

# Predictive model for sustaining biodiversity in tropical countryside

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**Growing demand for food, fuel, and fiber is driving the intensification and expansion of agricultural land through a corresponding displacement of native woodland, savanna, and shrubland. In the wake of this displacement, it is clear that farmland can support biodiversity through preservation of important ecosystem elements at a fine scale. However, how much biodiversity can be sustained and with what tradeoffs for production are open questions. Using a well-studied tropical ecosystem in Costa Rica, we develop an empirically based model for quantifying the “wildlife-friendliness” of farmland for native birds. Some 80% of the 166 mist-netted species depend on fine-scale countryside forest elements ( $\leq 60$ -m-wide clusters of trees, typically of variable length and width) that weave through farmland along hilltops, valleys, rivers, roads, and property borders. Our model predicts with  $\sim 75\%$  accuracy the bird community composition of any part of the landscape. We find conservation value in small ( $\leq 20$  m wide) clusters of trees and somewhat larger ( $\leq 60$  m wide) forest remnants to provide substantial support for biodiversity beyond the borders of tropical forest reserves. Within the study area, forest elements on farms nearly double the effective size of the local forest reserve, providing seminatural habitats for bird species typically associated with the forest. Our findings provide a basis for estimating and sustaining biodiversity in farming systems through managing fine-scale ecosystem elements and, more broadly, informing ecosystem service analyses, biodiversity action plans, and regional land use strategies.**

countryside biogeography | habitat use | Las Cruces | radio telemetry | remote sensing

Meeting food demands of the world's people in a sustainable manner will require a near-doubling of food production in the next 40 y while halting the loss of biodiversity and ecosystem services (1–5). The conflict inherent in these goals has produced much debate, yielding two contrasting strategies—each at an extreme of spatial scale (6, 7). At the large scale, a so-called “land sparing” strategy pursues maximal yields through intense industrial farming in places with high potential productivity while setting aside separate reserves for biodiversity. Its opposite is a “wildlife-friendly” approach that integrates agricultural production and conservation on a fine scale on land managed for both.

Wildlife-friendly farming balances tradeoffs within a single system (8, 9) with conservation benefits derived from much smaller, fine-scale ecosystem elements, whose sustainable contribution to biodiversity remains little known. These fine-scale ecosystem elements, such as single trees, charral (early secondary growth), live fences, fruit and timber plantations, and remnants of native forest of all sizes, determine the potential for farmland to support biodiversity and provide ecosystem services critical for food production (10–13). Quantifying the importance of fine-scale ecosystem elements in human-dominated landscapes has proven elusive. It requires high-resolution information of (*i*) species' utilization of different ecosystem elements and (*ii*) detailed information about ecosystem element configurations over a region.

Here, we develop an approach for quantifying the benefits conferred to biodiversity by fine-scale ecosystem elements in farmland and apply it to a landscape in Costa Rica. We focus on countryside forest elements comprising trees of all sizes and spatial arrangements that persist on farmland beyond tropical forest reserves (10). In much of the tropics, ribbons of forest elements loosely weave through the human-dominated landscape along hilltops, valleys, rivers, roads, and property borders. Countryside forest elements include individual and small clusters of trees as well as various sizes and qualities of remnant native forest patches; they can include structurally complex nonnative vegetation. We apply our approach to tropical birds but believe it to be generalizable, with a focus on different elements of ecological importance and different taxa in other regions. Our approach provides a basis for investigating how fine-scale ecosystem elements on farmland can enhance biodiversity.

To quantify the wildlife friendliness of tropical farmland, we (*i*) identify the sizes and configurations of countryside forest elements most important to bird communities, (*ii*) quantify the spatial scale at which countryside forest elements determined bird community composition, and (*iii*) develop and test a model using fine-scale remote sensing of countryside forest elements to predict bird community composition. We conducted three interrelated studies to investigate these issues. The first study used radio telemetry to determine patterns of habitat use by birds; the second used capture and survey techniques to calculate species occurrences in preferred habitats, namely, countryside forest elements; and the third was a detailed digitization of the distribution of forest elements over the entire study area to contextualize all results.

## Results

From 25,794 validated independent locations of individuals from six radio-tracked species over 6 y, we generated home ranges for 258 individuals (*SI Appendix, Fig. S1A*). Radio-tracking was conducted on three forest-dependent species (an ovenbird and two manakin species) and three open countryside generalists (a tanager and two thrush species) commonly found in agricultural plots. Countryside forest elements were strongly selected by the six species over all other ecosystem elements on farmland, especially in the regions of high use within home ranges (*SI Appendix, Fig. S1B* and *Tables S1–S4*).

We found that birds used countryside forest elements of all sizes and spatial configurations but to different degrees. Three species were identified as forest element-limited and carried out their life cycles, including nesting, on farmland by tailoring their home ranges to complex networks of fine-scale countryside forest

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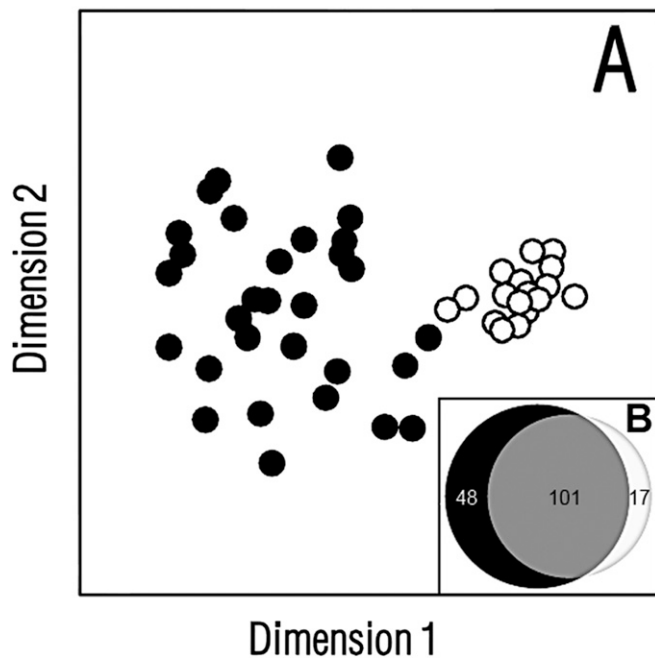
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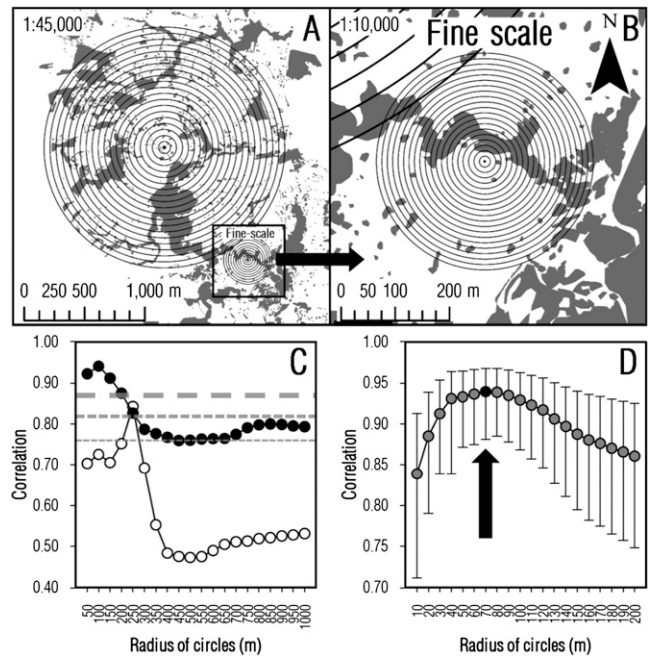
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elements ( $\leq 60$  m wide) that weaved through farmland and pastures. The remaining radio-tracked species used both forest elements and agricultural plots but centered their home ranges on the finest scale countryside forest elements in the landscape ( $\leq 20$  m wide) and used agricultural plots peripherally (*SI Appendix*, Fig. S1C and Tables S5–S11). These three species were also observed nesting in both countryside forest elements and agricultural plots. We found no evidence for selection of larger countryside forest elements ( $>60$  m wide) over fine-scale countryside forest elements ( $\leq 60$  m wide). Moreover, 43 individuals tracked over several years showed no signs of abandoning their territories in fine-scale countryside forest elements for larger forest elements with more forest interior.

After 4 y of mist netting in the landscape, we analyzed 26,288 ecosystem element-specific captures from 166 species and found birds organized into two partially overlapping communities: a forest community and an agricultural community (Fig. 1 *A* and *B*). Of the 166 species, 61% were found in both communities. Of the remaining species, 10% were forest reserve-limited (found only in the 262-ha forest reserve), 19% were forest element-limited (found only in countryside forest elements when captured outside of forest reserve), and 10% were agri-limited (found only in agricultural plots and seeming to avoid forest elements). These percentages do not include the four bird spe-



**Fig. 1.** Similarity plots show the forest and agricultural bird communities from mist netting in Costa Rica. (*A*) Multidimensional scaling plot based on Sørensen similarity coefficients (stress = 0.14); thus, each point summarizes species presence/absence data from capture studies on the landscape. Close proximity between points indicates a greater proportion of shared species (based on presence/absence data from capture studies). Black circles (●) represent samples from inside countryside forest elements ( $n = 30$ ), and open circles (○) represent samples from agricultural plots ( $n = 17$ ) (results of one-way analysis of similarity:  $R = 0.756$ ,  $P < 0.001$ ). (*B*) Inset of a two-way area-proportional Euler diagram summarizing bird community overlap. Numbers are total species encountered in each ecosystem element type. The circle composed of black and gray areas represents the forest community (species found in countryside forest elements), and the circle composed of white and gray areas is the agricultural community (species found in agricultural plots). The gray area represents community overlap with species found in both countryside forest elements and agricultural plots. Of the 48 species in the forest community, 17 are found exclusively in the 262-ha forest reserve.



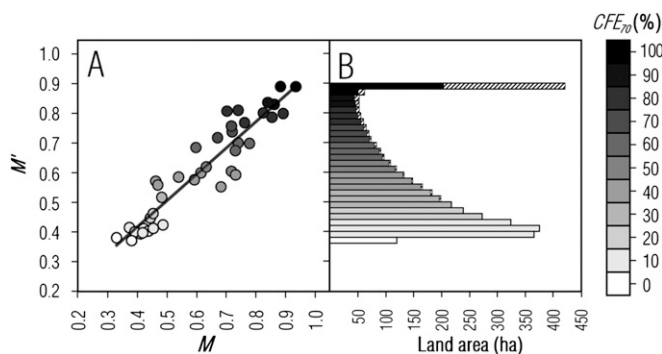
**Fig. 2.** Concentric circles are used to measure the proportion of countryside forest elements at different scales: landscape scales (*A*) and fine scales (*B*). Gray areas are countryside forest elements detected because they are  $\geq 4$  m<sup>2</sup> in size. (*C*) Correlation between community similarity index and the proportion of countryside forest elements at landscape scales. Each point represents the Pearson correlation coefficient ( $r$ ) for each landscape-scale sampling location on farmland ( $n = 15$ ) and the proportion of countryside forest elements within the radius on the horizontal axis. To demonstrate how critical even the smallest forest elements can be, we compare correlations between countryside forest elements from 2-m resolution aerial photographs (●) with forest cover calculated from 28.5-m resolution satellite images (○). Gray dashed lines represent correlation values corresponding to Holm’s adjusted  $P$  values: thick line,  $P < 0.001$ ; medium line,  $P < 0.01$ ; and thin line,  $P < 0.05$ . (*D*) Correlation between community similarity index and the proportion of countryside forest elements at fine scales. Each point represents the Pearson correlation coefficient ( $r$ ) for each fine-scale sampling location in farmland ( $n = 39$ ) and the proportion of countryside forest elements within the radius on the horizontal axis. The single black point is the highest correlation ( $r = 0.939$ ), indicated by the arrow. Error bars show 95% confidence intervals based on Fisher’s  $Z$  transformation. All correlations were significant (Holm’s adjusted  $P$  values at  $P < 0.001$ ).

cies extirpated from the region, presumably because of hunting pressure (on one species) and inability to cope with the human modifications of the landscape since 1960 (ref. 14, appendix b).

Through high-resolution classification of ecosystem elements, we then found that fine-scale countryside forest elements determined bird communities on tropical farmland (Fig. 2). Countryside forest elements most strongly correlated with a community similarity index that quantified the similarity of community composition to the forest reserve, a regional baseline, at a 70-m neighborhood scale ( $r = 0.939$ ) (Fig. 2*D* and *SI Appendix*). We developed a linear model, using countryside forest elements within 70 m of the point of interest (denoted as  $CFE_{70}$ ), to predict community composition (denoted as  $M'$ ) against the original community composition (denoted as  $M$ ):

$$M' = 0.3768 + 0.5187 \cdot CFE_{70} \quad [1]$$

Eq. 1 accurately predicted community composition relative to the original community composition values ( $R^2 = 0.865$ ,  $P < 0.001$ ;  $n = 39$ ) (Fig. 3*A*). Furthermore, Eq. 1 performed well when tested on an independent dataset of bird surveys conducted in the study area ( $R^2 = 0.755$ ,  $P < 0.001$ ;  $n = 68$ ), predicting with



**Fig. 3.** Empirical development and implementation of the equation (Eq. 1) to predict bird community composition using the proportion of countryside forest elements within 70 m of the point of interest ( $CFE_{70}$ ). Gray scale indicates the  $CFE_{70}$  value for each datum. (A) Plot of actual vs. predicted bird community using Eq. 1. (B) Distribution of land and its predicted community composition in the 4,220-ha study area (excluded edges where data were incomplete). Bars with a diagonal pattern indicate land in the 262-ha forest reserve.

approximately 75% accuracy (*SI Appendix* and *SI Appendix*, Fig. S2).

Using Eq. 1 to predict the bird community composition for each square meter of the classified portion of the landscape (4,220 ha) revealed that countryside forest elements on farms contributed approximately 260 ha of land predicted to support a bird community statistically equal to that found in the forest reserve (land with  $M'$  values within the SD of the mean  $M$  value for the reserve =  $0.93 \pm 0.06$ ,  $n = 8$ ). This suggests that countryside forest elements effectively doubled the effective size of the 262-ha reserve and provided substantial seminatural habitat when summed across the study area (Fig. 3B).

## Discussion

We found that fine-scale countryside forest elements largely determined the composition of bird communities on tropical farmland, confirming the generality of this relationship in other systems (14, 15). Habitat selection of the six radio-tracked species, coupled with community patterns derived from extensive mist netting, indicate that 80% of the 166 species sampled are partially or completely dependent on small woodlots, scattered trees, live fences, and the like to persist in farmland. In contrast, 10% of all species are so totally dependent on extensive stretches of forest that they are likely to go locally extinct in the absence of the forest reserve. Overall, our findings suggest that fine-scale countryside forest elements facilitate the persistence of biodiversity in farmland and promote biodiversity-driven ecosystem services vital to agriculture.

Our approach differs from previous attempts to sense biodiversity remotely in human-dominated landscapes in three fundamental ways. First, most studies are limited to a single species (16) or rely solely on species richness to quantify biodiversity (17). Species richness has been shown to be relatively high across some human-dominated ecosystems (15, 18, 19). In our approach, we quantify biodiversity in terms of community change using a large number of species.

Second, our approach used a highly accurate, manual, fine-scale ecosystem element classification, whereas remote sensing is frequently conducted at coarse scales and/or uses error-prone automated classification systems (17). In our heterogeneous study area, we found high bandwidth imagery to be coarse and automated classification to be highly error-prone (Fig. 2C). With advances, both in imagery and classification techniques, it is likely that these problems will soon be resolved (20, 21). Lastly, our approach combines habitat selection from multiple species,

extensive community surveying, and model testing in the context of an expansive fine-scale understanding of the landscape. The array and resolution of our techniques distill a suite of species-specific responses to human land use into a model that may be applied generally to other systems and taxa.

Our results indicate that countryside forest elements, especially at fine scales, should be included in analyses examining tradeoffs in biodiversity, agricultural yield, and ecosystem services in farmland (22). To be useful in studying other ecosystems where countryside forest elements are not the determining landscape feature, such as European grasslands, our approach will require modification and testing. Opportunities for further study include assessing how species that are dispersal-limited or require extensive areas of habitat use human-dominated ecosystems (23, 24), investigating how human land use influences population patterns and source-sink dynamics of countryside biota (25, 26), and quantifying yield tradeoffs (27). We believe careful integration of these factors into our general approach for predicting biodiversity on farmland can inform regional decisions to meet human demands and manage natural capital sustainably.

Finally, our results underscore the agency individual landowners have in managing biodiversity, ecosystem services, and natural capital on their properties. Conservation biology is commonly couched in the strategy of protected areas and national parks at large scales and by large social institutions. We show that modest management practices that include important natural and seminatural ecosystem elements at fine scales can dramatically improve the hospitality of a farm to biodiversity. Through fine-scale management, landowners possess the power to increase natural capital directly and manage for ecosystem services on their farmland, while helping to sustain biodiversity in the countryside.

## Methods

**Study Area.** The study was conducted in the countryside of Coto Brus, Puntarenas, Costa Rica, which was heavily deforested in the 1960s and 1970s. The countryside contains forest elements of variable sizes mixed with agricultural plots and pasture, which are virtually indistinguishable except at a fine scale. The landscape and biogeography have been described in previous literature (18, 19). Coto Brus' native habitat is classified as tropical premontane wet forest (28).

**Radio Telemetry.** Six resident (nonmigratory) focal species were used as bioassays to understand the importance of ecosystem features in a human-dominated landscape. The radio-tracked species spanned the spectrum of forest dependencies within the forest community, with three being found only in countryside forest elements (*Automolus ochrolaemus*, *Coropipo altera*, and *Lepidothrix coronata*) and three occurring in both countryside forest elements and agricultural plots (*Turdus assimilis*, *Tangara icterocephala*, and *Catharus aurantirostris*) (29).

Radio telemetry included the attachment of small temporary radio transponders to the backs of captured birds using a standard protocol at 12 of the 18 study locations from 2002 to 2006. After transponder attachment, birds were released and allowed to adjust for 24 h before being tracked and observed. Independent locations of birds were recorded in 30- to 120-min intervals for several days until sufficient independent locations were recorded or the transmitter fell off and was recovered. Independent locations were recorded when radio-tracked birds were seen, identified by unique color-band combinations, or determined to be within a <10-m area by short-distance triangulation (walking around a tree or thicket a bird was concealed in). Habitat substrate and behavior, including nesting, were recorded when possible. Only individuals with >25 independent locations were analyzed.

Home ranges of radio-tracked individuals were calculated using fixed kernel density estimates with a 2-m resolution. Least-squared cross-validation was used to calculate h-smoothing factors. Each home range was weighted by regions of predicted utilization and divided into nested subareas for analysis (30) (*SI Appendix*, Fig. S1). To compare each bird's use of different ecosystem elements relative to their availability in the landscape, we applied a proportional analysis method (*SI Appendix*) to each home range (31).

We tested for selection of countryside forest element size and configuration by the radio-tracked species. To do this, we used the interior core area,

a standard index of configuration related to both the size and shape of a countryside forest element (32). The interior core area is defined as the portion of a countryside forest element contained within a specified distance from the edge. Interior core areas were calculated at 10-m intervals from the edges of each countryside forest element polygon, up to 100 m deep in the largest countryside forest elements. Eleven maps for all countryside forest elements in the study area were created: 1 map for each interior core area interval from 0 to 100 m from each element's edge.

All home ranges were superimposed over each interior core area map to calculate each bird's use of countryside forest elements of different sizes and configurations. To compare each bird's interior core area preference of countryside forest elements, we applied a proportional analysis method (SI Appendix) to each home range and each interior core area map (31).

**Bird Community Sampling.** Bird sampling was conducted using constant-effort mist netting. Mist-netting protocols consisted of twenty  $12 \times 2.5$ -m, 32-mm mesh ground-level mist nets in a 3- to 5-ha plot haphazardly placed at each study location. Constant effort mist-netting sampling for birds took place between January 25 and May 12 for 4 y (2007–2010). Only species with >5 captures since the initiation of the study in 1999 and nets with >25 captures were included in all analyses. Understory passerines and near-passerines were sampled primarily, and these species comprise the majority of the avifauna in the area.

Capture data from mist nets were lumped or eliminated in two manners to analyze landscape-scale and fine-scale effects of ecosystem elements on bird community composition. In landscape-scale analyses, we combined all data from each sampling location (Fig. 2 A and C), that is, from 20 mist nets at each of the 18 study locations. In addition to fine-scale ecosystem element classification, coarse forest cover estimates calculated from satellite images with a resolution of 28.5 m were correlated with bird community composition. This revealed the importance of fine-scale ecosystem element classification (Fig. 2C).

In analyses of fine-scale effects, we combined data from limited groups of three mist nets, or triplets, placed within 0–5 m of each other (Fig. 2 B and D). To increase spatial independence, we eliminated data from intermediate nets between triplets (mean nearest neighbor distance between triplets in the same study location =  $102 \pm 18$  m, range: 81–147 m.) After eliminating intermediate nets between triplets, we were left with 47 triplets with at least 80 m spacing between them. Landscape-scale and fine-scale sampling locations inside the forest reserve served as a baseline for the community similarity index for mist net data. Additionally, point count surveys were conducted in the study area and used to test Eq. 1 (SI Appendix).

We determined the spatial scale at which countryside forest elements most strongly determined bird community composition by correlating the proportion of countryside forest elements at different neighborhood scales (Fig. 2) with a standard index of community similarity. Using the Sørensen index, we correlated the similarity of species composition in a bird sampling location on farmland with a set of sampling locations in the forest reserve, which provides a regional baseline. We defined  $M$  as the arithmetic mean of Sørensen similarity coefficients calculated for each farmland sample compared with the set of samples in the forest reserve (SI Appendix).

**Ecosystem Element Classification.** We classified ecosystem elements manually by digitizing Costa Rica Airborne Research and Technology Applications orthorectified aerial photographs from 2003 and 2005 with 2-m resolution. The ecosystem element map covered 4,750 ha, determined by 1-km radius buffers around each of the 18 study locations and several small areas where radio-tagged birds were active outside of 1-km buffers. The four ecosystem elements included (i) countryside forest elements [primary and secondary forest fragments of all sizes, single trees, charral (early secondary growth), live fences, hedgerows, nonnative timber and fruit tree plantations, and nonnative garden ornamentals]; (ii) agricultural plots (with the majority being sun coffee plantations but also including banana, plantain, tomato, and chili plantations); (iii) pasture; and (iv) rural infrastructure. Ground truthing was conducted to ensure accuracy of digitization. To compare resolution of ecosystem element classification, we used forest cover calculated from 28.5-m resolution satellite images was included from previous studies (17, 18).

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