

Optimizing carbon storage and biodiversity protection in tropical agricultural landscapes

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Abstract

With the rapidly expanding ecological footprint of agriculture, the design of farmed landscapes will play an increasingly important role for both carbon storage and biodiversity protection. Carbon and biodiversity can be enhanced by integrating natural habitats into agricultural lands, but a key question is whether benefits are maximized by including many small features throughout the landscape ('land-sharing' agriculture) or a few large contiguous blocks alongside intensive farmland ('land-sparing' agriculture). In this study, we are the first to integrate carbon storage alongside multi-taxa biodiversity assessments to compare land-sparing and land-sharing frameworks. We do so by sampling carbon stocks and biodiversity (birds and dung beetles) in landscapes containing agriculture and forest within the Colombian Chocó-Andes, a zone of high global conservation priority. We show that woodland fragments embedded within a matrix of cattle pasture hold less carbon per unit area than contiguous primary or advanced secondary forests (>15 years). Farmland sites also support less diverse bird and dung beetle communities than contiguous forests, even when farmland retains high levels of woodland habitat cover. Landscape simulations based on these data suggest that land-sparing strategies would be more beneficial for both carbon storage and biodiversity than land-sharing strategies across a range of production levels. Biodiversity benefits of land-sparing are predicted to be similar whether spared lands protect primary or advanced secondary forests, owing to the close similarity of bird and dung beetle communities between the two forest classes. Land-sparing schemes that encourage the protection and regeneration of natural forest blocks thus provide a synergy between carbon and biodiversity conservation, and represent a promising strategy for reducing the negative impacts of agriculture on tropical ecosystems. However, further studies examining a wider range of ecosystem services will be necessary to fully understand the links between land-allocation strategies and long-term ecosystem service provision.

Keywords: agroecosystems, birds, carbon sequestration, cloud forest, dung beetles, land-sharing, land-sparing, Tropical Andes

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Introduction

Agricultural land management is a vital component of global biodiversity preservation (Tilman *et al.*, 2002; Tschardt *et al.*, 2005; Sayer *et al.*, 2013) and plays an important role in climate change mitigation (Smith *et al.*, 2000; Knoke *et al.*, 2012). In tropical agriculture, biodiversity and carbon storage are both linked to the retention of woodland habitats within the landscape (Albrecht & Kandji, 2003; Stavi & Lal, 2013). While the importance of within-farm woodlands for biodiversity is well established (Hughes *et al.*, 2002; Daily *et al.*,

2003; Ranganathan *et al.*, 2008), levels of carbon sequestration in agricultural woodlands have received little study (Wade *et al.*, 2010). Consequently, it is unclear whether carbon and biodiversity values can be jointly optimized in agricultural landscapes through appropriately tailored land-management strategies.

Most work on carbon sequestration in tropical agriculture relates to agroforestry practices (e.g. Albrecht & Kandji, 2003; Bhagwat *et al.*, 2008; Stavi & Lal, 2013), whereas biodiversity conservationists typically focus on the value of un-managed woodland fragments that are often ubiquitous in tropical landscapes (Ricketts *et al.*, 2001; Hughes *et al.*, 2002; Daily *et al.*, 2003; Bhagwat *et al.*, 2008). As unmanaged woodlands require comparatively minimal investment on the part

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of farmers, policies promoting their retention or enhancement can offer a low-cost pathway to delivering carbon benefits alongside biodiversity (Sayer *et al.*, 2013). A key question concerns how these woodland habitats are best integrated into tropical farmland (Balmford *et al.*, 2005; Green *et al.*, 2005). Is it better to have many fine-grain habitat features throughout the landscape, or coarser blocks of contiguous forest? The extremes of this continuum are often referred to as 'land-sharing' and 'land-sparing' strategies (Green *et al.*, 2005; Fischer *et al.*, 2008). Land-sparing promotes the intensification of agriculture, allowing blocks of land to be spared for nature, while land-sharing promotes the integration of wildlife-friendly habitat features throughout farmland, typically via reductions in production intensity. Although these alternatives have received considerable interest among biodiversity conservationists (Edwards *et al.*, 2010a; Phalan *et al.*, 2011; Hulme *et al.*, 2013), the potential for synergies between biodiversity protection and carbon storage under either strategy remains untested.

Tree biomass, a primary component of tropical carbon sinks, can be sensitive to forest fragmentation and edge effects (Laurance *et al.*, 1998; Mesquita *et al.*, 1999; Laurance *et al.*, 2000). Carbon storage might therefore be maximized by maintaining larger contiguous habitat blocks (land-sparing) rather than smaller and more fragmented woodland features (land-sharing). Similarly, forest biodiversity is sensitive to fragmentation and edge effects (Klein, 1989; Sekercioglu *et al.*, 2002) and may also benefit from land-sparing strategies more than land-sharing in the tropics (Edwards *et al.*, 2010a; Phalan *et al.*, 2011; Hulme *et al.*, 2013). Conversely, land-sharing strategies can provide significant benefits for disturbance-tolerant species (Phalan *et al.*, 2011), as well as enhanced provision of ecosystem services such as pollination and soil protection (Perfecto & Vandermeer, 2010; Melo *et al.*, 2013). One issue that has not been addressed in previous comparisons is the nature of habitats protected under land-sparing allocations. Alongside intensive agriculture, spared lands could be designated to protect primary habitats, or alternatively to protect degraded lands that are allowed to naturally regenerate (Chazdon *et al.*, 2009; Phalan *et al.*, 2011). The latter strategy could provide important benefits for carbon stock enhancement in heavily degraded areas, a possibility that is often overlooked in discussions of climate mitigation in favour of a focus on avoided deforestation (Edwards *et al.*, 2010b). To our knowledge, the implications of these alternatives have not been compared for biodiversity or carbon.

Here, we report on surveys of carbon storage and biodiversity (birds and dung beetles) in agricultural

and forest landscapes of the Chocó-Andes, Colombia. This region straddles two biodiversity hotspots that support endemic-rich biological communities of major global importance (Myers *et al.*, 2000; Brooks *et al.*, 2002). Our samples span a broad continuum of woodland habitat integration within farmland, together with control sites in contiguous primary and secondary forests. First, we test whether carbon storage differs between plots in contiguous forests and those in woodland habitats embedded within pastoral farmland. Next, we model the occupancy dynamics of bird and dung beetle communities in farmland, examining how species occurrence varies in relation to the proportionate cover of woodland habitats within farmland. We use models derived from our datasets to predict whether land-sharing and land-sparing management strategies differ in the delivery of carbon and biodiversity cobenefits, considering a range of possible production levels. Finally, we test whether the potential benefits of land-sparing vary depending on whether primary or naturally regenerating forests are protected via spared land designations.

Materials and methods

Study area

We sampled three areas in the departments of Antioquia, Risaralda and Chocó, Colombia, spanning an altitudinal range of 1290–2680 m above sea level (Fig. S1, Table S1). We selected sites spanning the frontier between agricultural development and remaining contiguous forests, with all sites located adjacent to large forest tracts (>1 000 000 ha; Fig. S1). Cattle farming is the primary agricultural practice in the region, accounting for >90% of farmed lands at each site (Table S1). Other land-uses included small areas of maize and orchards of tamarillo *Solanum betaceum* (<10 ha total). Each site included both primary and secondary forests. Secondary forests spanned an approximate age range of 6–30 years (determined from interviews with reserve managers, plus local residents). We restricted our secondary forest samples to advanced stands (>15 years) in all analyses. All sampled secondary forests had some degree of connectivity to primary forest (Fig. S1).

Carbon sampling

We measured nonsoil carbon stocks at sampling points across the main habitat types (primary forest, advanced secondary forest and farmland) arrayed within randomly located 400 × 400 m squares (Fig. S1). We placed sampling points at 100 m intervals within squares, with up to five points in each square (fewer in cases where squares incorporated nonsampled habitats such as young secondary forests). As farmland sampling points seldom fell directly within woodland fragments, we placed an additional 34 nonrandom points inside woodland fragments surrounded by pasture (fragment size

range 0.1–27 ha), which we henceforth refer to as ‘woodland fragments.’ Finally, we also placed 16 points within the edges of contiguous primary forest (<30 m from agricultural boundary) to evaluate edge effects on carbon storage.

At each sampling point, we established a 15 × 5 m plot, within which we sampled living and nonliving carbon pools. We used a large number of relatively small plots ($n = 222$ in total, see Table S1 for breakdown by habitat) to better capture the small-scale heterogeneity in land-use history and topography typical of the Tropical Andes (Sierra *et al.*, 2007). To determine living tree biomass, we measured the diameter at breast height (dbh) of all trees >5 cm dbh and measured wood-specific gravity using tree cores extracted with an increment borer (two threads, 5.15 mm diameter; Haglöf, Sweden). We used these values in four allometric biomass estimation equations taken from harvested tree studies: Chave ‘Type II wet forest’ (Chave *et al.*, 2005), Feldpausch ‘Western Amazonia’ and Feldpausch ‘Pantropical’ (both from Feldpausch *et al.*, 2012), and Alvarez ‘Lower montane wet forest model I.3’ (Alvarez *et al.*, 2012). We took the mean of the four estimates as the final aboveground estimate for each tree. We then estimated root biomass using a published upland forest root/shoot ratio of 0.26 (Cairns *et al.*, 1997) and estimated vine biomass using an equation developed in Colombian montane forest (all vines >2 cm diameter, Sierra *et al.*, 2007).

For the nonliving carbon pool, we estimated biomass for all standing or fallen dead trees >5 cm dbh, applying a deadwood density of 0.31 g cm⁻³ taken from the literature (Gibbon *et al.*, 2010). We then exhaustively sampled the leaf litter layer from four 0.25 m² quadrats within each plot. We weighed these samples to the nearest 0.1 g and then used the fresh/dry weight ratio of an oven-dried subsample (10–20%) to estimate the dry biomass of litter (Nascimento & Laurance, 2002). We summed the biomass pools for each plot before multiplying by 0.5 to give an estimate of the total nonsoil carbon stock (Gibbon *et al.*, 2010).

Biodiversity sampling

We sampled bird and dung beetle communities within 400 × 400 m squares located across each of the main habitat types, overlapping directly with carbon sampling plots (Fig. S1; Table S1). For birds, we visited up to three points within each square (fewer when squares incorporated some nonsampled habitats), each spaced 200 m apart (146 points in total; Table S1). We conducted four point counts of 10-min duration at each point (06:00 to 12:00), avoiding conditions of rain or high winds (>10 mph). Every day, experienced surveyors (J. J. G. and D. P. E.) walked different routes between points to ensure that each location was visited both early and late in the sampling window. We recorded unknown vocalizations using Sennheiser ME66 microphones and Olympus LS11 recording devices, allowing subsequent identification using online reference material (www.xeno-canto.org). As we were interested in modelling community responses to local habitat features, we excluded records of highly mobile or transient species whose occurrence may be independent of the specific features of each site (e.g. large raptors, swifts and nonbreeding

trans-continental migrants). We restricted our analyses to detections within an estimated 100 m radius and assumed that each sampling point sampled the bird community effectively within that radius.

We sampled dung beetles in a subset of squares (Table S1), placing baited pitfall traps at up to five locations within each square, spaced 100 m apart (145 traps in total; Table S1). We baited traps with human dung, which attracts virtually all dung-feeding species (Davis *et al.*, 2001). Each trap was collected at 24-h interval across 4 days, with baits replaced after 2 days. We assumed traps were effectively sampling an area of 50 m surrounding each point (Davis *et al.*, 2001). Species determinations were made by F. Edwards, C. A. Medina, A. González and J. S. Cardenas using the reference collection housed at Instituto Alexander von Humboldt, Colombia.

Habitat variables

To assess whether the occurrence of species in farmland was influenced by levels of woodland fragment cover, we mapped the distribution of habitats via site walkovers in a 100-m radius around each biodiversity sampling point (following Phalan *et al.*, 2011), delimiting all grazed pasture and woodland fragments, as well as other nongrazed habitats (e.g. roads, buildings). We digitized these maps and used them to calculate the proportionate cover of woodland surrounding each point, applying a radius appropriate for the estimated area sampled around each point for each group: 100 m for birds and 50 m for dung beetles. To control for potential landscape-scale effects on species occupancy, we also estimated the distance of each farmland sampling point to the nearest contiguous forest edge. We did this using a ground-truthed map based on ALOS/PALSAR pantropical cloud-free forest cover data (Shimada *et al.*, 2010), combining the remote-sensed data with visual mapping and handheld GPS records to create an ArcMap layer delimiting contiguous forest across each site (i.e. including primary and secondary forests but excluding isolated fragments; Fig. S1).

Statistical analysis

Carbon stock variation across habitats. We assessed differences in each carbon pool across wooded habitat types (primary forest, primary forest edge, advanced secondary forest and woodland fragments) using analyses of covariance (ANCOVA), controlling for altitudinal variation as a model covariate. We log transformed all response variables prior to analysis and used Shapiro–Wilk tests to check normality. We also performed pairwise comparisons between each habitat class using Tukey’s honestly significant difference (HSD). In addition to comparing plot-level carbon stocks, we estimated carbon at the wider landscape-scale by extrapolating estimates across the 100 m radius surrounding each sampling point. In farmland, we assigned mean carbon values for each habitat across the mapped 100 m radius circle, before summing the total estimated carbon stock. For forest points, we extrapolated

the measured carbon stock value from each plot to a surrounding 100 m radius.

Biodiversity analyses. We calculated observed alpha diversity (number of species detected) for both taxonomic groups at each sampling point and estimated within-habitat turnover in species composition (beta diversity) using Chao-Jaccard similarity indices (Chao *et al.*, 2005). For each point, we computed pairwise comparisons against all other points within the same habitat category (primary forest, secondary forest and farmland), taking the mean values as a point-level index of within-habitat beta diversity. To evaluate community similarity across the three habitat classes, we also used nonmetric multidimensional scaling ordinations (NMDS) of the presence/absence data, which make no prior assumptions about habitat-level structuring in the data. All community analyses were performed using Program Estimate S (Version 9, <http://purl.oclc.org/estimates>).

Predicting community responses to alternative land-use strategies requires knowledge of species-level responses to variation in habitat availability within farmland (Phalan *et al.*, 2011). To evaluate this, we modelled variation in species occurrence probabilities across our sampling points using a Bayesian community-level hierarchical formulation (Dorazio & Royle, 2005; Dorazio *et al.*, 2006; Zipkin *et al.*, 2009). This approach allows species-level variation in detection probability to be explicitly modelled by conditioning on the number of times a species is detected over repeated sampling visits to each site (MacKenzie *et al.*, 2002). We modelled occurrence probabilities ψ for each species i at each sampling site j as a linear function of site-specific habitat variables, via a logit link:

$$\text{Logit}(\psi_{i,j}) = \alpha_{i,s} + \beta_1 \cdot D_j + \beta_2 \cdot D_j^2 + \beta_3 \cdot W_j + \beta_4 \cdot W_j^2 + \beta_5 \cdot P_j + \beta_6 \cdot S_j + \beta_7 \cdot A_j \quad (1)$$

where a is a random intercept accounting for unexplained species- and site-level variation (over-dispersion), β_1 to β_7 are parameter coefficients, D is the distance to nearest contiguous forest, W is the proportionate cover of woodland habitat surrounding farmland sites, P and S are binary indicators of whether the point is within primary or secondary forest, and A is altitude. We included both linear and quadratic terms for forest distance and woodland habitat cover to account for potential nonlinearity in species occupancy relationships. We centred and standardized all continuous predictor variables prior to analysis, ensuring that parameter estimates gave robust measures of the relative effect of each on occurrence probability (Schielzeth, 2010).

We incorporated community-level hierarchical structuring by specifying each parameter as a random draw from hyperparameter distributions representing the full spectrum of variability across the community (Gelman & Hill, 2007). We assigned diffuse uniform (0, 1) priors for hyperparameter means and inverse-gamma (0.1, 10) priors for variances and fitted the model in a Bayesian framework in WinBUGS version 1.4 (Spiegelhalter *et al.*, 2003). To minimize model uncertainty, we excluded species detected at fewer than three sampling

points from this analysis (88 bird species), leaving a total community of 243 bird species (all 28 dung beetle species were included).

Simulating land-allocation scenarios. To compare land-sharing and land-sparing strategies, we used our data-derived models to predict carbon stocks and species occurrence probabilities across simulated hypothetical landscapes. For robust comparisons, food production must be equal under both land-sparing and land-sharing scenarios, requiring two assumptions: (1) that cattle production per unit area is constant within our study areas and (2) that woodland fragments within farmland make zero contribution to yield. We therefore assumed that total food production is always equal in landscapes with the same proportionate cover of grazed pasture, regardless of the composition and distribution of habitats in the remaining portion.

In each simulation, we specified a fixed proportion of the landscape as grazed pasture, with the remainder either covered by woodland habitats present throughout the farm landscape (land-sharing) or a single block of contiguous forest (land-sparing). We considered two land-sparing scenarios: one in which the spared area is contiguous primary forest (henceforth 'primary-sparing'), and another in which the spared area is advanced secondary forest (henceforth 'secondary-sparing'). We simulated a range of production levels for each scenario, corresponding with observed variation in proportionate pasture cover across our sampling sites (from 20% to 80% grazed in increments of 10).

We constructed each landscape by combining 30 individual sites, assigning each a set of scenario-specific habitat values that were used to predict species occupancy and carbon stocks (see Appendix S1 for full details). We simulated 1000 replicate landscapes for each scenario; in each case, generating species occurrence probabilities by applying fitted versions of Eqn (1) to each simulated site, accounting for uncertainty by making random draws from the posterior distributions of each model parameter (i.e. β values). We used the mean landscape-wide occurrence probability to assess how each species responds to each land-allocation strategy, relative to an 'intact' landscape consisting entirely of primary forest. The optimal land allocation scenario for a given species is the one that maximizes mean occurrence probability. We generated carbon stock values by making random draws for each site from normal distributions representing each habitat type, with means and standard deviations derived from our data. We then summed these values across all 30 sites to generate a predicted carbon stock for each hypothetical landscape.

Results

Carbon stocks in forest and farmland

Woodland fragments in farmland held significantly less carbon per unit area than primary forest plots, both in the living plant material pool (Fig. 1a; HSD = 0.205, $P = 0.047$) and the dead plant material pool (Fig. 1b; HSD = 0.206, $P = 0.004$). Secondary forests and primary

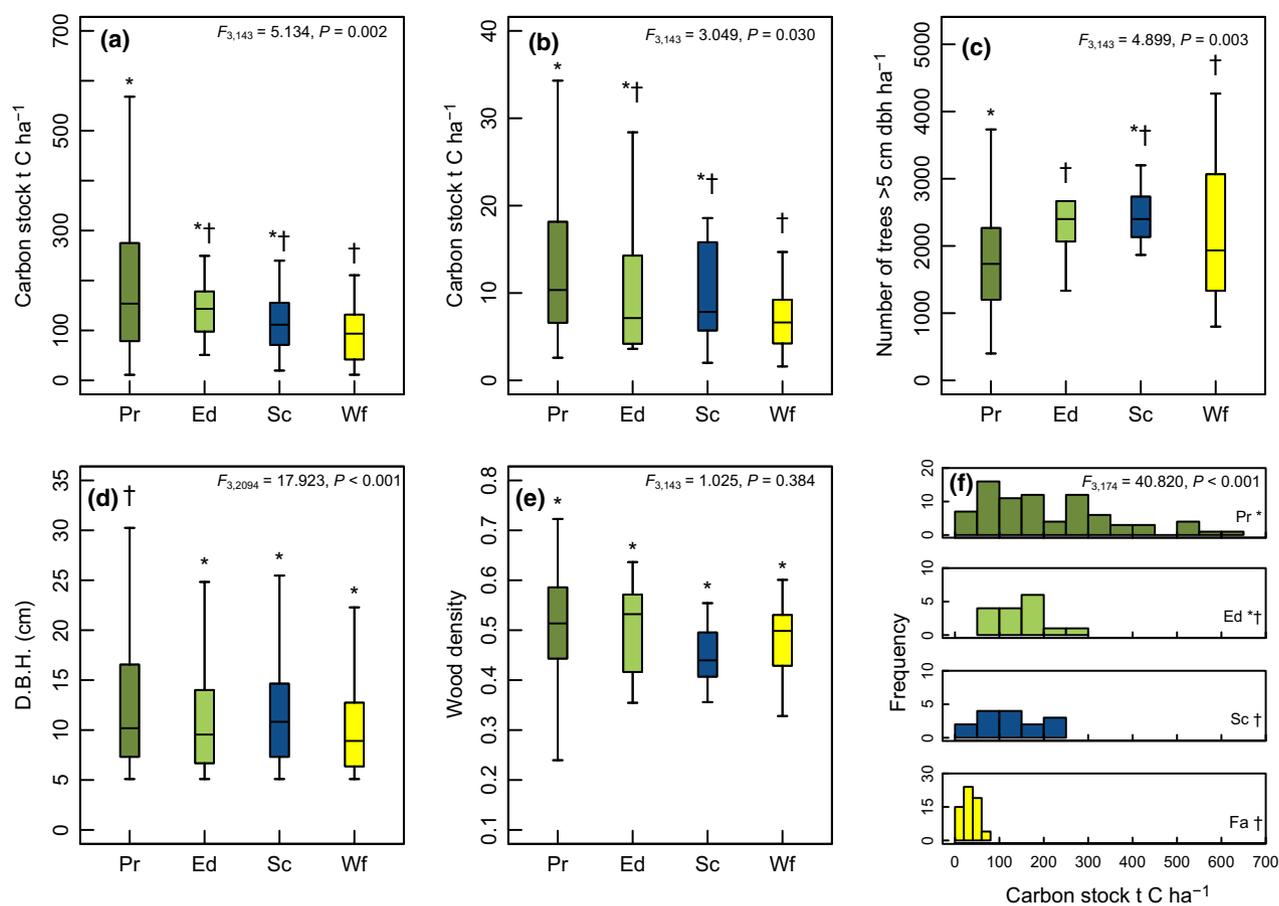


Fig. 1 Carbon stock characteristics of plots sampled in primary forest ('Pr'), primary forest edges ('Ed'), advanced secondary forests (15–30 years old, 'Sc') and woodland fragments within agricultural land ('Wf'). Box whisker plots show medians, interquartiles and 95% ranges for samples from each habitat, including living (a) and dead (b) plant material pools, densities of trees >5 cm dbh (c), tree size (d) and wood-specific gravity (e). Panel (f) shows frequency plots of total carbon stocks for landscapes surrounding sampling points in each forest habitat, together with farmland ('Fa'), estimated via extrapolation according to habitat coverage mapped across 100 m radii. In all panels, habitats with shared symbols do not differ significantly (Tukey's HSD, $P > 0.05$). Results of cross-habitat ANCOVA tests are reported in each case.

forest edge plots were intermediate between woodland fragments and primary forests (Fig. 1a and b). Primary forests held fewer, but larger trees per unit area than other habitats (Fig. 1c and d). Wood-specific gravity did not differ significantly across habitats (Fig. 1e). Summing all carbon pools, total stocks in woodland fragments were significantly lower than primary forest (HSD = 0.229, $P = 0.007$), although differences relative to forest edge and secondary forest plots were not significant (HSD $P > 0.05$ in each case).

At the landscape scale, estimated carbon stocks within farmland habitat were much smaller than all forest habitats (mean = 32.7 t ha⁻¹; Fig. 1f). Primary forests had the highest landscape-scale estimates of carbon stock (mean = 207.7 t ha⁻¹; Fig. 1f), with primary forest edge and secondary forest estimates being lower on average (means = 150.8 and 127.0 t ha⁻¹,

respectively; Fig. 1f). Pasture itself contributed relatively little to agricultural carbon stocks (mean = 12.0 t ha⁻¹), which were closely related to the proportionate cover of woodland fragments in the landscape (Pearson $R^2 = 0.86$).

Congruence of carbon stocks and biodiversity in agriculture

For both taxonomic groups, alpha and beta diversity peaked in primary and secondary forests, mirroring patterns of landscape-scale carbon storage (Fig. 2a and b). Within farmland, occurrence probabilities for most species were positively related to the proportionate cover of woodland habitats (Table S2 & S3). There was a significant positive correlation between bird alpha diversity in farmland and landscape-scale

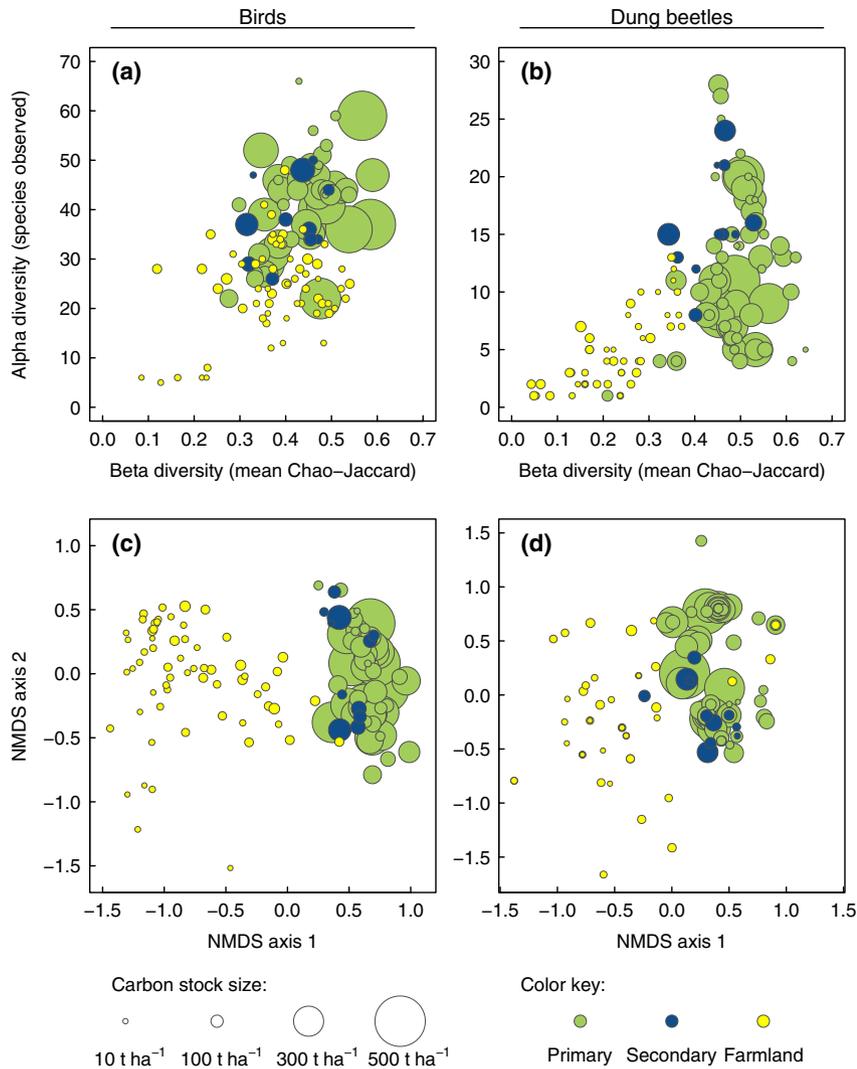


Fig. 2 Community characteristics of birds and dung beetles across primary forest, advanced secondary forest and pastoral agriculture. In each panel, points represent individual sampling locations, scaled to represent carbon stocks within a 100 m radius surrounding each point. The number of species observed at each point (alpha diversity), and pointwise contributions to within-habitat beta diversity (measured as the mean Chao-Jaccard similarity for all pairwise comparisons within a habitat class) are shown for birds (a) and dung beetles (b). Ordination plots show nonmetric multidimensional scaling analyses (NMDS) indicating the similarity of bird (c) and dung beetle (d) communities at each point.

carbon levels (Fig. S2a), but not dung beetle alpha diversity (Fig. S2b). Within-habitat beta diversity was uncorrelated with carbon levels in farmland for birds (Fig. S2c) and negatively correlated for dung beetles (Fig. S2d).

Ordination plots showed that communities of both taxonomic groups in farmland differed markedly from those of secondary and primary forests (Fig. 2c and d). Farmland sites with higher woodland habitat cover tended to be more similar to forests, leading to a significant correlation between the first NMDS axis and landscape-scale carbon levels (birds, Fig. S2e, dung beetles Fig. S2f). The second NMDS axis was uncorrelated with carbon levels for both taxonomic groups (birds, Fig.

S2e, dung beetles Fig. S2f), correlating more closely with altitude (birds: $R^2 = 0.632$, $P < 0.001$; dung beetles: $R^2 = 0.217$, $P = 0.007$).

Optimal land-allocation strategies

Mean predicted carbon stores per hectare were highest in the primary-sparing scenario, and lowest in the land-sharing scenario, while the secondary-sparing scenario was intermediate (Fig. 3). These differences were broadly consistent across all food production levels (Fig. 3). On average, carbon stocks in primary-sparing scenarios were 78% higher than those in land-sharing

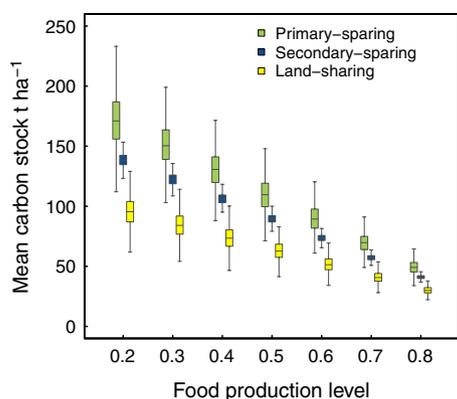


Fig. 3 Predicted mean carbon stocks across hypothetical land-sharing and land-sparing scenarios. Food production levels equate to the proportion of the landscape that is covered by grazing pasture. Land-sharing scenarios involve landscapes where woodland fragments are interspersed throughout farmland, whereas primary-sparing and secondary-sparing scenarios involve contiguous blocks of primary or secondary forest surrounded by grazing pasture.

scenarios, while secondary-sparing carbon stocks were 43% higher than land-sharing (Fig. 3).

Birds and dung beetle communities were also predicted to benefit most from land-sparing strategies (Fig. 4; Table 1). For both taxonomic groups, patterns of species occurrence were very similar under the two land-sparing scenarios (birds Fig. 4b and c, dung beetles Fig. 4e and f), reflecting the similarity of advanced secondary forests and primary forests for both communities (Fig. 2c and d). Species responses under land-sharing were more varied, showing a wide range of increases and declines relative to occurrence levels in intact primary forests (birds Fig. 4a, dung beetles Fig. 4c). The relative superiority of land-sparing strategies tended to increase at higher food production levels (Table 1), reflecting the increasing severity of declines under land-sharing for many species (birds Fig. 4a, dung beetles Fig. 4d).

Discussion

In our study region, woodland fragments within tropical farmland hold significantly less carbon per unit area than contiguous primary and secondary forests and support less diverse bird and dung beetle communities. Our simulations suggest that carbon and biodiversity co-benefits would be maximized in agricultural landscapes that retain larger blocks of contiguous forest (land-sparing) rather than smaller woodland features spread throughout farmland (land-sharing). This result is consistent across a range of production levels, and across both taxonomic groups. Within our study region,

the biodiversity benefits of land-sparing appear to be similar regardless of whether primary or advanced secondary forests are protected.

In tropical woodland fragments, carbon storage is influenced by both edge effects and regeneration processes (Tabarelli *et al.*, 2008). In contiguous secondary forests within our study areas, carbon accumulates at a rate of around $4.2 \text{ t C ha}^{-1} \text{ yr}^{-1}$ (J.J. Gilroy *et al.* unpublished data), which agrees broadly with values from other cloud forest studies (Fehse *et al.*, 2002; Sierra *et al.*, 2007). In regenerating woodland fragments, however, annual carbon accumulation is likely to be lower due to altered microclimates, seed dispersal dynamics and herbivory in fragmented sites (Mesquita *et al.*, 1999; Tabarelli *et al.*, 2008). Edge effects also lead to elevated tree mortality in mature fragments (D'Angelo *et al.*, 2004), implying that within-farm woodlands are unlikely to ever approach the per-unit-area carbon storage levels of contiguous forests, given the critical importance of large trees for forest carbon storage (Slik *et al.*, 2013). Active agroforestry management practices can significantly elevate the carbon storage potential of woodland fragments (Stavi & Lal, 2013), although the biodiversity costs and benefits of these techniques are mixed (Bhagwat *et al.*, 2008). Our results suggest that the carbon benefits of preserving unmanaged woodland fragments within farmland are small relative to the protection of fewer, larger blocks of contiguous primary or secondary forest.

Habitat fragmentation and edge effects also play important roles in driving differences in bird and dung beetle communities between farmlands and contiguous forests (Klein, 1989; Turner, 1996; Sekercioglu *et al.*, 2002; Tschardtke *et al.*, 2008). Even with relatively high levels of woodland fragment cover in farmland, alpha diversity of both taxonomic groups tended to be lower than in primary and secondary forests, while community composition was markedly different (Fig. 2). Many species within our study region are apparently dependent on contiguous forests, being absent from farmland sites even when relatively high levels of woodland habitat are retained. Our simulations suggest that community diversity will be higher in land-sparing landscapes, although this prediction depends on an assumption that spared forest reserves are ecologically similar to large contiguous forests. If spared habitat blocks are themselves subject to fragmentation and edge effects, this assumption would clearly be violated. To derive maximum benefits, land-sparing strategies need to be carefully designed to ensure that large contiguous forests are protected. This may require management decisions to be made at large spatial scales, coordinating across multiple farms and even geopolitical regions (Tschardtke *et al.*, 2005).

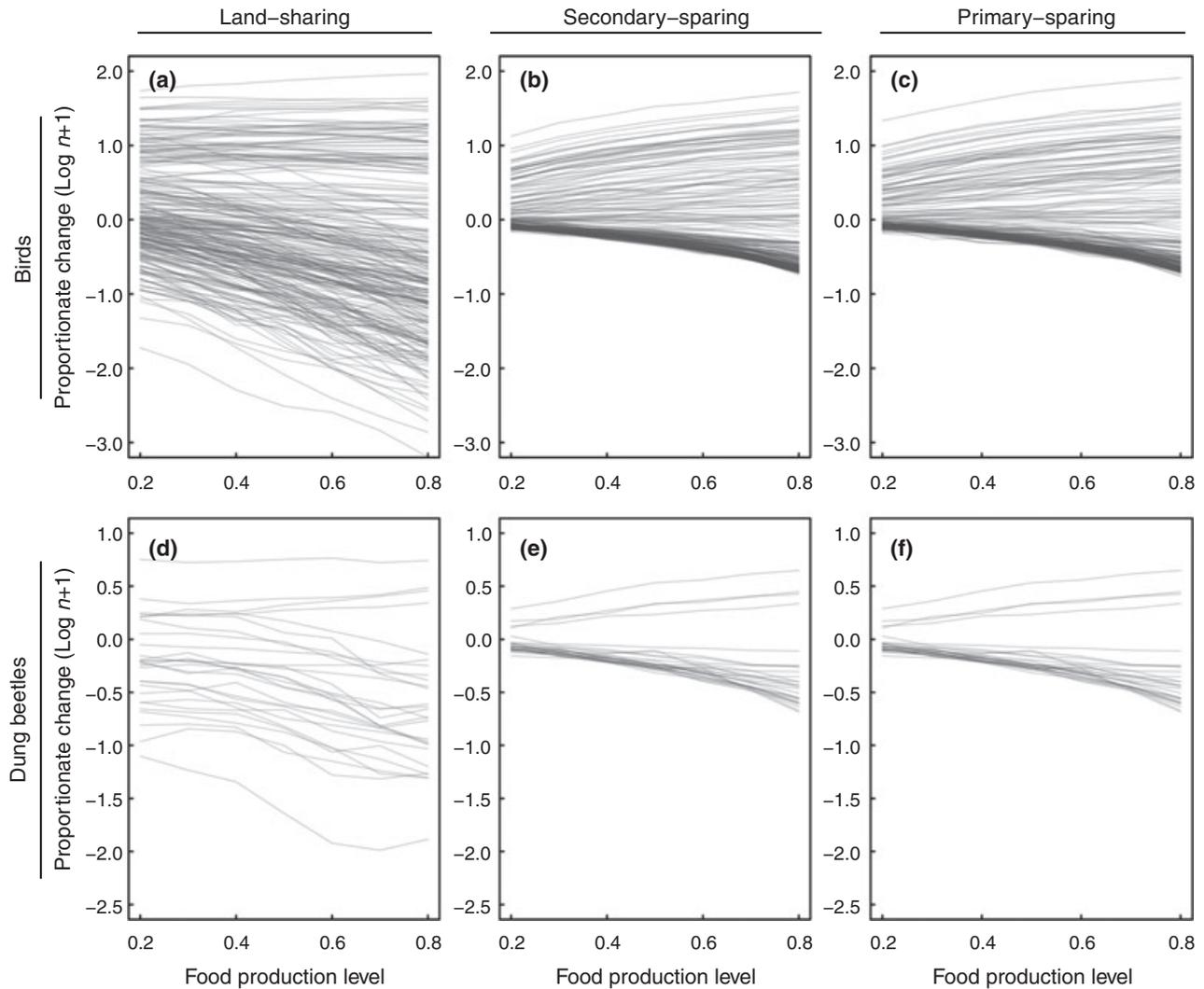


Fig. 4 Predicted changes in mean occurrence probability for each species of bird (a–c) and dung beetle (d–f) across landscapes representing a range of agricultural land-use scenarios. Lines indicate the proportionate change in occurrence relative to a primary forest landscape ($\text{Log}_{10} n + 1$ transformed) across a range of food production levels, which equate to the proportion of the landscape that is covered by grazing pasture. In land-sharing scenarios (a = birds, d = dung beetles), the remainder of the landscape is made up of woodland fragment habitats interspersed within farmland. In land-sparing scenarios, the remainder is either a contiguous block of primary forest (b = birds, e = dung beetles) or a contiguous block of advanced secondary forest (c = birds, f = dung beetles).

Land-sparing strategies provided similar benefits for biodiversity whether they involved sparing primary forests or advanced secondary forests. Our study region still supports large tracts of contiguous primary forest, making the primary-sparing strategy a viable option to bring maximum biodiversity benefit and carbon storage. However, recent evidence suggests that deforestation in the Colombian Andes may be slowing, a trend driven by low timber values and minimal economic rents from agriculture (Sánchez-Cuervo *et al.*, 2012) and potentially supported by additional yield gains in some agricultural sectors (García-Ulloa *et al.*,

2012). Primary forests may not therefore be under imminent threat from conversion to agriculture. In these circumstances, the regeneration of secondary forest blocks under land-sparing could deliver significant carbon stock enhancement in the region, while also bolstering population sizes for species persisting in secondary forests (Chazdon, 2008). Secondary-sparing strategies could also be beneficial in regions already denuded of primary forest, where habitat regeneration may be the only option for a land-sparing approach. It is important to note, however, that our samples are derived exclusively from secondary forests with

Table 1 Relative biodiversity benefits of land-sparing and land-sharing strategies, predicted using landscape simulations. For each species, we evaluated the superiority of each strategy by assessing the mean change in landscape-wide occurrence probability from 1000 replicate simulations. We compared a range of production levels by varying the proportion of the hypothetical landscape that is grazed under each scenario

Scenario	Number of species benefiting (% of total)		
	All birds (total = 243)	Forest birds (total = 212)	Dung beetles (total = 28)
<i>Primary forest land-sparing vs. land-sharing</i>			
Lowest production level (20% grazed)			
Primary-sparing better	124 (51)	123 (58)	20 (71)
Land-sharing better	119 (49)	87 (42)	8 (29)
Highest production level (80% grazed)			
Primary-sparing better	152 (63)	151 (71)	22 (79)
Land-sharing better	91 (37)	61 (29)	6 (21)
Mean across all production levels			
Primary-sparing better	138 (57)	137 (65)	19 (68)
Land-sharing better	105 (43)	75 (35)	9 (32)
<i>Secondary forest land-sparing vs. land-sharing</i>			
Lowest production level (20% grazed)			
Secondary-sparing better	113 (47)	112 (53)	20 (71)
Land-sharing better	130 (53)	100 (47)	10 (29)
Highest production level (80% grazed)			
Secondary-sparing better	154 (64)	153 (72)	22 (79)
Land-sharing better	89 (36)	59 (28)	6 (21)
Mean across all production levels			
Secondary-sparing better	138 (57)	137 (65)	19 (68)
Land-sharing better	105 (43)	75 (35)	9 (32)

direct connectivity to large primary forest tracts. Biodiversity and carbon cobenefits in secondary forests that are isolated from primary forest could be significantly reduced (Chazdon, 2008). Furthermore, as our biodiversity analyses use simple presence/absence metrics, we cannot exclude the possibility that populations in secondary forests are maintained by immigration from primary forest sources (Brawn & Robinson, 1996).

For land-sparing strategies to work in practice, it is essential to maximize the intensity of food production in a sustainable manner. An important caveat concerns the role that small-scale habitat features play in the local provision of ecosystem services such as soil protection, water flow regulation and pollination (DeFries & Rosenzweig, 2010; Perfecto & Vandermeer, 2010; Melo *et al.*, 2013). Our land-sparing simulations assume that within-farm woodlands can be replaced with pasture to meet food production targets, but this overlooks potential negative impacts on long-term agricultural sustainability (Scherr & McNeely, 2008). Equally, large contiguous habitat blocks are likely to be important for landscape-scale ecosystem service provision, potentially influencing the sustainability of surrounding agriculture. To better assess the merits of land-sharing and sparing strategies, there is an urgent need to evaluate the relative contributions of small- and large-scale habitat features to critical ecosystem service provision. Our work clearly demonstrates the importance of large habitat blocks for tropical biodiversity and carbon storage, but further studies are needed to fully determine the long-term benefits of different land allocation policies. Ultimately, agricultural sustainability may be best served by a balance featuring elements of both land-sparing and land-sharing approaches. Finding the optimal level for this balance is a key priority for future research.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Simulating land-sparing and land-sharing strategies.

Figure S1. Map of study region.

Figure S2. Correlations between biodiversity metrics and carbon storage levels.

Table S1. Details of study sites.

Table S2. Posterior means and standard deviations of bird species occupancy parameters.

Table S3. Posterior means and standard deviations of dung beetle species occupancy parameters.