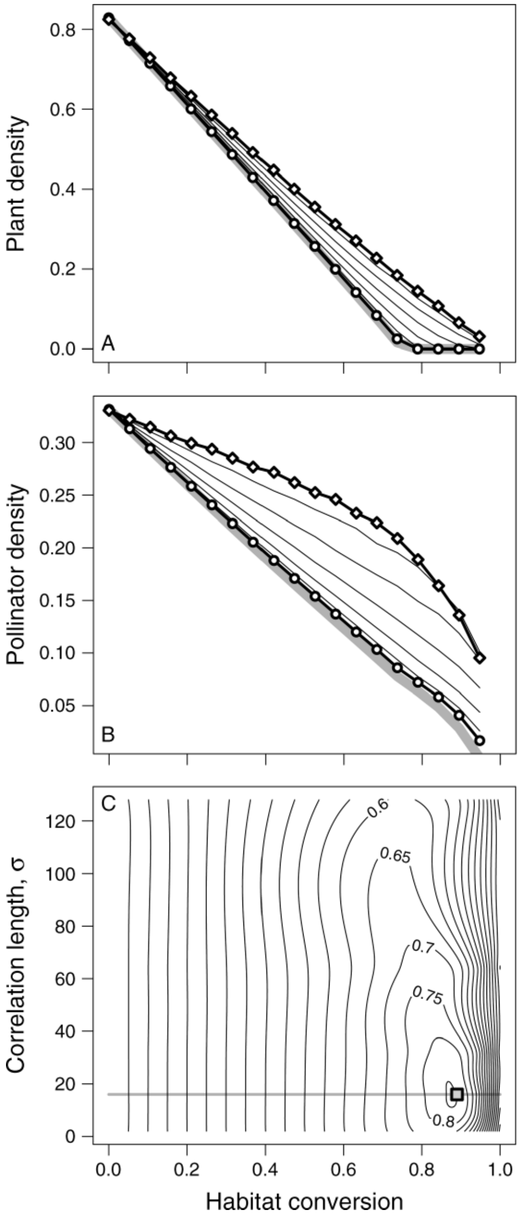

FIG. 6. Simulation results using Gaussian landscapes. Autocorrelation (σ) ranged from 2 to 128 increasing by powers of 2. Mean dispersal and foraging distances were 16 cell widths ($\vartheta = 0.0625$). Simulation grids were 256 × 256 cells. Results were averaged over 10 simulations. Standard errors were negligible and are omitted. (A) Plant density as a function of habitat conversion ($1 - \Lambda$). The bold lines show results for the smallest and largest values of σ (circles, $\sigma = 2$; diamonds, $\sigma = 128$). The thick gray line gives the mean-field prediction. (B) Pollinator nest density as a function of habitat conversion. Symbols are as in panel (A). (C) Contour plot showing pollination services as a function of autocorrelation and habitat conversion. The average dispersal and foraging distance is indicated by a gray line. The location of maximum average services (83%) is indicated by a square symbol. All parameters are at default values.

initial density. Interestingly, this may be an effective strategy to recover wild plants and pollinators in areas where habitat conversion has caused widespread declines. Absent bistable dynamics, pollinators should easily spread into mixed cultivated landscapes (provided sufficient nesting habitat in addition to pollen resources) and subsequently sustain reinvasion of pollinator-dependent wild plants.

This study suggests a number of general management and conservation recommendations. First, mutualistic species are disproportionately sensitive to habitat fragmentation owing to positive feedback and resulting survival thresholds. The model suggests that extinction thresholds for plant–pollinator systems occur at 50–60% habitat loss depending on whether pollinators nest in converted habitat. If crops planted in the converted habitat provide pollen, the threshold for pollinators can be extended above 90%, or may disappear entirely if pollinators nest in cultivated areas. At this level of habitat conversion, I predict that pollinator-dependent plants will go extinct in remnants owing to loss of metapopulation collapse. However, precise estimates of the extinction thresholds cannot be generalized to all situations as the outcome will depend critically on biological details of particular systems. For example, Ricketts (2004) found persistence of pollinator services in a coffee plantation despite a high percentage of habitat conversion (approximately 85%) and a lack of nesting in the cultivated area. It is also important to consider habitat alteration that may occur beyond the boundaries of a particular management unit. Simulations in this study were run with periodic boundaries to emulate a uniform percentage of habitat conversion across the landscape. In practice, patterns of habitat conversion may change abruptly from one parcel to the next and these boundary effects should be taken into account in any real planning scenario. Nonetheless, as a general rule conservation efforts should pay close attention to trends in extent and pattern of habitat conversion as early as possible and certainly as soon as crop land becomes the dominant land cover. Additionally, in cases where extensive habitat conversion has already occurred, restoration of wild habitats should be considered, however habitat restoration alone may not be sufficient to restore pollination services owing to the Allee effect discussed above. After restoration, an active reintroduction program may be needed to attain a sustainable pollinator community.

One of the more intriguing and possibly the most general result of this study is the importance of matching the scale of habitat pattern to scales of pollinator foraging and dispersal. In both the Gaussian-autocorrelation and island landscape models, I found that a habitat-gap distance equal to the mean dispersal and foraging distances was optimal for pollination services in the gap areas. To my knowledge the first spatially explicit theoretical result dictating a specific recipe to optimize pollination services in agroecosystems (see also Brosi et al. 2008). Islands of nesting habitat should be spaced apart a distance equal to the average foraging and dispersal distances of pollinators. Island widths should be one-half of the distance between patches. Further studies need to determine whether alternative dispersal functions (e.g., gamma, Gaussian, heavy-tailed, and so on) will alter the outcome. Also, the particular recipe might change when combined with other strategies, such as attracting pollinators to field margins (Pywell et al. 2005, Carvell et al. 2007, Olson and Wackers 2007). Fortunately, it should be relatively easy to test the scale-matching hypothesis experimentally by allocating nesting habitat in different patterns and assessing pollination limitation in the field.

Recently, Brosi et al. (2008) considered optimal size and spacing of pollinator "reservoirs" within an agricultural landscape. Brosi et al. simulate pollinator dynamics along one-dimensional transects and use optimization methods to discover configurations that maximize potential crop yield. Although the goals of our work are somewhat different, there are many interesting areas of both agreement and disagreement in results. A general area of agreement is the importance of dispersal and foraging scales when designing landscapes. Clearly very long-range dispersal negates any configurational effects as pollinators can reach any point in the landscape: all that is required is sufficient habitat to maintain the pollinator population somewhere in the landscape. Shorter dispersal distances generally require distances between crops and reservoirs to be closer. One of the interesting findings of Brosi et al. is solutions involving both large and small clusters of habitat for pollinators: large blocks of habitat to buffer metapopulation effects and smaller dispersed blocks to spread pollinators around. Generally, hierarchical patch-size models did poorly under scenarios considered in this paper. The discrepancy may have to do with particular assumptions driving the models, i.e., one dimension vs. two dimensions and boundary conditions. I consider a very general landscape with periodic boundaries whereas Brosi et al. focus on a single management unit where foraging beyond the management boundary is discounted. Brosi et al. also separate foraging from dispersal distances and it appears that short dispersal distance combined with larger foraging distances tends to favor larger clusters of pollinator habitat. While the results of Brosi et al. and those presented here form a basis for theoretical understanding of pollinators in agricultural landscapes, major challenges remain. Two areas warranting further consideration are the influences of pollinator foraging behavior and pollinator community composition on pollination services.

The models presented here are dramatically simplified versions of real agricultural landscapes. While these simplifications resulted in a more tractable framework for understanding effects of habitat conversion on pollination services, there are a number of areas in which the models could be profitably extended. First and foremost would be to incorporate life history variation among plants and pollinators to more accurately reflect the complexity of natural communities. Species embedded in plant–pollinator interaction networks express a range of adaptive strategies from generalist to highly specialized (Pellmyr and Thompson 1996, Ringel et al. 1996, Waser et al. 1996, Johnson and Steiner 2000, Bascompte et al. 2003, Vázquez and Aizen 2004), and it would be interesting to incorporate complex interaction structure into spatially explicit modeling of pollination services (see Fortuna and Bascompte [2006] for a spatially explicit model of fragmentation effects on pollinator networks). Another effect of life history variation would be to increase the variance in dispersal and foraging distances. A number of studies have demonstrated strong species-specific variation in foraging distances (Klein et al. 2008, Kohler et al. 2008). Variation in foraging distances could lead to aggregate community-level patterns quite distinct from that of individual species. For example, a mixture of species-specific exponential distributions would combine to form a gamma distribution at the community level (Gleser 1989). Changes in movement pattern are likely to alter optimal landscape configuration for pollination services. A wide range of species-specific movement patterns could for example favor a landscape with a broad range of patch sizes as would be the case with a hierarchical or fractal-type landscape.

Other areas where the models could be extended to include foraging behavior and population genetics. The inclusion of an optimal foraging module would be interesting as it is known that pollinator foraging activities can be altered by landscape configuration (Steffan-Dewenter and Kuhn 2003) and resource quality (Cartar 2004). Additional factors that might affect outcomes are plant self-fertilization and behavioral resource switching by pollinators, both of which can reduce the strength of Allee effects (Morgan et al. 2005). Positive density dependence can also be enhanced by genetic mechanisms such as self-incompatible alleles (Wagenius et al. 2007), inbreeding depression (Lennartsson 2002), and complementary sex determination as occurs in many Hymenoptera (Zayed and Packer 2005). While the focus of this paper is on spatial patterns and mutualistic feedbacks, it is important to remember that many if not all pollination systems include nectar robbery (Irwin and Brody 1998, Bronstein 2001) and other forms of exploitation (Pellmyr et al. 1996, Yu 2001, Morris et al. 2003) with potentially important consequences for population persistence and pollination services.

An important issue not considered here is the phenology of crop and wild plant flowering. In the current model, pollinators can survive solely on crop pollen. This is an unrealistic assumption as many crops have relatively brief flower production. Coffee for example blooms over a four-day period (Ricketts 2004) and pollinators must thus forage on other sources for the remainder of the year. With short duration flowering, estimates of maximum pollination services reported here are certainly too large and I would expect to see joint extinction of wild plants and wild pollinators in the vicinity of 50% habitat conversion to croplands (the exact value would depend on details of the specific ecosystem). Future work needs to explore various phenological scenarios to ascertain the effect of flowering sequence on potential crop pollination by wild pollinators. Certainly if crop pollen alone is insufficient to maintain wild pollinators, it greatly emphasizes the importance of wild plants in agroecosystems.

A final consideration is the importance of nonequilibrium dynamics. In previously degraded landscapes experiencing natural regrowth or active restoration, facilitating re-invasion and reassembly of the wild pollinator community may be an equal concern to optimizing pollination services. Habitat connectivity may play an important role in restoration efforts. For example, Keitt et al. (2001) showed that a strong Allee effect coupled with habitat fragmentation can halt an invasion when there is insufficient immigration into peripheral patches to overcome positive density dependence (although this effect may be overcome to some extent by the availability of crop pollen). There are likely trade offs between landscape configurations for optimal pollination services and those that promote re-invasion (e.g., the spanning-tree landscape is highly connected, but as a result sacrifices some spillover into crops). In cases where agroecosystems may be subjected to aerial spraying or other large scale disturbances, managers should consider, in addition to those that promote crop pollination, landscape designs that will assist in rebuilding pollinator communities to restore wild pollination services as quickly as possible.

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APPENDIX A

Figures comparing simulation and mathematical model outputs (*Ecological Archives* A019-062-A1).

APPENDIX B

Model sensitivity analysis (*Ecological Archives* A019-062-A2).

APPENDIX C

Pollination services in fragmented landscapes: additional landscapes (*Ecological Archives* A019-062-A3).