

Effects of land use on bird populations and pest control services on coffee farms

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Global increases in both agriculture and biodiversity awareness raise a key question: Should cropland and biodiversity habitat be separated, or integrated in mixed land uses? Ecosystem services by wildlife make this question more complex. For example, birds benefit agriculture by preying on pest insects, but other habitat is needed to maintain the birds. Resulting land use questions include what areas and arrangements of habitat support sufficient birds to control pests, whether this pest control offsets the reduced cropland, and the comparative benefits of “land sharing” (i.e., mixed cropland and habitat) vs. “land sparing” (i.e., separate areas of intensive agriculture and habitat). Such questions are difficult to answer using field studies alone, so we use a simulation model of Jamaican coffee farms, where songbirds suppress the coffee berry borer (CBB). Simulated birds select habitat and prey in five habitat types: intact forest, trees (including forest fragments), shade coffee, sun coffee, and unsuitable habitat. The trees habitat type appears to be especially important, providing efficient foraging and roosting sites near coffee plots. Small areas of trees (but not forest alone) could support a sufficient number of birds to suppress CBB in sun coffee; the degree to which trees are dispersed within coffee had little effect. In simulations without trees, shade coffee supported sufficient birds to offset its lower yield. High areas of both trees and shade coffee reduced pest control because CBB was less often profitable prey. Because of the pest control service provided by birds, land sharing was predicted to be more beneficial than land sparing in this system.

Hypothenemus hampei | agroecology | agroforestry | Caribbean | warbler

Agricultural demand is expected to double by 2050 (1), making integration of efficient agricultural production with biodiversity conservation a global challenge (2, 3). This challenge has sparked a debate over contrasting land use approaches, summarized as “land sparing” (i.e., maximizing agricultural yield in some areas and sparing others for nature) vs. “land sharing” (i.e., wildlife-friendly farming, with lower yields and more area under cultivation to meet demand) (4, 5). To date, empirical evidence suggests that land sparing may be better for crop production and wildlife, especially for forest species (6, 7). However, previous work has not adequately considered the capacity for wildlife to provide ecosystem services that boost yield (5). A more complete understanding of the complex relationships among crop yield, biodiversity conservation, and ecosystem services is needed to enable more effective allocation of land use (8). For mobile wildlife, these relationships are even more complex, given that biodiversity and ecosystem services are affected by the spatial arrangement as well as the variety of different land uses (9–11).

The recent discovery that birds provide important pest control services on coffee farms (11–13) illustrates the interactions of land use, conservation, and agricultural production. Coffee farms are an example agricultural system in which mobile predators provide insect pest control, but pest insect populations are too variable over time and space to support predator populations by themselves. Coffee production is often a mix of monoculture and diverse agriculture, with monoculture having higher crop yield but little wildlife habitat and often higher pest insect infestation

rates. These characteristics make coffee farms excellent model systems for studying key questions of how land use decisions affect wildlife populations, the pest control services that wildlife provide, and agricultural production.

Is it economically beneficial to preserve prey-rich habitat for birds so they provide pest control? If so, how much habitat should be conserved? Is prey-rich habitat more beneficial when it is less fragmented (likely better for bird foraging) or more dispersed among the crops (perhaps making birds more likely to find and consume pests)? More generally, which is better for birds or for agriculture: separate large areas of intensive monoculture and large natural habitat or a mosaic of diverse agriculture and habitat patches? Such questions epitomize the land sparing vs. land sharing debate (4, 6, 14, 15).

We address the foregoing questions in the coffee farm system. The world’s most economically damaging insect pest in coffee is *Hypothenemus hampei*, the coffee berry borer (CBB). Gravid adult females of this tiny (<3 mm) beetle bore into a coffee berry, where they lay a brood of 30–120 eggs. The larvae mature and mate with their siblings inside the berry, and gravid adult females emerge 23–28 d later to disperse to another berry (16). Field research in Jamaica has confirmed that migratory insect-eating warblers (family Parulidae) consume CBB in amounts sufficient to diminish pest abundance and crop damage, and provide a substantial economic benefit (12, 13). Native forest birds also consume CBB in Costa Rican plantations where CBB has recently invaded, and provide a substantial economic benefit (11). CBB by themselves cannot sustain bird populations, owing to their small size and episodic availability. Our observations from Jamaican coffee farms indicate that CBB make up <10% of the warbler diet. Thus, habitat that produces other prey is necessary to sustain bird populations if the birds are to control CBB outbreaks. Such habitat includes intact forest, trees and forest fragments (referred to herein as “trees”), and shade coffee (i.e.,

Significance

How land use can support both natural and agricultural resources is a key sustainability question. This question is more complicated when nature and agriculture support each other; here, birds consume pest insects, and coffee provides bird habitat. We used a model based on field research to study the effects of agricultural and natural land uses on birds, the pest control services that birds provide, and crop production on Jamaican coffee farms. Our conclusions address whether small forest-like areas are more valuable for pest control than large intact forest, how the size and number of natural patches affect birds and crop production, and whether replacing sun coffee (a monoculture) with more diverse and tree-rich shade coffee increases pest consumption to a degree sufficient to offset the reduced yield.

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coffee grown under tree canopy that has habitat value but a lower average coffee yield).

The interactions among land use types and arrangements, bird populations, and pest control are impossible to understand via field experiments alone, owing to the number and complexity of interactions and difficulty of controlling such variables as the number of birds arriving from migration and pest outbreak timing and intensity. Thus, modeling is essential. To make our study tractable while still capturing complexities of real systems, we used an individual-based model of insect-eating birds and CBB closely based on field studies conducted on Jamaican coffee farms (17).

The model simulates foraging of individual birds in landscapes that are artificial (allowing manipulation of the areas of various habitat types) while capturing essential characteristics (e.g., habitat types, patch sizes) of real landscapes (Fig. 1). Prey availability and foraging success rates vary among habitat types

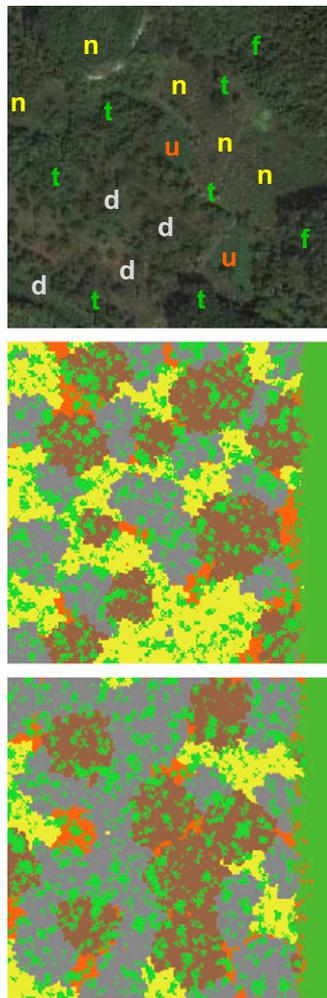


Fig. 1. Example landscapes. Model landscapes were generated stochastically but represent the general land use characteristics of real farms. (Top) 500 × 500 m of a typical Jamaican coffee farm, with patches of forest (f), sun (monoculture) coffee (n), shade coffee (d), and pasture (u), with trees and forest fragments (t) throughout. (Source: 18°20′19.28″N, 77°54′41.30″W; Google Earth image dated January 7, 2011, accessed January 9, 2014.) (Middle) The model's 1,000 × 1,000 m synthetic landscape with the baseline habitat areas (Table 1). The dark-green border on the right side is forest, small light-green patches are trees habitat, gray is shade coffee, yellow is sun coffee, and brown and orange are pasture and other land uses unusable by birds. (Bottom) Model landscape for the scenario with 80% of coffee production in shade.

and between CBB and other prey. Model birds continually move to any adjacent patch offering higher food intake and consume either CBB or other prey, thereby depleting the prey. The model represents prey availability and bird foraging, and also addresses processes (e.g., spatial arrangement of habitat, foraging behavior, prey depletion, competition) that are clearly important but would make a mathematical model very complex.

Here we address three specific land use trade-offs: (i) the relative area of prey-rich, noncoffee habitat (forest adjacent to a farm and trees within a farm) vs. coffee habitat; (ii) the spatial arrangement of trees habitat (fewer large patches vs. more small patches); and (iii) the relative areas of coffee habitat without and with shade cover (“sun” and “shade” coffee, representing monoculture vs. diverse cropland). We examine the effects of these trade-offs on both coffee production and bird population density, and identify ecological processes and uncertainties that seem particularly important for a better understanding of the ecosystem services provided by birds.

The questions that we address are certainly not unique to the bird-coffee-pest system. Similar questions—essentially, how much of the natural ecosystem do we need, and in what configuration—arise in any system in which ecosystems, and especially mobile animals (10, 18, 19), provide services to humans. In particular, the issue of alternative foraging habitat and prey availability are inevitable in systems where birds—which require reliable food sources because of their rapid metabolism and limited ability to store energy—consume agricultural pest insects, which are of episodic abundance by nature. This study provides an example of the use of spatially explicit, theory-based modeling to address such questions.

Results

Our first simulation experiment evaluated the importance of the area of contiguous forest that borders one side of the 100-ha model landscape. Increasing the area of forest at the expense of coffee production area produced a slight decrease in bird density and lower production of uninfested coffee (Fig. 2A). Bird densities decreased because our shade coffee habitat supports higher densities than forest, owing to the higher foraging success parameter for shade coffee (Table 1). We obtained a negative regression slope between forest area and bird density in 71% of 512 simulations that used all combinations of low and high values of nine key parameters; almost all of the exceptions had high values of parameters representing prey production and foraging success for forest and low values of those parameters for shade coffee. Coffee production decreased with increasing forest area, mainly because coffee production area was replaced with forest. Coffee production also decreased because CBB infestation increased slightly with the lower bird density, from an average of 13% berries infested with no forest to 16% infestation with 20% forest.

Repeating this experiment with no trees habitat yielded qualitatively different results. Increasing forest area in the absence of trees produced a slight increase, rather than a decrease, in bird density (Fig. 2B); however, bird densities were much lower without trees and, consequently, CBB infestation rates were much higher (28–29%). Coffee production was slightly higher without trees, simply because trees were replaced with coffee. Without trees, forest habitat was more important for bird densities but supported an insufficient number of birds to provide CBB control. The bird density was lower in the absence of trees habitat in part because trees habitat supports higher bird densities compared with the coffee habitat that it replaces. However, an even more important factor in the lower bird density is our assumption that birds roost overnight in either forest or trees habitat. Without trees, all birds roosted in the forest and started foraging from the forest each morning, and never reached much of the nonforest habitat before the end of the day. (Zero forest area is omitted in Fig. 2B, because there would be no roosting sites with no trees and no forest habitat.)

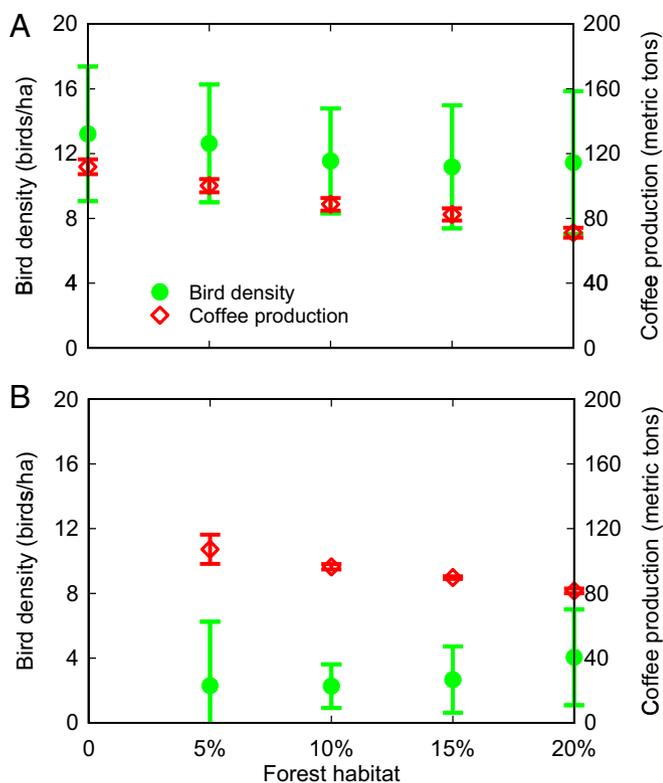


Fig. 2. Simulated responses of bird density (left axis) and total production of uninfested coffee (right axis) to area of forest habitat (as percentage of total area) with 20% of nonforest area as trees habitat (A) and with no trees habitat (B). Error bars represent 1 SD in results from 512 model runs with low and high values of nine uncertain parameters.

The second experiment investigated the effects of the trees habitat patches—large trees and forest fragments dispersed throughout the coffee farm. Trees habitat appeared more important than forest to bird populations and CBB control. As the area of trees habitat increased from 0 to 20% of the landscape in this experiment, bird density increased fivefold (Fig. 3A). Net coffee production peaked at a 5% trees habitat, indicating that (compared with zero trees) the 5% loss of coffee production area was offset by the higher CBB consumption by the larger bird population. CBB infestation rates decreased with increasing trees area, with just a 5% area in trees reducing sun coffee infestation by 60% (Fig. 3B). These results were robust to parameter uncertainty; there was a positive regression slope between trees area and bird density under all parameter combinations, and the 5% trees scenario produced the highest coffee production under 89% of the parameter combinations.

We next examined how the value of trees habitat depends on its degree of fragmentation. Varying the size and number of trees patches from 1,000 mostly very small patches to 50 large patches had relatively little effect on bird density or CBB infestation rate.

On average (across the 512 parameter combinations), bird density varied by only 18%, and coffee production varied by only 11%, among the different patch size scenarios. The number of trees patches producing the highest bird density was not consistent among parameter combinations; the 1,000-patch scenario produced the most birds in 12% of the parameter combinations, 500 patches produced the most birds in 28% of the combinations, and 50 patches produced the most birds in 57% of the combinations. The small effect of trees patch size appears to be related to the fact that in all scenarios, trees and coffee habitat remained sufficiently close together to allow birds to readily feed in both. Even with only 50–100 trees habitat patches, the mean distance of coffee cells to trees was 30–70 m, compared with an observed mean hourly bird displacement of 33 m (*SI Methods*).

In our final experiment, we examined how the relative areas of shade and sun coffee affect birds and total net coffee production. We found a moderate effect of the area of shade vs. sun coffee habitat when forest and trees habitat was available at baseline levels (Fig. 4A). Bird density increased with the percentage of coffee production area in shade under 99% of the parameter combinations. CBB infestation rates remained relatively low in all shade scenarios, and total net coffee production was highest when it was all sun coffee; there was a negative regression slope between percentage shade coffee and uninfested coffee production under 90% of the parameter combinations.

The relative area of coffee shade types had different effects when trees habitat was absent (Fig. 4B). Bird densities were overall much lower, so CBB infestation was high. Increasing the area of shade coffee supported higher, but still low, bird densities that reduced the infestation of sun coffee by a only relatively small degree. Without trees habitat, total net coffee production was higher (because trees habitat was replaced by coffee), and surprisingly insensitive to the amount of coffee grown in sun vs. in shade, despite the lower yield of shade coffee (Table 1). Bird densities were always too low to reduce CBB infestation in shade coffee. As the area of shade coffee increased, the increasing bird density reduced CBB infestation in sun coffee (from 36% with no shade coffee to 29% with 80% shade coffee), but sun coffee made up less and less of total production. Total net coffee production was highest at intermediate shade levels; 59% of the parameter combinations predicted the highest production at 20% shade coffee, 32% of the parameter combinations predicted the highest production at 80% shade coffee, and the highest production was at 100% shade coffee in only 9% of the combinations.

To clarify the relationship between bird density and control of CBB (expressed as percent reduction in infestation rate from that in the absence of birds) in our simulation experiments, we examined this relationship across all experiments except the trees patch size experiment. This overall relationship indicates that any landscape management that supports even a modest bird density is likely to suppress CBB in sun coffee (Fig. 5). In contrast, CBB control in shade coffee was modest unless bird density was relatively high. However, CBB suppression decreased again at a bird density close to the initial density of 20, which indicates ample prey availability.

Table 1. Habitat types and calibrated parameter values

Type (percentage of baseline landscape area)	Prey production, g/m ² /d	Foraging success, m ² /h; time to catch half of cell's prey, h*	Maximum CBB infestation rate, mean ± SD among cells	Coffee density, berries/m ²
Forest (10%)	0.032	15; 1.1	–	–
Trees (20%)	0.026	29; 0.6	–	–
Shade coffee (22%)	0.022	38; 0.4	0.2 ± 0.05	220
Sun coffee (22%)	0.0085	71; 0.2	0.4 ± 0.1	270
Unusable (26%)	0.0	–	–	–

*Parameter value; and the time for one bird to catch half of the prey in a cell, which depends solely on foraging success.

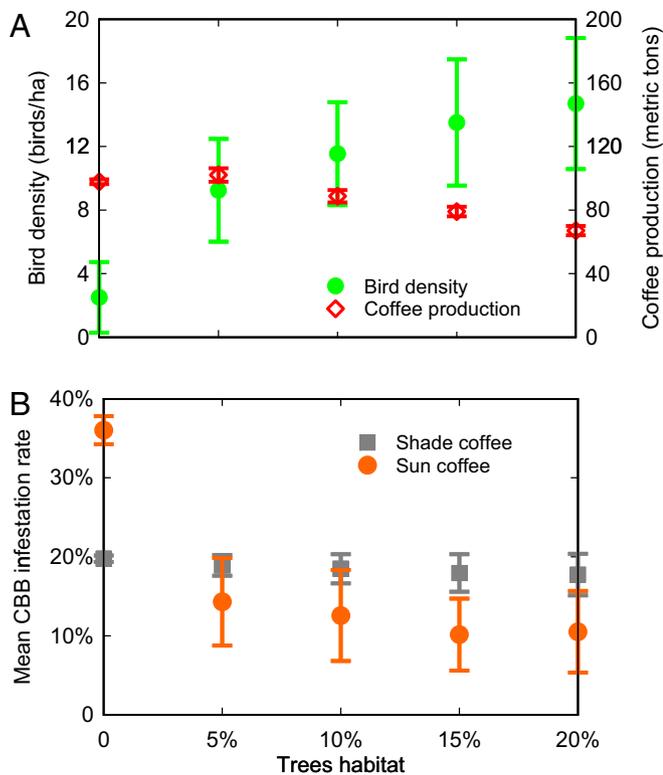


Fig. 3. Simulated responses to variation to area of trees habitat (as percentage of nonforest habitat). (A) Response of bird density and total uninfested coffee production. (B) Response of CBB infestation rates in shade coffee and sun coffee. Error bars are as in Fig. 2.

Discussion

Disentangling the complex relationships among availability of natural habitat, delivery of ecosystem services, and crop production is an important problem in applied ecology (8, 15). This problem is unlikely to be answered by field studies alone, given the many variables and processes that must be controlled and observed (8). Our approach of using a simple spatial simulation model closely based on a real system has revealed complex, sometimes unanticipated, but yet plausible relations among land use, bird populations, and agricultural pest control. Our model is useful because it represents key processes driving the system: how crop production depends on the area in each crop type (monoculture vs. diverse) and on pest control provided by birds, and how bird density varies with the area, spatial arrangement, and prey characteristics of important habitat types. After testing verified that it could reproduce nine key patterns observed in the real system (17), the model was calibrated to observations. Important results proved robust to uncertainty in the prey production and bird foraging parameters.

Our study indicates that ecosystem services provided by wildlife—here, pest control by birds—can be very important to the land sharing vs. land sparing debate. Because of this service, land sharing benefits both bird populations and crop production. Mixes of coffee with trees habitat, or shade coffee instead of sun (monoculture) coffee, would support more birds and also produce more uninfested coffee than separating the landscape into sun coffee and forest. Without CBB control by birds (and similar infestation rates in sun and shade coffee), coffee production would be maximized by all sun coffee, at a severe cost to bird abundance.

Several other advantages of land sharing have been noted previously. First, the trade-off between biodiversity and agricultural production is often examined at large scales (15), prompting the major criticism that without proper land use

regulation, the land sparing strategy actually might not lead to spared land (20, 21). Second, land sharing, or sparing at a finer scale such as individual farms, is arguably more tractable, because markets could provide incentives and rewards for farm owners to include land for conservation (3, 22). For coffee production, such incentives could include higher prices for shade-grown and organic coffee, subsidies and guidance for introducing shade trees, and (as our findings indicate) a reduced need for insecticides. Moreover, conservation at smaller scales may better fit the existing agricultural matrix and sociopolitical structure of the tropics (14), where agricultural expansion likely will be most intense (1).

Several conclusions from this study appear to be applicable to other agricultural systems in which birds provide pest control. First, our results confirm that prey-productive natural habitat is important for maintaining bird populations at levels sufficient to control pest insects (18). Second, because birds are mobile and can forage over long distances, areas of prey-productive habitat, such as our trees habitat, need not be highly dispersed among cropland, but instead can occur in relatively few, large patches (10). However, foraging distances are limited (and vary among animals), so longer distances among prey-productive habitat patches could reduce the value of such “stepping stones” for animals that provide ecosystem services (23). Third, if monoculture agriculture has higher pest infestation rates than more diverse agriculture, such as shade coffee, then replacing some monoculture with diverse cropland could have two crop production benefits: supporting higher densities of birds that then consume more pests, and reducing the percentage of cropland that is highly vulnerable to infestation. Finally, it seems reasonable to expect a very high availability of prey-productive bird habitat to decrease pest control by reducing the incentive of birds to consume crop pests.

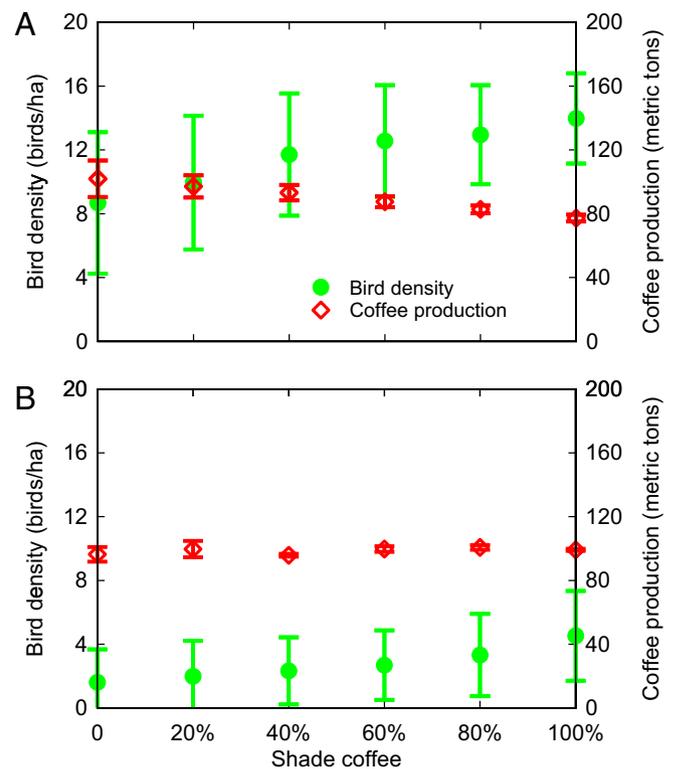


Fig. 4. Simulated responses of bird density and production of uninfested coffee to relative area of sun coffee vs. shade coffee habitat (as a percentage of total coffee area in shade) with trees habitat (A) and with no trees habitat (B). Format is as in Fig. 2.

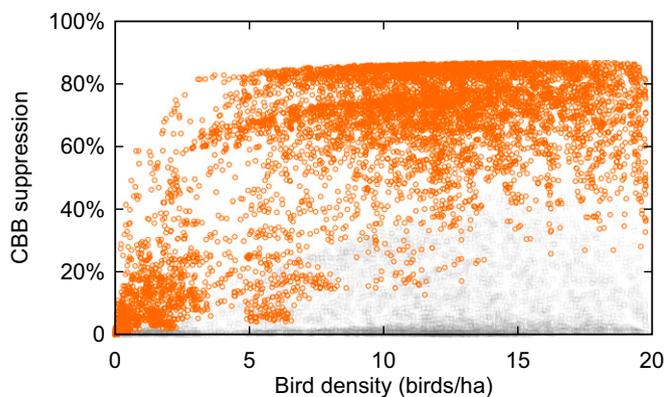


Fig. 5. CBB suppression (percentage by which birds reduce infestation rate over the entire growing season) vs. bird density. Symbols represent each of 512 parameter combinations of all scenarios in all experiments except the trees patch size experiment. The orange circles represent CBB in sun coffee, and the gray squares represent CBB in shade coffee. The calibration analysis indicated that the model somewhat overpredicts CBB suppression in sun coffee and underpredicts it in shade coffee (*SI Methods*).

This modeling study has identified several key uncertainties that can be best resolved via targeted field studies. First, our results depend strongly on the foraging submodel, especially the functional response and its parameters. For example, our simulated birds consumed CBB because we assumed that CBB are easy to see and capture; otherwise, their small size makes CBB unattractive as prey. In contrast, low foraging success in forest made this prey-rich habitat relatively unproductive for feeding. Although functional response has been quantified in shorebirds and farmland birds (24, 25), little literature exists on tree-feeding insectivores of the kind that often provide insect pest control. Estimates of prey production rates (by habitat area) are also important for modeling, but are challenging to obtain empirically. Knowledge of the factors that cause birds to switch habitat and prey is vital to an understanding of pest control and ecosystem services in general (26).

More complete and conclusive knowledge of how birds use habitat, especially forest, for purposes other than feeding could clarify the importance of habitat for both conservation and ecosystem services. Nighttime roosting is a clear example in this study. Our model includes the observation that birds roost and begin foraging in either trees or forest habitat (27), which strongly affected the simulated benefits of trees habitat; without roosts throughout the landscape, birds never foraged in much of the coffee habitat. Our modeling results could differ if other kinds of habitat were used as roosts or if birds were found to “commute” directly between resting and foraging habitat, as observed in other animals (28).

Methods

Our general approach was to conduct and analyze simulation experiments varying the areas of different habitat types. We describe the study system and model, along with the simulation experiment designs.

Study System. We modeled artificial landscapes based closely on the Jamaican coffee farms where the field studies used to design and test the model were conducted (12, 13, 27, 29). These farms, like other tropical coffee plantations (11), have complex and diverse habitat mixes, which we simplified into five types. “Forest” represents large, intact forest where bird prey is assumed to be abundant but relatively difficult to capture because of low light levels and high vegetation density. “Trees” habitat ranges from individual large trees to forest patches of >0.5 ha, without coffee bushes, occurring throughout the nonforest habitat. “Shade coffee” represents coffee under at least 50% shade cover; the canopy is assumed to provide high production of bird prey that is moderately easy to capture (29, 30). “Sun coffee” represents coffee with <25% shade cover. Here bird prey is assumed to occur only on coffee bushes and thus is relatively scarce but easily captured. Coffee

yield (gross kg/ha) is assumed to be 22% higher for sun coffee compared with shade coffee. “Unusable” habitat represents land uses, such as pasture and roads, that do not provide suitable structure and prey for forest-associated insectivorous birds.

The birds in the model represent the small, insectivorous, migratory songbirds of the family *Parulidae* that migrate from North America to inhabit Jamaican coffee farms in winter. These birds prey on a variety of vegetation-associated arthropods and can opportunistically focus on CBB (13). Birds likely capture CBB while the beetles are drilling through the exocarp of the coffee berries, because this process can take several hours, occurs predictably at the apex of the berry, and makes the black beetles highly visible against the green or red berries.

The Coffee Farm Model. In our model, bird densities and CBB suppression emerge from how individual simulated birds select foraging habitat and prey over small distances and times, as well as from the spatial arrangement of habitat types. The model has been described in detail previously (17), except for the small changes identified below. Nine characteristic patterns observed in real coffee farm systems were used to design the model, select appropriate foraging theory for the simulated birds, and demonstrate the model’s ability to reproduce the processes driving the system (17). Model calibration is described in *SI Methods*. Here we summarize the model’s key characteristics.

Model Structure. The model is spatially explicit and individual-based. It runs at a daily time step (except for bird foraging, described below) for the 151-d period (December–April) of coffee production in Jamaica, which coincides with overwinter presence of North American songbirds. Space is represented as a 100-ha landscape, a 200×200 grid of 5×5 m cells. Each cell belongs to one of the five habitat types (Table 1), and habitat types are assigned in a way to produce irregular patches of each type (*Initialization*). Cells have a variable for non-CBB prey availability and two variables representing CBB: infestation rate (fraction of coffee berries drilled into by CBB and thus ruined as crop) and availability of CBB to birds. CBB are assumed to be available as bird prey only when drilling into a coffee berry, so CBB availability is proportional to the rate of increase in infestation rate; the number of CBB drilling into coffee berries at any time is both the number of beetles available as bird prey and the number of berries being infested. Birds are represented explicitly as mobile individuals, with state variables for their location (current cell) and daily prey consumption.

Schedule. The model executes six simple actions on each simulated day. First, each cell resets its non-CBB prey availability (g/m^2) to its daily production rate ($\text{g/m}^2/\text{d}$), which depends on habitat type (Table 1). Second, cells of the two coffee habitat types update their CBB infestation rate and availability of CBB as bird prey (g). The daily increase in infestation rate is a logistic function of current infestation rate, but is decreased by the number of drilling female CBB captured by birds on the previous day. Third, the birds reset their daily prey consumption to zero. Fourth, birds select habitat and forage, using the theory described below. This action is repeated for each “foraging time step” of 3 min over a 12-h foraging day. The order in which birds execute this action is randomly shuffled at each foraging time step. Fifth, birds return to their “home” cell (explained below) to roost overnight. Finally, any birds that did not obtain a daily minimum consumption of 5 g experience a probability of death (or emigration out of the modeled landscape) of 0.2. Thus, the bird population declines rapidly if it exceeds the landscape’s “carrying capacity.”

The bird foraging theory is simple yet causes the model to reproduce a diversity of patterns observed at our Jamaican study sites at both individual and population levels (17). At each 3-min foraging time step, a bird (*i*) stops if its daily prey consumption exceeds its daily maintenance requirement of 5 g; (*ii*) calculates the prey intake rate at its current cell and at the eight surrounding cells, from either non-CBB prey or CBB; (*iii*) moves to the cell offering the highest prey intake rate; and (*iv*) consumes either CBB or prey—whichever offers the highest intake—by adding that intake to its daily consumption and subtracting it from the amount remaining available in the cell. The prey intake rate is equal to the prey’s availability (g/m^2 cell area) times a foraging success parameter (m^2/h ; Table 1). This is a Holling type 1 functional response (31) that neglects handling time because the model does not represent individual prey items or capture events. Foraging success represents the relative difficulty of detecting and capturing prey in each habitat type.

Initialization. Before a simulation is run, the model creates a landscape and populates it with birds. Landscapes are generated via a stochastic process that uses model parameters to set the size of the forest patch (which is always along the landscape’s right-hand border) and the number of patches and fraction of total landscape area in shade coffee, sun coffee, unusable, and

trees habitat types. The stochastic process starts creating each patch by identifying a "seed" cell located at least 200 m from another seed cell of the same type, and then adding randomly selected adjacent cells to the patch. This process can create reasonably realistic landscapes with widely ranging availability of individual habitat types.

The baseline landscape scenario used for calibration (Fig. 1) was designed to represent typical Jamaican coffee farms (13, 29, 32). The 100-ha landscape comprises 10 ha of forest; 1,000 patches totaling 20 ha of "trees" habitat, with patch size drawn from a random exponential distribution with mean of 0.02 ha; 22 ha each of shade coffee and sun coffee, in 20 patches of each coffee type; and 26 ha (26%) of unusable habitat, including 10 large pastures plus random small pieces.

The bird population is initialized by simply placing each of 2,000 simulated birds (20 birds/ha, a relatively high landscape-scale average) into a randomly selected "home" cell to which it returns to roost each night. The model was modified so that home cells are selected from among only the forest and trees habitat types, as indicated by recent field observations (27) of strong selection for forest and trees habitat for nocturnal roosting. This change allowed the model to better reproduce another pattern observed in the field (11, 17): lower densities of foraging birds at high distances from trees or forest habitat.

Simulation Experiments. We explored the effects of land use by synthesizing landscapes to represent wide ranges of variation in amount and distribution of habitat types. Bird foraging was simulated in each synthetic landscape. We analyzed the bird density data at the end of a 151-d simulation, as an indicator of the landscape's bird conservation value, and total net production of uninfested coffee, as a measure of economic consequences. Net production (kg) of each coffee type (shade and sun) was calculated as $N_T \times A \times D_{CT} \times (1 - I_T) \times W_C$, where N_T is the number of cells of a coffee type, A is cell area (25 m²), D_{CT} is the parameter for coffee density (berries/m²), I_T is the mean final infestation rate, and W_C is a typical coffee berry weight (0.0010 kg). Values of D_{CT} (Table 1) were estimated from harvest data for Jamaican farms (17).

Parameter uncertainty is a concern with our model. The prey production and foraging success parameters have strong effects on results, and we could estimate their values only via calibration; thus, instead of simply running the model using the parameter values in Table 1, we executed each simulation experiment 512 times, using all combinations of low and high values ($\pm 20\%$

of the values in Table 1) of parameters for prey production and foraging success in forest, trees, and coffee habitat plus *CBB*-success. The $\pm 20\%$ range does not represent the expected range of "true" parameter values, but instead was chosen somewhat arbitrarily to evaluate the robustness of the model results to parameter values by, for example, considering how many of the 512 combinations produced a particular outcome.

Effects of intact forest area were evaluated by running the model with five landscape scenarios varying in forest area from zero to twice the baseline value (0–20% of total area). Forest was assumed to replace, or be replaced by, coffee habitat in equal parts shade and sun. As the area of forest and coffee habitat varied, the number of coffee patches was adjusted to maintain a constant size. The forest and trees habitat types have similar prey characteristics (Table 1) and are the only types assumed to provide nocturnal roosts. Because trees habitat could make up for a lack of forest and vice versa, we repeated the forest area experiment in the absence of trees habitat.

Effects of trees habitat were studied by varying the area of trees habitat from zero to twice the baseline value of 20% of nonforest area, keeping the mean patch size constant. Trees habitat was assumed to replace all other habitat types except forest, so changes in the area of trees produced proportional but opposite changes in the area of coffee and unusable habitat.

Effects of trees habitat patch size were evaluated by holding the total area of trees habitat constant at 20% of nonforest area while decreasing the number of patches from the baseline of 1,000 to 500, 250, 100, and 50 (mean patch areas of 0.02, 0.04, 0.08, 0.2, and 0.4 ha).

Effects of coffee type were simulated by holding the total area of coffee production constant and varying the percentage of shade coffee from 0 to 100%. We expected that this experiment would be strongly affected by the availability of trees habitat, which has bird prey production characteristics similar to shade coffee (Table 1). This interaction is important for coffee management, because monoculture coffee has both low shade coffee and little trees habitat; thus, we repeated this experiment with no trees.

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Supporting Information

Railsback and Johnson 10.1073/pnas.1320957111

SI Methods

Calibration of the Coffee Farm Model. During its design, the coffee farm model's structure and foraging theory were tested and found to reproduce a variety of observed patterns, even before calibration (1). For this study, we calibrated the model to field observations, using a hierarchical approach starting with bird foraging behavior, followed by population-level foraging patterns (which emerge from foraging behavior and parameters for food and foraging in the various habitat types), and ending with coffee berry borer (CBB) consumption (which depends on foraging behavior, foraging on other food sources, and parameters for CBB). For individual-based models, the hierarchical approach has the advantages of calibrating the underlying individual-level mechanisms before calibrating the full-model results that emerge from what individuals do (2), and limiting the number of calibration simulations to a feasible number.

We performed manual calibration experiments, running the model with various parameter value combinations and examining the results to identify combinations that caused the model to meet specific criteria. We took this approach instead of an optimization approach because uncertainty in the calibration criteria and data did not justify a more precise calibration, and because it was computationally tractable.

The first step in calibration was to adjust parameters for individual foraging habitat selection to fit 474 observations of the distances between locations of individual birds at 1-h intervals (1). These observations were approximately lognormally distributed; the natural logs of distances between hourly observations had a mean of 3.5 m and an SD of 1.0 m. The corresponding distribution of hourly movement in model results was sensitive to the model's foraging time step and the radius over which birds are assumed to select habitat cells at each step. We calibrated these two parameters by running the model with five values of the foraging time step (1–5 min) and three levels of foraging radius (the current cell plus 8 surrounding cells, the 13 cells with centers within a radius of 10 m, and the 21 cells with centers within 12 m) and then identifying the combination that best produced the observed lognormal distribution. The calibration experiment ran the model for 20 d, sufficient for the distribution to stabilize, then output the distance between each bird's location and its location 1 h earlier, once per hour over 1 d. One simulated landscape was used for all of the experiments. A foraging time step of 3 min and sensing area of nine cells (birds select among their current cell and the eight surrounding cells) provided the best fit, closely reproducing the observed mean with a simulated SD of 0.7 m.

We next calibrated the prey parameters (i.e., prey production and foraging success) of each landscape type to target values of bird densities and foraging times (mean hours per day that birds forage). The first calibration target, based on several types of observations (3) and the potential limitations and biases of each, was a landscape-wide mean density of 15 birds/ha. The second calibration target was that bird density in shade coffee should be roughly twice that in forest, a target based on published density estimates for small insectivorous birds in coffee habitat (4–7). The third calibration target was bird densities two to three times

higher in shade coffee compared with sun coffee, observed at a study site with characteristics similar to those in the model (8). The final calibration target was a mean foraging time of 10–11 h/d. This range is lower than the typical dawn-to-dusk foraging behavior of real birds demonstrated in radiotelemetry studies (9), because the model does not let birds forage longer than the minimum to meet their daily maintenance consumption and does not represent any nonforaging behaviors that use up time during the day.

We began the calibration of bird densities and foraging times by varying the prey production and foraging success parameters of all habitat types by the same ratios and observing the resulting bird densities and mean hours spent foraging on the last simulated day. These preliminary experiments showed that the calibration targets were best met by increasing food production and reducing catchability parameters. Thus, we generated 13 levels of prey production in each habitat type by multiplying precalibration values by factors ranging from 1.0 to 1.6 in steps of 0.05, and generated 11 levels of foraging success by multiplying precalibration values by factors ranging from 0.3 to 0.8 in steps of 0.05. We then applied all 143 combinations of those levels to each of five replicate landscapes, all with the baseline area of each habitat type. The results of this experiment indicated that precalibration values of prey production should be multiplied by ~ 1.2 and foraging success should be multiplied by ~ 0.4 . We used a similar experiment varying only prey production for forest habitat to calibrate the relative densities of birds in forest and high-shade coffee.

The calibrated prey parameters (Table 1) met the calibration targets. The simulations using five replicate landscapes produced a mean (over the final 100 d) of 15 birds/ha and 10.0 h of foraging per day. The simulated mean density of feeding birds was 11 birds/ha in forest, 21 birds/ha in shade coffee, and 8 birds/ha in sun coffee.

Calibration of CBB dynamics was based on field observations that indicate birds reduce CBB infestation rates (compared with rates in enclosures that prohibit bird consumption of CBB) by 30–50% in shade coffee and by 50–70% in sun coffee (8, 10). To calibrate the model toward these targets, we adjusted the most uncertain CBB parameter, *CBB-success*, which reflects how easily birds can capture the CBB. We executed model runs with 11 values of this parameter (1.0–3.0 times the precalibration value of 420 m²/h) in five replicate landscapes, and recorded the mean reduction in infestation rates caused by birds at the end of the 151-d simulation. The best fit to the target CBB infestation reductions were at a *CBB-success* value of approximately 1,100 m²/h. This value corresponds to a time of 1 min to remove half of the CBB from a cell, which is not unreasonable because these prey, although small, are visually conspicuous in predictable, exposed locations on coffee berries and likely require minimal handling. The model produced slightly lower CBB reductions than those seen in shade coffee (20–25%) and higher reductions than those seen in sun coffee (80%). These differences will affect absolute predictions of CBB control by birds, but would be expected to have less important effects on relative predictions, such as the direction of change in infestation rates with changes in habitat availability.

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