The payoff of conservation investments in tropical countryside

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Communicated by Paul R. Ehrlich, Stanford University, Stanford, CA, October 22, 2008 (received for review September 10, 2008)

The future of biodiversity and ecosystem services hinges on harmonizing agricultural production and conservation, yet there is no planning algorithm for predicting the efficacy of conservation investments in farmland. We present a conservation planning framework for countryside (working agricultural landscapes) that calculates the production and conservation benefits to the current baseline of incremental investments. Our framework is analogous to the use of reserve design algorithms. Unlike much countryside modeling, our framework is designed for application in data-limited contexts, which are prevalent. We apply our framework to quantify the payoff for Costa Rican birds of changing farm plot and border vegetation. We show that installing windbreaks of native vegetation enhances both bird diversity and farm income, especially when complementing certain crop types. We make predictions that differ from those of approaches currently applied to agri-environment planning; e.g., although habitat with trees has lower local species richness than farm plot habitats (1–44% lower), replacing any plot habitat with trees should boost regional richness considerably. Our planning framework reveals the small, targeted changes on farms that can make big differences for biodiversity.

biodiversity | conservation planning | countryside biogeography | ecological-economic models | matrix

The design of reserve networks was revolutionized by site-selection planning algorithms, but there are no analogues for agri-environment schemes. We know that reserve networks are unlikely to protect more than a tiny fraction of Earth’s biodiversity over the long run (1–5), and recent research focused on agricultural systems suggests that significant biodiversity might be protected there (6–12). However, the scientific basis for informing investments on farmland is weak, even in Europe where conservation in farmland has been practiced for decades (13), and the window of opportunity for harmonizing human activities with biodiversity conservation is closing rapidly (14). Thus, although the future of biodiversity and ecosystem services hinges on harmonizing agricultural production and conservation (15), there is no general planning algorithm for predicting the efficacy of conservation investments in farmland.

Here, we develop a framework for systematic conservation planning in the countryside, recognizing that such planning has been developed thoroughly for network design (site selection). Network design involves choosing sites to protect occurrences of biodiversity features based on their incremental contributions to current and planned reserves, focusing on the complementarity of alternative sites. Most countryside conservation research does not address complementarity, so it will fall short of contributing optimally to conservation policy. Researchers characterize the conservation value of habitats based on their species density (e.g., refs.13, 16, and 17), rarefaction curves (e.g., refs.18 and 19), or species detection probabilities (e.g., ref. 20). These are important first steps, but they do not account for complementarity of sites.

When countryside modeling does account for complementarity, it generally fails to account for a second component of incremental contributions: the current baseline. Researchers project the impacts of land-use change on biodiversity generally by considering drastic, wholesale changes—such as removing all trees from a landscape—or single “optimal” landscape configurations (21–24). Because it is unlikely that countryside conservation could be achieved by fiat, our approach focuses on incremental changes from the current baseline—the landscape as it exists today. This approach parallels the changes that are sought by payment for environmental service (PES) programs (25, 26), the principal tool of countryside conservation. A primary benefit of incremental contributions is that they permit the integration of economic and ecological considerations, as in the use of return-on-investment analysis (27).

Although network design algorithms assess incremental contributions, these algorithms are currently inappropriate for countryside conservation because of key differences in scale and approach. (Scale) Traditional network design focuses on eco-regional to global extents, whereas countryside conservation involves local to regional planning. (Approach) Network design assumes protection to be the primary lever whereas, in the countryside, numerous management options are evaluated. Given these differences, our planning framework is the analogue of network design algorithms, but with 3 crucial revisions. (Objectives) Network design focuses primarily on globally relevant diversity. In local-to-regional countryside planning, we may be interested in local diversity and abundance, even of common species. These factors may be of greater local concern because of their contribution to tourism, aesthetics, crop pollination, seed dispersal, pest control, and other ecosystem services. (Habitat) Terrestrial network design commonly involves the assumptions that species of concern can occupy reserves and that they will not persist long outside reserves (28). In contrast, our countryside approach recognizes that species may survive outside reserves, depending on habitat and microhabitat conditions, recognizing that favorable conditions vary from species to species. (Configuration) Network design is at its heart a spatial exercise, pinpointing particular sites. Countryside conservation is inherently different because it depends largely on voluntary incentive programs, which do not specify particular sites. Consequently, we intentionally model a spatially implicit conservation approach that encourages particular land uses and habitat features in certain contexts, but not in particular places.

If they are to be used widely, conservation frameworks must be applicable when data are scarce. For example, Butler et al.’s (15) risk assessment framework is an important advance in

Author contributions: K.M.A.C. and G.C.D. designed research; K.M.A.C. performed research; K.M.A.C. contributed new reagents/analytic tools; K.M.A.C. analyzed data; and K.M.A.C. and G.C.D. wrote the paper.

The authors declare no conflict of interest.

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This article contains supporting information online at www.pnas.org/cgi/content/full/ 0810522105/DCSupplemental.

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conservation planning for individual species, but the data requirements for each species are sufficiently strict to inhibit the application of the framework to most places in the world. Effective conservation requires the development of planning methods that can be applied with simple assessments of species presence and abundance, such as we develop here.

Here, we apply this theoretical framework by integrating empirical information on the biodiversity and economics of farms in Costa Rica, to explore 3 central questions. First, focusing on birds and the tropics, how do incremental changes in plot and border vegetation affect the bird community supported by countryside? (Where plots are the predominant vegetation at a 1-ha resolution and borders are the strips of vegetation at the edges of these.) Second, how could landscape management enhance bird conservation, especially for rare, forest specialist or migratory species? Third, what bird conservation could be achieved at little or no cost to farmers? We identify nonintuitive cost-effective conservation investments, focusing pragmatically on realistic changes in farmland that could increase its conservation value.

Although many aspects of agricultural practice impact biodiversity (including chemical inputs, timing of activities, and hydrological alterations (29), vegetation cover and associated resources are essential and often limiting (30, 31). We therefore focus on the impacts of habitat change on biodiversity, predicting that incremental impacts will vary immensely.

Model and Methods

We develop a model to explore the impact of small changes in land cover on countryside biodiversity, based on an example of Costa Rican birds. Using a database of bird–habitat associations from the Costa Rican countryside, we project the effect of small, incremental changes in habitat occurrence on bird diversity.

The model is a randomization jackknife procedure that takes as input census data of biodiversity associated with particular types of countryside habitat. The model gives as output the marginal changes in species richness, composition, and abundance predicted under different scenarios of incremental change to countryside habitat. We apply the model using the terrestrial avifauna and major farm habitat types that occur in a study circle of 15-ha radius, centered on the Las Cruces Biological Station in southern Costa Rica (6). The study area was largely deforested by the 1960s and today comprises a mix of countryside habitats (see below).

We use the bird census data collected by Hughes et al. (21), who surveyed birds in the study circle using strip transects and noted the habitat within which each bird was detected. Following Hughes et al. (21), we classify farm habitat as “plot” or “border.” There were 6 types of plot habitats: active pasture (31%), coffee (25%); mostly sun-grown, with bananas and other small trees for shade), fallow fields (22%), residential (8%), strips of trees (mostly riparian strips with some second-growth forest; 8%), and mixed (e.g., small, mixed plantings of sugar cane, palm, yuca, etc.; 6%). There were 8 types of border habitat (at the edge of plots): bare ground (including sparse herbaceous cover) and the 7 possible combinations of shrubs, trees, and tangle (sprawling vegetation >0.5 m tall, mostly shrubs and vines). Plot habitats were sampled in proportion to their abundance in the study circle (21).

We model the hypothetical destruction of habitat by removing the bird records associated with a habitat. From the census data, we created a database of the surveyed habitat, where each unit of habitat (corresponding to 1 minute of observation time—observers walked at a constant speed) was associated with some number of bird observations (many were zero). When birds were observed in a border, the adjacent plot habitat was also recorded. We assume that species can occur only in plot–border combinations in which they were observed empirically and that they could potentially be observed in any such suitable habitat (see Discussion). Accordingly, we assume that removing a unit of habitat has an equal chance of removing each bird observation associated with that habitat type.

In an ideal world, we might know the extent to which each species depends on each particular patch of habitat, and conservation schemes might be able to pinpoint particular patches. Because we do not have such detailed data, we adopt this spatially implicit approach of lumping together common habitat types and assuming that observed bird–habitat associations are predictive of impacts on species. This approach meshes well with available data (transect data) and applicable conservation programs (voluntary incentive schemes).

We used regressions based on series of removals (jackknives) to predict the impacts of removing and replacing habitat (regressions were not always linear, but all produced good fits for changes of at least 25% of the landscape feature in question; see supporting information (SI Text). We predict the impacts of habitat conversion by manipulating observation time from the dataset, making use of (i) the associations of bird observations with the above habitat types and (ii) the correspondence between observation time and area covered by the observers. Thus, to estimate the impact on species richness (S) of removing 5% of the coffee plots, we randomly removed 5% of the observation time associated with coffee plots and calculate the new S for the study circle (Fig. 1). We report averaged results of 1,000 jackknife replicates. This method simultaneously accounts for rarity and complementarity, following the logic of rarefaction that is central to richness estimation (32).

We calculated the effect of habitat additions indirectly, extrapolating from regressions based on removals (see SI Text). We partitioned the bird community into subsets based on migratory status (neotropical migrants and residents) and habitat affinity (forest specialists, agricultural specialists, habitat generalists) (see SI Text).

The model reports impacts on the bird community in terms of species richness (S), abundance (N, the grand sum across all species), Shannon–Wiener diversity index ($H'$), and Shannon–Wiener evenness ($J'$) (33).

We compare our marginal-impact predictions for plot habitat conversion with those derived from measures that typically underlie countryside conservation policy (e.g., based on the
species density of a typical site—\( \sim 50 \) min of observation). We calculated these species densities using analytically calculated rarefaction curves [the converse of species accumulation curves (34)] of expected number of species observed in a plot habitat as a function of observation time. Whole-community rarefaction curves were constructed by summing probability curves of observing individual species (as functions of observation time, counting observations of flocks as single observations and assuming no replacement of observation time).

There is one important complication with the data: Although observers always noted the border habitat in which birds were observed, the border habitat was not noted when no birds were observed. These detailed, fine-scaled but extensive data on negative observations are critical for assessing marginal effects, and the need for them is likely a primary reason that predictions of marginal impacts are so difficult and uncommon. We used the waiting times between observation events to parameterize border-turnover and bird-observation rates using maximum-likelihood estimation of a double Poisson process (see SI Text).

Conservation data are frequently limited in such a manner, so we are frequently faced with a choice to wait for better data or to make assumptions (which can be supported somewhat by the data—see SI Text). We fear that too much is lost while waiting.

All database manipulations and regressions were performed by using ForecastS, a program written in C++ using the genrand random number generators [Makoto Matsumoto and Takuji Nishimura (1997) genrand and genrand2 (35)]; and see the Mersenne Twister Home Page (www.math.sci.hiroshima-u.ac.jp/~m-mat/MT/emt.html).

Results

In general, impacts are small in absolute terms. Small absolute impacts on landscape \( S \) (e.g., \( <1\% \) change per \( 1\% \) change in landscape plot or border habitat) are expected for 2 reasons. First, the accumulation of species with area or observation time generally diminishes with added area or time. Second, the landscape includes both plot and border habitats, so even \( 100\% \) change in one or the other should have \( <100\% \) impact on landscape abundance and diversity indices.

The impact on \( N \) of adding a border habitat is positively correlated with the habitat’s vertical complexity (Fig. 2). Because of the relatively small amounts of some border habitats associated with each plot type, there is considerable variability in the predicted changes in \( S \) (changes in \( N \) are much less variable).

Our model predicts a marked decline in \( S \) with the expansion of residential land (Fig. 3). Conversion of habitat with trees has the greatest impact on \( S \), followed by the mixed habitat type (Fig. 3). Changes from coffee plantations to pasture—as associated with the drop in global coffee prices at the turn of the 21st Century—are associated with much smaller impacts on \( S \) (see SI Text).

Our jackknife model suggests that conversion of habitat to “strips of trees” (such as riparian strips and small wooded areas) should boost \( S \) and \( H' \) strongly (Fig. 4). These predictions differ from predictions based on rarefaction curves (Fig. 4).

Our model predicts that converting bare ground/low herbaceous cover in plot borders to complex vegetation will be the most effective means of increasing overall \( S \) (Fig. S1A). At the plot scale (Fig. S1B), conversion of active pasture to riparian strips and wooded areas is most beneficial for \( S \), followed closely by conversion of coffee farms or residential plots to the same. Although replacing agricultural or residential habitat with “strips of trees” has a strong positive impact on \( S \) (Fig. 4), this impact is proportionately greater on forest specialists (Fig. 5).

Our model suggests that the overlapping set of neotropical migrants is also especially responsive to strips of trees (Fig. S2).

Three kinds of changes to border habitat beside pasture and coffee plots have contrasting effects, with windbreaks of complex native vegetation having the greatest positive effects on \( S \), \( N \), and \( H' \) (Fig. 6). The effects on biodiversity are not proportional to the costs to farmers, which enables the apparent win–win solution of complex native windbreaks (Fig. 6; see Discussion).

Discussion

We have developed a modeling approach that allows us to project the impact of subtle land-cover changes on species communities, using only habitat-specific census data. The approach enables the estimation of impacts associated with very specific landscape changes, such as replacement of one kind of border vegetation with another, adjacent to a particular plot habitat. Comparing such predicted impacts across plot types, it appears that the effect of change in border vegetation depends strongly on adjacent plot type (Fig. 2).

Our results are suggestive of a complementarity effect: Border vegetation that offers a structure type unavailable in adjacent plots may especially boost overall bird abundance (Fig. 2). For instance, adding tangle—which does not occur within coffee

![Figure 2](image-url)

**Fig. 2.** The incremental impact on abundance (N) of adding different border types to coffee plots (A) and to pasture (B). Impacts are presented per 1% change in the landscape border habitat, relative to a whole-landscape baseline of 4,987 observed birds (N); missing bars are projected zero impacts. Only coffee and pasture results are shown because these habitats were the most prevalent in the study area, and other plot types had more variable results. Border types are ordered by roughly increasing vertical complexity of vegetation. Error bars represent 95% confidence intervals about the mean.

![Figure 3](image-url)

**Fig. 3.** The predicted incremental impact associated with the conversion of plot habitat to residential land. Change in species richness (S) is from a baseline of 141 species. The results for “trees” are conservative, because they only include the impacts of converting plot habitat on the adjacent borders, not the changes in the plots themselves (plots of trees were not sampled).
In contrast, the growth in household numbers is a major driver of biodiversity. Residential land (Fig. 3) adds support to the idea that rapid pasture conversion is impacting richness. Adding trees to the borders of largely treeless pastures has a lesser effect. Similarly, adding trees to the borders and riparian strips are important partly because some species specialize in riparian zones. The predicted increase in species richness from converting bare ground/low herbs to complex vegetation (Fig. 4) agrees well with previous findings of the importance of borders (18, 31), and the added value of complex vegetation (19, 39). In our landscape, it seems that these changes are approximately as important as creating second-growth forest or maintaining riparian strips (Fig. S1), the conservation value of which has also been documented elsewhere (19, 40, 41). It may be that complex forest borders and riparian strips are important partly because some species use them as connecting habitats.

To address our second question—how landscape management can enhance conservation of segments of the bird community of special interest or concern—we contrasted findings for groups delineated on the basis of abundance, forest dependence, and migratory status. [Because only 3 of the species observed are endemic to the South Central American Pacific Endemic Bird Area (42), we did not analyze endemism.]

Unsurprisingly, forest-specialist birds appear to be more closely associated with riparian strips and wooded areas than non-forest-specialists (Fig. 4). A similar relationship seems to hold for migrant vs. resident birds: Whereas the impact of replacing each habitat type, in the model, with strips of trees would entail local losses of richness of 1–44% (Fig. 4). These predicted positive impacts are completely at odds with predictions based on the nonmarginal measure of the species density of habitats (through species accumulation curves), which do not account for species rarity or site complementarity relative to the study area. According to species density, one might expect the model to predict that converting certain habitats to strips of trees would entail local losses of richness of 1–44% (Fig. 4). These differing predictions underpin the critical importance of accounting for rarity and complementarity in conservation planning for countryside. These concepts have long been recognized as fundamental for systematic design of reserve networks (37), but they have not yet received due attention in countryside conservation planning.
Harvey, personal communication). Missing bars are projected zero impacts. Farmers within 3 years (46), whereas living fences are costly to install (C.

...diversity of 5.74 (S/N11032) would account for in our plot–border combinations, we may over- or underestimate contributions to diversity. For example, if riparian strips are beneficial to bird diversity because they happen to connect patches of second-growth forest, and there are no more such patches to connect in the region, our approach would overestimate the benefits of adding new riparian strips.

Other advances in landscape planning include spatial population models, but these models can only be run for relatively small numbers of species (e.g., refs. 28, 44, and 45) and not the hundreds of bird species that characterize tropical countryside. Only with such complex models, informed by detailed demographic data on each species, could we account for important complications in predictions of biological impacts, such as the possibility that some habitats may be ecological traps for some species by attracting birds but impeding successful reproduction. In light of the large number of habitat and microhabitat classes, the huge number of possible spatial interactions for each of hundreds of species, and the few cases in which we can identify important interactions a priori, our approach may be the most practical.

Conservation policy must account for interests of stakeholders (here, landowners), and conservation science is more useful when it makes tradeoffs explicit. Marginal impact models do this and allow incorporation of economic benefits and costs of alternative conservation policies. Here, they reveal some possible win–win land-use changes.

Installing windbreaks is expected to be profitable to farmers in developing nations in 3 years, because of increased production of beef/dairy products and coffee (46), whereas replacing fences with living fences of trees costs approximately U.S. $350/km net (47). Windbreaks increase yields by protecting plot vegetation from desiccation and reducing stress on cattle (46). They may take the form of dense exotic shrubs (e.g., Dracaena spp.) or complex native vegetation, with far greater conservation value in the latter (Fig. 6). Indeed, installing windbreaks of complex native vegetation is a win–win strategy, benefiting farmers while significantly augmenting bird diversity (89% of the maximum gain of S; Fig. 6), easily outperforming the more costly installation of living fences.

Our model therefore suggests that such measures can have considerable biodiversity benefits with no net economic cost (for windbreaks of complex native vegetation), lesser benefits for a small cost (for living fences), or mixed impacts for no net cost (for windbreaks of exotic shrubs; Fig. 6). Unfortunately, the apparent win–win solution is not without impediments and will require creative tinkering. For instance, some farmers are unwilling to allow complex native vegetation in plot borders for fear of snakes. If we are to tap the vast conservation potential of human-dominated landscapes in a cost-effective manner, we must develop and use practical marginal-impact ecological models that sensitive to economic and cultural constraints.

Because this approach is intended to support voluntary incentive schemes, economic costs and cultural constraints can structure conservation actions without centrally consolidated information. One might use this scheme to design incentives for conservation actions based only on expected benefits for biodiversity and ecosystem services; landowners can choose to participate or not, demonstrating their costs and constraints through their choices. That such incentive schemes provide a way for costs and constraints to influence conservation action without information gathering is a principal advantage over schemes that dictate particular actions in particular places.

Our model demonstrates the importance of marginal-impact research for conservation decision making. This approach yields important results that differ from traditional measures of conservation value. For example, although strips of trees have a lower species density than other habitats (1–44% lower), we predict that adding strips of trees in any habitat would yield significant gains in regional richness (Fig. 3). Such

**Fig. 6.** The predicted incremental impacts on richness (A), abundance (B), and diversity (C) of changes to border habitat beside coffee plantations or active pasture: either installing windbreaks (dense border vegetation that cuts the wind; as exotic shrubs or complex native vegetation) or living fences (rows of small pruned trees, whose trunks serve as fence posts). Impacts are presented per 1% change in landscape border habitat, relative to landscape baselines of 141 species (S), 4,987 observed birds (N), and Shannon–Wiener diversity of 5.74 (H'). Both forms of windbreaks are likely to be profitable to farmers within 3 years (46), whereas living fences are costly to install (C. Harvey, personal communication). Missing bars are projected zero impacts.

<table>
<thead>
<tr>
<th>Border Change</th>
<th>% Change in S</th>
<th>% Change in N</th>
<th>% Change in H'</th>
</tr>
</thead>
<tbody>
<tr>
<td>exotic shrub</td>
<td>-0.06</td>
<td>-0.04</td>
<td>-0.2</td>
</tr>
<tr>
<td>complex shrub</td>
<td>0.02</td>
<td>0.04</td>
<td>0.08</td>
</tr>
<tr>
<td>native fence</td>
<td>0.06</td>
<td>-0.02</td>
<td>0.1</td>
</tr>
<tr>
<td>living fence</td>
<td>0.08</td>
<td>0.06</td>
<td>0.12</td>
</tr>
</tbody>
</table>

enhances S of resident species, the effect is pronounced for neotropical migratory species (Fig. S2), a group in decline for decades and of particular interest to many North Americans (43). Numerous studies have found neotropical migrants to be more tolerant of agricultural modification than residents (10, 40), suggesting an important conservation opportunity in agricultural habitats. Our data support the utility of protecting and restoring second-growth forest and riparian strips for wintering-ground conservation of neotropical migratory birds, which seem to depend on these landscape elements even more than do resident birds.

Our approach averages over effects of habitat configuration, as appropriate for conservation programs that operate in the countryside (see Introduction). Insofar as the benefits of a particular plot or border are due to aspects of configuration that (i) would not apply to added plots or borders, or (ii) we do not account for in our plot–border combinations, we may over-
gains, achieved piecemeal over tropical agricultural landscapes could, in aggregate, preserve a substantial portion of the diversity now considered under threat of extinction and do so at moderate cost.

Supporting Information

Chan and Daily 10.1073/pnas.0810522105

SI Text

Regressions to Calculate Habitat Additions and Replacements. We calculated the effect of habitat additions indirectly, extrapolating from regressions based on removals. To estimate the impact of adding tree–tangle border in coffee, for instance, we first calculated the impact of removing portions of this habitat (e.g., 5%, 10%, 15%, 25%, 30%, ... 50%); in reality, we removed 10 multiples of observation minutes to total at least 25% of the minutes associated with the habitat in question, e.g., 4, 8, 12, ..., 40, but we report by percentage change in response variables per 1% change in total habitat for ease of comparison across habitat types. We replicated this jackknife procedure 1,000 times, and used these replicates to calculate a regression with multiple y values for each x (where x is amount of coffee removed). Finally, we used the best-fit line associated with this regression to calculate the impact of adding varying levels of tree–tangle border in coffee (Fig. 1), calculating the confidence intervals associated with the mean impact. Of course, habitat is not removed without the addition of some other habitat, and vice versa. Accordingly, we also calculated the impact of habitat replacements as removals followed by additions. We calculated context-specific additions: e.g., for replacing pasture with coffee, we calculated a regression of the effects of removing coffee after removing the pasture to predict the impact of replacing pasture with coffee.

We used linear regression, except in the few cases of significant deviations from linear regression [by F tests of appropriate fit that were made possible by the multiple values for the dependent variable (1)]. Then we tried a logarithmic regression, based on the logarithmic form typical of species accumulation curves. In the very few cases in which each of these regressions failed to characterize the data appropriately (also according to the F test for deviations from regression), it was because the linear relationship close to the baseline became curved close to the origin. In such cases, we restricted the range of areas included in the regression to characterize more appropriately the relationship around the baseline, which is the range of interest.

The approach we used here—the use of regressions on the impacts of habitat removals to predict the impacts of additions—implies certain assumptions. In particular, we assume that the dynamics governing the accumulation of individuals, species, etc., in the existing habitat are equivalent to the dynamics governing the accumulation of further habitat. This assumption is only valid for small changes to the current context (<25% change relative to current extent of a habitat in the landscape), as assured by the regressions and F tests (see above), but since our interest is in such marginal realistic changes, the assumption is appropriate.

Partitioning the Bird Community: Migratory Status and Habitat Affinity. We partitioned the bird community into subsets based on migratory status and habitat affinity. We determined migratory status from Stiles and Skutch (2). We determined habitat affinity based on G. C. Daily (unpublished data of 10,108 observations of 254 species in the study area). Birds that were observed ≥3 times and >90% of the time in forest were classified as forest specialists (83 species); those observed ≥3 times and >90% of the time in agricultural habitats were classified as agricultural specialists (89 species); those birds observed ≥3 times but not falling into the above categories, or observed at least once in both forest and agricultural habitats, were classified as habitat generalists (51 species); the remainder were left as unclassified (31 species).

Maximum-Likelihood Estimation of Absence Data Using a Double-Poisson Process. There is one important complication with the data: although observers always noted the border habitat in which birds were observed, the border habitat was not noted when no birds were observed. These absence data are critical for assessing marginal effects and are likely one of the primary reasons that predictions of marginal impacts are so difficult and uncommon. We used the waiting times between observation events to parameterize rates of border turnover and observation.

We modeled these processes from the perspective of the observer walking at a constant pace. As the observer walks, border types change sporadically (the first Poisson process), and within each border type, birds are observed (the second Poisson process, with a rate that is characteristic of the border type). In the dataset, however, we have only bird observations with their accompanying border type. From these data we can derive waiting times characteristic of border types (the times between sequential observations in the same border type), which collectively provide estimates of the border-specific observation rates.

Borders also turn over at different rates, however. We can derive estimates of these turnover rates for each border type from the distribution of durations of contiguous border type (times during which the border appeared to remain constant based on sequential observations of birds in the same border).

With observation rates and border turnover rates in hand, we can use maximum likelihood analysis to characterize the border types that were present between bird observations.

To illustrate this maximum-likelihood approach, consider a simple example in which borders turn over at equal rates. If we observed a bird in a tree–tangle border in minute 4 and a bird in a bare-ground border in minute 11, we are unsure of the border type for minutes 5–10. According to this approach, the most likely time that tree–tangle border became bare ground is dictated by the observation rates of the 2 border types: if the tree–tangle observation rate is double that of bare ground, the most likely time of transition is between minutes 6 and 7 (thus, 2 min of nonobservation in tree–tangle and 4 min of nonobservation in bare ground).

We found that the border-turnover rates and observation rates varied significantly between borders and plots. For the various habitat types and border types within them, we tested the fit of the distribution of waiting times to the Poisson distribution using “G” goodness-of-fit tests (1). The vast majority of these tests were nonsignificant, and in those that were significant, the difference between predicted and observed distributions was small.

We also performed sensitivity scenarios in which we assumed that border turnover or observation rates were constant and equal; the model results from these scenarios generally diverged little from the best-fit model.

Predicted Impacts Associated with Drop in Coffee Prices. The drop in world coffee prices is likely to have had considerable impacts on biodiversity globally (3), and given the prominence of coffee plantations in the Las Cruces region, we considered its likely impacts in our system. In Costa Rica, the drop in coffee prices is likely to have had considerable impacts on farming, either leaving their fields to lie fallow or converting them to pasture. We predict that both of these plot conversions
should have had very small impacts, boosting species richness (conversions of up to 25% of coffee plots to pasture are predicted to increase $S$ linearly up to 0.79 species; 1.45 for conversions to fallow), but having mixed impacts on abundance (fallow: linear +19.7 birds/25% coffee; pasture: linear −32.4 birds/25% coffee).

Fig. S1. The greatest predicted incremental impacts on species richness (S): from increasing the complexity of border habitat (A) and replacing plot habitat (B). Impacts are relative to a landscape baseline of 141 species. In A, we replace bare ground with tangle, trees, tangle–shrub, tree–shrub, tree–tangle, or tree–tangle–shrub in the proportions that these border habitats occur with each plot type. In B, trees are added to plots as border strips (due to constraints of the empirical data), giving a lower-bound estimate of their impact that nonetheless is greater in magnitude than the most significant changes between other plot types.
Fig. S2. The impact of replacing habitat with strips of trees on species richness ($S$) of 17 neotropical migrant species relative to the impact on 124 resident species (expressed as a percentage of these 2 species communities).