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RESEARCH ARTICLE

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Avian phylogenetic and functional diversity are better conserved by land-sparing than land-sharing farming in lowland tropical forests

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Abstract

1. The transformation of natural habitats for farming is a major driver of tropical biodiversity loss. To mitigate impacts, two alternatives are promoted: intensifying agriculture to offset protected areas (land sparing) or integrating wildlife-friendly habitats within farmland (land sharing). In the montane and dry tropics, phylogenetic and functional diversity, which underpin evolutionary values and the provision of ecosystem functioning and services, are best protected by land sparing. A key question is how these components of biodiversity are best conserved in the more stable environments of lowland moist tropical forests.
2. Focusing on cattle farming within the Colombian Amazon, we investigated how the occupancy of 280 bird species varies between forest and pasture spanning gradients of wildlife-friendly features. We then simulated scenarios of land-sparing and land-sharing farming to predict impacts on phylogenetic and functional diversity metrics.
3. Predicted metrics differed marginally between forest and pasture. However, community assembly varied significantly. Wildlife-friendly pastures were inadequate for most forest-dependent species, while phylogenetic and functional diversity indices showed minimal variation across gradients of wildlife-friendly features.
4. Land sparing consistently retained higher levels of Faith's phylogenetic diversity (~30%), functional richness (~20%) and evolutionarily distinct lineages (~40%) than land sharing, and did so across a range of landscape sizes. Securing forest protection through land-sparing practices remains superior for conserving overall community phylogenetic and functional diversity than land sharing.

5. *Synthesis and applications*: To minimise the loss of avian phylogenetic diversity and functional traits from farming in the Amazon, it is imperative to protect large blocks of undisturbed and regenerating forests. The intensification required within existing farmlands to make space for spared lands while meeting agricultural demand needs to be sustainable, avoiding long-term negative impacts on soil quality and other ecosystem services. Policies need to secure the delivery of both actions simultaneously.

KEYWORDS
biodiversity conservation, cattle farming, Colombia, habitat loss, land-use change, pasture, sustainability

1 | INTRODUCTION

The impacts of human activities on natural ecosystems are increasing rapidly. Conversion of natural habitat to agricultural land is a dominant driver of biodiversity loss worldwide (Jaureguiberry et al., 2022). There have been severe declines in most indicators of biodiversity during the last 50 years (Díaz et al., 2019), and increased biotic homogenisation and alteration of ecosystem functioning globally (Newbold et al., 2018). Land-use change is particularly intense in the tropics, which harbours the most biodiversity-rich areas on Earth (Laurance et al., 2014). For instance, 219 million hectares of moist tropical forest were lost between 1990 and 2019 (Vancutsem et al., 2021), mainly driven by agriculture (Pendrill et al., 2022), highlighting a critical threat to tropical biodiversity.

One approach to determining how best to protect biodiversity while meeting increasing global food demand is the sharing/sparing land-allocation management scheme (Phalan et al., 2011). Land-sparing advocates for intensifying farming in small areas and saving space to protect natural areas. Land-sharing aims to achieve conservation by integrating wildlife-friendly features (hereafter WFF) within farmland. In tropical forests, land sparing often provides better results for the conservation of species richness and abundance than land sharing across taxa and regions (Balmford et al., 2015; Chandler et al., 2013; Edwards et al., 2021; Gilroy et al., 2014; Luskin et al., 2018; Williams et al., 2017), although the scale of the benefits can vary with landscape size or connectivity (Grass et al., 2019; Valente et al., 2022). In addition to taxonomic metrics, it is increasingly common to evaluate phylogenetic and functional diversity. These measures are linked to greater resilience to environmental changes, stability within ecosystems and the provision of ecosystem services (Chapman et al., 2018; González-Orozco & Parra-Quijano, 2023; Li et al., 2020).

There is limited evidence of how sharing/sparing impacts phylogenetic and functional diversity in the tropics. In the montane Chocó-Andes region of Colombia, land-sparing strategies consistently conserved higher levels of avian phylogenetic (Edwards et al., 2015) and functional diversity (Cannon et al., 2019) than land sharing. Additional evidence in tropical dry habitats in Mexico revealed that the conversion of forest to farmland leads to a decrease in dung beetle phylogenetic diversity and that increasing farmland heterogeneity (akin to land sharing) does not positively affect it (Alvarado et al., 2018). A key question is how are phylogenetic and functional diversity affected by sharing/sparing practices in lowland moist tropical forests, which are global epicentres of biodiversity (Barlow et al., 2018) and differ markedly from tropical montane and dry forests studied previously.

We focus on avian biodiversity in the Amazon, a priority area for conservation. Birds are good indicators of the response of multiple taxa to disturbances (Edwards et al., 2014), have a well-characterised functional space (Tobias et al., 2022) and a complete phylogeny for all extant species (Jetz et al., 2012). Using survey data from the Colombian Amazon, Bayesian hierarchical multi-species occupancy models and farmland simulations, we address three core objectives related to phylogenetic and functional diversity: (1) assess the impact of converting forests to pasture with varying levels of WFF; (2) compare the effect of land-sparing and land-sharing management practices; and (3) determine the influence of farm size on land-sharing and land-sparing comparisons.

2 | MATERIALS AND METHODS

2.1 | Study area and sampling

Three study sites were located within the Caquetá moist ecoregion of the Colombian Amazon, spanning an altitudinal range of 103–283 m.a.s.l. in the Amazonas, Putumayo and Guaviare departments. Surrounding forest cover is sparse and more fragmented in Guaviare, due to a greater proportion of forest conversion to pasture while the Amazonas and Putumayo sites are closely surrounded by varying amounts of primary and secondary forest (Figure 1). Fieldwork was conducted during the regional dry season from July to September 2019 under the national biodiversity sampling permit of Instituto Humboldt Colombia (humboldt.org.co). No ethics approval was required.

Sampling points were located in clusters of three, except two farmland clusters with only two points due to small area of pasture. Sixteen clusters were allocated to each habitat, resulting in a total

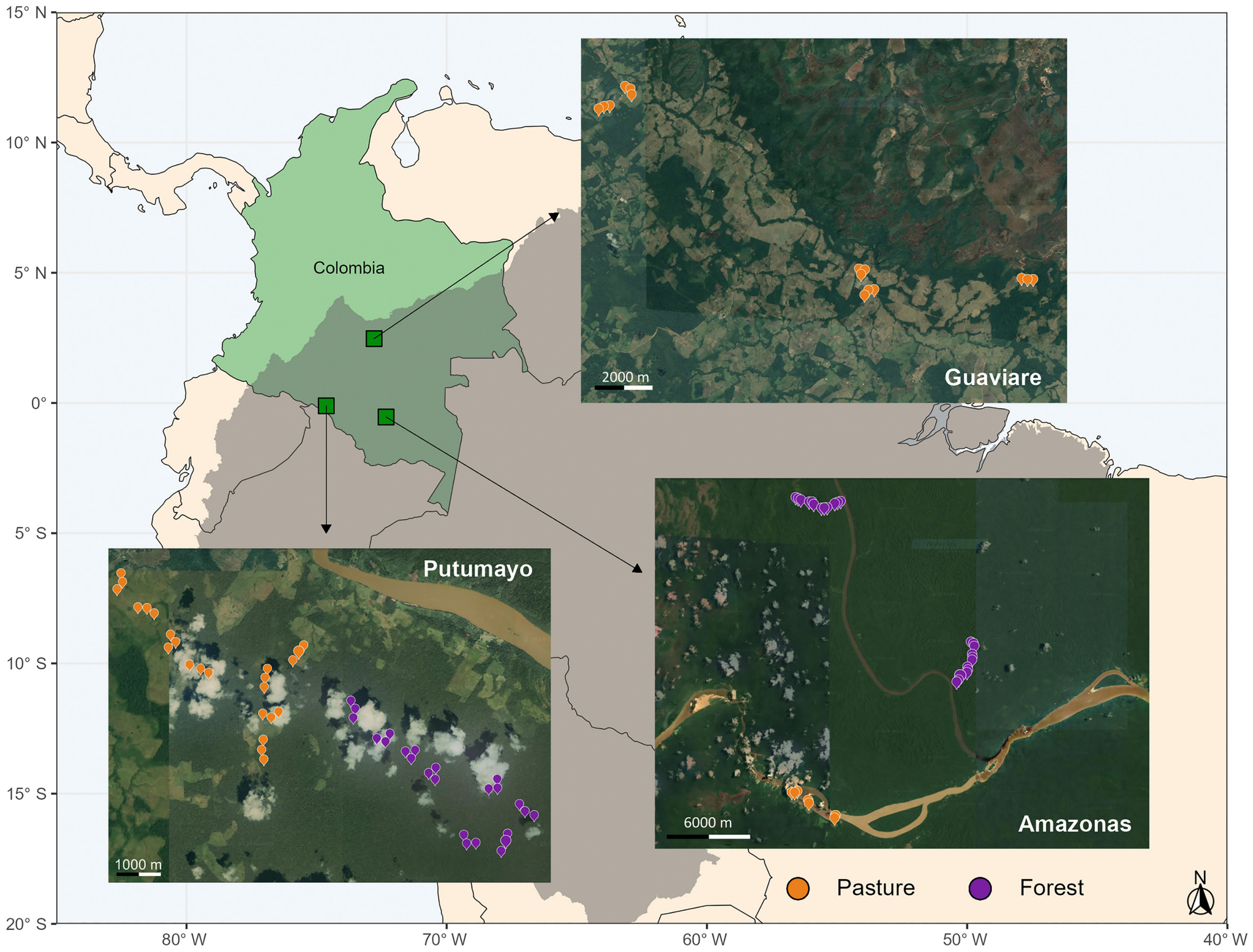

FIGURE 1 Location of the study area in Colombia. Inset maps show satellite images of the three study sites (Amazonas, Putumayo and Guaviare), with pasture (orange) and forest (purple) points. Study sites exhibit varying amounts of primary, secondary, and/or fragmented forest, resulting from differential pressures to conversion into cattle ranching at each site. The Amazon basin is shown in grey shading in the background (northern South America) map.

of 94 sampling points. Points within clusters were separated from each other (mean distance = 260.3 m, range 199.8–461.1 m) to ensure community independence (Pearman, 2002). The minimum distance between clusters was 670 m. Forest points were situated at least 200 m from a forest edge to minimise the influence of edge effects. Spatial sampling bias was unavoidable due to logistical constraints and spatially autocorrelated habitat distribution. This was accounted for with the inclusion of site random effects during modelling. A single experienced observer (JBS) performed bird sampling via 10-min repeat-visit point counts on four consecutive mornings between 06:00 and 10:00, varying the daily visitation order of points. Presence–absence of species detected by sight or hearing within a 100 m radius was registered (Bicknell et al., 2015; Hill & Hamer, 2004; Mills et al., 2023; Pearman, 2002; Socolar et al., 2019), along with continuous sound recording using a Sennheiser ME62 microphone and Tascam DR-100 digital recorder, for later identification of unknown vocalisations.

Grazed pasture and WFF (such as forest fragments, scrubland vegetation, hedgerows, isolated trees, and riparian strips) were mapped manually in the field via visual inspection within the 100 m radius in pasture points following Gilroy et al. (2014). These were used in combination with satellite imagery to quantify the proportion of WFF within a 100 m radius of each point, as the sum of WFF cover area divided by the total area of the sampling point (Figure S1). Forest points were assigned a value of zero WFF.

2.2 | Modelling species occupancy

Bayesian multispecies occupancy models were used to understand how species ($n = 280$) vary in occupancy between forest and pasture points across gradients of WFF, accounting for imperfect detection and considering factors expected to influence it (Socolar et al., 2022). These models combine two components (*occupancy* and *detection*) into a single model, and use repeated surveys to separate absences from detection errors, thus estimating species presence even in sampling units where they went undetected, an advantage over raw-data models (Tingley et al., 2020). Habitat associations are an important determinant of how birds respond to land-use change (Socolar & Wilcove, 2019); therefore, we included this by categorising the level of forest dependency of each species using their Birdlife classification (datazone.birdlife.org) into three categories: (1) low, not reliant on intact forest for breeding and foraging or not dependent, (2) medium, frequently found in forest but not reliant on intact forest in the landscape and (3) high, requiring intact forest in the landscape for breeding and foraging.

The *occupancy* component of the model included the effect of habitat, proportion of WFF, interactions between these main effects and forest dependency, as well as their species-level random intercept and slopes. We also included a site-fixed effect and random intercept term for site-species to account for possible variation in occurrence probabilities between the three study sites due to biogeographic filtering. Additionally, a cluster effect was incorporated into the model as a random intercept to account for nonindependence of clusters of points. The *detection* component includes a random effect to allow species to vary in their detectability, time of visit of a point (as a species-specific effect) and habitat class to account for differences in detectability in forest and pasture.

2.3 | Simulating bird communities

We used the posterior occupancy probabilities to predict presence/absence of each species at forest and pasture points via Bernoulli trials. Each trial represents a single species at a single point, with a probability of success determined by the predicted species occupancy from the model. Points used for prediction were forest, intensive pasture (0% WFF) and pastures of varying proportions of WFF according to observed field data (0.1, 0.2, 0.3, 0.4, 0.5 and 0.6). Using a prediction matrix of 1000 posterior draws in each case.

To compare agricultural practices, we simulated scenarios by merging predicted communities at points according to sharing/sparing schemes. These scenarios allocate land for conservation and production, with conservation represented by forest points or WFF, and production by intensive pasture. We defined two production levels: high (0.9 production, 0.1 WFF) and low (0.4 production, 0.6 WFF); that is, a low-production farm reserves 0.6 of land for conservation and the remaining for production. Farms were simulated for increasing sizes (points = 10, 50, 100, 150, 200, 250, 300, 350, 400 and 450). Land-sparing farms had a mix of forest and intensive pasture points while land-sharing farms only had wildlife-friendly pasture points (Figure 2). Predicted species-site matrices for habitats (forest, wildlife-friendly pastures) and 40 farming scenarios were used to calculate phylogenetic and functional diversity metrics.

2.4 | Phylogenetic diversity metrics

A subset of 10,000 phylogenetic trees for the observed species was downloaded from vertlife.org (Jetz et al., 2012). We calculated Faith's Phylogenetic diversity: the sum of the phylogenetic tree branch lengths of all species in a community (Faith, 1992); Mean Pairwise Distance: the average distance in the phylogenetic tree between all combinations of species pairs; and Mean Nearest

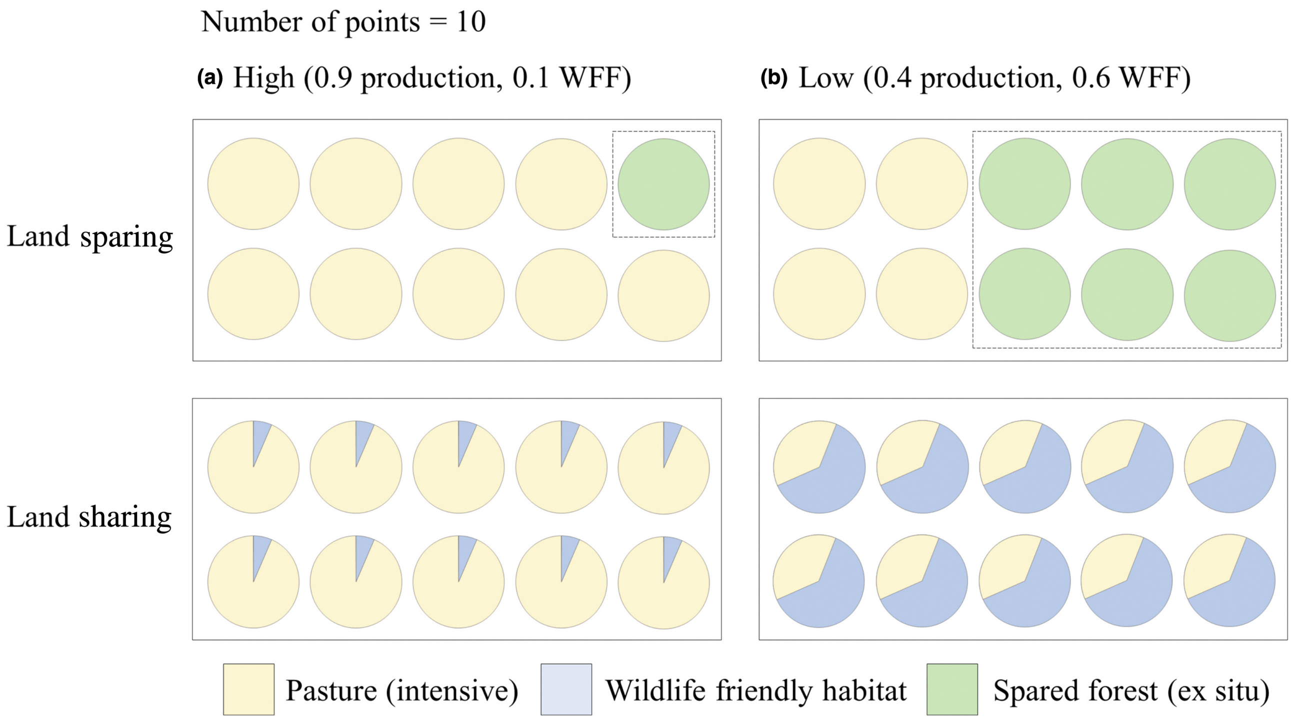

FIGURE 2 Schematic representation of land-sharing and land-sparing simulated landscapes consisting of *n* points ($n = 10$ in this example), for high (a) and low (b) production scenarios. Land sparing offsets natural forest for protection elsewhere in the region (dashed boxes) by farming at higher intensities (no in-farm WFF). Land sharing exclusively retains WFF within the farmland (boxes).

Taxon Distance: the average distance between a species and its most closely related species. As these metrics positively correlate with species richness, we used a null model approach to compute the standardised effect size (SES) of each metric (Swenson, 2014). Positive values suggest phylogenetically dispersed communities, that is, with species distributed across clades that diverged a long time ago on the evolutionary tree. Negative values suggest communities consisting of species with more recent common ancestors or phylogenetically clustered (Webb et al., 2002). Additionally, we used two metrics of evolutionary uniqueness: Evolutionary Distinctiveness and Evolutionary Distinctiveness Rarity. Species with no extant close relatives in the phylogenetic tree (i.e. more evolutionarily unique) have high evolutionary distinctiveness values (Isaac et al., 2007). Evolutionary Distinctiveness Rarity is a measure of distinctiveness adjusted by species' global range; communities with higher Evolutionary Distinctiveness Rarity contain species of conservation interest with high extinction risk due to small global ranges (Jetz et al., 2014).

2.5 | Functional diversity metrics

We compiled a data set of 17 functional traits for the observed species (Bird et al., 2020; Tobias et al., 2022; Tobias & Pigot, 2019), including 11 morphological, 2 dietary and 4 life-history traits. (Table S1). The previous was used to obtain the best quality functional space (Maire et al., 2015), reducing dimensionality using Gower distance and principal coordinate analysis, following Palacio et al. (2022). The resulting multidimensional functional space was used to compute a set of four indices (scaled 0–1). Functional richness: the total space volume occupied by a species assemblage. Higher values suggest a greater range of functional traits and hence greater utilisation of resources. Functional evenness: the regularity of species abundance distribution within the trait space, which is related to resource use efficiency. Functional divergence: accounts for the abundance of species with extreme or unique functional traits. Functional Dispersion: the abundance-weighted deviation of species trait values from the centre of the functional trait space of an assemblage. Additionally, the SES of the four functional diversity indices were computed using a null model approach. Positive values show that functional indices are greater than expected by chance leading to functional overdispersion, negative values indicate functional clustering and values close to zero imply that stochastic processes lead the community assembly (Swenson, 2014).

2.6 | Computation details

Occupancy models were fitted in Stan (Stan Development Team, 2023) using the R package *flocker* (Socolar & Mills, 2022) using standardised and centred variables and weakly informative priors that avoid densities strongly concentrated around 0 and 1 on the probability scale; with 4 chains each running for 1000 iterations, for a total of 4000 post-warmup draws. Phylogenetic metrics were calculated using a randomly sampled tree for each posterior iteration using the *PhyloMeasures* package (Tsirogiannis & Sandel, 2016). Evolutionary Distinctiveness in the *picante* package using the fair proportions method (Kembel et al., 2010) and Evolutionary Distinctiveness Rarity using species global range values from Tobias et al. (2022). Functional space reduction was computed in the package *mFD* (Magneville et al., 2022) and metrics in *fundiversity* (Grenié & Gruson, 2023; Villéger et al., 2008). Matrix randomisations for standardised effects size metrics were performed 1000 times using the function *RandomizeMatrix* in *picante* (Kembel et al., 2010). All analyses were performed in the R software version 4.2.1 (R Core Team, 2022).

2.7 | Differences in predicted metrics

We compared metrics by subtracting predicted distributions. For habitats, we computed the differences as forest minus pasture. For farming scenarios, land sparing minus land sharing. Differences were summarised using percentage differences (median and 95% Bayesian credible intervals), to show how higher or lower is a metric from the baseline (forest or land-sparing). We used the probability of direction index of effect existence (Makowski et al., 2019) which expresses the probability that a difference is strictly in the direction determined by the median percentage difference sign. For ease, when referring to metrics in the Section 3, we only use median values.

3 | RESULTS

3.1 | Phylogenetic and functional diversity across habitats

Differences in predicted metrics between forest and pasture diminish with higher proportions of WFF (Figure 3). However, forest habitats consistently showed higher values for Faith's phylogenetic diversity (19.03% to 33.76%, Figure 3a), evolutionary distinctness (30.84% to 48.37%, Figure 3g) and evolutionary distinctness rarity (68.30% to 117.06%, Figure 3h). Conversely, mean nearest taxon distance is lower in forests (−13.87% to −23.96%, Figure 3c). Mean pairwise distance differences were minimal (<2%) between habitats (Figure 3e). SES Faith's phylogenetic diversity indicated a clustered community assembly in forests (median = −2.07), that is not observed across wildlife-friendly pastures (Figure 3b). Similar patterns were observed for SES mean pairwise distance and SES mean nearest taxon distance, being negative in forests but positive or close to zero in pastures (Figure 3d,f).

Functional richness, evenness and dispersion were slightly lower in forests compared to pastures (−5.19% to −2.96% for richness, −18.60% to −20.70% for evenness and −13.61% to 14.99% for

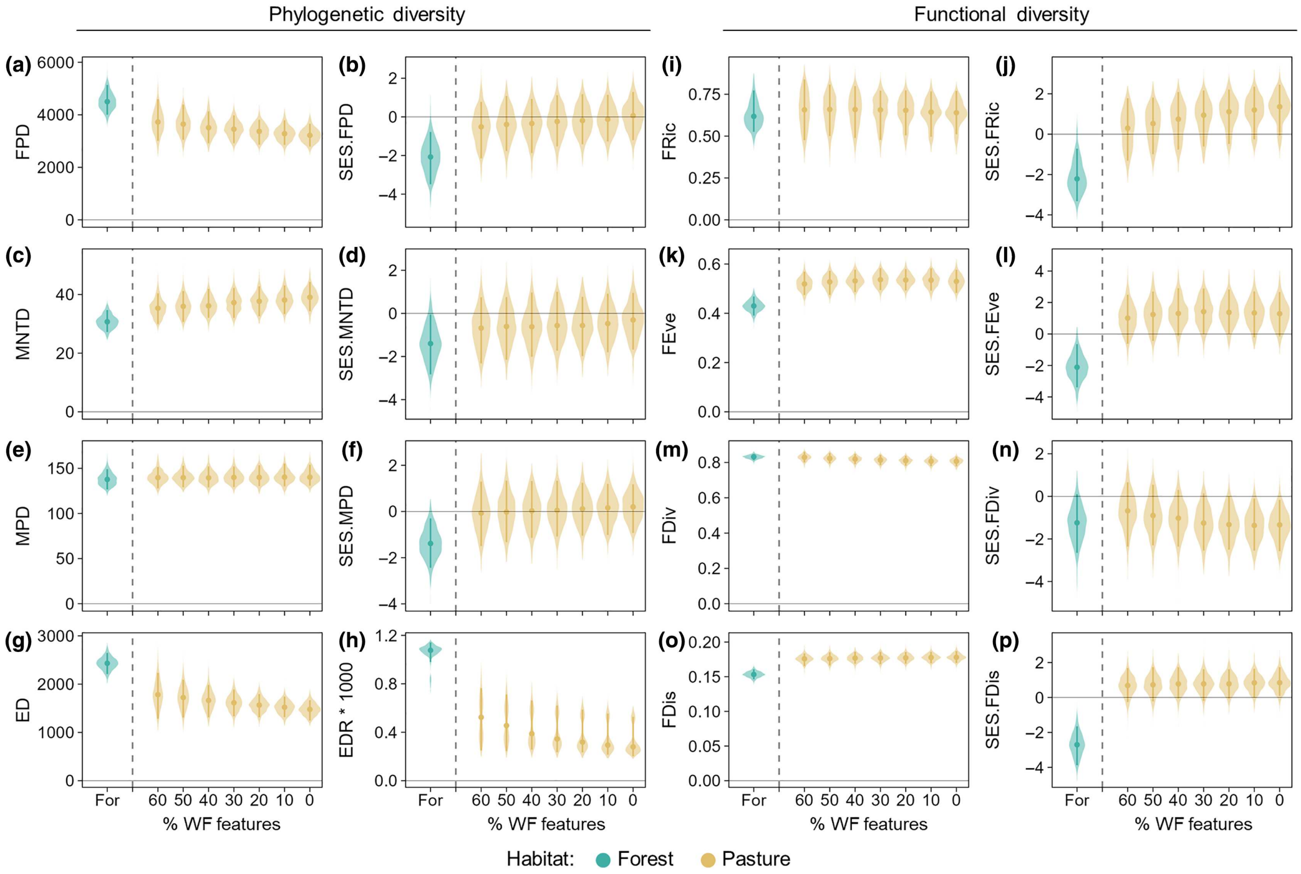

FIGURE 3 Phylogenetic (a–h) and functional (i–p) diversity metrics and their standardised effect size values (SES) for predicted communities in forest and pasture points across levels of WFF. (a, b) Faith's Phylogenetic diversity (FPD). (c, d) Mean nearest taxon distance (MNTD). (e, f) Mean pairwise distance (MPD). (g) Evolutionary distinctness (ED). (h) Evolutionary distinctness rarity (EDR). (i, j) Functional richness (FRic). (k, l) Functional evenness (FEve). (m, n) Functional divergence (FDiv). (o, p) Functional dispersion (FDis). Violin plots display frequency distributions of indices from 1000 simulations, with point median and 95% Bayesian credible interval line ranges.

dispersion, Figure 3i,k,o), suggesting dominance of specific functional traits in forests. Functional divergence remained relatively low and consistent across habitats (<3%, Figure 3m), indicating high trait similarity across species. However, SES values for all functional diversity metrics were negative in forests, indicating functional clustering, which was not observed across wildlife-friendly pastures (Figure 3j,l,n,p). Detailed comparisons in Table S2 and Figure S2.

3.2 | Impacts of land-sharing and land-sparing

Predicted values of phylogenetic and functional diversity indices varied throughout management practices and production levels for simulated farms of 100 points (Figure 4). Land sparing retained more Faith's phylogenetic diversity than land sharing, values were 34.80% and 25.20% higher at high and low production levels, respectively (Figure 4a). Similarly, evolutionary distinctness was 49.12% and 36.88% higher (Figure 4g), evolutionary distinctness rarity was 68.34% and 45.63% higher (Figure 4h), and functional richness was 22.50% and 18.93% higher (Figure 4i). In contrast, mean nearest taxon distance was lower in forest than pasture at high (−16.19%) and low (−10.25%) production levels (Figure 4c). Significance was achieved for all of the previous with probabilities of direction higher than 97.5% (Table S3). Marginal differences were noted for the remaining metrics, across management scenarios and production levels (Figure 4e,k,l,o). SES values for phylogenetic (Figure 4b,d,f) and functional diversity (Figure 4h,l,n,p) fell within the ±1.96 range, indicating random community assembly in simulated farmlands.

3.3 | Effect of size in comparisons of land-sharing and land-sparing

The differences in predicted phylogenetic and functional diversity metrics between management practices become smaller as the number of points under comparison increases (Figure 5). There is a major overlap in the distribution of predicted metrics at high and low production levels. However, land sparing consistently retains significantly higher predicted values of indices at increasing sizes (Figure S3), except for mean nearest taxon distance which was lower in land sparing than in land sharing (Figure 3c). SES metrics were not affected by size (Figure 5b,d,f,j,l,n,p).

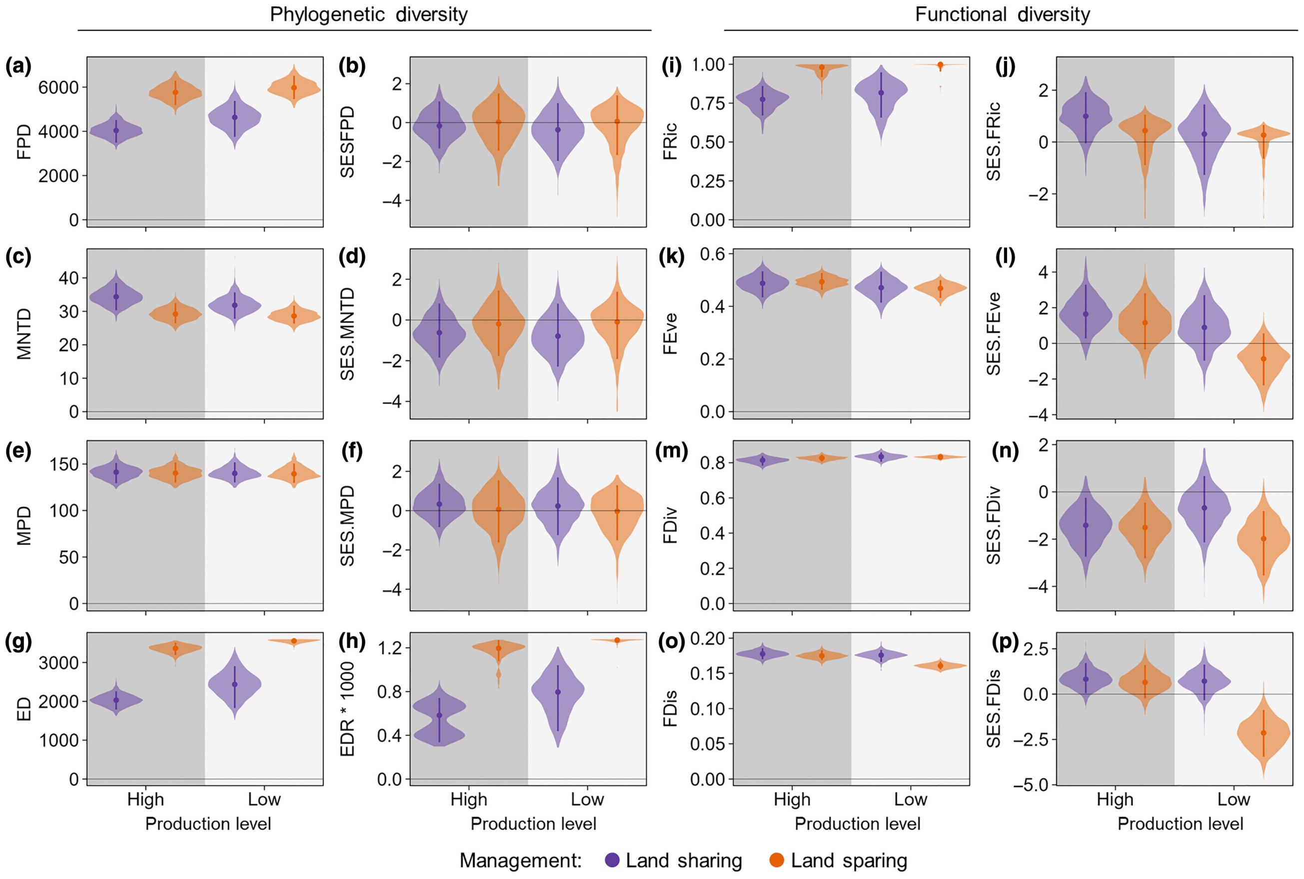

FIGURE 4 Phylogenetic (a–h) and functional (i–p) diversity indices and their standardised effect sizes (SES.) for simulated bird communities on agricultural scenarios of 100 points for land-sparing (orange) and land-sharing (purple) at high (grey background) and low (white background) production levels. (a, b) Faith's phylogenetic diversity (FPD). (c, d) Mean nearest taxon distance (MNTD). (c, d) Mean pairwise distance (MPD). (g) Evolutionary distinctness (ED). (h) Evolutionary distinctness rarity (EDR). (i, j) Functional richness (FRic). (k, l) Functional evenness (FEve). (m, n) Functional divergence (FDiv). (o, p) Functional dispersion (FDis). Violin plots display frequency distributions across 1000 iterations, with point median and 95% Bayesian credible interval line ranges.

4 | DISCUSSION

Understanding how different agricultural land-use practices affect biodiversity is crucial for effective conservation. We found that land sparing consistently retained higher levels of avian Faith's phylogenetic diversity, Functional richness, and evolutionarily distinct lineages, and did so across a range of hypothetical landscape sizes. Investing in natural habitat protection along with sustainable high-yield agriculture therefore appears to represent an effective strategy for lowland tropical forest conservation.

4.1 | Impacts of conversion from forest to wildlife-friendly pastures

Forest loss had contrasting impacts on phylogenetic and functional diversity in Amazonian lowland bird communities. Faith's phylogenetic diversity, Evolutionary distinctness and Evolutionary distinctness rarity decreased, consistent with previous evidence of loss due to agricultural conversion (Chapman et al., 2018; Frishkoff et al., 2014; Kusuma et al., 2018). However, the marginal differences in functional metrics after conversion indicate minimal overall impact on the structure of functional space, mirroring findings for Afrotropical birds, where land-use change reduced species richness without affecting the functional structure of communities (Rurangwa et al., 2021).

The small difference in functional richness may be due to hyperdiversity in the Amazon, where high functional redundancy offsets the loss of species' traits by the prevalence of other functionally similar species (Nunes et al., 2021). However, the effects of such functional simplification might worsen after accumulation through time (Reich et al., 2012; van der Plas, 2019). Notably, SES phylogenetic and functional diversity metrics were consistently negative in forests, suggesting more functionally and phylogenetically similar species (specialists), while pastures host species with a broader suite of functional traits across lineages (generalists).

Wildlife-friendly pastures fail to support forest-dependent species, especially evolutionary lineages of high conservation concern (Figure 3g,h) that were absent from pastures regardless of WFF proportion (Figure S4). This suggests that conversion to pastures

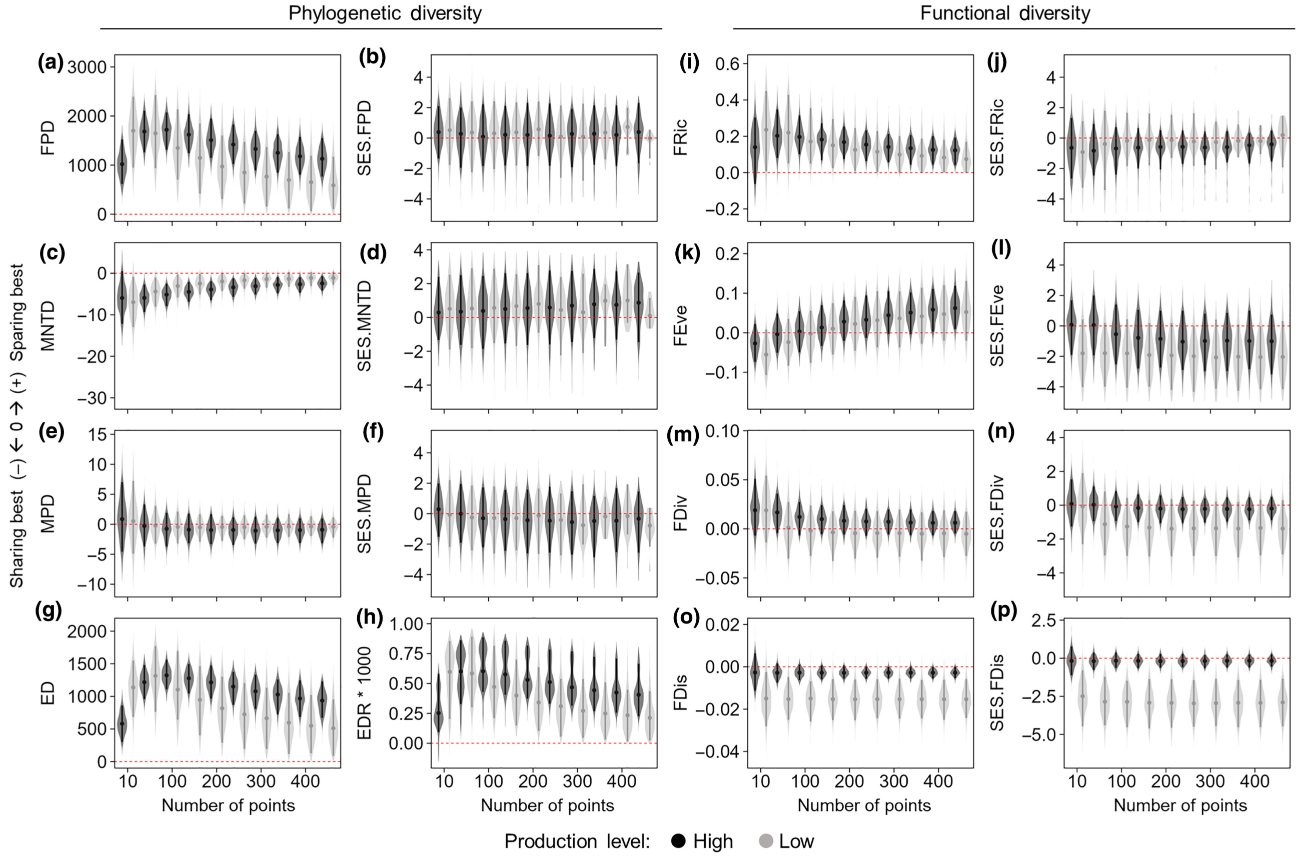

FIGURE 5 Comparisons in phylogenetic (a–h) and functional (i–p) diversity indices and their standardised effect sizes (SES.) for simulated bird communities across land-sharing and land-sparing scenarios. Each plot shows the subtraction between land-sparing minus land-sharing metrics across an increasing number of simulation points, at high (dark grey) and low (light grey) production levels for (a, b) Faith's phylogenetic diversity (FPD). (c, d) Mean nearest taxon distance (MNTD). (e, f) Mean pairwise distance (MPD). (g) Evolutionary distinctness (ED). (h) Evolutionary distinctness rarity (EDR), (i, j) Functional richness (FRic). (k, l) Functional evenness (FEve). (m, n) Functional divergence (FDiv). (o, p) Functional dispersion (FDis). Violin plots display frequency distributions across 1000 simulations, with point median and 95% Bayesian credible interval line ranges.

leads to greater community dominance of generalist species that are less evolutionarily distinct and have larger global ranges (Edwards et al., 2015; Valente et al., 2022). Retention of wildlife-friendly pastures appears insufficient to secure the protection of species with high evolutionary distinctness, as well as functional traits of forest dependents. Failure to secure such species could have negative implications for the delivery of functions and services over long timescales (Leitão et al., 2016) and is achieved only by protecting native forest habitats.

4.2 | Impacts of land sparing and land sharing

Phylogenetic metrics were affected by sharing/sparing practices and production levels, high production led to greater declines due to smaller proportions of land being allocated for protection. Land sparing conserved more Faith's Phylogenetic Diversity relative to land sharing, while its SES showed no variation, implying that predicted differences between land allocation schemes are driven by the difference in species richness. The benefits of land sparing became more apparent for Evolutionary Distinctness and Evolutionary Distinctness Rarity, revealing that an important amount of evolutionary uniqueness might be lost under land-sharing practices. Prioritising these metrics helps to protect more of the tree of life, particularly by securing the persistence of restricted-range evolutionarily unique species (Molina-Venegas, 2021). Mean Pairwise Distance and its SES remained unchanged across sharing/sparing, while Mean Nearest Taxon Distance was reduced in land sharing, pointing to a loss of evolutionarily recent taxa. These contrast with findings in the Colombian Chocó-Andes region, where lower Mean Pairwise Distance in land sharing than land sparing evidenced the disproportionate loss of deep evolutionary relationships within the phylogenetic tree (Edwards et al., 2015).

Functional Diversity metrics showed limited variation across simulated scenarios, except Functional Richness which was ~20% lower in land sharing, supporting previous findings (Cannon et al., 2019; Edwards et al., 2021). Overall, Functional Diversity metrics suggest that the functional structure is not altered much by agricultural practices in these landscapes; species are tightly packed within the functional space (FDis) and have an even distribution (FEve) and high redundancy (FDiv) of functional traits, suggesting high resilience to disturbances (Laliberté & Legendre, 2010).

Land-sharing practices cannot maintain the levels of biodiversity found in land sparing because they consist only of wildlife-friendly pastures and do not secure forest areas, which are irreplaceable for many species. Conversely, land sparing achieves higher biodiversity value by retaining both forest and pasture communities, which differ according to SES metrics across habitats (Figure 3). Therefore, securing contiguous forest protection through land-sparing practices remains superior to conserving overall community phylogenetic and functional diversity.

4.3 | Influence of size across sharing/sparing simulations

Faith's Phylogenetic Diversity, Evolutionary Distinctness, Evolutionary Distinctness Rarity and Functional Richness remained higher under land sparing regardless of farm size, although, at the largest sizes the relative benefit was reduced. The lack of forest points in land sharing leads to very low predicted occupancy of forest-dependent species, meaning that a large landscape (consisting of more points) is needed for those species to occur in at least part of the landscape, albeit at potentially very low abundances. On the other hand, land-sparing landscapes rapidly reach their maximum as the number of management units increases. Thus, whether a small or large amount of land is dedicated to these strategies, the benefits of land sparing outweigh those of land sharing. Maintaining over 40% of forest patches in agricultural landscapes in the tropics is key for species protection (Arroyo-Rodríguez et al., 2020). This points to the adoption of land-sparing practices for biodiversity conservation even at wide spatial scales.

4.4 | Study limitations

We assumed that the proportion of land under production translates equally into yield in both sharing and sparing. Within wildlife-friendly pastures, barbed-wire fencing usually meant that patches of habitat were not accessible to cattle and thus unlikely to improve yield. However, in other farming systems, land-sharing features can enhance yield by provisioning ecosystem services such as shading or pest biocontrol (Grass et al., 2019). In cases where land-sharing practices can be implemented without incurring a yield cost relative to intensive farming, both sparing and sharing strategies could potentially be applied simultaneously without impacting overall food production. Accounting for yield data and type of farming in future simulations might help to explore such potentials (Phalan, 2018).

Sparing scenarios also rely on the assumption that forest is effectively spared within contiguous blocks, but if the spared forest is of poor quality due to fragmentation effects (Laurance et al., 2014) then the potential benefits would likely reduce relative to sharing. Equally, sharing assumes effective protection of patches within farmland, but these are often at risk from seasonal fires (Cammelli et al., 2020), which could dramatically reduce their value (Barlow & Silveira, 2009). Forest sampling points were located within contiguous protected areas ensuring minimal edge effects, which indicates that the conservation of larger forests provides greater benefits.

The distance from forest to farmed points was not accounted for. In the Andes, the presence of contiguous forests near pastures reduced the apparent benefits of land sparing over land sharing. Yet, land sparing was always superior to sharing for the conservation of avian taxonomic (Gilroy et al., 2014), phylogenetic (Edwards et al., 2015) and functional (Cannon et al., 2019) diversity. It has been argued that applying land-sharing practices at a wide scale can create a more wildlife-friendly agricultural matrix for biodiversity (Kremen, 2015). However, Birch et al. (2024) found that accounting for the amount of WFF in the broader landscape does not have detectable effects on predicted occupancy in lowland tropical forests, therefore this component was not included in our model. Finally, although birds are good indicators of how biodiversity responds to disturbances, the impacts of land sharing/sparing for other taxonomic groups was not explored and might vary.

4.5 | Management implications and conclusions

Landscape management schemes in the tropics should prioritise land sparing because forest protection offers major benefits towards biodiversity conservation, global warming mitigation and carbon neutrality targets (Mackey et al., 2020). Sparing secondary forests is also highly beneficial (Hughes et al., 2020), recovering 90% of primary forest taxonomic diversity in the Brazilian Amazon (Lennox et al., 2018), and equivalent functional and phylogenetic diversity in 15–30 years in the Colombian Andes (Edwards et al., 2021). Primary and secondary forest protection is particularly valuable in lowland tropical regions highly prone to agricultural expansion and deforestation, such as the Congo Basin, Borneo, New Guinea, and the Amazon (Potapov et al., 2022). Intensification in land-sparing schemes needs to be sustainable to avoid the long-term negative impacts on soil, water, and other ecosystem services associated with more industrial approaches (Cassman & Grassini, 2020).

Land-sparing and land-sharing practices might support different aspects of biodiversity and be complementary conservation initiatives. Ultimately, the ideal management strategy will depend on local contexts and goals. Further research using similar simulation-based approaches could explore these aspects across various habitats and regions. Given evidence of accelerated conversion of forests into cattle grazing within protected areas in the study area (Murillo-Sandoval et al., 2023), land sparing needs to be simultaneous with actions halting the expansion of agriculture into natural habitats and restart farming on abandoned lands. In Colombia, there has been an increase in policies on biodiversity conservation with a socio-ecological approach to improve the sustainable use of land and natural habitat protection, for instance by promoting the intensification of cattle grazing through silvopasture (Echeverri et al., 2023), which could ease the adoption of land sparing. We argue that land-sparing rather than land-sharing represents a more effective method of minimising the impacts of agriculture in lowland tropical forests, by protecting undisturbed and regenerating forest in conjunction with sustainably intensifying productivity within existing farmland. Government and business policies need to secure both actions simultaneously.

AUTHOR CONTRIBUTIONS

David P. Edwards, Giovanny Pérez, Simon C. Mills and James J. Gilroy conceived the ideas and designed the methodology. Jacob B. Socolar, Diego E. Martínez-Revelo and Torbjørn Haugaasen collected the data. Giovanny Pérez and Simon C. Mills analysed the data. Giovanny Pérez led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflicts of interest to declare.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.n5tb2rc40 (Pérez, 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Distribution of observed proportions of wildlife-friendly habitat features within pasture points ($n=46$).

Figure S2. Percentage difference between the posterior predicted values of metrics in forest and wildlife-friendly pasture of varying proportions for phylogenetic (A–E) and functional (F–I) diversity metrics.

Figure S3. Percentage difference between the posterior distribution of land-sparing and land-sharing predicted phylogenetic (A–E) and functional (F–I) diversity metrics, at high (yellow) and low (blue) production levels.

Figure S4. Phylogenetic distribution of 280 observed Amazonian birds in forest and pasture habitat points with varying proportions of wildlife-friendly features within (60%, 10% and 0%) Coloured tiles indicate each species' mean estimated occupancy probability within habitats.

TableS1. Birds functional traits: Cat: Categories: M: Morphological, D: Dietary, F: Foraging behaviour, L: Life history. Type of variable: C: continuous, T: categorical.

Table S2. Summary of comparisons for predicted phylogenetic and functional diversity metrics between habitats.

Table S3. Summary of comparisons for predicted phylogenetic and functional diversity metrics computed as land-sparing minus land-sharing.

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