Article:

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Sparing land for secondary forest regeneration protects more tropical biodiversity than land sharing in cattle farming landscapes

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SUMMARY

Effectively managing farming to meet food demand is vital for the future of biodiversity[1, 2]. Increasing yields on existing farmland can allow the abandonment (sparing) of low-yielding areas that subsequently recover as secondary forest[2-5]. A key question is whether such 'secondary sparing' conserves biodiversity more effectively than retaining wildlife-friendly habitat within farmland ('land sharing'). Focusing on the Colombian Choco-Andes, a global hotspot of threatened biodiversity[6], and on cattle farming, we examined the outcomes of secondary sparing and land sharing via simulated scenarios that maintained constant landscape-wide production and equal within-pasture yield: (1) for species and functional diversity of dung beetles and birds; (2) for avian phylogenetic diversity; and (3) across different stages of secondary forest regeneration, relative to spared primary forests. Sparing older secondary forests (15-30 years recovery) promotes substantial species, functional, and phylogenetic (birds only) diversity benefits for birds and dung beetles compared to land sharing. Species of conservation concern had higher occupancy estimates under land-sparing compared to land-sharing scenarios. Spared secondary forests accumulated equivalent diversity to primary forests for dung beetles within 15 years, and within 15-30 years for birds, highlighting the need for longer-term protection to maximise the biodiversity gains of secondary sparing. Promoting the recovery and protection of large expanses of secondary forests under the land-sparing model provides a critical mechanism for protecting tropical biodiversity, with important implications for concurrently assisting in the delivery of global targets to restore 350 million hectares of forested landscapes[7, 8].

Keywords: Ecosystem functioning, forest and landscape restoration FLR, natural secondary regeneration, Scarabaeinae, South America, tropical forest conservation

RESULTS AND DISCUSSION

Does older secondary-sparing or land-sharing farming best protect species and functional diversity?

Many studies have shown that the intensification of farmland to prevent expansion into spared primary forests would best protect species richness (SR), phylogenetic and functional diversity relative to land sharing[9-11]. However, an untested suggestion is that intensification of agriculture to allow abandonment of marginal farmland and sparing of regenerating secondary forest would deliver positive outcomes for tropical biodiversity[2-5]. A land-sparing approach best protected biodiversity in secondary forest-dominated landscapes recovering from logging in Poland (pers comm. A. Balmford[12]) and hurricanes in Mexico[4], but substantial seed and sapling banks, as well as faunal diversity, remain after forest degradation. The potential for land sparing of secondary forest regrowth on fully transformed farmland is thus a key question.

In this study, we assess areas of secondary forest regenerating on land that was previously deforested for cattle pasture. Large blocks of primary forest are not considered in our management scenarios, but are part of the wider study landscape. Across three large and widely spaced study landscapes, each containing contiguous secondary forest, primary forest, and low-intensity cattle farms, which spanned multiple land holdings, we recorded 318 bird and 27 dung beetle species, of 8,470 and 17,686 individuals, respectively. Dung beetles and birds are reliable indicators of wider biodiversity impacts of land-use change[13], representing a broad range of key ecosystem functions[14, 15]. Using hierarchical species-habitat occupancy models, we simulate land-use scenarios to examine biodiversity outcomes of secondary-sparing in Andean landscapes, and compare these to land-sharing approaches where small-scale wildlife-friendly habitat features, including forest fragments, hedgerows, and isolated trees, are retained within farmland (Figure 1). Across simulated scenarios, we maintain constant landscape-wide production and equal within-pasture yield.

When low to moderate levels of land are spared for secondary forest regeneration (i.e. 20-60% spared, 40-80% under intensive production), older secondary sparing (recovery >15 years) resulted in higher predicted mean SR of dung beetles than equivalent land sharing (i.e. 20-60% small-scale wildlife-friendly features, Figure 2A). At the highest percentage of spared land considered (80% spared land and 20% remains under production), dung beetle SR was marginally higher under land sharing than secondary sparing (Figure 2A). For birds, across all percentages of land area remaining under production, secondary sparing resulted in substantially higher predicted mean SR than land sharing (Figure 2B).

The total connecting branch lengths of a functional dendrogram (functional diversity, FD) and the total volume of a functional convex hull occupied by the community (functional richness, FRic) of dung beetles were higher under older secondary sparing than land sharing when low to moderate percentages of land were abandoned (Figures 2C and 2E). At the highest abandonment level (80% spared land and 20% land remains under production), FD (Figure 2C) and FRic (Figure 2E) were marginally greater under a land-sharing strategy. For birds, across all abandonment levels, secondary sparing resulted in substantially higher predicted mean FD and FRic than did land sharing (Figures 2D and 2F). Marginal increases in predicted dung beetle SR, FD, and FRic under land sharing relative to secondary sparing with low production (20%; Figure 2) are likely linked to the persistence of functionally unique forest species when a high proportion of 'wildlife-friendly' features (i.e. patches of remnant forest, isolated trees, riparian strips and hedgerows) are present[16], alongside other functionally distinct species that favour more open pasture habitat[17].

The regularity of species distribution within functional space relative to their abundance (functional evenness, FEve; Figure 2G), the relative abundance of species with the most extreme functional traits (functional divergence, FDiv; Figure S1), and the distribution of species traits accounting for the mean distance of species from the centre of functional space and weighted by abundance (functional dispersion, FDis; Figure S1) of dung beetles did not differ between older secondary sparing and land sharing at each level of abandonment. Similarly, bird FDiv and FDis did not differ between older secondary sparing and land sharing at any abandonment level (Figure S1). However, bird FEve at low to moderate abandonment levels was higher under older secondary sparing than land sharing, although there was no difference at the highest abandonment level (Figure 2H). This variation is again likely due to the mosaic of habitats created by low-intensity farming, such as scrub lands, with the availability of open habitat, allowing functionally unique bird species to be present in the community[18].

Most of the 40 bird species of conservation concern showed higher relative abundances under land-sparing than land-sharing scenarios (Table S2). At the lowest abandonment level (20% spared land, 80% land remains under production), 34 species (85%) had greater mean relative abundances, which were on average 74% higher under land sparing than land sharing (Table S2). Species favouring land-sparing scenarios are typically those associated with large tracts of intact forest, such as *Bangsia aureocincta* and *Entomodestes coracinus*, which had >96% higher mean relative abundances compared to land sparing. Threatened bird species that did better under land sharing included those favouring grassland and scrubland habitats, such as *Synallaxis moesta* and *Diglossa gloriosissima* (which had 81% and 53% higher mean relative abundances, respectively, compared to land sparing), and riverine strips, including *Hypopyrrhus pyrohypogaster* (53% higher mean relative abundance compared to land sparing). A reduction in the area of land remaining in production (20% production, 80% spared) favoured 95% of species of conservation concern (n = 38; Table S2). In addition, four of eleven species of conservation concern that were recorded only anecdotally (i.e. outside of point counts) were noted solely in secondary forests, whereas only two were recorded solely in pasture (Table S2; the remaining five species were either restricted to primary forest or sighted in multiple habitats). This highlights the value of secondary forests for conservation concern species, as well as cementing the irreplaceable value of intact primary forests.

The nine dung beetle species with ranges estimated to be restricted to the Western Cordillera of Colombia showed similar patterns to the overall community. Restricted-range species on average had 47% higher mean relative abundances under land sparing than land sharing with high production (80% land remains under production, 20% spared land) (Table S2). This pattern shifted to restricted-range species, on average, having 51% higher mean relative abundances under land sharing than land sparing when production was reduced (20% land remains under production, 80% spared land) (Table S2). As with the overall community, this pattern highlights the requirement of restricted-range dung beetle species for sufficient vegetation cover.

Previous work showed that as the remoteness of farmland from contiguous forest increases, the relative benefits of sparing primary forest increase relative to land sharing[11, 19]. However, for secondary forest sparing, we show no impact of farmland distance to forest on the relative benefits of SR, FD, FRic, and FEve for dung beetles (Figure S2), whereas for birds, older secondary sparing was increasingly valuable for SR, FD, and FRic (but not for FEve) when farmland is further from forest edge (Figure S2). This further supports the suggestion that high species and functional diversity within low-intensity, ‘wildlife-friendly’ farmland can be confounded with spill-over effects from nearby forest[20, 21], via source-sink dynamics[22] or periodic movements from natural to farmed habitats[23]. Consequently, while intensifying farmland (for example, through increased stocking rates and/or improved pastures) to promote contiguous secondary forest regeneration would remove features that can provide high connectivity across farmland[24], our results indicate that many bird species and associated ecological functions are unlikely to persist in larger land-sharing landscapes that lack areas of contiguous forest. Even when wooded features and apparent connectivity are high under land sharing, the ability of species to disperse through the agricultural matrix is highly variable, being dependent on taxon-specific morphology, behaviour, and matrix type[25, 26], resulting in many species that are unable to exploit these features for dispersal.

Does older secondary-sparing or land-sharing farming best protect avian phylogenetic diversity?

Land sparing of primary forest would best protect phylogenetic diversity (PD)—the total evolutionary history shared across all species within a community—relative to land sharing[10], but whether sparing older secondary forest would deliver equivalent positive outcomes is unknown. Across the avian phylogeny (Figure 3A), the majority of species had high predicted occupancy under older secondary sparing (dark blue; Figure 3A). By contrast, many non-passerine groups (especially Trochilidae and Piciformes), and Oscine (e.g., Corvoidea, Muscicapoidea) and Suboscine (e.g., Furnaridae, and clusters of Tyrannidae) families performed poorly under land sharing irrespective of production level (pale yellow; Figure 3A, only high production [80% land remains under production, 20% spared land] is presented; for species names see supplementary material Figure 1B in[27]).

At all abandonment levels, there was substantially higher predicted mean PD with secondary forest sparing, with a predicted gain of over 1,100 million years of evolutionary history at 20% abandonment relative to land sharing (Figure 3B). However, phylogenetic diversity standardized against a null expectation (sesPD) did not reveal a difference between older secondary sparing and land sharing (Figure 3C), indicating that higher PD under secondary sparing is largely driven by higher species richness (Figure 2B). Abundance-weighted metrics can reveal key insights into the phylogenetic makeup of communities under each strategy. The average number of years of evolutionary history separating species in a community (mean pairwise distance), standardized against a null expectation (sesMPD), was marginally lower under land sharing than older secondary sparing, especially with greater levels of abandonment (Figure 3D), indicating that communities under land sharing have species distributed across clades that diverged more recently than communities under older secondary sparing (i.e., land-sharing communities are more phylogenetically clustered). Across abandonment levels, the average number of years separating each species from its closest relative in the community (standardized mean nearest taxon distance, sesMNTD) did not differ between older secondary sparing and land sharing (Figure S1), suggesting equal co-occurrence of closely related species under both strategies.

Agricultural intensification could favor species with lower evolutionary distinctiveness (ED)[28]. Older secondary sparing had marginally higher predicted mean ED than did land sharing (Figure 3E), especially at lower abandonment levels, indicating that species represented more unique evolutionary history under secondary sparing. As shown previously for primary sparing[10], the benefit of older secondary sparing relative to land sharing increased for PD with distance to forest, although there was limited impact for sesMPD and ED (Figure S2). Thus, many bird species with higher-than-average contributions to PD persist only in land-sharing landscapes when large tracts of forest are nearby, again suggesting that high PD within low-intensity, 'wildlife-friendly' farmland[28] could be confounded by source-sink dynamics[22].

Benefits of older secondary sparing relative to young secondary and primary sparing

Species richness, functional and phylogenetic diversity tend to increase with forest age[17, 29-33], although the rate of species recovery is taxon specific. For dung beetles, biodiversity benefits relative to land sharing were similar whether spared secondary forest was older or young (15 years or less recovery; Figure 4), and irrespective of the percentage of land under production. This indicates a rapid recovery of dung beetle diversity after land abandonment[17], as also occurs for surface-active ants in this region[34], likely supported by the rapid re-establishment of a canopy that offers a diverse array of micro-habitats and buffers temperature fluctuations to generate more stable micro-climates[35].

For birds, the magnitude of the benefit for sparing relative to land sharing was reduced with young secondary sparing for SR, FD, and PD, and marginally so for FRic (but not for FEve, sesPD, sesMPD or ED) (Figure 4). This indicates that full conservation benefits are not achieved until regenerating forests are older. Bird communities may be under strong environmental filtering at earlier stages of forest regeneration, as shown across other taxonomic groups[31], potentially driven by variation in the establishment of fruiting and flowering food plants, and of epiphytes, mosses and bromeliads that are used as foraging and nesting substrates[36, 37]. In the Amazon, for example, avian communities remain depauperate across decadal timescales, lacking habitat specialists and key functional groups compared to those in primary forest[38].

Primary forest often harbours higher diversity relative to older secondary forest[27, 39, 40], suggesting that the relative benefits of older secondary sparing may be lower than equivalent primary sparing[4, 9, 11]. For dung beetles, however, the relative benefits of sparing for species richness and functional diversity were similar whether spared forest was older secondary or primary (Figure 4), and a similar pattern was shown for all bird species richness, functional, and phylogenetic diversity metrics (Figure 4). The sparing-sharing approach implicitly scales across multiple farms and, in the case of sparing, a conserved forest block; thus, our results indicate landscape-level diversity, not how alpha- (local) or beta-diversity vary under these scenarios.

We did not assess the biological merits of active restoration, which may increase the rate of biodiversity recovery relative to the passive regeneration occurring within our sampled forests, nor did we investigate the potential for silvopasture, which involves active planting of nitrifying trees (e.g. *Alnus* in this region) within extensive cattle pastures. These alternative restoration pathways are very infrequent in our study region and were not sampled. Evidence from small-scale trials suggests that silvopasture can enhance yields, whilst sequestering carbon[41, 42], and would support some forest- and edge-dwelling species[43, 44], resulting in landscapes similar to our land-sharing scenarios where wildlife-friendly features (including trees) are retained within pasture. Our results suggest that the biodiversity value of these landscapes, even at the maximum level of retained wildlife-friendly features, still tends to be lower than an equivalent secondary-sparing scenario.

Forest regeneration is dictated by land ownership, which underpins willingness to participate and financial investment to intensify pasture; geographic location and associated climate conditions; seed bank quality and soil structure resulting from land-use history; and landscape configuration and its relationship with seed dispersal potential. Consequently, the scale, quality and rate of forest regrowth will vary across localities[45, 46]. In some landscapes, the practical distinction between land-sparing and land-sharing scenarios will thus be blurred and the localised spatial arrangement of farmed and abandoned lands will guide solutions for biodiversity conservation.

Our study locations were in secondary forests directly connected to primary forests, but understanding how the isolation, size, and edge density of spared secondary forest impacts land-sparing, land-sharing relationships remains an important question. Furthermore, across our simulated scenarios in which the same landscape-wide production is achieved, we assume that within-pasture yields are equal across scenarios. However, under a land-sparing scenario, yields might be enhanced via improved fodder grass selection, fertilisation, better breed selection and veterinary care[45]. The feasibility of yield increases depends on the potential for financial investment and education/training programs, the accessibility of which will vary. Equally, wildlife-friendly features within pasture can improve soil stability and provide shade for cattle, potentially enhancing yields[47, 48].

Overall, our results uniquely provide support for multidimensional biodiversity benefits of secondary sparing, suggesting that farming intensively alongside secondary recovery in abandoned areas could enhance biodiversity recovery relative to equivalent low-intensity farming scenarios. Land abandonment is increasingly occurring in marginal farmland areas, particularly in areas too steep or dry for modern agriculture, and with increasing rural to urban migration[49]. In Latin America and the Caribbean, for instance, 36 million hectares of woody vegetation recovered on abandoned farmland between 2001 and 2010[50]. Our results also underscore the conservation importance of protecting secondary forest blocks in regions where increasing agricultural demand is driving clearance of secondary forests, akin to findings highlighting the importance of sparing primary forests relative to land sharing[4, 9-11, 51].

To maximise the conservation benefits of secondary sparing, effective land-use planning must be underpinned by policy and financial drivers to balance environmental and socio-economic outcomes[5]. Secondary sparing will be particularly valuable in regions where the majority of primary forest cover has been already lost, such as the tropical Andes, Brazilian Atlantic, African tropical moist belt, and Himalaya[52]. Secondary sparing in marginal farmlands also provides an alternative when high opportunity costs make primary forest sparing unattainable[53]. Across the tropics, the majority of secondary regeneration occurs adjacent to remnant primary forests[46, 54, 55]. Further targeting of land abandonment in areas close to existing natural habitat and which spans elevation bands would increase recolonization potential, buffer edge-affected forests, and enhance the size of remaining forest blocks, thus reducing the risks of long-term, area-driven extinctions[28, 56]. Indeed, increasing landscape forest cover is the determining factor in successful restoration of biodiversity in secondary forests under either passive or active intervention[46].

Our study underscores the importance of long-term protection of spared secondary forests for delivering biodiversity gains (see also[38, 57]), in addition to other ecosystems services, such as carbon stocking[29, 46, 58, 59] and preventing landslides or soil erosion[60]. However, regenerating forests tend to be poorly protected, with laws, policies and socioeconomic conditions that can work against long-term persistence. In Brazil, the lack of protection status given to secondary forests has driven steadily increasing deforestation rates in secondary forests from 2000 to 2014[61]. Similarly, in Costa Rica, young regenerating forests are excluded from the laws that protect forests, thus these sites are often cleared to prevent reclassification to protected forest once they advance, which would remove owners' land-use options[62, 63] (see[5] for further examples). This highlights the urgent need for adequate legal recognition of the value of secondary forest, and in particular the protection of younger secondary forests as future repositories of biodiversity. Regulation and monitoring of secondary forests is also needed to prevent the perverse outcome of abandonment driving agricultural displacement and subsequent clearance of native vegetation elsewhere[64, 65].

Schemes including government subsidies and carbon-based payments for ecosystem services (PES) could provide mechanisms for change[58, 66]. Carbon-based PES schemes that promote carbon enhancements via secondary forest regrowth are a cost-effective opportunity. For example, given the low opportunity costs of marginal cattle pastures in the Tropical Andes and shifting agriculture in North-east India[67, 68], it is more profitable for landowners to grow carbon rather than cows (Andes) or crops (NE India) even at low carbon prices. More broadly, there are ambitious global commitments under the Bonn Challenge to restore tree cover to 350 million hectares via forest and landscape restoration, mainly in the tropics. The potential of secondary sparing highlights a major biodiversity-friendly pathway by which we can deliver on these challenging global targets for restoration. This will often require the combination of agricultural training, inputs and stocks of high-yielding, pest and drought resilient varieties, with proactive management to focus forest regeneration towards larger spared blocks of abandoned farmland. These will represent vital conservation resources in the coming decades.

STAR Methods

Detailed methods are provided in the online version of this paper and include the following:

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- Biodiversity sampling
- Species of conservation concern

METHOD DETAILS
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- Functional trait matrices and diversity metrics
- Avian phylogenetic diversity and evolutionary distinctiveness measures

QUANTIFICATION AND STATISTICAL ANALYSIS
- Stimulating land-sparing and land-sharing scenarios

SUPPLEMENTAL INFORMATION

Supplemental Information includes two tables and three figures, and can be found with this article online at INSERT LINK HERE

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AUTHOR CONTRIBUTIONS

FAE and DPE conceived the study idea; FAE, JJG and DPE collected the data; FAE, MRM, CCPC, and PGC analysed the data and produced the figures; FAE wrote the first draft of the manuscript, with all coauthors contributing edits.

DECLARATION OF INTERESTS

The authors declare no competing interests.

MAIN-TEXT FIGURE/TABLE LEGENDS

Figure 1: Visualisation of secondary-sparing and land-sharing management strategies

Blocks of secondary forest recover on abandoned land (secondary-sparing) by consolidating production within remaining farmed areas, while land sharing maintains small wildlife-friendly habitat features within the pasture. We simulate these strategies through hypothetical landscapes composed of management units (of 100 m radii), represented by circles (5 units per scenario are present here; 52 units were used in our simulations), based on field data from three large and widely spaced landscapes, which included multiple land holdings, in a tropical Andean agriculture system. Secondary-sparing management units consist of spared secondary forest sites adjacent to contiguous forest and paired with intensive farmland sites (i.e. all non-grazed land is consolidated into larger habitat blocks, as is farmland), while land-sharing units are composed of farmland within which a proportion of wildlife-friendly habitat (e.g. riverine stripes or isolated trees) is retained. Four scenarios were run with different proportions of land remaining under production (high production at 80% through to low production at 20%), in which the same landscape-wide production is achieved and within-pasture yield is assumed to be equal across all scenarios.

Figure 2: Variation in dung beetle and bird species richness and functional diversity under secondary-sparing versus land-sharing strategies

Species richness (A, B), functional diversity (C, D), functional richness (E, F) and functional eveness (G, H) of communities simulated under older secondary-sparing (blue) and land-sharing (orange) management strategies. Metrics are generated across four scenarios varying the percentage of land area remaining under production, and in turn the amount regenerating as secondary forest or preserved as land-sharing features. Error bars represent 95th percentiles, points represent mean values from randomisations (per scenario), while violin plots represent the frequency distribution of these randomisations. See also Figure S1, Figure S2 and Table S1.

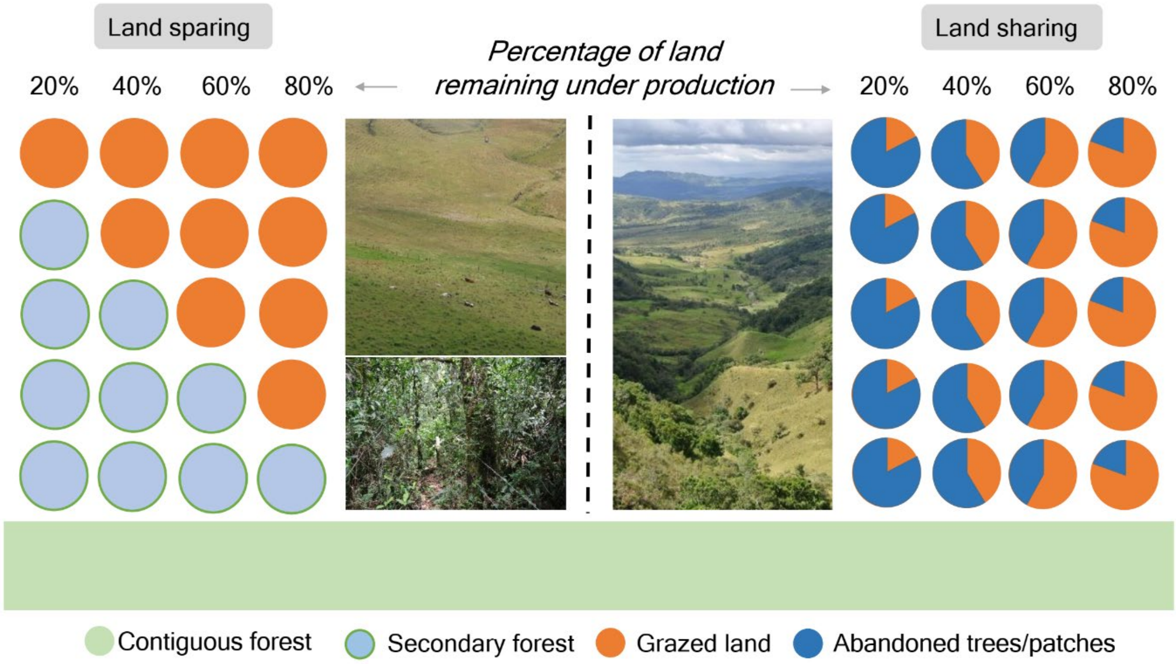
Figure 3: The phylogenetic relationships and diversity of Chocó-Andean birds under secondary-sparing versus land-sharing strategies

(A) The phylogenetic distribution of Chocó-Andean birds generated under a low-abandonment scenario where 20% land area is abandoned for natural regeneration while 80% remains under production. Spots show the proportion of simulated communities for which a species was present. The strength of colour is scaled from 0 (white) to 100% (full colour) for both strategies. Major nodes indicate passerines (Pa), suboscines (Su), and oscines (Os), while outer bars (black and grey) distinguish family groups. Figure 3A with species names labelled is available from the authors upon request. Variation in avian phylogenetic diversity (B), standard effect size of phylogenetic diversity (C), standard effect size of mean pairwise distance (D), and evolutionary distintiveness (E) are shown across four scenarios varying the percentage of land area remaining under production, and in turn the amount regenerating as secondary forest or preserved as land-sharing features. Error bars represent 95th percentiles, points represent mean values from randomisations (per scenario), and violin plots represent the frequency distribution of these randomisations. All scenarios simulate two land management strategies, land sparing (blue) and land sharing (orange), and consider older secondary forest as conserved habitat. See also Figure S1 and Figure S2.

Figure 4: Variation in species richness, functional and phylogenetic diversity across different habitats under land-sparing land-sharing strategies

The amount of species richness (A, B), functional diversity (D, E), functional richness (G, H), and functional evenness (J, K), and bird phylogenetic diversity [PD] (C), standard effect size of PD (F), standard effect size of mean pairwise distance (I), and evoluntionary distintiveness (L) under simulated land-sparing (blue) and land-sharing (orange) management scenarios. Young secondary, older secondary and primary forest are considered as conserved habitat. Metrics are generated under a low-abandoment scenario (20% land area is abandoned for natural regeneration while 80% remains under production). Error bars represent 95th percentiles, points represent mean values from randomisations (per scenario), and violin plots represent the frequency distribution of these randomisations. See also Table S1.

Figure 1


Land sparing
Percentage of land remaining under production
Land sharing
20%
40%
60%
80%
20%
40%
60%
80%
Contiguous forest
Secondary forest
Grazed land
Abandoned trees/patches

411 **Figure 2**

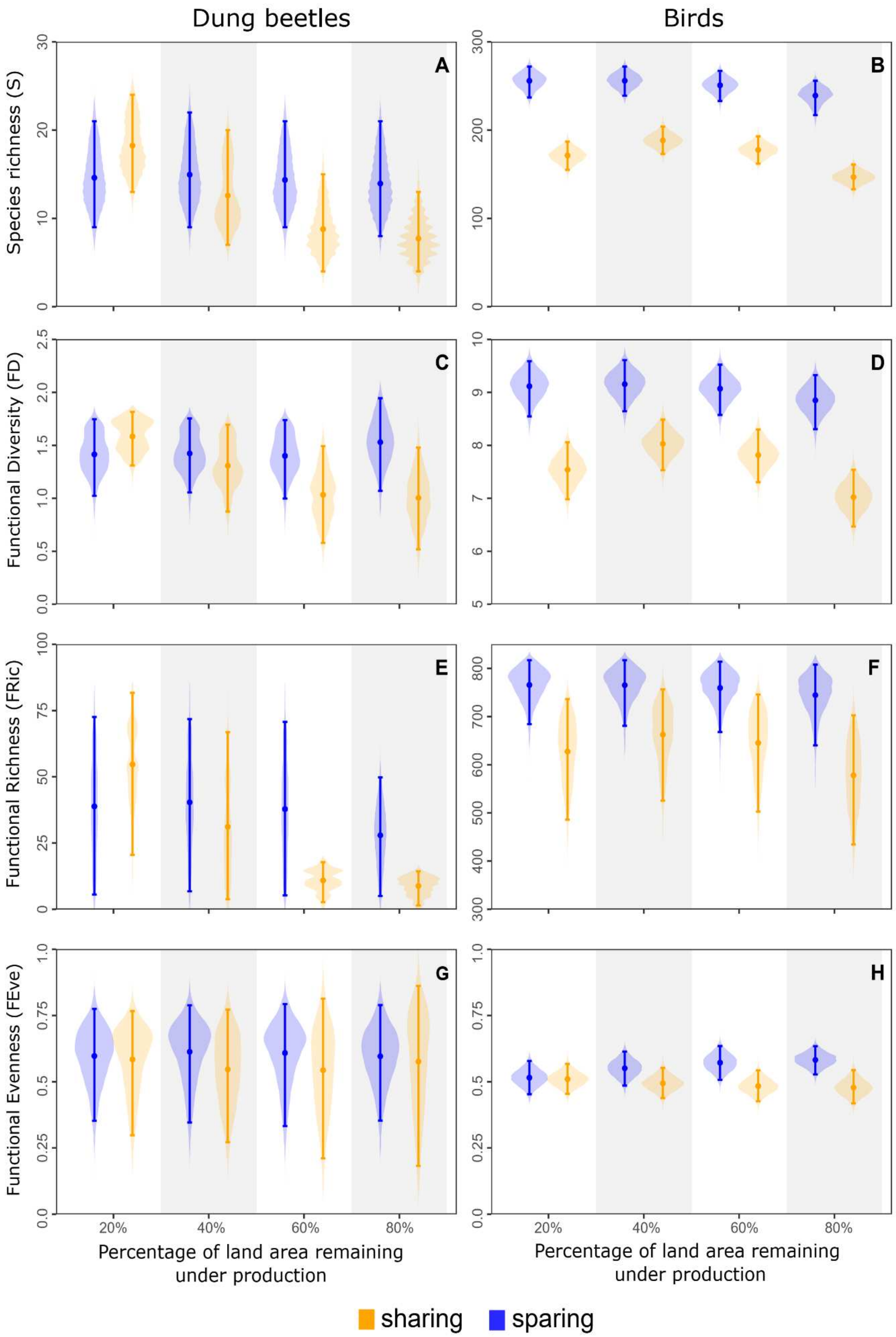

Dung beetles
Birds
Species richness (S)
Functional Diversity (FD)
Functional Richness (FRic)
Functional Evenness (FEve)
A
B
C
D
E
F
G
H
0
10
20
30
100
200
300
0.0
0.5
1.0
1.5
2.0
2.5
5
6
7
8
9
10
0
25
50
75
100
300
400
500
600
700
800
0.0
0.25
0.5
0.75
1.0
20%
40%
60%
80%
Percentage of land area remaining under production
sharing
sparing

Figure 3

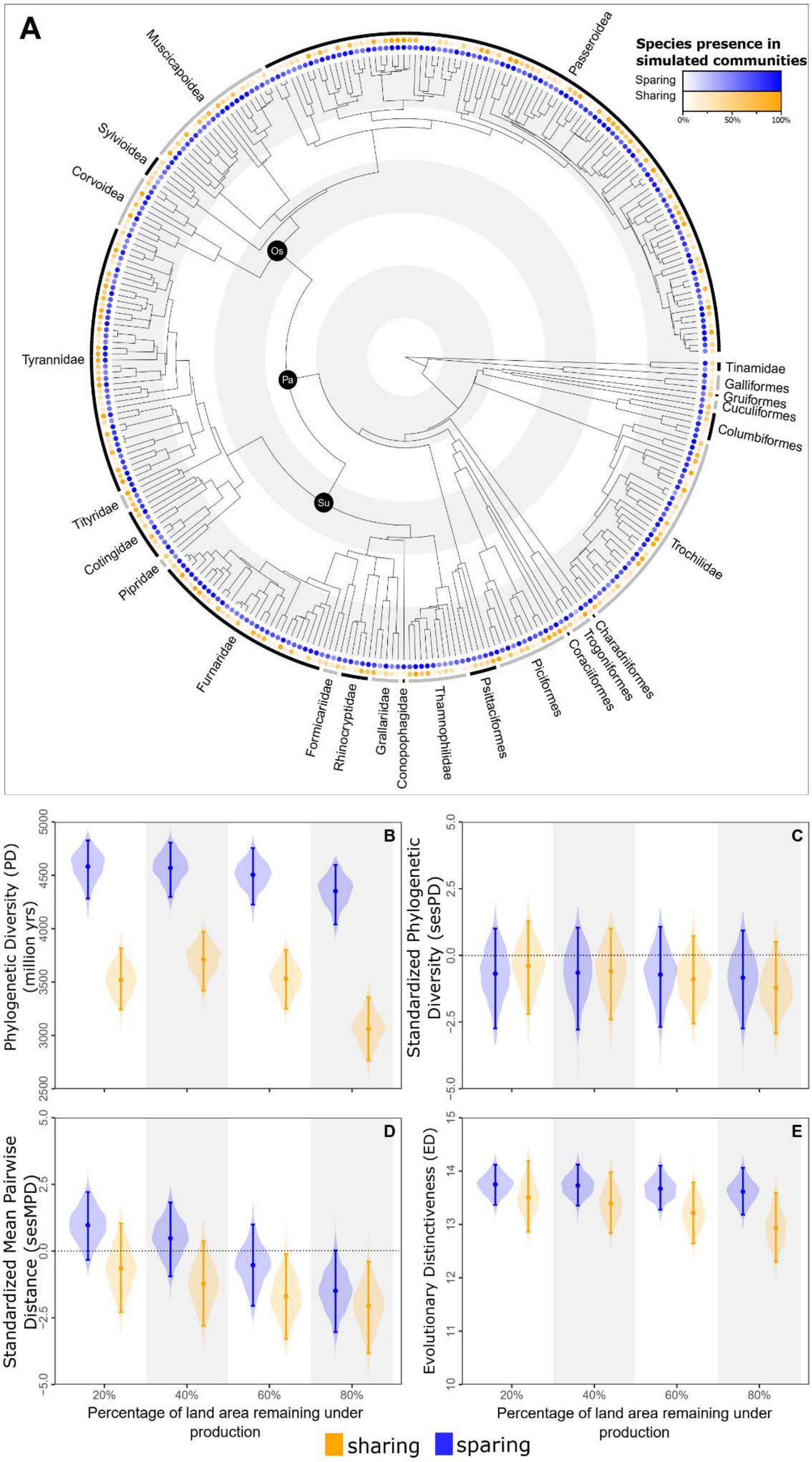
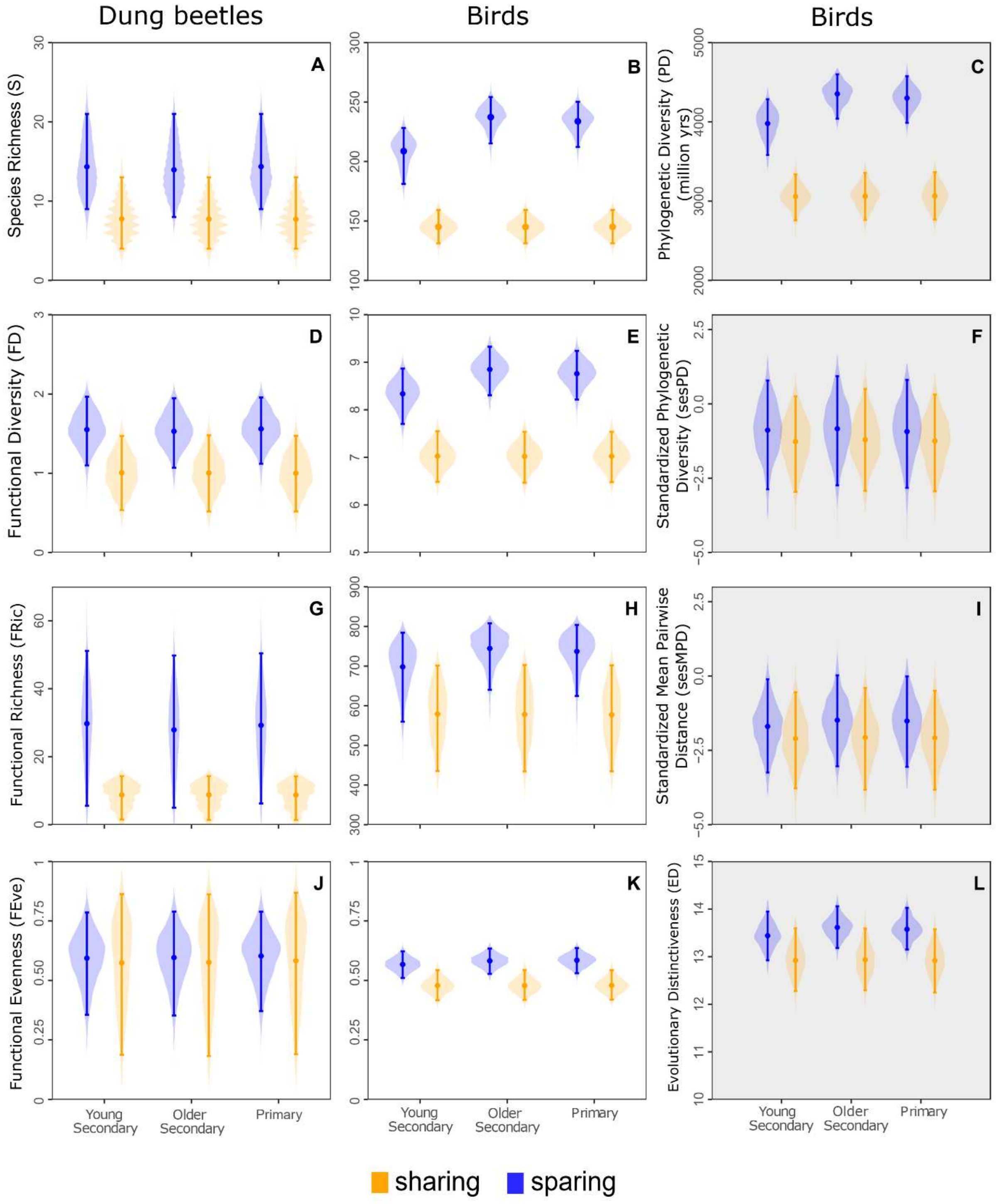

A
Species presence in simulated communities
Sparing
Sharing
0%
50%
100%
Os
Pa
Su
Passeroidea
Muscicapoidea
Sylvioidea
Corvoidea
Tyrannidae
Tityridae
Cotingidae
Pipridae
Furnariidae
Formicariidae
Rhinocryptidae
Grallariidae
Conopophagidae
Thamnophilidae
Psittaciformes
Piciformes
Coraciiformes
Trogoniformes
Charadriiformes
Trochilidae
Columbiformes
Cuculiformes
Gruiformes
Galliformes
Tinamidae
B
Phylogenetic Diversity (PD) (million yrs)
5000
4500
4000
3500
3000
2500
C
Standardized Phylogenetic Diversity (sesPD)
5.0
2.5
0.0
−2.5
−5.0
D
Standardized Mean Pairwise Distance (sesMPD)
5.0
2.5
0.0
−2.5
−5.0
E
Evolutionary Distinctiveness (ED)
15
14
13
12
11
10
20%
40%
60%
80%
Percentage of land area remaining under production
sharing
sparing

Figure 4


Dung beetles
Birds
Birds
A
Species Richness (S)
0
10
20
30
B
100
150
200
250
300
C
Phylogenetic Diversity (PD) (million yrs)
2000
3000
4000
5000
D
Functional Diversity (FD)
0
1
2
3
E
5
6
7
8
9
10
F
Standardized Phylogenetic Diversity (sesPD)
−5.0
−2.5
0.0
2.5
G
Functional Richness (FRic)
0
20
40
60
H
300
400
500
600
700
800
900
I
Standardized Mean Pairwise Distance (sesMPD)
−5.0
−2.5
0.0
2.5
J
Functional Evenness (FEve)
0
0.25
0.50
0.75
1
K
0
0.25
0.50
0.75
1
L
Evolutionary Distinctiveness (ED)
10
11
12
13
14
15
Young Secondary
Older Secondary
Primary
sharing
sparing

STAR Methods

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Biological Samples		
Dung beetle specimens	Colecciones biológicas, Instituto Alexander von Humboldt, Colombia	
Deposited Data		
Original data and code	[69]	10.6084/m9.figshare.c.5234441
Specimen identifiers for morphometric traits	[11]	https://onlinelibrary-wiley-com.sheffield.idm.oclc.org/doi/full/10.1111/gcb.14601
Software and Algorithms		
R version 4.0.2, on platform: x86_64-w64-mingw32/ x64 (64-bit)	The R Foundation for Statistical Computing	https://cran.r-project.org/mirrors.html
R studio Version 1.1.463	RStudio	https://rstudio.com/products/rstudio/download/
Other		
Global bird species distribution maps	[29], [70]	http://datazone.birdlife.org/
Taxonomy and assessment data (non-spatial) for birds.	[71]	https://www.iucnredlist.org/

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Felicity Edwards (felicityedwards10@gmail.com).

Materials Availability

This study did not generate new unique reagents.

Data and Code Availability

Selected datasets and code written for this paper will be deposited using figshare: 10.6084/m9.figshare.c.5234441

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study Areas

Sampling occurred in three sites in the departments of Antioquia, Risaralda and Choco, Colombia (1290–2680 m above sea level[67]), spanning between 1,737 and 3,295 ha[29]. Sites were characterised by sub-montane to sub-tropical Andean contiguous primary cloud forests (>1,000,000 ha) and adjacent secondary forests (3 - 30 years recovery) within a wider matrix of cattle pasture (predominant agricultural practice in the region[72]). Secondary forest locations were connected to primary forests, and time since agricultural abandonment was determined from interviews with reserve managers and local residents. Land-sharing features (e.g. hedgerows, isolated trees, forest patches) contained a mix of primary and naturally regenerating vegetation. At each site multiple sampling squares were surveyed, arranged more than 400 m apart from another within a habitat, and more than 300 m between habitats.

Biodiversity sampling

We sampled birds using standardised point count surveys spaced 200 m apart (total across study *n* = 174) and run on four consecutive days for 10 minutes. All birds seen or heard were noted, while unknown vocalizations were subsequently identified from each digitally recorded survey. We excluded migrant or highly mobile species, such as large raptors or swifts, from our analyses as we were specifically interested in community patterns, which reflected local-scale changes in habitat. Dung beetles were sampled using standardised baited (with human dung) pitfall traps spaced 100 m apart within each sampling square (total across study *n* = 145). Traps were set-up in the field for four days, re-baited after 48 hours and samples collected every 24 hours. All individuals were identified to species or morpho-species. Species determinations were made by; F. Edwards, C. A. Medina, A. Gonzalez, and J. S. Cardenas at the Instituto Alexander von Humboldt, Colombia, where specimens were also deposited.

Species of conservation concern

Overall community metrics provide a valuable insight into the diversity, functional composition and potential redundancy within a community. However, they can obscure important shifts in species of conservation concern. We therefore examine how land-sparing and land-sharing simulated scenarios might impact species of conservation concern. We assessed the mean relative abundance indices of species, across all 52 simulated sites, based on the occurrence probabilities generated by our Bayesian hierarchical occupancy models (described below). We extract these relative abundance indices from both land-sparing and land-sharing scenarios where older secondary forest is 'spared' land and with 20% and 80% of land area remaining under production (Table S2). We also extract the mean relative abundances for these species in primary forest as a baseline comparison.

We highlighted 40 bird species of conservation concern, either listed as threatened by IUCN (status listed as critically endangered, endangered, vulnerable, or near threatened; n = 22)[71] or as having a restricted geographic range determined by Birdlife International range maps[70] as per[29] (n = 18). We assess dung beetle species as being of conservation concern when their known range is restricted to the Occidental Cordillera in western Colombia, which includes the states of Antioquia, Chocó, Risaralda and Valle del Cauca (n = 9). Species' ranges were assessed through specimen records in the Entomological collection of the Instituto Alexander von Humboldt (IAvH-E) database, datasets published in the Global Information Biodiversity Facility (GBIF[73]) with expert validation across records (pers. comm. D. Martinez), and records of species in the Universidad Nacional de Colombia, Medellin, Colombia.

METHOD DETAILS

Habitat variables

To generate relationships between species communities and landscape composition, we firstly calculated the proportion of 'wildlife-friendly' habitat across our grazed landscapes, within a radius of all farmland (pasture) sampling points. We selected taxonomically relevant distances, 100 m for birds and 50 m for dung beetles, using distances of the known spatial turnover of tropical bird[74, 75] and dung beetle[76] communities. Wildlife-friendly features were visually mapped and included patches of remnant forest, isolated trees, riparian strips and hedgerows. The area occupied by these different features was calculated. Roads and other human infrastructure were excluded from the area calculations to focus solely on land cover, which could benefit biodiversity. Using this information, we calculated our wildlife-friendly index, relative to the area grazed, for each point as: $Wr = Fr/\,(\mathrm{Pr} + Fr)$

Where, for a given radius r, Fr is the proportion of wildlife-friendly cover, and Pr is the proportion of pasture cover. The index ranges from one (100% forest cover, applied to all forest sampling points) to zero (entirely pasture with no wildlife friendly habitat). Secondly, as sampled pasture points varied in the distance from contiguous forest edge we calculated the distance to the nearest contiguous forest edge (ranging from 50 - 1550 m) using remote-sensed data (ALOS/PALSAR)[77] combined with information from hand-held GPS devices. Contiguous forest in this case was a mixture of primary and secondary forests due to the uncertainty of forest age across the wider landscape. Sampling points located within forest were assigned a distance of 0 m.

Functional trait matrices and diversity metrics

In addition to species richness, we assessed functional diversity, which was evaluated using a range of life history and morphological traits, for each individual bird and dung beetle species (Table S1). We included resource use (i.e. dietary range), behavioural (i.e. foraging mode) and morphological traits, which have previously been shown to be functionally important for our study taxa[78, 79].

Avian traits included foraging guild(s), foraging strata, foraging mode, degree of territoriality, predominant habitat type association[80], and seven morphological measurements following[11]: tarsus length, tail length, hand-wing index (measured via wing length x Kipp's distance) and bill width, depth, shape and length (measured as both nares to tip and exposed culmen). Morphometric data was measured from museum specimens and obtained from a minimum of two males and two females, with the exception of bill shape, which was gathered from the literature[80].

Dung beetle traits included nesting strategy, activity period, diet preference (sourced from research articles and expert knowledge) and three morphological measurements: body size, front:back leg ratio, and size adjusted front leg area (as per[79]) measured from collected specimens. All morphological measurements were calculated using ImageJ[81], from photographs of our collected specimens. The number of individuals measured per species varied due to the availability of specimens (*n* = 1 - 27). Information for behavioural traits were gathered from the literature[82-88], when multiple sources of trait information were available, we took the majority consensus. When such information was not available, for example for morpho-species, species of the same genus were recorded as sharing similar behaviours, following[79].

To account for generalist behaviours in some species, a subset of trait categories (avian foraging guild, strata and mode, and the activity period of dung beetles) were analysed as multiple independent binary traits. This allows an individual species to be assigned multiple traits within these broad categories (for example, a species can be frugivorous and insectivorous, feeding in the mid- and under-storey strata, Table S1)[89].

Using this trait data, we calculated five complementary measures of functional diversity across our land-use scenarios:

1. **Functional Diversity (FD)** – measures the total connecting branch lengths of a functional dendrogram[90]. FD is produced from a distance matrix derived from an original trait matrix. We used the extended Gower distance measure to calculate our distance matrices, which allows for different variable types to be accounted for[91]. We used an unweighted pair-group arithmetic average (UPGMA) clustering method.
2. **Functional richness (FRic)** – measures the total volume of functional space occupied by a given set of species. Communities with greater functional space occupied are likely to have a broader range of functional traits, which translates to potential increased resource utilisation.
3. **Functional evenness (FEve)** – measures how even species abundances are distributed in functional trait space and is bounded by 0-1. A value close to 1 represents communities with an even distribution of species abundances across functional space,

implying low functional redundancy. A value close to 0 represents an uneven distribution of species and overlapping functional roles (high functional redundancy).

4. **Functional divergence (FDiv)** – measures how the relative abundance of species is related to the most unique functional traits (those furthest from the centroid of functional space), and describes the patterns of niche differentiation in a given functional space. A high value of FDiv means the most abundant species are at the extreme of functional space, while a lower FDiv value indicates the most abundant species are close to the centroid of functional space.
5. **Functional dispersion (FDis)** – measures the mean weighted (via relative abundance) distance of species traits to the centroid of trait space[92]. Greater FDis implies increased representation of more unique traits in a given community.

For the calculation of FRic, FEve, FDiv and FDis traits act as coordinates in multidimensional functional space and were weighted equally, while species were weighted by their abundance. The distance matrices (derived from our trait matrices) were calculated using the extended Gower distance measure[91] and principal coordinate analyses (PCoA) were then run to gain the transformed coordinates[93] used to calculate the functional metrics. Analyses were run in the FD[94] and picante package[95] of R[96].

Avian phylogenetic diversity and evolutionary distinctiveness measures

To assess the phylogenetic impact of secondary sparing we calculated five complementary phylogenetic diversity metrics:

1. **Phylogenetic diversity (PD)** – measures the sum of branch lengths of a phylogenetic tree and represents the total evolutionary history within a community.

2. **Standard effect size of PD** - measures PD accounting for species richness. Positive values indicate higher than expected values of PD for a given species richness, vice versa for negative values.
3. **Standard effect size of mean pairwise distance (MPD)** - measures MPD (calculated as the average distance separating species in a community on a phylogenetic tree, weighted for species abundance, representing the number of years of evolutionary history) accounting for species richness. Positive values indicate higher than expected values of MPD for a given species richness, vice versa for negative values.
4. **Standard effect size of mean nearest taxon distance (MNTD)** - measures MNTD (calculated as the average number of years separating each species from its closet relative in the community, weighted for species abundance) accounting for species richness. Positive values indicate higher than expected values of MNTD for a given species richness, vice versa for negative values.
5. **Evolutionary distinctiveness (ED)** – measures the degree of isolation a given species is from the global phylogeny (9,993 species). A high ED value indicates a species has no extant close relatives.

We used 500 unique phylogenetic trees, 250 trees of both the Hackett[97] and Ericson[98] backbones obtained from[99], each one representing an individual hypothesis of species evolutionary relationships. The mean value of the phylogenetic diversity metrics and the median ED value, from all 500 trees, were used to account for phylogenetic uncertainty. Metrics were calculated using the picante package[95] in R[96].

QUANTIFICATION AND STATISTICAL ANALYSIS

Simulating land-sparing and land-sharing scenarios

We used a landscape simulation process based on ‘spared’ older secondary forest, to assess how species, functional, and phylogenetic diversity could be conserved within landscape scenarios[10, 11, 19] (Figure 1).

Firstly, we estimated the relationship between species occurrences and habitat variables using Bayesian hierarchical occupancy models, run separately for birds and dung beetles. For each species, we modelled occupancy probability across sampling locations as a function of habitat (categories primary, mature secondary, young secondary and farmland), elevation, distance to contiguous forest, and wildlife-friendly index, including site as a random effect to ensure the large spatial variation across the three study sites was accounted for. Bird species were divided into those recorded in forest (n = 288) and those found solely in pasture (n = 30), these were then analysed separately in community-level models (dung beetles were run as a full community as the number of species was far fewer). We controlled for imperfect detection across habitats (i.e. detectability will be easier in open pasture), and in relation to time of day (i.e. vocal activity decreases through the day) for avian models, via a state-space formulation, where species detection probabilities are estimated from repeated samples under an assumption of site-level closure within the study period[29, 100]. Parameters were estimated using

WinBUGS version 1.4[101] (see[19] for full model specifics), using 50,000 iterations, following a burn in of 20,000.

We used these occupancy model outputs to estimate site-level abundances in our simulated land-sharing, land-sparing landscape scenarios. To do this, for each hypothetical scenario we divided the simulated landscape into 'management units', each consisting of 52 'sites', with each site corresponding to a circle of 100 m radius, akin to our sampled locations. For each site, we predicted species occupancy probabilities and assigned habitat characteristics dependent on a given set of conditions (Figure 1). We converted the resulting probabilities into abundance metrics by summing Bernoulli trials for each site across the landscape, generating an index of relative prevalence for each at the landscape scale[11]. We repeated this process for 10,000 posterior-predictive samples of site-level species occurrence probabilities to generate posterior distributions for each derived biodiversity metric. To make avian phylogenetic analyses computationally tractable, we reduced the number of replicates to 1,000 posterior-predictive samples for phylogenetic metrics.

For secondary-sparing strategies, landscapes were separated into 'spared forest' units and intensive pasture units (0% wildlife-friendly features), such that within habitat features are removed and non-grazed land is consolidated into larger habitat blocks, while grazed land is intensified in a smaller land area[102]. Contrastingly, land-sharing strategies landscapes were designated as fully pasture with varying amounts of wildlife-friendly features retained within[102]. In both cases, we assessed a range of abandonment levels, representing the proportion of the landscape devoted to either regenerating forest (sparing) or wildlife-friendly features (sharing; Figure 1). Across all simulated scenarios, we maintained the same landscape-wide production and assume that within-pasture yields were equal.

Abandonment levels were based on the limits of pasture cover across the farmland study sites (20%, 40%, 60%, 80%). Pasture units were assigned a given distance from contiguous forest, these distances were set at 500 m, 750 m, 1,000 m, 1,250 m, and 1,500 m. Results presented in the main text are taken from the mid distance (1,000 m) from contiguous forest.

Within scenarios, the aggregate level of cattle production is held constant, thus allowing the performance of each strategy to be examined independent of production, under an assumption that yield is constant across all pastures[5, 25]. We acknowledge that local variation in yield might occur under both land-sparing and land-sharing scenarios (see Discussion).

These analyses were repeated considering young secondary forest (15 years or less recovery) and primary forest as ‘spared’ forest to compare with mature secondary forest simulations. In our results, we present a scenario of 20% abandoned land, higher percentages of abandoned land showed no difference in patterns across the forest types. All analyses were carried out in R[96] using custom code[69].

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