

# The payoff of conservation investments in tropical countryside

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**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 ecoregional 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

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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.

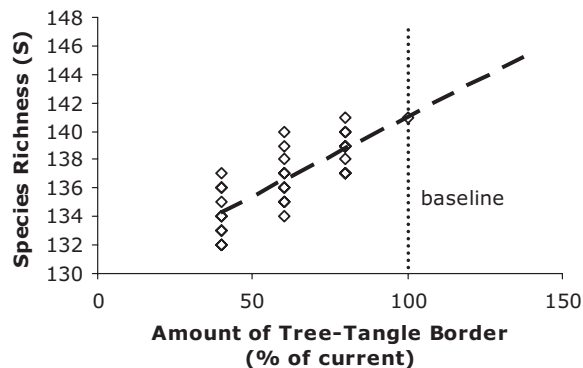
### Model and Methods

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  $\approx 15$ -km 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, yucca, 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



**Fig. 1.** A hypothetical illustration of the methodology for predicting the impacts on a biodiversity metric (species richness,  $S$ ) of adding marginal amounts of a given habitat element (tree-tangle border habitat adjacent to coffee plots). In this example, there is a baseline (dotted line) of 100 quanta (observation minutes) of tree-tangle border and a corresponding 141 species observed in the entire study area (rightmost diamond). Diamonds to the left represent the number of species observed in the study area given simulated removal (jackknifing) of 20, 40, and 60 quanta of tree-tangle border (and correspondingly, observation time). These diamonds from jackknifing runs (1,000 in actual analyses) are then used in a regression to predict impacts of addition of habitat, represented by the dashed regression line.

*Discussion*). Accordingly, we assume that removing a unit of habitat has an equal chance of removing each bird observation associated with that habitat type.

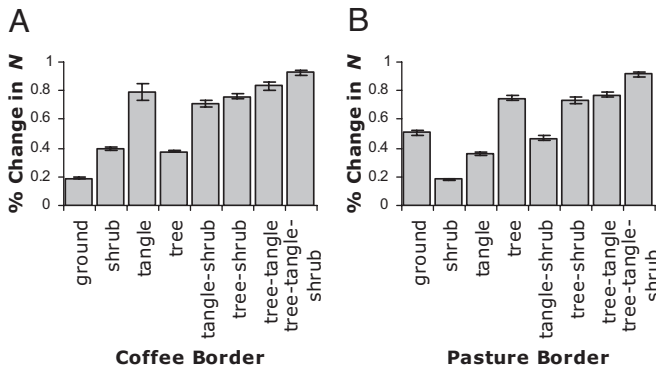
In an ideal world, we might know the extent to which each species depends on each particular patch of habitat, and conservation schemes might be able to pinpoint particular patches. Because we do not have such detailed data, we adopt this spatially implicit approach of lumping together common habitat 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



**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.

species density of a typical site— $\approx 50$  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).

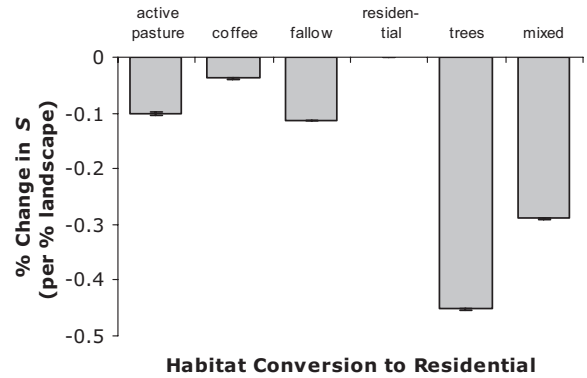
There is one important complication with the data: Although observers always noted the border habitat in which birds were observed, the border habitat was not noted when no birds were observed. These detailed, fine-scaled but extensive data on negative observations are critical for assessing marginal 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](http://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



**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 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.

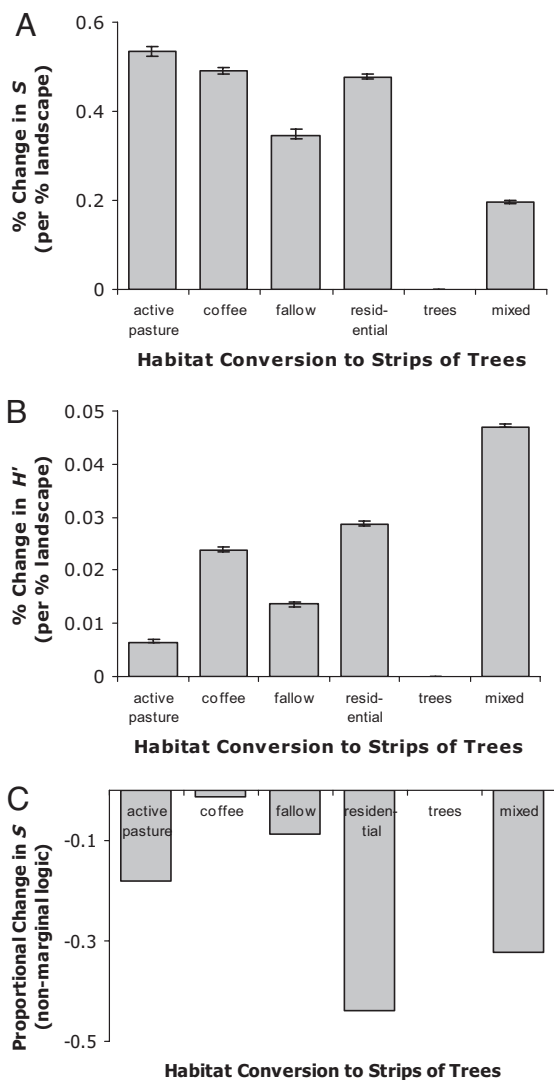
Although replacing agricultural or residential habitat with “strips of trees” has a strong positive impact on  $S$  (Fig. 4), this impact is proportionately greater on forest specialists (Fig. 5). Our model suggests that the overlapping set of neotropical migrants is also especially responsive to strips 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; and 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

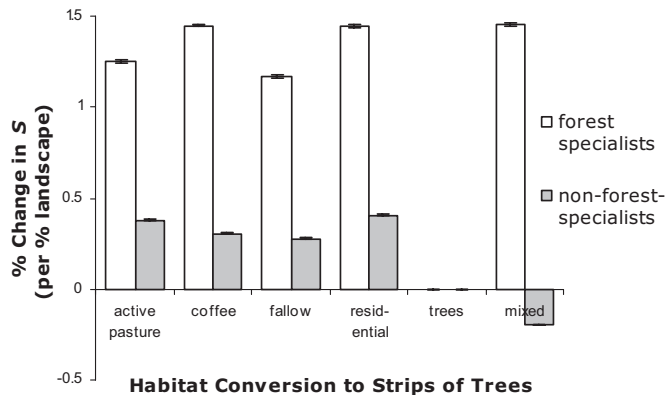


**Fig. 4.** The predicted marginal impacts on the bird community in borders of replacing each of the major plot types with strips of trees (riparian strips and second growth forest). (A and B) The units are percentage of change in number of species (A) and landscape  $H'$  (B) per percentage of change in the landscape borders. (C) For comparison also shown are the predictions of change in local richness based on site species densities derived from rarefaction curves, a standard measure of the conservation value of habitat (by which strips of trees are relatively species poor). This is nonmarginal logic, because it is solely based on local richness, unlike A and B, which are based on each habitat's contribution to landscape richness.

plots—along coffee borders greatly enhances  $N$ ; adding trees, which do occur in coffee plots, has a lesser effect. Similarly, adding trees to the borders of largely treeless pastures has a stronger effect than adding tangle, which often occurs within pasture.

Our model's predicted decline in  $S$  with the expansion of residential land (Fig. 3) adds support to the idea that rapid growth in household numbers is a major driver of biodiversity loss (36). In contrast, the *ca.* 2000 drop in global coffee prices—which triggered conversion in the study circle of coffee plantations to pasture and fallow land—is predicted to have impacts an order of magnitude smaller, enhancing  $S$  slightly by augmenting habitat for numerous rare pasture- and fallow-dependent species (SI Text).

We predict that adding riparian strips and small wooded areas to agricultural lands would boost  $S$  and  $H'$  strongly (Fig. 4).



**Fig. 5.** The impact of replacing habitat with strips of trees on species richness ( $S$ ) of 18 forest specialist species relative to the impact on 96 nonforest specialists (expressed as a percentage of these 2 species communities). Results are conservative, because they include only the impacts of converting plot habitat on the adjacent borders and not the changes in the plots themselves (plots of trees were not sampled).

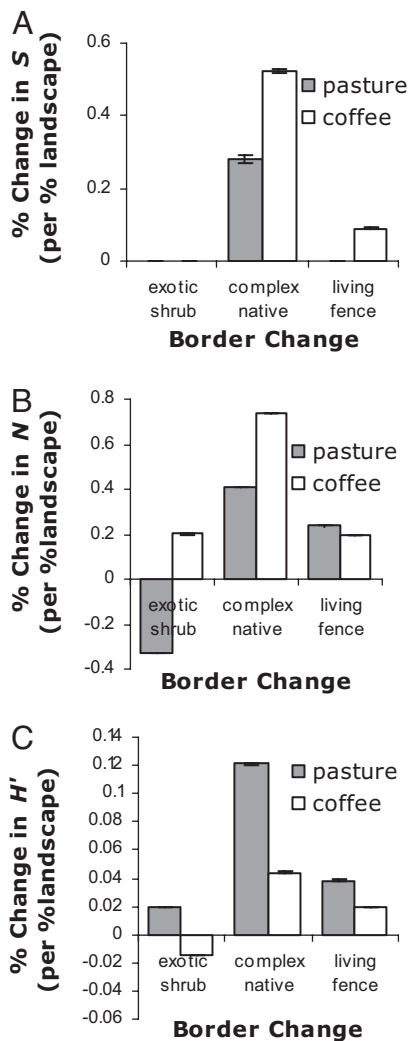
These predicted positive impacts are completely at odds with predictions based on the nonmarginal measure of the species density of habitats (through species accumulation curves), which do not account for species rarity or site complementarity relative to the study area. According to species density, 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.

The impacts of such transitions to “strips of trees” indicate the importance of the use of multiple metrics to assess biodiversity patterns. Although the largest impacts on  $S$  occur by conversion of pasture to strips of trees and the smallest by conversion of mixed, this pattern is reversed for  $H'$  (Fig. 4). This is for 2 reasons: The species that might be lost by loss of mixed habitat are those that are very rare and contribute little to diversity measures like  $H'$ ; meanwhile, loss of pasture makes numerous species considerably rarer, undermining the gain in richness associated with adding strips of trees by reducing evenness.

The predicted increase in species richness from converting bare ground/low herbs to complex vegetation (Fig. S1) agrees well with previous findings of the importance of borders (18, 31, 38) 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 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



**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.

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-

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

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.

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