LETTER

Balancing biodiversity with agriculture: Land sharing mitigates avian malaria prevalence

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Abstract

Debate over balancing agricultural production and biodiversity conservation has generated two opposing strategies: a "land sparing" approach involving large-scale nature reserves, versus a "land sharing" approach where agricultural areas support wildlife through fine-scale conservation. As a result of this debate, studies focus almost exclusively on species diversity and food production, while ignoring other critical ecosystem processes such as disease dynamics. Here we quantify how tropical avian malaria in an abundant sedentary bird species responds at fine spatial scales in a "land sharing" system. We find the proportion and configuration of countryside forest elements within a radius of 400 m, proximity to the nearest river, and habitat type explains malaria prevalence across the region. We simulate "land sparing" and "land sharing" land use strategies and model malaria prevalence to find that land sharing mitigates malaria prevalence more effectively. With these analyses, we gain a better understanding of how biodiversity, ecosystem services, agricultural yield, and human well-being intersect in complex ecosystems.

Introduction

Balancing the conservation of biodiversity with humanity's demand for food and resources is one of the primary challenges of the 21st century. Two contrasting strategies have emerged from this predicament. A large scale, so-called "land sparing" strategy proposes to maximize yields through intensification of arable portions of the planet while setting aside separate reserves for biodiversity. In contrast, a fine scale, "land sharing" approach integrates agricultural production and conservation on land managed for both (Green *et al.* 2005; Vandermeer & Perfecto 2005; Fischer *et al.* 2008; Phalan *et al.* 2011). As a result of this debate, studies focus almost exclusively on species diversity and food production, while ignoring other critical ecosystem processes affected by land use (Phalan *et al.* 2011; Tscharntke *et al.* 2012). The important role of land use in the mitigation of infectious diseases has been appreciated only recently (Allan *et al.* 2003; Millennium Ecosystem Assessment 2005; Wood *et al.* 2007). How land use strategies affect disease dynamics remains largely unknown, despite human modified habitats constituting roughly 75% of the all global land surfaces, and recent focused debate on land sparing versus sharing (Ellis *et al.* 2010; Fischer *et al.* 2011).

At large scales vector-borne disease dynamics, and in particular, malaria, have been observed to differ between natural and human-dominated ecosystems. In Peru, for example, feeding rates of the primary vector of human malaria, *Anopheles darlingi*, were nearly 300 times higher in deforested areas (Vittor *et al.* 2006), and models have been developed for predicting avian malaria based on regional environmental variables (Sehgal *et al.* 2011). Despite these findings, we lack an understanding of how

Figure 1 We gathered data on the relative abundance, habitat use, and blood parasite prevalence of Orange-billed Nightingale-Thrush (OBNT; *Catharus aurantiirostris*) from 18 study locations in Coto Brus, Costa Rica.

disease responds to land use at the scales relevant to small-scale, agricultural practices typical of the tropics and relevant to comparing land sharing and land sparing strategies (Ellis *et al.* 2010; Fischer *et al.* 2011).

Using a combination of field studies and theoretical modeling we quantify how tropical avian malaria in an abundant, sedentary bird species responds to tropical agricultural land use strategies. Our study has three overarching objectives: (1) to quantify how avian malaria varies across a tropical land sharing agricultural system; (2) to identify relationships between patterns of avian malaria and landscape features, spatial scales, and landscape habitat configurations; and (3) use results from the first and second objectives to simulate and compare how malaria prevalence changes under land sparing and land sharing land use strategies.

Methods

Field methods

To quantify how avian malaria varies across a tropical land sharing agricultural system we gathered data on the relative abundance, habitat use, and blood parasite prevalence of Orange-billed Nightingale-Thrush (OBNT; *Catharus aurantiirostris*; Figure 1) in 18 study locations situated in the premontane farming countryside of Coto Brus, Costa Rica. Study locations were separated with an average nearest neighbor distance greater than 1.2 km. The total area encompassing all study locations measured approximately 4,300 ha. Within the study area, locations were selected to span a gradient of human land uses, ranging from the Las Cruces Biological Reserve, which protects 262 ha of rainforest; intermediate habitats of forest fragments and secondary forest; to sun coffee plantations ranging in local tree cover from less than 5% to over 25%.

At each study location, bird sampling was conducted using constant-effort mist netting. Mist netting protocols consisted of twenty, 12 m × 2.5 m, ground-level mist nets in a 3–5 ha plot arbitrarily placed in a single habitat type at each study location. Constant effort mist-net sampling for birds took place between January 25 and May 12 for 8 years (2002–2009) at most study locations. OBNT were captured, banded with a unique leg band, blood was collected and stored in lysis buffer (Chasar *et al.* 2009), and birds were released on-site shortly after processing. At 12 of the 18 study locations from 2002—2006, some birds were selected to be fitted with small, temporary radio transponders. Birds captured in agricultural areas were slightly favored for radio telemetry for the purposes of another study (see Sekercioglu *et al.* 2007).

After radio transponder attachment, birds were released and allowed to adjust for 24 hours before being tracked and observed. Independent locations of birds were recorded in 30–120 minute intervals for several days until sufficient independent locations were recorded. For more detailed information on radio-telemetry methods and analyses refer to Sekercioglu *et al.* (2007) and Mendenhall *et al.* (2011).

Malaria prevalence

To determine the presence of *Plasmodium* in OBNT blood samples, DNA was extracted from avian whole blood using the Animal Tissue Wizard SV genomic purification kit (Promega Corporation, Madison WI, USA) and polymerase chain reaction (PCR) was used to determine if a sample was positive for blood parasites. To increase sequence length for analysis, two different PCRs were utilized, both amplifying sections of the mitochondrial cytochrome *b* gene as described in Chasar *et al.* (2009). All reactions contained positive and negative controls and were run on 1.8% agarose gels and stained with ethidium bromide.

Positive samples were sequenced on an ABI Prism 3100 Genetic Analyzer (Applied Biosystems, Carlsbad, CA, USA). These sequences were edited and aligned using Sequencher 4.8 (GeneCodes, Ann Arbor, MI, USA) and were classified to species by sequence similarity in GenBank using the NCBI BLAST search. Novel sequences of malaria lineages were deposited in GenBank and accession numbers are the following: OBNT1 (JN819327), OBNT17 (JN819337), OBNT23 (JN819350), OBNT14 (JN819352), OBNT15 (JN819354), and OBNT9 (JN819353).

Habitat mapping

To identify relationships between patterns of avian malaria and landscape features, spatial scales, and landscape habitat configurations we mapped the study area extensively. To overcome the difficulties of mapping fine-scale and complex configurations of habitat in a land sharing agricultural landscape, we digitized Costa Rica Airborne Research and Technology Applications (CARTA) orthorectified aerial photographs from 2003 to 2005 with 2-m resolution. The habitat map covered 12,400 ha and included all study locations. The habitat categories included: (1) "forest elements," or forest patches and treed remnants too small to be remotely sensed (e.g., primary and secondary forest fragments of all sizes, single trees, *charral* [early secondary forest], live fences, hedgerows, nonnative timber and fruit tree plantations, and nonnative garden ornamentals); (2) agricultural plots (the majority being sun coffee plantations, but also including banana, plantain, tomato, and chili plantations); (3) pasture; and (4) rural houses and infrastructure. Habitat digitization was conducted by the lead author and two assistants who worked closely to ensure accuracy and consistency. The final map was verified in the field from multiple vantage points, comparison with previous studies in the landscape, and comparison with 150 random samples across the landscape.

In addition to the habitat classification, existing models of river systems at a 5-m resolution (Centro Nacional de Investigación GeoAmbiental, Costa Rica) were also included because of their known effects on malaria distributions (Wood *et al.* 2007).

Data analysis

OBNT abundance and habitat use

Individual captures were used to approximate relative abundance of OBNT for each study location. OBNT are common birds that were selected for this study because they are frequent in forest and nonforest habitat types.

Home ranges of radio-tracked individuals were calculated using fixed kernel density estimates. Least-squared cross validation was used to calculate h-smoothing factors. Home range was considered the area that fell within the 99% utilization distribution.

Malaria prevalence modeling approach

To identify which landscape features affect malaria prevalence in OBNT we employed generalized linear models (GLM). Specifically, logistic regressions were used to model the prevalence as a function of landscape features and their interactions. We used stepwise model selection based on Akaike information criterion (AIC).

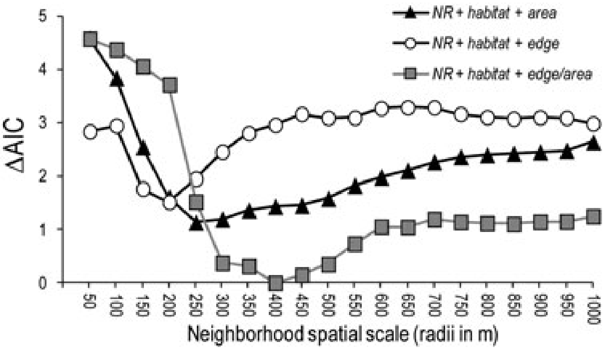

Figure 2 Model selection for malaria *A* prevalence predicted by forest element variables of *area*, *edge*, and *edge/area* calculated at multiple neighborhood spatial scales using concentric circles centered on the middle of each study location. ΔAIC values are the top three competing model structures that included: proximity to the nearest river (*NR*); habitat type as forest or non-forest (*habitat*); and the specified forest element variable and neighborhood spatial scale.

The landscape features used in our analysis included proximity to the nearest river (*NR*), habitat type as forest or nonforest (*habitat*), total area of forest elements at multiple neighborhood spatial scales (*area*), total sum of forest element edges at multiple neighborhood spatial scales (*edge*), and an additional index, also at multiple neighborhood spatial scales, of total forest element edge divided by total forest element area (*edge/area*). The *edge/area* index was included to capture both area and configuration because of its relevance when comparing land sparing and land sharing systems and because *area* and *edge* variables were collinear. Neighborhood spatial scales for forest element *area*, *edge*, and *edge/area* were calculated using concentric circles centered on the middle of each study location.

The *area*, *edge*, and *edge/area* forest element variables were iteratively calculated at each spatial scale from 50 to 1000 m radii from the center of study locations at increments of 50 m. Only one spatial scale of each variable was represented in any given model. Spatial scales were compared and selected based on AIC in stepwise model selection (Figure 2).

Variables were tested for collinearity and normality. Only variables that were independent from each other were used in model construction (e.g., *area*, *edge*, and *edge/area* were all collinear and were not considered in model selection). Modeling was conducted in R (R Development Core Team 2012).

Theoretical landscape simulation approach

After patterns of malaria and their relationship to the landscape were determined we conducted an analysis

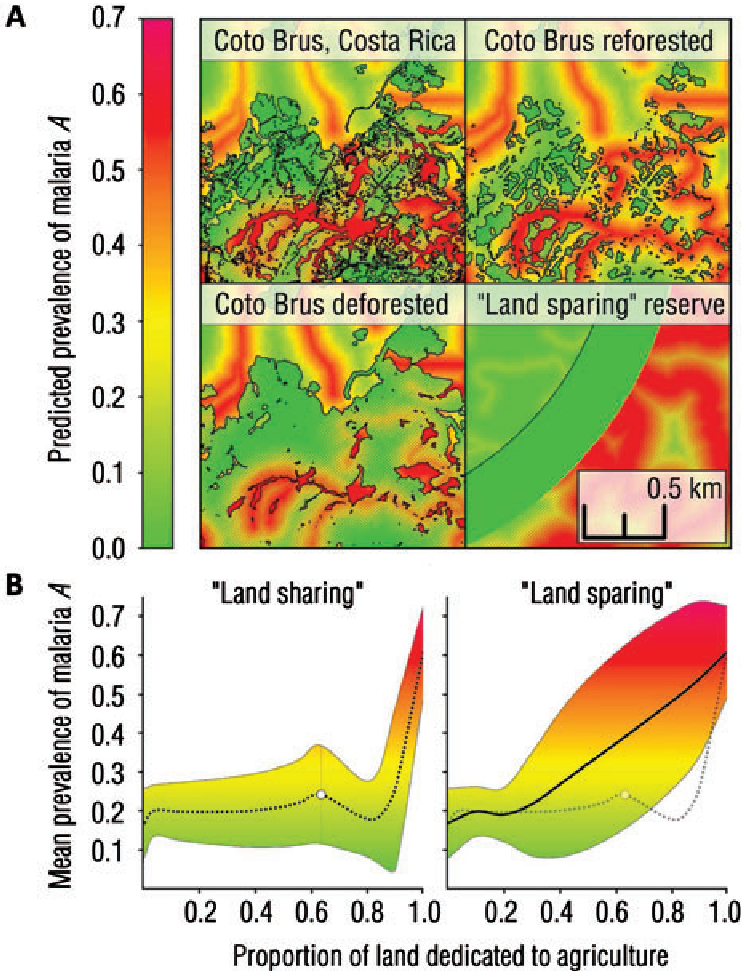

Figure 3 (A) Approximately 1 km^2 views of study area and land use simulations with predicted malaria *A* prevalence (non-forest habitats indicated by hashing). Land sharing simulations altered the proportion of land dedicated to agriculture by expanding or contracting the size of existing countryside forest elements. Land sparing simulations altered the proportion of land dedicated to agriculture by expanding or contracting a single, large forest reserve in the general location were the Las Cruces Forest Reserve is located. The land sparing reserve view shows the border of the single, large forest reserve and the non-forest habitat in which it is embedded.
(B) Predicted mean prevalence of malaria *A* (mean is middle line, solid for land sparing and dashed for land sparing, colored areas denote ± 1 SD) for the full extent of simulated landscapes. Open circle denotes unmodified Coto Brus, Costa Rica study area used to seed simulations. Both land sparing and land sharing end points (0 and 1.0 proportion dedicated to agriculture) are identical. Land sharing mean malaria *A* prevalence without SD, dashed line, is overlaid with land sparing for comparison.

Table 1 Statistical modeling of malaria *A* prevalence in OBNT predicted by landscape features

Variable	Parameter estimate	*Z*	*P*
(Intercept)	−1.7954 ± 0.5684	−3.158	0.002
NR	−0.0070 ± 0.0024	−2.907	0.004
habitat	0.9360 ± 0.4223	2.216	0.027
edge/area$_{400}$	0.0006 ± 0.0003	2.164	0.030

The results of generalized linear modeling of malaria *A* are shown; predicted proximity to the nearest river measured in meters (*NR*), habitat type classified as forest (1) or non-forest (0) (*habitat*), and the total forest edge/ total forest area within a 400 m radius measured in meters/ hectare (*edge/area*$_{400}$); using binomial errors and a logit link. Those predictors remaining after model optimization are shown with statistics describing their contribution to the final model.

to compare how malaria prevalence might change under land sparing and land sharing land use strategies. Land sparing and land sharing are difficult to compare because they often occur in different regions and biomes (Phalan *et al.* 2011). To resolve this difficulty, we employed theoretical landscape simulations of forest element extent and configuration in our study area. Because Coto Brus, Costa Rica has been referenced by the architects of the "land sparing versus land sharing debate" as a land sharing model landscape, we used our 12,400 ha habitat map of Coto Brus, Costa Rica as a configuration baseline from which to manipulate the extent of forest elements in a land sharing agricultural system (Green *et al.* 2005; Fischer *et al.* 2008). For a land sparing agricultural system's configuration we simulated a large, circular reserve embedded in a matrix of farmland (Figure 3A).

For land sparing and land sharing, we simulated changes in the extent of forest elements consistent with configurations of each land use strategy (Figure 3A). For example, the land sharing system's forest element extent was increased and decreased (i.e., reforested and deforested) by expanding and contracting existing Coto Brus, Costa Rica forest elements from their edges. Often isolated, small forest elements disappeared with deforestation simulations, but would merge with surrounding forest elements in reforestation simulations (Figure 3A). The forest element extent in the land sparing system was changed by adjusting the proportion of the single, continuous forest reserve relative to surrounding nonforest habitat.

Because areas of absolute agriculture and pasture were not observed in Coto Brus, Costa Rica and are likely rare in land sharing and land sparing tropical systems (e.g., no trees, live fences, or garden ornamentals within 400 m radius), simulated treeless areas were given observed values of forest element *area*, *edge*, and *edge/area* from intensely farmed areas from the 12,400 ha habitat map. Therefore, the minimum forest element *area* was limited to 2.5 ha (~5% of a 400 m radius circle), the maximum forest element *edge* was 12,500 m, and the maximum *edge/area* was calculated to be 5,000 m/ha. Forest element area gained by these minimum and maximum value replacements were not counted toward the total extent of forest elements in any simulation (i.e., proportion of land dedicated to agriculture).

All simulations were conducted using the unmodified river system models for Coto Brus, Costa Rica. Landscape simulations were conducted in ArcINFO 10.0 (ESRI 2011).

Results

OBNT relative abundance and habitat use

A total of 456 individual OBNT were captured between 2004 and 2009 at the 18 study locations. Because our focus was malaria, we did not conduct abundance modeling using capture-mark-recapture analysis methods to obtain better estimates of OBNT abundance. Rather, we coarsely estimated OBNT distributions by comparing total captures across study locations. For this comparison, we removed six study locations whose sampling only spanned from 2007 to 2009 and assumed that OBNT were detected identically in different habitat types. Of the remaining 352 OBNT individuals captured in the remaining eight forest study locations and four agricultural study locations there were no differences in OBNT abundances between forest elements and non-forest elements ($t_3 = 0.26$; $P = 0.81$) with approximately five individuals detected per site per year. Despite previous results that OBNT are dependent on the smallest forest elements in agricultural areas (see Mendenhall *et al.* 2011 and Mendenhall *et al.* 2012), we assumed that OBNT evenly blanketed the landscape for the purposes of our investigation in malaria prevalence and land use strategy.

We radio tracked a total of 68 individual OBNTs. We found birds to be sedentary with small home ranges (mean = 6.17 ha ± 0.98 SE) and to frequently use forest elements and agricultural areas. We found no evidence of home range size dependence on a given habitat type. There were no differences in home range sizes among birds whose home range included high (66–95%; $n = 7$), medium (33–66%; $n = 20$), and low (0–33%; $n = 41$) percentages of forest elements (ANOVA $F_{2,65} = 1.73$; $P = 0.19$). Based on radio-telemetry results we concluded that OBNT are sedentary birds with small home ranges that do not vary much with landscape context.

Malaria prevalence and relationship to landscape features

We determined the prevalence of avian malaria (*Plasmodium spp.*) from 260 individuals at 18 study locations. Twenty five percent of OBNTs were infected with malaria. Nearly 90% of infections were caused by *Plasmodium* grouped into a single lineage (GenBank accession number: OBNT1, JN819327). Focusing on this lineage to simply parasite and vector variability (hereafter malaria *A*), we found OBNT malaria prevalence to be explained by a GLM dependent on the following variables: (1) proximity to the *NR* measured in meters, (2) habitat type classified as forest or non-forest (*habitat*), and (3) the total forest edge/ total forest area within a 400 m radius measured in meters/hectare ($edge/area_{400}$; Table 1; Figure 2).

We found malaria *A* prevalence to increase with increased forest element edge and decreased forest element area ($edge/area_{400}$) both inside and outside of forest elements. We also found that increased proximity to rivers (*NR*) corresponded in increased malaria *A* prevalence in OBNT. Finally, forest elements hosted a higher prevalence of malaria than nonforest. The presence of forest elements on farmland intuitively decreased the prevalence of malaria *A* in surrounding nonforest habitats within 400 m. Consistent with our model, our field studies confirmed that the highest malaria *A* prevalence were observed in the smallest forest elements and most deforested agricultural plots. Forest elements metrics were also not correlated with proximity to rivers in our study locations, for example, a linear regression between *NR* and $edge/area_{400}$ was not significant ($R^2 = 0.06$; $P = 0.32$; $n = 18$).

Theoretical comparison of land sparing and land sharing

We extrapolated the GLM from Table 1 to the study area to estimate malaria *A* prevalence in Coto Brus, Costa Rica. We calculated the malaria *A* prevalence for the study area to be approximately 24% (± 0.13 SD) (open circle in Figure 3B).

Through our landscape simulations we estimate land sharing to mitigate malaria *A* prevalence better than land sparing (Figure 3B). We observed that deforestation increased malaria *A* prevalence dramatically with land sparing configurations because forest elements in land sharing systems play a critical role in reducing malaria *A* prevalence in surrounding, nonforest habitats. By measuring the prevalence of malaria *A* holistically (e.g., taking forest and nonforest habitats into account) land sparing configurations mitigate malaria *A* prevalence better than land sparing at nearly all agricultural extents.

Because there are nearly infinite possible configurations of a landscape's habitat elements, our simulation of avian malaria under land sharing deforestation and reforestation are expectedly differently shaped as we move away from the actual Coto Brus, Costa Rica landscape (i.e., the shape of the dashed line from to the left and right of the open circle in Figure 3B). Improvements that move beyond our simplified landscape simulations can be greatly improved by using existing landscape and ecosystem services modeling tools, such as Marxan and InVEST (Watts *et al.* 2009; Kareiva *et al.* 2011).

Discussion

Many previous studies have shown that disease dynamics, especially those mediated by animal vectors, are altered by deforestation and human land use (Allan *et al.* 2003; Vittor *et al.* 2006; Wood *et al.* 2007; Chasar *et al.* 2009). Our results show how fine-scale landscape features, namely the proportion and configurations of clusters of trees on farmland, influence tropical avian malaria prevalence in a human-dominated ecosystem. We recognize that our extrapolation of avian malaria to theoretical landscapes may be somewhat limited, especially at the furthest ends of our landscape simulations. Moreover, further study is required to better understand the mechanisms driving the observed patterns in our study system, but it is likely that fine-scale landscape features, such as forest elements on farmland, are influencing abiotic factors, such as sun and moisture, that affect vector habitat use and, therefore, disease dynamics (Wood *et al.* 2007; Yasuoka and Levins 2007; Knowles *et al.* 2011).

Despite limited knowledge of the vector dynamics and the theoretical assumptions that OBNT and malaria respond predictably at the extremes of our simulations (e.g., extensive deforested areas where OBNT may not persist), the patterns observed in our study are strengthened by a deep understanding of the common, yet sedentary avian host and the high resolution mapping of a land sharing agricultural system. Moreover, our use of wild birds to quantify disease dynamics, rather than humans, has the advantage of being an honest indicator that is not confounded by socioeconomic constraints that are often linked to human malaria prevalence patterns (Koram *et al.* 1995).

Because of the strong relationship between avian malaria prevalence and landscape features in our study we were able to use avian malaria prevalence as a case to test how an ecosystem process, in this case disease dynamics, is affected by human land use. By examining how avian malaria prevalence is affected by agricultural intensity (e.g., land sharing vs. land sparing configurations) and agricultural extent (e.g., the proportion of land dedicated to agriculture), we were able to compare how an ecosystem process varies in a realistic land sharing system (Vandermeer and Perfecto 2005) and an extreme land sparing system. We believe this kind of analysis to be the starting point for a better understanding how biodiversity, ecosystem services, agricultural yield, and human well-being intersect in increasingly human-dominated landscapes. The ongoing debate between land sparing and land sharing thus far has been unidimensional. Here we offer an example of how land use strategy is more than a balancing act between factors of food production and species diversity, but an opportunity to manage ecosystem processes, ecosystem services, natural capital, and human quality of life.

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