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A Small-Scale Land-Sparing Approach to Conserving Biological Diversity in Tropical Agricultural Landscapes

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Abstract: *Two contrasting strategies have been proposed for conserving biological diversity while meeting the increasing demand for agricultural products: land sparing and land sharing production systems. Land sparing involves increasing yield to reduce the amount of land needed for agriculture, whereas land-sharing agricultural practices incorporate elements of native ecosystems into the production system itself. Although the conservation value of these systems has been extensively debated, empirical studies are lacking. We compared bird communities in shade coffee, a widely practiced land-sharing system in which shade trees are maintained within the coffee plantation, with bird communities in a novel, small-scale, land-sparing coffee-production system (integrated open canopy or IOC coffee) in which farmers obtain higher yields under little or no shade while conserving an area of forest equal to the area under cultivation. Species richness and diversity of forest-dependent birds were higher in the IOC coffee farms than in the shade coffee farms, and community composition was more similar between IOC coffee and primary forest than between shade coffee and primary forest. Our study represents the first empirical comparison of well-defined land sparing and land sharing production systems. Because IOC coffee farms can be established by allowing forest to regenerate on degraded land, widespread adoption of this system could lead to substantial increases in forest cover and carbon sequestration without compromising agricultural yield or threatening the livelihoods of traditional small farmers. However, we studied small farms (<5 ha); thus, our results may not generalize to large-scale land-sharing systems. Furthermore, rather than concluding that land sparing is generally superior to land sharing, we suggest that the optimal approach depends on the crop, local climate, and existing land-use patterns.*

Keywords: agricultural intensification, agroforestry, integrated open canopy coffee, land sharing, land sparing, shade coffee

Un Método para Reservar Tierras a Pequeña Escala para Conservar la Biodiversidad en Paisajes Agrícolas Tropicales

Resumen: *Se han propuesto dos estrategias contrastantes para la conservación de la biodiversidad al mismo tiempo que se satisface la demanda creciente de productos agrícolas: sistemas de producción mediante la reservación de tierras o el uso múltiple de tierras. La reservación de tierras implica incrementar la productividad para reducir la cantidad de tierra requerida para la agricultura, mientras que las prácticas de uso múltiple de tierras incorporan elementos de ecosistemas nativos en el sistema de producción mismo. Aunque el valor de conservación de estos sistemas ha sido debatido extensivamente, hay escasez de estudios empíricos. Comparamos las comunidades de aves en café de sombra, un sistema de uso múltiple de tierras practicado ampliamente en el que se mantienen árboles de sombra dentro de la plantación de café, con las comunidades*

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de aves en un sistema de producción de café novedoso, a pequeña escala, en tierras reservadas (café de dosel abierto integrado o DAI) en el que los pequeño productor obtienen mayor producción bajo poca o ninguna sombra al mismo tiempo que conservan una superficie de bosque igual al área bajo cultivo. La riqueza y diversidad de especies de aves dependientes del bosque fueron mayores en las plantaciones de café DAI que en las de café de sombra, y la composición de la comunidad fue más similar entre el café DAI y el bosque primario que entre el café de sombra y el bosque primario. Nuestro estudio es la primera comparación empírica de sistemas de producción mediante la reservación de tierras y el uso múltiple de tierras bien definidos. Debido a que las parcelas de café DAI pueden ser establecidas permitiendo que los bosques en suelos degradados se regeneren, la adopción extensiva de este sistema podría llevar a incrementos sustanciales de la cobertura de bosques y del secuestro de carbono sin comprometer la producción agrícola ni amenazar la forma de vida tradicional de los pequeños productores. Sin embargo, estudiamos parcelas pequeñas (<5 ha); por lo tanto, pueden que nuestros resultados no sean generalizables a sistemas de reservación de tierras a mayor escala. Más aun, en vez de concluir que la reservación de tierras generalmente es superior al uso múltiple de tierras, sugerimos que la aproximación óptima depende del cultivo, el clima local y de los patrones de uso de suelo existentes.

Palabras Clave: agroforestería, café de dosel abierto integrado, café de sombra, intensificación agrícola, reservación de tierras, uso múltiple de tierras

Introduction

The importance of tropical agricultural landscapes to global conservation is widely appreciated due to the rapid conversion of natural ecosystems for agriculture and the limitations of protected areas for conserving biological diversity (Rodrigues et al. 2004; Foley et al. 2005). In Central America alone, more than1.2 million km^2 of land are used for agriculture, which represents over 50% of the total land area (FAO 2013). In contrast, protected areas comprise only 2.2% of this area, do not represent ecosystem diversity, and are not always compatible with local societal needs (WDPA 2006; Gaston et al. 2008; Agrawal & Redford 2009). The disparity between protected and unprotected land is especially important in tropical regions, which contain a disproportionately large share of Earth's biological diversity (Dirzo & Raven 2003).

Although the importance of tropical agricultural landscapes for conserving global biological diversity is widely recognized, conservationists disagree about the strategies required to achieve these goals (Green et al. 2005; Fischer et al. 2008). A fundamental disagreement hinges on the role of agricultural intensification (Tilman et al. 2002), and 2 contrasting approaches have been proposed. The first strategy, referred to as land sharing or wildlife-friendly farming (Green et al. 2005), involves integrating components of native ecosystems (e.g., shade trees) into the cultivation system. Support for this approach is based on research that indicates low-intensity agricultural systems with greater representation of components of native ecosystems, such as tree-dominated agroforestry systems, support more biological diversity than intensively cultivated agricultural systems (Perfecto et al. 2003; Philpott et al. 2008). The second approach, known as land sparing, involves maximizing yields to make other lands available for conservation (Balmford et al. 2005; Green et al. 2005). Supporters of this approach emphasize that protecting native ecosystems is a higher conservation priority than protecting elements of native habitats (Rappole et al. 2003; Phalan et al. 2011*b*).

Both land-sharing and land-sparing agricultural methods have been criticized on environmental, economic, and social grounds. Critics of land sharing note that such agricultural systems do not explicitly protect native habitats and can be economically prohibitive if yields are low and income is not compensated for by adequate premiums (O'Brien & Kinnaird 2003; Rappole et al. 2003). It has also been emphasized that more land must be cultivated to support low-yield, land-sharing agricultural practices relative to high-yielding methods (Evenson & Gollin 2003; Phalan et al. 2011*b*). Critics of the land-sparing approach argue that increasing yields does not ensure conservation of biological diversity and may stimulate further agriculture-driven deforestation (Chappell et al. 2009). Agricultural intensification is typically associated with increased inputs of chemical fertilizers and pesticides, which often contaminate local food chains and water supplies (Pimentel et al. 2005). Furthermore, the land-sparing approach is characterized as treating the needs of human and biological diversity conservation as inherently opposed and could encourage large monocultures at the expense of small farmers and their traditional livelihoods (Perfecto & Vandermeer 2010).

Coffee (*Coffea* spp.) production systems have been at the center of this research and debate. Coffee is the second largest legally traded commodity in Latin America, and coffee-production and processing methods can strongly affect local and regional environments via habitat loss, erosion, water pollution, and energy consumption (Arce et al. 2010). Traditionally, coffee was cultivated under a canopy of native trees, but as part of efforts to increase yield, many of these shade-coffee farms were converted to sun-coffee farms that structurally resemble other unshaded monocultures (Moguel & Toledo 1999).

Results of numerous studies show that species richness and composition of various taxa are more similar to native forest in shade coffee than in sun coffee (Greenberg et al. 1997; Perfecto et al. 2003; Philpott et al. 2008). Furthermore, survival can be high for some migratory bird species that use shade coffee (Johnson et al. 2006); thus, shade coffee is considered an example of an effective land-sharing farming system.

Although clearly preferable to sun coffee, there are important limitations to the conservation value of shade coffee (O'Brien & Kinnaird 2003; Rappole et al. 2003). Shade-coffee certification programs do not conserve native ecosystems, and price premiums for shade coffee can encourage deforestation (Rappole et al. 2003; Tejeda-Cruz et al. 2010). Although species richness can be similar between shade coffee and primary forest, community composition often differs, with generalist species being more prevalent than forest-dependent species (Tejeda-Cruz & Sutherland 2004). Furthermore, the degree to which forest-dependent species use shade coffee depends on landscape context, indicating that the presence of adjacent forest can exert stronger influence on community structure than local farm-level attributes such as tree density or structure (Batáry et al. 2011). Economic factors also constrain the utility of shade coffee because yield decreases as shade cover increases above 40%, the minimum allowed by some shade-coffee certification programs (Perfecto et al. 2005; Philpott et al. 2007), and high shade cover can increase disease prevalence in growing regions with limited sunlight and high precipitation (Beer et al. 1998; Avelino et al. 2006).

The debate over land sparing is nearly 10 years old, yet no empirical studies have compared the conservation value of well-defined land-sparing and land-sharing production systems. One reason for this is that few land-sparing systems have been identified that explicitly link increased yield with conservation. One such system, however, is integrated open canopy (i.e., IOC coffee). Integrated open canopy coffee requires farmers to conserve an area of forest equal to the area under cultivation and to not cut forest when establishing new farms (Arce et al. 2010). Although IOC coffee receives no formal recognition as a production system, variations of IOC coffee are being implemented throughout the coffee-growing world because forest adjacent to coffee plantations protects coffee plants from wind damage, contributes organic material, reduces erosion, and yields fuel wood. Integrated open canopy coffee farms can be small and thus managed by single families, so this system is not subject to the liabilities associated with large monocultures. Nonetheless, IOC coffee is clearly a land-sparing system in that it involves linking increased yields to the protection of native forest. Coffee yield can be 2–5 times higher in low-shade farms compared with heavily shaded farms (Soto-Pinto et al. 2000; Avelino et al. 2006; Arce et al. 2010); thus, an IOC farm of half coffee and half forest could yield 2.5 times as much coffee as a shade-coffee farm of the same total area. Furthermore, yield can be higher in coffee farms adjacent to forest than in isolated farms because many pollinators are forest dependent (Ricketts et al. 2004).

We hypothesized that protection of actual forest, rather than just elements of native forest (e.g., canopy trees), leads to higher species richness and diversity of forest-dependent bird species in small-scale land-sparing IOC coffee than in land-sharing shade coffee and that community composition is more similar between IOC coffee and native forest than between shade coffee and forest sites. We also assessed the degree to which Neotropical–Nearctic migratory birds used land-sparing IOC coffee because the high diversity of migratory birds in land-sharing farms has been used to justify environmental certification and marketing of shade coffee.

Methods

Study Area

The study area was approximately 50 km^2 located between 800 and 1600 m on the Pacific slope of the continental divide in the Cordillera de Tilarán, Costa Rica (N10°13′ W84°39′) (Fig. 1) within the Río Aranjuez watershed. The lower elevations of the study area contained fragments of premontane moist forest and were embedded in a mosaic of small coffee farms and cattle pastures. This agricultural landscape lies adjacent to the >28,000-ha Monteverde Reserve Complex (MRC), which includes the Monteverde Cloud Forest Preserve, the Children's Eternal Rainforest, and Alberto Manuel Brenes Biological Reserve. The forests above 1200 m are classified as upper montane wet forest. Mean annual temperature ranges from approximately 18 °C at high elevations (1500 m) to 24 °C at lower elevations (700 m).

Field Methods

We sampled birds in 8 replicates of shade coffee, IOC coffee, secondary forest, and primary forest sites November–March in 2006–2008. Shade-coffee sites were sampled if they had at least 40% shade cover and 10 species of native trees because these are the primary requirements of most certification schemes (Philpott et al. 2007). Under the classification system of Moguel and Toledo (1999), these farms would be considered commercial polyculture systems, which is the only commonly used shade-coffee system in Costa Rica (Somarriba et al. 2004). Rustic shade coffee farms with the original forest canopy partially intact are extremely rare in Costa Rica due to low yields. The coffee portion of the IOC sites had few or no shade trees and could have been classified as either unshaded monocultures or shaded

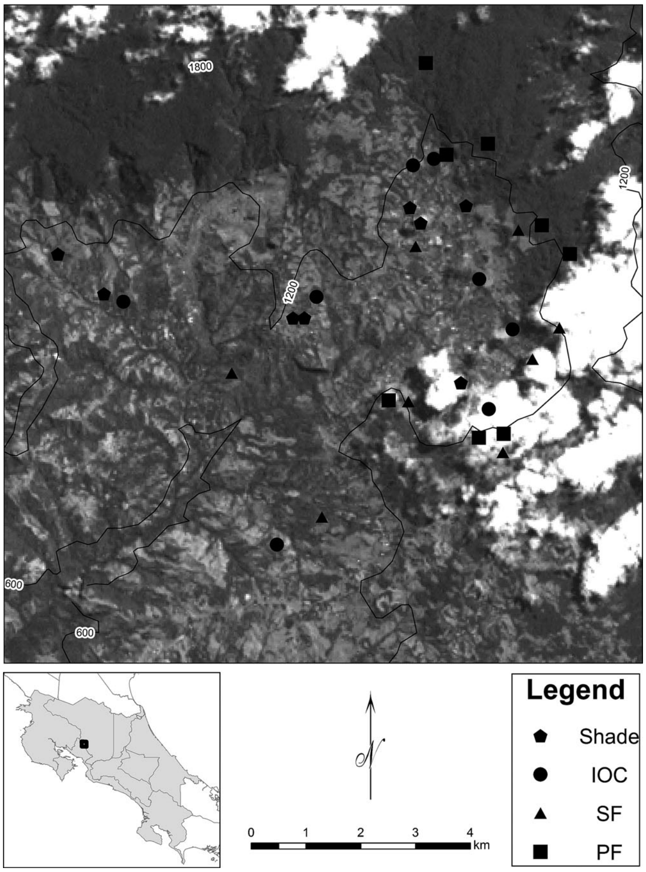

Figure 1. 2003 Landsat image of the study area in the Cordillera de Tilarán, Costa Rica (dark gray, forest; lighter areas, agriculture). The large forested area to the north and east is the Monteverde Reserve Complex. The 32 study sites are also shown (shade, shade coffee; IOC, integrated open canopy coffee; SF, secondary forest; PF, primary forest).

monocultures (Moguel & Toledo 1999). The forested portions of IOC sites consisted of 10- to 30-year-old stands formed from natural regeneration following pasture abandonment. Only farms that had approximately equal amounts of forest and cultivated land were included as IOC sites. Secondary forest consisted of 10- to 30-year-old stands formed from natural regeneration following pasture abandonment. Primary forest had never been cleared, although there was evidence of the removal of individual trees at some sites. Vegetation characteristics for the 4 farm and forest types are presented in Table 1. All sites were $\geq$0.5 km apart. Farms were small (1–3 ha under cultivation) and operated by individual families organized in a small cooperative, La Cooperativa Montes de Oro.

To sample bird communities, we established grids of 10 mist nets (12 × 2.5 m, 32- and 36-mm mesh) spaced 25 m apart in each site. Each of the 32 sites was surveyed once over the duration of the study. In IOC coffee farms, 5 nets were in the coffee portion of the farm and 5 were in the adjacent forest. Thus, the IOC sample unit included both the coffee and forest portion of the farm. We sampled for 7 h/d over 3 consecutive days at each site.

Statistical Analyses

We modeled variation in species richness, diversity, and similarity. We used a recently developed hierarchical model that allows for inference about community parameters by modeling the underlying patterns of occurrence or abundance of each species at each sample location (Dorazio & Royle 2005). We tested for differences in community parameters between the 2 coffee-production systems and the forest sites for 3 species groups: all species, forest-dependent species, and Nearctic migrants (see Supporting Information for species classifications). The model allows for direct estimation of capture probability, which is important because capture probability can be affected by variables such as species' traits, environmental conditions, or survey effort, and unmodeled heterogeneity in capture probability can bias estimators of species richness if ignored (Nichols et al. 1998).

A detailed description of the model is presented in Supporting Information. Here, we briefly describe the basic structure. The abundance $\left(N_{ij}\right)$ of species ***i*** at site ***j*** was regarded as a Poisson random variable with mean λ_{ij}, which we modeled as a log-linear function with an analysis-of-covariance structure. The main effect was the farm and forest type (i.e., IOC coffee, shade coffee, secondary forest, or primary forest), and the continuous covariate was the distance from the MRC. We included distance from the MRC because landscape-level patterns affect diversity in agroforestry systems (Batáry et al. 2011). The log-linear model for mean abundance was thus

$$\log\left(\lambda_{ij}\right) = \beta 0_i + \beta 1_i \times \mathrm{IOC}_j + \beta 2_i \times \mathrm{Shade}_j + \beta 3_i \times \mathrm{SF}_j + \beta 4_i \times \mathrm{DISTMRC}_j, \qquad (1)$$

where IOC, shade, and SF are dummy variables and DISTMRC is the distance from the MRC. Because we hypothesized that forest-dependent species respond differently to land-sparing and land-sharing production systems, we allowed β coefficients to be species specific and functions of the degree of forest dependence. Specifically, the β coefficients were modeled as $\beta_i \sim$ normal $(\mu_{\beta_g}, \sigma_\beta^2)$, where μ_{β_g} is the mean value of the coefficient for species in forest-dependence class g and σ_β^2 is the variance. The model for the effect of forest dependence was $\mu_{\beta_g} = \mu_{\beta_0} + \mu_{\beta_1} \times \mathrm{FORDEP}_g$, where FORDEP is an index of forest dependence that is based on intensive observations by Costa Rican naturalists (Stiles 1985). Recent work indicates that many more species require forest than is recognized by this classification (Ruiz-Gutiérrez et al. 2010). By estimating the parameter μ_{β_1} we were able to evaluate the validity of this system.

Table 1. Summary statistics of environmental, geographical, and survey effort variables for our study of land-sparing and land-sharing coffee production systems.

Variable	*Habitat*[a]	*Mean*	*SD*	*Minimum*	*Median*	*Maximum*
Elevation (m)	PF	1289	93	1120	1280	1401
	SF	1105	127	863	1151	1240
	Shade	1080	87	912	1080	1180
	IOC	1073	107	923	1076	1196
Distance from Monteverde Reserve Complex (m)	PF	1261	797	226	1129	2893
	SF	2145	1678	155	1867	4465
	Shade	2821	941	1680	2750	4263
	IOC	2512	1542	997	2126	5398
Total dbh[b] (cm)[c]	PF	857	391	566	712	1429
	SF	363	278	137	307	819
	Shade	319	313	169	332	422
	IOC	312	381	80	311	618
	IOC coffee	97	242	0	32	767
	IOC forest	678	353	160	633	1583
Mean dbh (cm)[c]	PF	17	3	14	17	20
	SF	10	6	7	9	18
	Shade	13	5	9	13	18
	IOC	13	5	8	12	19
	IOC coffee	11	4	6	11	18
	IOC forest	16	6	7	16	27
Trees[c]	PF	51	22	33	45	85
	SF	38	32	18	28	96
	Shade	24	14	19	24	30
	IOC	23	23	10	22	42
	IOC coffee	9	17	0	4	57
	IOC forest	44	18	9	45	91
Canopy height (m)[c]	PF	25	6	18	25	31
	SF	7	4	4	6	15
	Shade	7	11	4	7	11
	IOC	8	9	0	9	17
	IOC coffee	4	6	0	3	15
	IOC forest	18	9	8	16	35
Canopy cover (%)[c]	PF	93	11	80	94	100
	SF	79	29	43	88	96
	Shade	56	18	43	50	75
	IOC	49	43	38	45	73
	IOC coffee	14	34	0	5	70
	IOC forest	94	25	65	95	100
Net-hours	PF	1289	93	1120	1280	1401
	SF	1105	127	863	1151	1240
	Shade	1080	87	912	1080	1180
	IOC	1073	107	923	1076	1196

[a] *Abbreviations: PF, primary forest; SF, secondary forest; shade, shade coffee; IOC, integrated open canopy coffee; IOC coffee, coffee portion of IOC farm; IOC forest, forest portion of IOC farm.*
[b] *Diameter at breast height.*
[c] *Variables measured at each net are shown for the coffee nets and the forest nets in integrated open canopy coffee farms.*

To model capture probability, we used a classical capture-recapture model as the observation process in our hierarchical model. This part of the model describes the process by which the data arise, conditional on N_{ij}. The specific capture-recapture model we chose is known as a removal model because only new captures, not recaptures, on each consecutive sampling occasion are considered; thus, there is no need to estimate behavioral responses, such as bird net avoidance. To model capture probability $\left(p_{ijk}\right)$, we used the following logit-linear model in which the intercept was considered a random species-level effect. Additional effects were effort (net hours), wind velocity, and habitat,

$$\begin{aligned}\operatorname{logit}\left(p_{ijk}\right) &= \alpha 0_i + \alpha 1 \times \mathrm{NETHOURS}_{jk} + \alpha 2 \times \mathrm{Wind}_{jk} \\ &\quad + \alpha 3 \times \mathrm{IOC}_j + \alpha 4 \times \mathrm{Shade}_j + \alpha 5 \times \mathrm{SF}_j. \end{aligned} \tag{2}$$

After estimating abundance for each species, corrected for imperfect capture probability, we were able to compute posterior distributions of community parameters such as species richness, diversity (Shannon index), and similarity as simple derived quantities. We used 3 measures of community similarity to compare shade coffee, IOC coffee, and secondary forest with primary forest: number of shared species, number of unique species (i.e., those occurring in primary forest but not in the other habitats), and Chao–Jaccard similarity index, which accounts for differences in species-specific abundance.

We adopted a Bayesian method of analysis for computational reasons and because it allowed us to evaluate our hypotheses with direct probability statements. We regarded an effect as significant if the posterior probability of a difference was >0.95. Posterior distributions were simulated with Markov chain Monte Carlo (MCMC) implemented in JAGS (version 3.2–0) (Plummer 2011). We generated 4 Markov chains with 150,000 burn-in iterations and 150,000 subsequent posterior samples. We used vague uniform or normal priors for all model parameters. Additional details and code are in Supporting Information. The posterior probabilities (hereafter posterior p values) reported are the probability an effect was greater than zero according to the fitted hierarchical model. All point estimates are posterior means.

Results

Abundance

We captured 2298 individuals of 148 species during 6629 net-deployment hours (Supporting Information). Thirty-six of these species were forest-dependent species and 25 were Nearctic migrants (Supporting Information). The index of forest dependency was highly informative of how abundance varied among the farm and forest types. Generally, forest-dependent species were most abundant in primary forest, followed by secondary forest, then IOC coffee (land-sparing production system). Forest-dependent species were least abundant in shade coffee as demonstrated by the effect sizes of the μ_{β_1} parameters and the 95% confidence intervals that did not include zero (Supporting Information). Capture probability varied greatly among species, but in general increased with effort, decreased with wind velocity, and was highest in secondary forest (Supporting Information).

Species Richness and Diversity

For all species pooled, richness was 14.1% higher in IOC coffee than in shade coffee (posterior $p = 0.98$) (Fig. 2). Overall richness was 27.0% higher in IOC coffee than in secondary forest (posterior $p = 0.99$) and 54.3% higher than in primary forest (posterior $p > 0.99$). Species diversity was highest in secondary forest and did not differ between IOC coffee and shade coffee (posterior $p = 0.60$) (Supporting Information).

Consistent with our primary hypothesis, more forest-dependent species occurred in IOC coffee than in shade

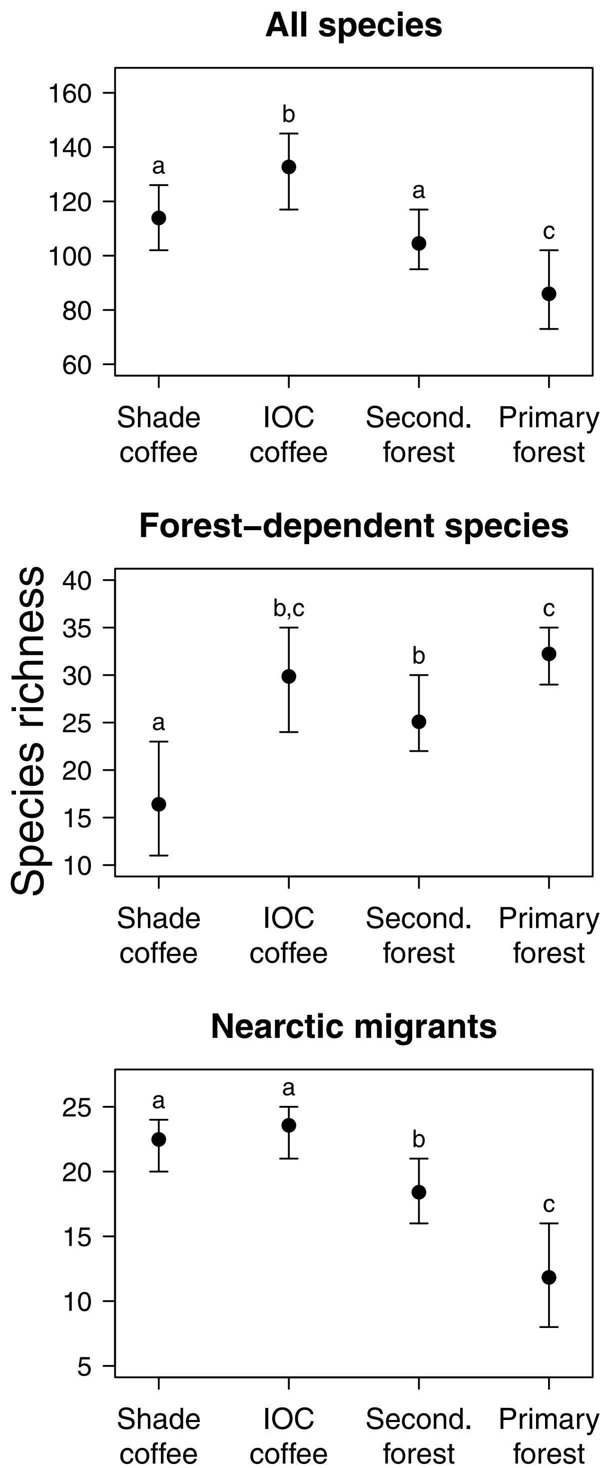

Figure 2. Species richness of all bird species, forest-dependent species, and Nearctic migrants in shade coffee (land sharing), integrated open-canopy coffee (IOC) (land sparing), and primary and secondary forest. Estimates are posterior means with 95% Bayesian credible intervals. Matching letters indicate no significant difference. Data are from mist-net captures of birds in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006–2008.

coffee. Specifically, 82% more forest-dependent species were found in IOC coffee than in shade coffee (posterior $p > 0.99$) (Fig. 2), and species diversity was 2.1 times higher in IOC coffee than in shade coffee (posterior $p > 0.99$) (Supporting Information). There was no significant difference in richness of forest-dependent species between IOC coffee and secondary forest (posterior $p = 0.89$) (Fig. 2); however, diversity was higher in secondary forest than in IOC coffee (posterior $p > 0.99$) (Supporting Information). Both richness and diversity of forest-dependent species were significantly higher in primary forest than in shade coffee or secondary forest (posterior $p > 0.99$) (Fig. 1 & Supporting Information). Diversity was also higher in primary forest than IOC coffee, but species richness did not differ (posterior $p = 0.70$).

Species richness of Nearctic migrants was not significantly different between shade coffee and IOC coffee (posterior $p = 0.66$), but was lower in secondary forest, and lowest in primary forest (posterior $p > 0.99$) (Fig. 2). Diversity of Nearctic migrants showed a similar pattern to richness, but diversity was significantly higher in shade coffee than in IOC coffee or shade coffee (posterior $p > 0.99$) (Supporting Information).

Species Composition

Community similarity was higher between IOC coffee and primary forest than between shade coffee and primary forest. This was evident in terms of the number of shared species (Fig. 3), the number of unique species (Fig. 4), and the Chao–Jaccard similarity index (Supporting Information). The IOC coffee and primary forest shared an estimated 77 species, whereas shade coffee and primary forest shared 62 species (23.8% difference, posterior $p > 0.99$) (Fig. 3). Similarly, an estimated 8 species were found in primary forest but not in IOC coffee, and 23 species occurred in primary forest but not in shade coffee (Fig. 4).

For forest-dependent species, the patterns in community similarity were much more pronounced than when all species were pooled. The number of forest-dependent species shared with primary forest was 75.3% higher in IOC coffee than in shade coffee (posterior $p > 0.99$) (Fig. 3). Integrated open canopy coffee was also more similar to primary forest in terms of the number of unique species than were either shade coffee or secondary forest (Fig. 4). For example, an estimated 17 forest-dependent species occurred in primary forest but not in shade coffee—more than 3 times higher than the number of species occurring in primary forest but not in IOC coffee (Fig. 4). The Chao–Jaccard index, which accounts for difference in abundance, revealed consistent patterns of similarity, although secondary forest was significantly more similar to primary forest than either coffee production system (Supporting Information).

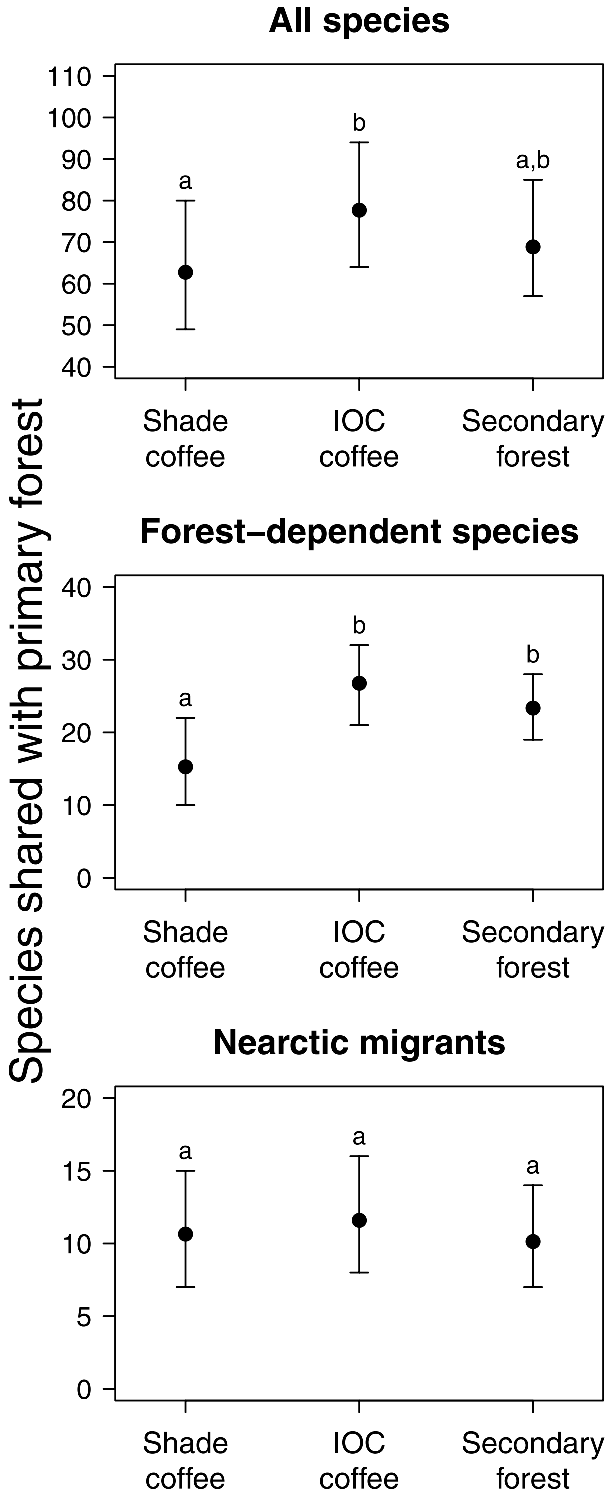

Figure 3. The number of species in shade coffee (land sharing), integrated open-canopy coffee (IOC) (land sparing), and secondary forest that also occurred in primary forest. Estimates are posterior means with 95% Bayesian credible intervals. Matching letters indicate no significant difference. Data are from mist-net captures of birds in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006–2008.

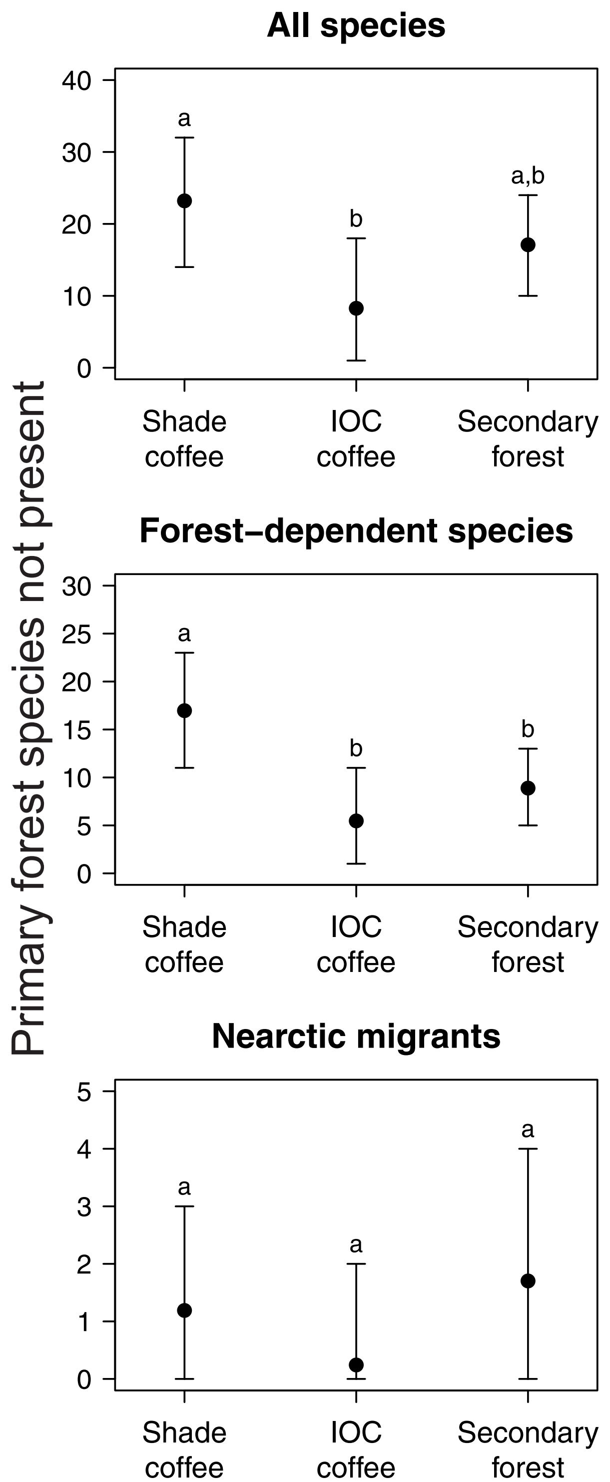

Figure 4. The number of species that occurred in primary forest but not in shade coffee (land sharing), integrated open-canopy coffee (IOC) (land sparing), or secondary forest. Lower values indicate higher similarity. Estimates are posterior means with 95% Bayesian credible intervals. Matching letters indicate no significant difference. Data are from mist-net captures of birds in 32 sites in the Cordillera de Tilarán, Costa Rica, 2006–2008.

For Nearctic migrants, few species occurred in primary forest, thus community similarity was generally very low when comparing primary forest to the other farm and forest types. Shared species (Fig. 3), unique species (Fig. 4), and the Chao–Jaccard similarity index did not differ significantly among shade coffee, IOC coffee, and secondary forest with respect to primary forest (Supporting Information).

Discussion

The debate over whether agricultural practices should be intensified to increase yield and spare land for conservation or whether low-intensity land-sharing practices should be favored has failed to produce coherent conservation strategies or recommendations for effective implementation of either approach. This can be attributed in part to a lack of empirical comparisons. We have presented and evaluated the first well-defined land-sparing system that could be institutionalized for conservation, and our results indicate this land-sparing production system, IOC coffee, has important advantages over an existing land-sharing production system, shade coffee. Nonetheless, we emphasize that land-sharing systems do not always involve trade-offs between agricultural yield and biological diversity (Clough et al. 2011), and the question of which approach is optimal depends largely on local conditions such as climate and existing land-use patterns. For example, in cases where shade coffee already exists, and no land is available for restoration, the best conservation strategy may be to support existing shade-coffee farmers.

A unique aspect of the land-sparing system we studied was that it was implemented by small farmers, which raises questions about the importance of scale in the land-sparing debate. For instance, some have argued that scale must be a component of the definition of land sparing and land sharing (Phalan et al. 2011*a*), with land sharing referring exclusively to large-scale production systems. Although we agree that scale is an important consideration, we believe that including scale in the definition unnecessarily complicates the debate. For instance, because all species perceive scale differently, it would necessitate the establishment of size thresholds across a range of species and taxa with a common affinity for native forest but differing in their area requirements. Thus, we argue that it is the mechanism by which yields are linked to conservation that is important, with land sparing being equated with systems that increase yield and explicitly conserve native ecosystems. This perspective is consistent with Green et al.'s (2005) idea that " . . . the best route to meeting both food production and conservation goals may be to increase yields on already converted land, thereby reducing the need to convert remaining intact habitats, and potentially freeing up former farmland for restoration to a more natural state." Integrated open canopy coffee is clearly a land-sparing system according to these definitions; however, the relatively small scale on which IOC coffee is practiced results in smaller forest patches and a more variegated landscapes, which, although valuable for many species, will differ fundamentally from larger land-sparing approaches.

Regardless of the semantics in the land-sparing debate, our results demonstrate that IOC coffee improves on alternative agroforestry systems from the standpoint of biological diversity conservation by accommodating forest-dependent bird species that are of high conservation concern and that do not use shade coffee. This is consistent with the results of other studies in which forest-dependent species are absent or uncommon in shade coffee (Tejeda-Cruz & Sutherland 2004) and other land-sharing production systems (King et al. 2006). Our finding that >80% more forest-dependent species occurred in IOC coffee than in shade coffee shows that IOC coffee is more effective at providing habitat for these threatened bird species. In addition, Nearctic migrants, whose occurrence in shade coffee has been used to justify its environmental certification, were abundant in IOC coffee even though the coffee-plantation portion of the farms had few or no shade trees. The value of this land-sparing system is further demonstrated by higher community similarity between IOC coffee and primary forest than between shade coffee and primary forest. As forest on IOC farms matures, the similarity between IOC coffee and primary forest is expected to increase, making our estimates of similarity between these 2 habitats conservative. Species composition in IOC coffee was more similar to secondary forest than was shade coffee, which is important because secondary forest patches can be important to maintaining biological diversity (Mendenhall et al. 2011). Unlike in previous studies, however, we present a market-based mechanism for protecting or regenerating secondary forest in agricultural landscapes.

One limitation of our study is that we were unable to directly compare IOC coffee with rustic shade-coffee systems, which are considered to have the highest conservation value among shade coffee systems (Moguel & Toledo 1999) and thus would have compared more favorably with primary forest than the commercial polycultures in our study. However, the lack of rustic farms in our study area is typical of coffee-growing regions (Philpott et al. 2007) because these farms, as depicted by Moguel and Toledo (1999), have very low yields. As a result, rustic coffee cultivation is not practiced at a scale large enough to affect a significant amount of bird habitat (Somarriba et al. 2004), and its inclusion in this study would not have been informative. Furthermore, the shade-coffee farms we worked in met many of the requirements of current certification programs (Philpott et al. 2007). An additional limitation of our study was that many of the shade coffee farms were adjacent to forest remnants; thus, some species captured in these farms probably would not have occurred there if the farms were truly isolated (Sekercioglu et al. 2007). However, if the shade coffee farms had been isolated, our estimates of forest bird abundance in shade coffee would have been even lower. Although our study was restricted to birds, multitaxa studies of agroforestry indicate that patterns of bird diversity among habitats are also reflected by other taxa (e.g., mammals, reptiles, and amphibians [King et al. 2006]).

Our results suggest that widespread adoption of IOC coffee could have a transformative effect in tropical agricultural landscapes by increasing forest cover while allowing for high agricultural yields. Widespread adoption of this land-sparing production system is possible because IOC coffee farms can be established by allowing forest to regenerate on degraded land. Degraded land is extremely common in the Neotropics, and restoration of this land would result in biological diversity conservation and carbon sequestration without any cost in terms of yield. Farmers that regenerate forest on degraded land could also benefit from carbon offset payments. Furthermore, the regenerating forest would offer economic benefits from wind protection, erosion control, increased organic material deposition, and habitat for pollinators. Additional economic incentives in the form of an environmental certification, such as is given to shade coffee, could also promote the establishment of IOC coffee and would ensure that protected forest remains protected. We therefore suggest that this simple land-sparing scheme offers tremendous potential for conserving biological diversity in tropical agricultural landscapes without compromising agricultural yield. The utility of this land-sparing system for other agricultural crops needs to be investigated to determine its applicability beyond coffee-growing regions of the Neotropics.

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Supporting Information

Capture data (Appendix S1), summarized posterior distributions (Appendix S2), species diversity results (Appendix S3), and community similarity results (Appendix S2) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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