Article:

Birch, B.D.J. orcid.org/0000-0003-1740-264X, Mills, S.C. orcid.org/0000-0002-1880-8425, Socolar, J.B. orcid.org/0000-0002-9126-9093 et al. (3 more authors) (2024) Land sparing outperforms land sharing for Amazonian bird communities regardless of surrounding landscape context. Journal of Applied Ecology, 61 (5). pp. 940-950. ISSN 0021-8901

https://doi.org/10.1111/1365-2664.14596

Received: 25 May 2023 | Accepted: 3 January 2024

DOI: 10.1111/1365-2664.14596

Journal of Applied Ecology
BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Land sparing outperforms land sharing for Amazonian bird communities regardless of surrounding landscape context

Benjamin D. J. Birch[1] | **Simon C. Mills**[1] | **Jacob B. Socolar**[2,3] | **Diego E. Martínez-Revelo**[4] | **Torbjørn Haugaasen**[2] | **David P. Edwards**[1,5]

[1]Ecology and Evolutionary Biology, School of Biosciences, University of Sheffield, Sheffield, UK

[2]Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences, Ås, Norway

[3]NCX, Inc., San Francisco, California, USA

[4]Grupo de Investigación en Ecología de Agroecosistemas y Hábitats Naturales (GEAHNA), Departamento de Biología, Facultad de Ciencias Naturales y Exactas, Universidad del Valle, Cali, Colombia

[5]Department of Plant Sciences and Conservation Research Institute, University of Cambridge, Cambridge, UK

Correspondence
Benjamin D. J. Birch
Email: bjdbirch1@gmail.com

David P. Edwards
Email: dpe29@cam.ac.uk

Funding information
Norges Forskningsråd, Grant/Award Number: 208836; Natural Environment Research Council, Grant/Award Number: NE/R017441/1

Handling Editor: Marc-André Villard

Abstract

1. Two strategies are central to the debate regarding agricultural development: one integrates farming and conservation (land sharing), and the other separates farming and conservation, intensifying production to allow the offset of natural habitat (land sparing). The role of wildlife-friendly habitat in the wider surrounding landscape (landscape wildlife friendliness (WF)) in promoting farmland diversity is potentially an unexplored benefit of land sharing.
2. We sampled birds across primary forests and cattle pastures in the western Amazon, where terrestrial biodiversity peaks. We tested the hypothesis that increased landscape WF will lead to increased species richness (SR) on farmland, even at low levels of 'on-farm' wildlife-friendly habitat (farm WF).
3. We show that while there is a minor increase in SR linked to increased levels of landscape WF, a large component of the avian community is functionally absent. Most forest-dependent species are missing from pasture, even at high levels of farm WF. For these species, the preservation of blocks of contiguous forest under land sparing is vastly superior.
4. We modelled both strategies under different levels of production. Land sparing always retained significantly higher SR than land sharing, regardless of the level of landscape WF.
5. *Synthesis and applications*. Landscape wildlife friendliness (WF) provided through land sharing is of limited benefit to many tropical forest-dependent species that are unable to move across or utilise pasture, even at high levels of farm and landscape WF. To ensure the persistence of these species, policymakers should urgently implement sustainable intensification mechanisms to increase farmland productivity while enabling the protection of large blocks of spared natural habitat.

KEYWORDS
agricultural sustainability, agroecosystems, birds, cattle farming, deforestation, fragmentation, habitat loss, land-use planning

---

1 | INTRODUCTION

The conversion of natural habitats to agriculture is the greatest threat to terrestrial biodiversity (Fischer et al., 2008). Currently, around 40% of the Earth's land surface is under production, with about two-thirds used for grazing livestock, making farmland the single greatest land use globally (Cannon et al., 2019; Lamb et al., 2016). Projections show an increase in the demand for agricultural products of 70%–100% by 2050, in conjunction with human population growth (Kamp et al., 2015; Zabel et al., 2019). Balancing conservation with farming is critical, with the future of global biodiversity firmly in the hands of agricultural policy makers (Fischer et al., 2008; Winkler et al., 2021).

Central to the debate surrounding agricultural development and biodiversity protection are two contrasting land-allocation strategies (Green et al., 2005). Land sharing integrates farming and conservation on the same land through less intensive production techniques. This allows some biodiversity to be maintained throughout the farmed landscape, but requires a greater land-use footprint. Land sparing separates farming and conservation, and production is intensified to require a smaller land-use footprint, allowing the protection of remaining natural habitats from agricultural conversion. These strategies are not mutually exclusive, and both have key roles to play in agricultural policy (Fischer et al., 2014). It has also been suggested that they may play complementary roles, with land sharing promoting landscape-level connectivity between areas conserved through land sparing (Fischer et al., 2014; Gilroy & Edwards, 2017; Grass et al., 2019; Kremen, 2015).

Across the tropics, land sharing supports substantial amounts of biodiversity through increased habitat complexity, as well as sustaining relatively high yields through the provision of pest control and other beneficial ecosystem services (Gilroy et al., 2014). Furthermore, land sharing can promote metapopulation dynamics by facilitating dispersal across landscapes, thus enabling rescue effects; both of which are essential to sustain species populations in fragmented habitats (Grass et al., 2019; Van Schmidt & Beissinger, 2020). However, low-intensity land-sharing practices also involve removing some land within farmed landscapes from production, thereby promoting further encroachment into pristine habitats to meet production demands (Green et al., 2005). Moreover, evidence shows that many species of high conservation importance, including forest specialists and endemics, do poorly even in shared landscapes with high levels of wildlife friendliness (WF) (Abrahamczyk et al., 2008; Edwards et al., 2021; Williams et al., 2017).

Many empirical studies reveal that land sparing is best for biodiversity and carbon capture (Balmford, 2021), with proximity to undisturbed natural habitat playing a pivotal role in governing species assemblages in agricultural landscapes and thus the apparent benefits of land sharing. For example, in the Western Colombian Andes, land sharing becomes increasingly inferior to land sparing at greater distances from contiguous forest, causing reductions in species richness (SR) of birds and dung beetles (Gilroy et al., 2014), as well as for functional and phylogenetic diversity of birds (Cannon et al., 2019; Edwards et al., 2015, 2021). As a result, many species of conservation importance only persist in farmed landscapes where large amounts of natural habitat occupy adjacent areas. To date, research has focused on the linear distance to contiguous forest, overlooking the influence of the intermediate habitat matrix on farmland diversity; a key argument for land sharing (Grass et al., 2019). A matrix providing important feeding, breeding or sheltering resources to fauna could facilitate greater movement across landscapes, thus enabling the persistence of species within land-sharing farmland (Grass et al., 2019; Reider et al., 2018).

Here, we examine how the proportion of WF in the landscape habitat matrix influences biodiversity under different land-sharing and land-sparing scenarios, using birds as an indicator taxon due to their broad range of sensitivities to human disturbances (Moura et al., 2016). We use field data collected from the Colombian Amazon, which constitutes part of the western Amazon, one of the world's most biodiverse ecosystems and the largest remaining area of intact tropical forest spanning ~1.5 million km^2 (Lessmann et al., 2019). We model bird communities across low-intensity cattle pastures, with varying levels of 'on-farm' WF (the proportion of wildlife-friendly habitat within a 100 m radius of farm points), and assess the influence of landscape-level WF (the proportion of forest cover within a 1000 m radius of farm points). The resulting model is then used to predict species responses across a range of land-sharing and land-sparing scenarios that vary in production output and landscape WF. We assess whether the proportion of WF habitat in the wider landscape affects farmland species occupancy, and predict that higher levels of landscape WF will lead to more species being present on even high-production farms.

2 | MATERIALS AND METHODS

2.1 | Study areas

We sampled three study areas in the departments of Amazonas, Putumayo and Guaviare, Colombia (Figure S1), which reside in the Caquetá Moist ecoregion of Amazonia, and span an altitudinal range of 103–283 m a.s.l. (Sánchez-Cuervo et al., 2012). We focused on low-intensity cattle farming, which constitutes most farmed land in our study areas, and is reflective of broader land-use patterns across Colombia where pastures cover over a third of the country's land area (Lerner et al., 2017). The Amazonas (Puerto Santander, PSP1-PSP7) and Putumayo (Puerto Leguizamo, PLP1-PLP24) sites are closely surrounded by varying amounts of primary and secondary forest, while the Guaviare (San José del Guaviare, SGP1-SGP15) site has sparser, more fragmented, surrounding forest cover resulting from a greater proportion of pasture conversion (Figures S1 and S2).

We sampled bird communities at points arrayed within 400 × 400 m squares, summing to 16 squares in farmland and 16 squares in contiguous forest (Figure S1). All forest points were situated within primary forest deemed to be unaffected by edge effects. Squares were randomly allocated within study sites, and a minimum spacing of 300 m was applied for squares within different habitats and 400 m for squares within the same habitat.

All fieldwork was conducted under the national collection permit of Instituto Alexander von Humboldt. No ethical approval was required for this study.

2.2 | Bird surveys

All sampling was conducted by JBS during the dry season running from July to September 2019. Bird communities were sampled at 94 points (48 forest, 46 pasture) using repeat-visit point counts. Following Gilroy et al. (2014), points were placed in clusters of three, save for two clusters that had only two points due to the small farm size. Within a cluster, points were spaced in a triangular pattern 200 m apart from one another, while between-cluster distances exceeded 600 m. We recorded all individual birds detected within a 100 m radius based on previous evidence for the grain of spatial community turnover in tropical forests (Hill & Hamer, 2004). Each point was visited between 06:00 AM and 12:00 PM on four consecutive mornings (10-min duration), avoiding adverse conditions such as strong wind or rain. Routes between sampling points were varied each day to ensure each point was visited at varying times throughout the sampling window. Species detected within a 100 m radius of the point were recorded, excluding flyovers and nonbreeding migrants (as per Gilroy et al., 2014). We continuously recorded sound during all point counts using a Sennheiser ME62 microphone and Tascam DR-100 digital recorder for later identification of unknown vocalisations. Unknown vocalisations were identified in consultation with multiple experts and online recording archives.

2.3 | Habitat variables

Squares within farmland showed mixed levels of remnant forest habitat, including forest fragments, riparian strips, scrubland vegetation, isolated trees and hedgerows or other woody growth with three-dimensional structure. We classed these features as wildlife-friendly habitat, and visually mapped them in the field within an estimated 100 m radius of the points. Grazed pasture and any other non-pasture habitats were also mapped following Gilroy et al. (2014). These maps were used in combination with Esri® satellite imagery to quantify the proportion of wildlife-friendly features within a 100 m radius of each point using QGIS (2021). Any other habitats such as roads and sheds were excluded from this calculation. All forest points were assigned a farm WF value of zero.

WF was also calculated for a 1000 m radius around each point using Landsat data from 2019 (Hansen et al., 2013). Maps were imported into R version 4.0.3 using the python Google Earth Engine API via the Reticulate package (Allaire et al., 2017; Gorelick et al., 2017) and manipulated using the sf package (Pebesma, 2018) (Figure S2). Landscape WF was calculated as the total proportion of forest cover in a 1000 m radius surrounding each point (including the 100 m radius farmed area), with a value of >50% pixel coverage classified as forest. To confirm that Landsat-generated maps were consistent with forest cover at the time of sampling, we made visual comparisons with satellite imagery from the date of sampling, finding no cases of mismatch between the Landsat imagery and forest cover at the time of sampling. Surrounding forest cover was calculated for radii of 500–5000 m around each point by increments of 500 m, but 1000 m was deemed the most suitable for this study, balancing sufficient variation between sampling locations (Figure S3), with sufficient spatial breadth to reflect landscape-scale patterns (Wu, 2018). All forest points were assigned a landscape WF value of zero.

2.4 | Statistical analysis

2.4.1 | Modelling species responses to farm (100 m radius) and landscape (1000 m radius) WF

Hierarchical Bayesian models were used to assess individual species responses to farm and landscape WF. Unique bird species were categorised according to their Birdlife forest dependency (FD) classification (BirdLife International, 2021) for all but one species, *Ortalis guttata*, which had a Birdlife FD status of 'unset'. We categorised this species ourselves using the Birds of Peru field guide (Schulenberg et al., 2010). The categories consisted of low FD (merging of Birdlife's 'low' and 'not normally found in forest' categories; low reliance on intact forest for breeding and/or foraging), medium FD (frequently found in forest but not reliant on intact forest in the landscape) and high FD (require intact forest in the landscape for breeding and/or foraging). We chose to classify species in this way to allow for pooling of variance across groups that are a priori expected to have broad differences in how they respond to land-use change and WF, as well as allowing us to identify potentially important compositional changes, that is, the replacement of forest specialists by generalists (Phalan et al., 2011).

We fitted hierarchical detection-occupancy models to make inferences about occupancy across gradients of habitat (forest vs. pasture) and WF in pasture (local and landscape-scale) while accounting for imperfect detection and including covariates that were expected to influence detection (Dorazio & Royle, 2005; Gilroy et al., 2014; Socolar et al., 2022). The occupancy component of the model includes terms that capture how species' occupancy varies between pasture and forest (habitat), as well as with variation in the pasture points' local- and landscape-scale WF. As responses are expected to be strongly structured according to a species' level of FD, separate fixed effects are estimated for each FD category. The occupancy model is thus:

$$\psi_{i,k} \sim \alpha_{\text{site}[i]} + \gamma_{\text{site}[i],k} + \beta_{0,k,\text{dep}[k]} + \beta_{1,k,\text{dep}[k]}\text{habitat}_i$$
$$+ \beta_{2,k,\text{dep}[k]}\text{wf\_lscape}_i + \beta_{3,k,\text{dep}[k]}\text{wf\_point}_i,$$

where *i* indexes points, *k* indexes species, *site* indexes which of our three sites a point belongs to, and *dep* indexes which of the three FD classes a species belongs to. Occupancy can thus vary systematically between sites, by species, and, to account for possible variation in occurrence probabilities between the three study areas due to biogeographic filtering, by site × species combination. The effects of habitat and landscape WF are estimated separately for each FD class and are also able to vary across species. All species-specific effects, as well as the site × species intercept term, were fitted as normally distributed random effects.

The detection component of the model included a random effect on species, allowing species to vary in their overall detectability, the time of day a point was visited (as a species-specific effect), as well as by broad habitat class to account for systematic differences in detectability in pasture and in forest. The detection model is therefore:

$$\theta_{i,j,k} \sim \delta_{0,k} + \delta_{1,k}\text{time}_{ij} + \delta_{2,k}\text{habitat}_i,$$

where j indexes visit. As before, all species-specific terms are fitted as normally distributed random effects. Models were fitted with weakly informative priors that avoid densities strongly concentrated around 0 and 1 on the probability scale (Northrup & Gerber, 2018), while also overstating our prior uncertainty about parameter values. Models were fitted using four chains each running for 1000 warmup iterations and 1000 sampling iterations, resulting in a total of 4000 post-warmup draws. Models were fitted in Stan (Stan Development Team, 2021) using the R package flocker (Socolar & Mills, 2022). We assessed convergence based on a lack of divergences in Stan's leapfrog integrator and rank-normalised folded r-hat statistics of less than 1.01 for all model parameters (Vehtari et al., 2021).

2.4.2 | Calculating land-sharing and land-sparing scenarios

To assess the relative benefits of each scenario, we calculated predicted community patterns under hypothetical land-sharing and land-sparing agricultural landscapes (Figure 1). These landscapes were divided into management units (analogous to individual farms) that consisted of varying numbers of sites (each site was 3.14 ha, calculated from the 100 m radius surrounding sampling points). The number of sites per management unit was varied to display how this influences biodiversity outcomes for each land-allocation scenario (Figure 5a). Units were surrounded by an increasing proportion of landscape WF spanning the observed variation (20%–80% at 15% intervals; Figure 1 only shows 0.2, 0.5 and 0.8 for illustrative purposes) within a 1000 m radius from the point. Within each management unit, the proportion of farm pasture remained constant and the amount of WF was either allocated throughout the management unit (land sharing, Figure 1), or allocated as a protected area within contiguous forest (land sparing, Figure 1). As per Gilroy et al. (2014), we made two key assumptions: (1) the rate of cattle production is constant for pastures within the study areas and (2) WF features within farms have no contribution to yield. As a result, food production relies entirely on the proportion of farm pasture.

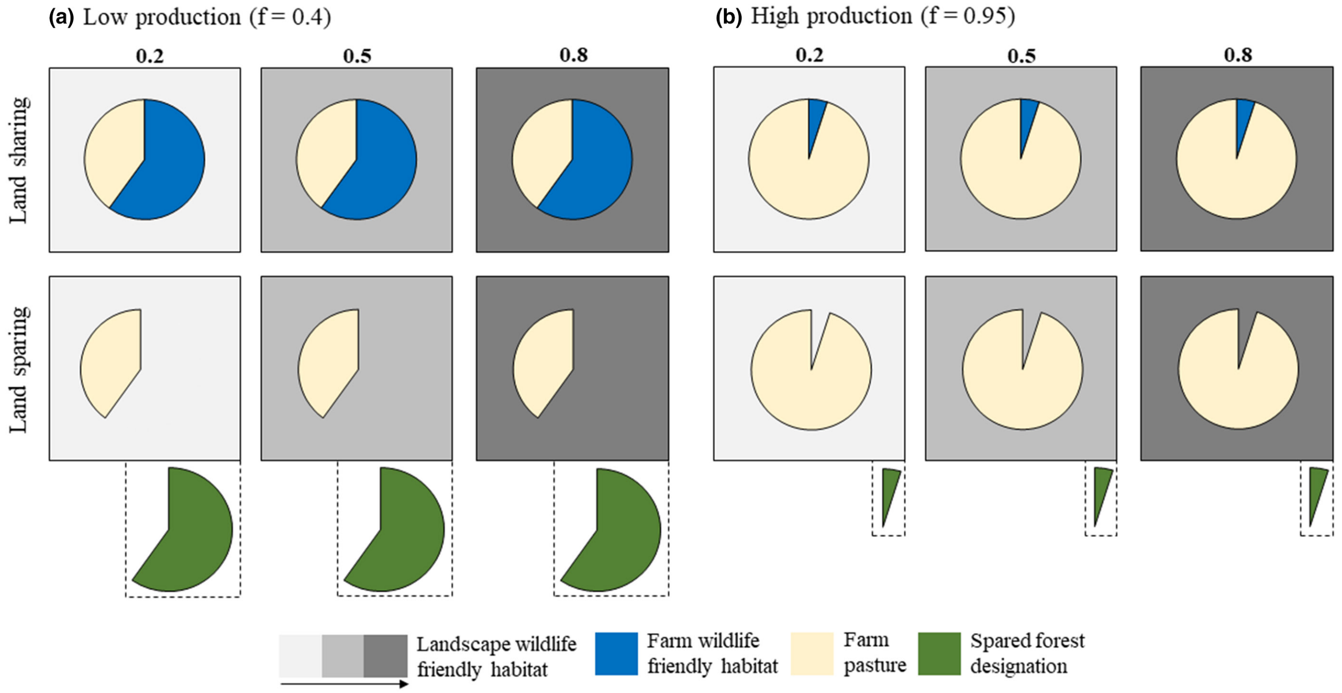


FIGURE 1 Examples of land sharing and land-sparing strategies for low (a) and high (b) production scenarios (f = proportion of farm pasture). Land sharing retains small areas of wildlife-friendly habitat within farmland, whereas land sparing protects blocks of natural forest externally (dashed boxes) by farming at higher intensities. Hypothetical landscapes are built to simulate these strategies, containing sets of management units (analogous to individual farms) each consisting of n sites (circles, $n = 1$ in this example). Farmed portions of both shared and spared farms are surrounded by varying proportions of landscape wildlife friendliness (WF) (20%, 50% and 80% in greyscale) within a 1000 m radius of the point (denoted as squares around the farmed study sites in circles). Land-sharing management units exclusively comprise sites containing a proportion of wildlife-friendly habitat (within box), whereas land-sparing management units retain no farm WF, but instead are paired with spared natural forest blocks located offsite in contiguous forest.

Calculations were made for two production levels (production level = 'area of production'), equal to the minimum and maximum levels of farm pasture observed during sampling: low production = 40% farm pasture (Figure 1a); and high production = 95% farm pasture (Figure 1b). To demonstrate, under a low production land-sharing simulation 40% of land would be pasture and 60% would be designated farm WF habitat for each individual site within a management unit, whereas under a land-sparing simulation, 40% of all sites within a management unit would be pasture with the remaining 60% allocated to contiguous forest (see Figure 1a for visual explanation).

2.4.3 | Predicting winners and losers and intermediates from farmland conversion

Winners were calculated as species that always have a higher mean occurrence index in pasture than the equivalent land covered entirely by contiguous forest. Conversely, 'losers' are species that always have a lower mean occurrence index in pasture than if the equivalent land was covered entirely by contiguous forest. Intermediates were calculated as species that have a lower mean occurrence index across at least one level of WF. Such species may do well in WF pasture, but worse in contiguous forest or pasture with low levels of WF. Winners and losers were also categorised by each species' FD status to understand the relative impact of agricultural conversion on these groups.

2.4.4 | Estimating species richness for land-sharing and land-sparing scenarios

To estimate the total number of species that would occur under land-sharing and land-sparing scenarios, a prediction matrix was made that included all the combinations of values needed to generate SR for each management unit. The probability of each species being present in each scenario for each iteration was calculated from our model, and the probability of presence across all species in a scenario and iteration was then summed to generate the predicted number of species for each posterior iteration. Total SR was then generated by calculating the mean number of species across all posterior replicates; medians and 95% credible intervals were calculated on this. We plotted SR across varying sizes of management units to show how this affects the differences between the two strategies.

3 | RESULTS

3.1 | Species responses to farm and landscape WF

We recorded 1426 birds from 288 species and 47 families (Table S1), of which 23% were classified as low FD, 38% as medium FD and 39% as high FD. A total of 184 species were recorded at forest sites (4% Low FD, 38% medium FD, 58% high FD), and 136 species were recorded at pasture sites (46% low FD, 42% medium FD, 12% high FD). Our model found habitat to have a strong effect on occupancy for birds of all levels of FD, with low FD birds responding negatively to forest cover ($\beta_{\text{forest,low}} = -1.79$; 95% CI: [−2.58, −1.05]; Figure 2), while medium and high FD birds responded positively ($\beta_{\text{forest,medium}} = 1.32$; 95% CI: [0.61, 2.07]; $\beta_{\text{forest,high}} = 3.01$; 95% CI: [1.88, 4.19]; Figure 2), with the largest positive effect seen for high FD birds. Farm WF had positive effects on medium and high FD species ($\beta_{\text{farm WF,medium}} = 0.22$; 95% CI: [0.03, 0.41]; $\beta_{\text{farm WF,high}} = 0.29$; 95% CI: [−0.06, 0.62]; Figure 2), with 95% CI overlapping 0 in the case of high FD species, and negative effects on occupancy for low FD species ($\beta_{\text{farm WF,low}} = -0.2$; 95% CI: [−0.37, −0.03]; Figure 2). For landscape WF, coefficients strongly overlapped 0 for all FD categories, indicating that the model has little confidence in the direction of effect of this variable (Figure 2).

There was a strong association between FD and whether a species was a winner, loser or intermediate from farmland conversion. Most low FD birds were winners that decreased in occupancy across pasture as farm WF increased (Figure 3a). Medium FD birds varied in their responses, showing a mixture of winners, losers and intermediates. Almost all species in this category increased in occupancy with farm WF, although they varied in their responses to forest with some species showing increased occupancy, while others decreased (Figure 3a). High FD species largely consisted of losers, with some species showing a slight increase in occupancy with farm WF (Figure 3a), although due to most forest species being absent from pasture altogether, farm WF had little effect on this grouping (Figures 2 and 3a). Landscape WF showed similar patterns to farm WF for medium and high FD species. However, low FD species showed a mixture of responses, with some decreasing in occupancy and others increasing (Figure 3b). Almost all low FD species decreased in occupancy between maximum landscape WF and contiguous forest (Figure 3b).

Habitat type and farm WF had the biggest effect on whether a species was a winner, loser or intermediate from farming (Figure 4). Winners showed a negative effect from both habitat (transition from pasture to forest) and farm WF, while intermediates showed a minimal response to habitat but showed a positive effect from farm WF. Losers showed a strong positive effect on both habitat and farm WF (Figure 4c).

3.2 | Estimating species richness across strategies

Species richness was higher under land sparing than land sharing across all scenarios (Figure 5). This was most pronounced at low production levels where land sparing retained 97% of all bird species, but land sharing retained 67% (Figure 5b). The difference in SR between sparing and sharing remained similar in high-production scenarios, although the percentage of total bird species dropped for both strategies to 85% and 54%, respectively (Figure 5d). The influence of landscape WF was minimal for all scenarios. Low production SR saw a decline of 3% between 20% and 80% landscape WF for land sparing, while no difference was recorded for land sharing. High production SR saw a decline of 5% between minimum and maximum landscape WF for land sparing, while land sharing gave rise to a 6%

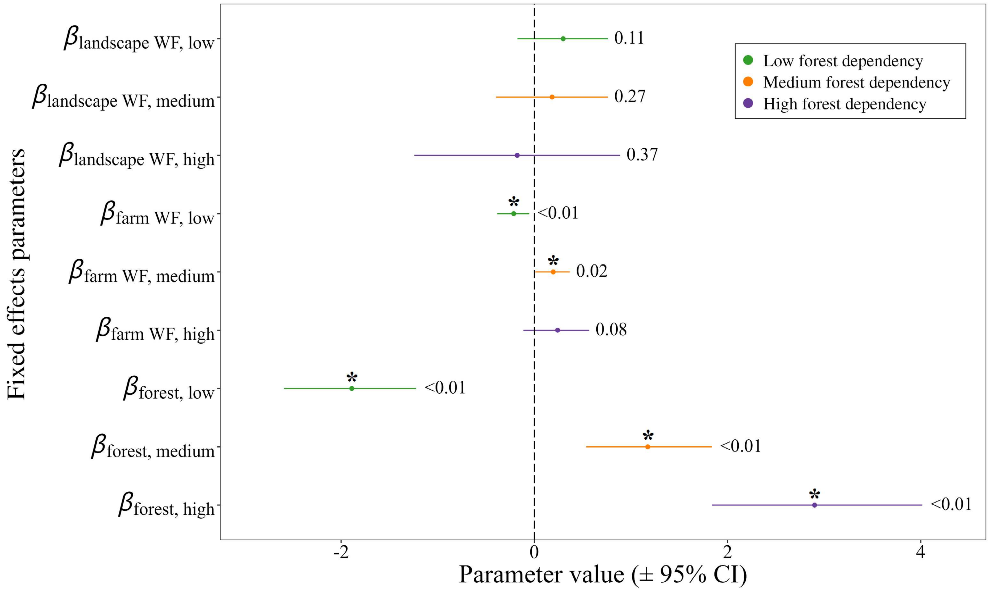


FIGURE 2 Coefficients for the fixed effects of habitat, farm wildlife friendliness (farm WF) and landscape wildlife friendliness (landscape WF), coloured according to forest dependency category. Lines indicate the 95% credible intervals (CIs) for each estimate, and the adjacent numbers display the probability of direction of effect (PD) with stars where CIs do not overlap zero. Predictor variables were standardised prior to analysis, and the binary habitat variable was effects coded as −1 for pasture and 1 for forest. Habitat effects (i.e., β_{forest} terms) correspond to the difference in occupancy between forest and 0-WF pasture.

increase in SR. The difference in SR between sparing and sharing strategies depended on the size of the management area, diminishing as the number of points per management unit, and therefore total area, became very large (Figure 5a,c).

4 | DISCUSSION

Increasing agricultural production without causing significant biodiversity loss is a major conservation challenge. We investigated how wildlife-friendly features in the surrounding landscape influence the relative benefits of land sharing vs land sparing on farmland bird communities. Specifically, we tested whether high levels of surrounding forest can rescue the ability of WF to support biodiversity locally. Our results reveal that both farm and landscape WF are weak predictors of farmland species occupancy. These findings indicate that farmland connected by a wildlife-friendly matrix remains limited in its ability to preserve occupancy for a large proportion of the Amazonian bird community, pointing to the need for the conservation of large habitat blocks under land sparing.

Many high FD species are functionally absent from pasture points at all levels of WF, and variation in occupancy across the gradient of WF is only observed in the non-forest component of the community (Figure 3). Consequently, the preservation of large tracts of contiguous forest through land sparing harboured significantly more biodiversity than wildlife-friendly farming (land sharing), which supported lower SR across all levels of landscape WF and production (Figure 5), adding to increasing evidence that extreme land sparing outperforms extreme land sharing (Balmford et al., 2019; Cannon et al., 2019; Edwards et al., 2015, 2021; Gilroy et al., 2014; Williams et al., 2017). The association between species occupancy and FD suggests strong environmental filtering in farmland, leading to the loss of forest specialists likely to be of significant conservation importance (Dambros et al., 2020; Socolar & Wilcove, 2019; Solar et al., 2015). These findings indicate that environmental filtering may be more important than dispersal limitations in determining patterns of bird assemblages in agricultural landscapes, given that many forest species are unable to disperse through the agricultural matrix, even with high levels of WF in the matrix (Karp et al., 2012).

Regional variations in FD (due to varying proportions of generalists vs. forest specialists) or considering alternative production systems that do not involve wholesale conversion to grassland could generate a result less starkly in favour of land sparing. Valente et al. (2022), for example, investigated the response of the bird community to coffee production in the Sierra Nevada de Santa Marta, Colombia, finding differences in SR between shared and spared landscapes that were less clearly in favour of one single strategy. Importantly, though the community-level patterns of alpha and gamma diversity were more equivocal in this context, they were underpinned by the same loss of forest specialists, offset by gains of open habitat specialists and generalists, as we observed here.

Medium FD birds showed the most variation in responses to farmland conversion and had the highest number of 'intermediate' species (Figure 3). This result was expected, due to edge-tolerant species falling into this category that do best in high levels of farm and landscape WF, but poorly in low WF habitat and full forest (Feniuk et al., 2019). Nevertheless, despite medium FD birds not being entirely reliant on intact forest for survival, forest still

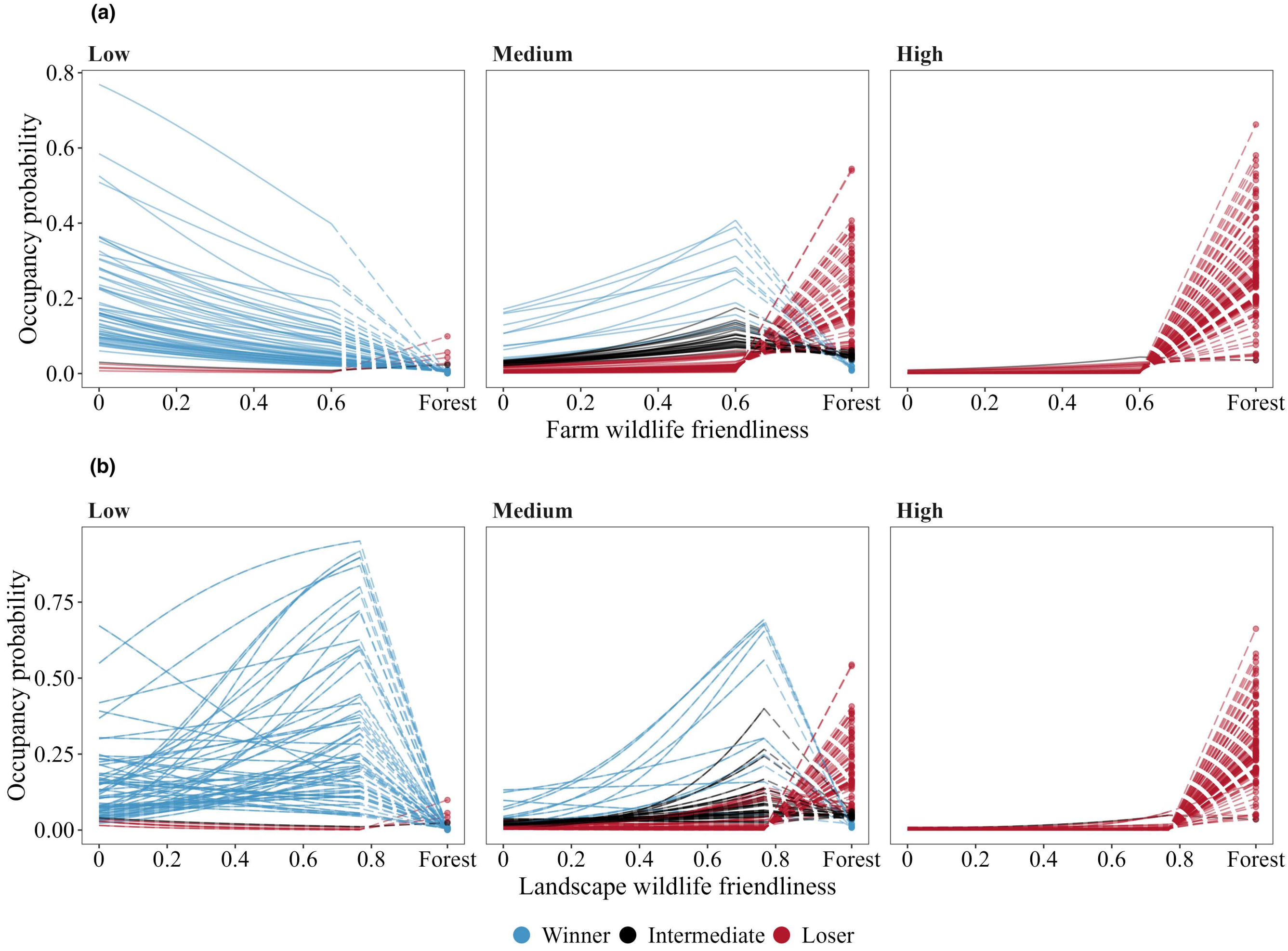


FIGURE 3 Bird species response curves showing the influence of the proportion of farm wildlife friendliness (WF) (a) and landscape WF (b) on occupancy probability. Each line represents a species. Birds are classified by forest dependency status (Low, Medium, High), as well as whether they are a winner (blue), loser (red) or intermediate (black), from farmland conversion. The occupancy probability of birds in forest sites is included for comparative purposes (circles). The difference in occupancy between forest and maximum farm and landscape WF is also shown (dashed lines).

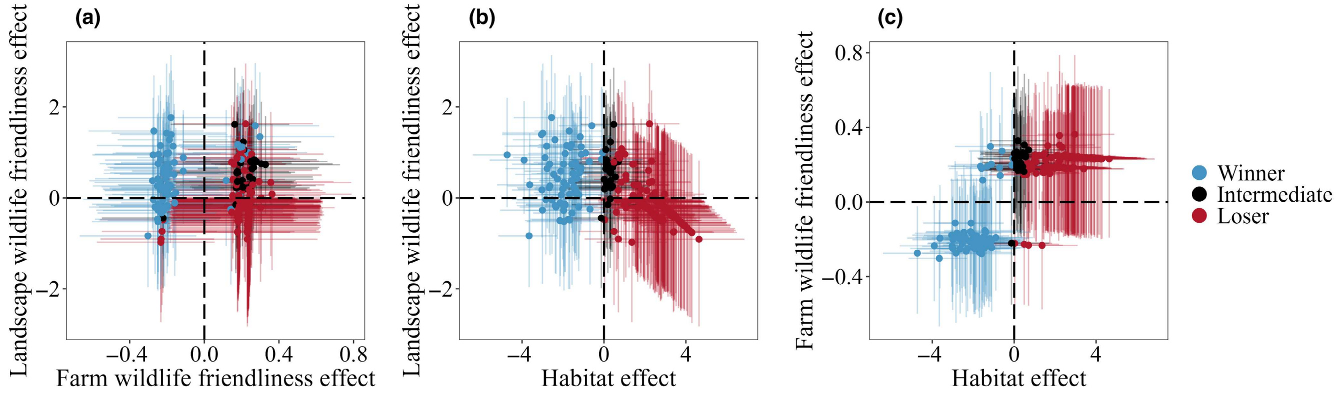
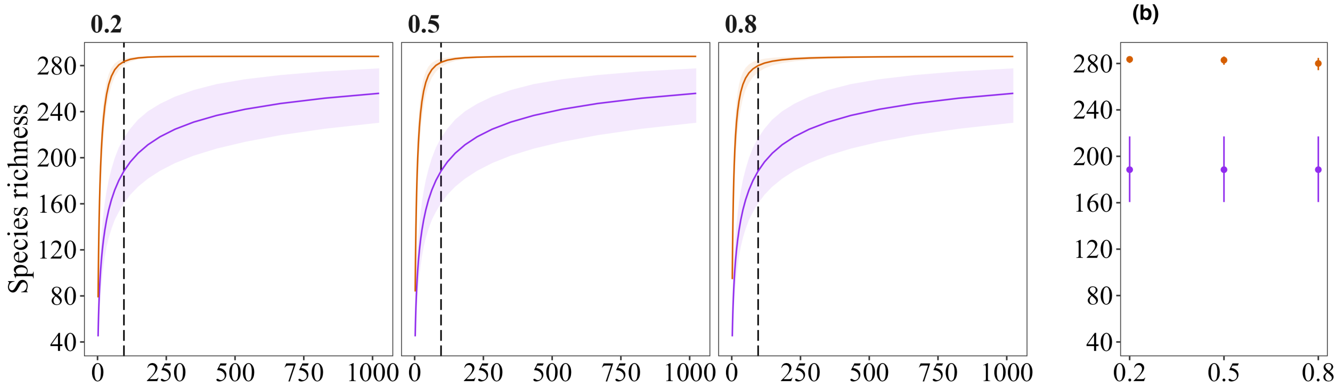


FIGURE 4 Pairwise correlation of effect sizes between landscape wildlife friendliness (WF) and farm WF (a), landscape WF and habitat (b), and farm WF and habitat (c). The habitat effect shows the transition from pasture to forest. Each circle represents a species that are classified by whether they are a winner (blue), loser (red) or intermediate (black), from farmland conversion. Error bars represent 95% credible intervals, and habitat effects (i.e., β_{forest} terms) correspond to the difference in occupancy between forest and 0-WF pasture.

(a) Low production (f = 0.4)



(c) High production (f = 0.95)

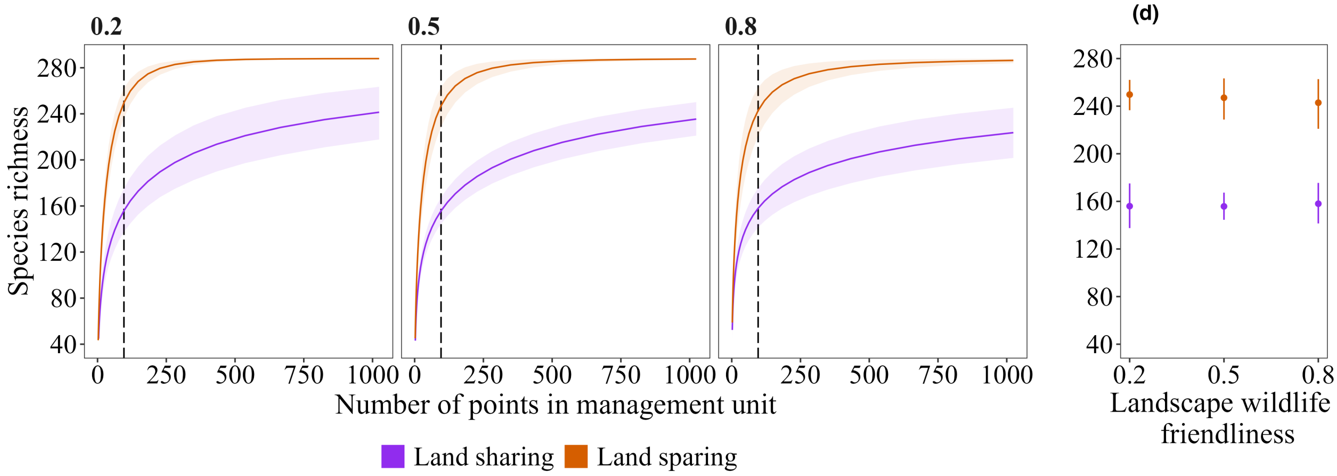


FIGURE 5 Comparisons of bird species richness at different levels of landscape wildlife friendliness (WF) across varying sizes of management units between land sharing (purple) and land sparing (orange) land-allocation strategies (a, c). Hypothetical land management units were created for low and high levels of agricultural production (f = proportion of farm pasture), where the proportion of ungrazed land is allocated as either wildlife-friendly habitat (land sharing) or contiguous forest (land sparing). An arbitrary number of points per management unit (dashed line) was chosen to illustrate the mean differences between land-allocation strategies across a gradient of landscape WF for low (b) and high (d) production levels.

constitutes a major component of overall habitat for many of these species (Table S1; BirdLife International, 2021). Their occurrence on farmland could be driven by source-sink dynamics, where nearby forest permits the immigration of individuals from areas with positive population growth rates, meaning that SR on farmland may poorly correspond to underlying population productivity (Gilroy & Edwards, 2017). This was demonstrated in the Brazilian Atlantic Forest, where the abundance and richness of bird assemblages in farmland was strongly related to forest cover at a landscape scale (Morante-Filho et al., 2016). This is concerning as the farms in our study were all surrounded by at least 20% landscape WF within a 1000 m radius (Figure S3), meaning that greater isolation from forest in broader-scale agricultural landscapes could reduce the benefits of land sharing even further (Lamb et al., 2016).

Land sparing is most effective when large areas of contiguous forest are protected upwards of 1000 ha (Lamb et al., 2016), thus being large enough to sustain viable populations unaffected by edge effects (Phalan et al., 2011). In our study, spared land was designated in core areas of protected contiguous forest and not subject to edge effects. Even large spared habitats can lose species over time if they are situated within landscapes with poor levels of connectivity, reducing the relative biodiversity benefits of land sparing (Grass et al., 2019). For example, the benefits of land sparing for birds in Ghana diminish in increasingly fragmented landscapes, such that land sharing performs marginally better when spared lands are subject to severe fragmentation and edge effects (Lamb et al., 2016). Similar findings have been found for Indian birds, although imperfections in land sparing are unlikely to be detrimental enough to make land sharing a more desirable option (Balmford et al., 2019). Nevertheless, the degradation of spared lands near farmland could exacerbate the negative biodiversity impacts of land sharing if populations are somewhat reliant on spillover effects from adjacent natural habitat (Gilroy et al., 2014). Hence, a landscape perspective is key to effectively balance the conservation of biodiversity in both spared and farmed land.

4.1 | Study caveats and conclusions

Our study has four main caveats: two relating to biodiversity; and two relating to socio-economic implications. Firstly, we only focused on one taxon, although birds are a good indicator of land-use impacts in other taxa (Barlow et al., 2007; Edwards et al., 2014), including in land sharing/sparing research (Edwards et al., 2021). Secondly, we assumed that the productivity of pasture is fixed and does not vary depending on the characteristics of the surrounding forest (e.g., spillover effects), or through WF features enhancing productivity on point (Hamer et al., 2021). Some forms of WF farming, particularly silvopasture systems, can benefit yields while reducing the agricultural land footprint via sustainable intensification (Clough et al., 2011; Lerner et al., 2017; Murgueitio et al., 2006). If WF features are capable of enhancing productivity on the land left under production, it would act to reduce some of the observed differences between sparing and sharing strategies. The extent to which the WF habitat we sampled is capable of enhancing productivity is however unclear. It typically consisted of scrub-like habitat and isolated trees rather than silvopasture, with these features often inaccessible to cattle due to barbed wire fences. As productivity is unlikely to be much higher at points containing WF features, and, given that many of the species recorded in our study are highly reliant on forest and have poor prospects in shared landscapes regardless of WF levels, this simplification is unlikely to significantly influence our results (Abrahamczyk et al., 2008; Edwards et al., 2021).

Regarding socio-economic implications, farmland intensification can drive both increases in land rents, resulting in further demand for land (at least in the short-term), and decreases in commodity price that enables market substitution or creation to utilise the cheaper crop (Lim et al., 2017). This requires strong legislation and land-use zoning to protect spared areas from leakage (Ford et al., 2020). Finally, smallholder farming is the most prevalent form of agriculture globally and provides livelihoods and food security to many of the planet's most vulnerable populations (Samberg et al., 2016). However, larger farms, typically associated with intensive agriculture, tend to be owned by the state or commercial companies. Increased demand for more intensive agriculture via land sparing could potentially contribute to environmental injustices by displacing smallholders through unethical practices such as land grabbing (Busscher et al., 2020). Therefore, the implications of land sparing on food resilience, sociocultural values and economic returns need to be accounted for, as well as the acknowledgement that sparing need not be dependent on industrial intensification (Balmford, 2021).

In conclusion, our results suggest that the preservation of large tracts of natural habitat is imperative to prevent major biodiversity losses, given no apparent benefits of landscape WF through land sharing for many high FD species. The intensification of agriculture on existing farmlands through the wider uptake of silvopasture—rather than ad hoc patches of native habitat found in our study areas—provides a possible solution, due to their low costs, high productivity gains and greater provision of ecosystem services, relative to more intensive systems (Braun et al., 2016; Lerner et al., 2017). Such practices would align with policies advocating sustainable intensification, thereby minimising negative ecological impacts on natural environments, and discouraging further agricultural expansion (Phalan et al., 2016), while providing the space for the preservation of forest tracts vital for the conservation of high FD species.

AUTHOR CONTRIBUTIONS

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

ACKNOWLEDGEMENTS

We thank the staff at the Instituto Alexander von Humboldt at Villa De Leyva, Colombia, in particular Claudia Alejandra Medina Uribe for logistical support. We thank Dan Lane for sharing his expertise in Amazonian birdsong. Funding was provided to D.P.E. by the Natural Environment Research Council (grant number: NE/R017441/1) and to T.H. and D.P.E. by the Research Council of Norway (grant number: 208836). This is publication #35 of the Biodiversity, Agriculture and Conservation in Colombia (Biodiversidad, Agricultura, y Conservación en Colombia [BACC]) project.

CONFLICT OF INTEREST STATEMENT

There was no conflict of interest.

DATA AVAILABILITY STATEMENT

Data are available from the Zenodo Digital Repository https://zenodo.org/doi/10.5281/zenodo.10501055 (Birch et al., 2024).

ORCID

Benjamin D. J. Birch https://orcid.org/0000-0003-1740-264X
Simon C. Mills https://orcid.org/0000-0002-1880-8425
Jacob B. Socolar https://orcid.org/0000-0002-9126-9093
Torbjørn Haugaasen https://orcid.org/0000-0003-0901-5324
David P. Edwards https://orcid.org/0000-0001-8562-3853

REFERENCES

Abrahamczyk, S., Kessler, M., Dwi Putra, D., Waltert, M., & Tscharntke, T. (2008). The value of differently managed cacao plantations for forest bird conservation in Sulawesi, Indonesia. *Bird Conservation International*, *18*(4), 349. https://doi.org/10.1017/S0959270908007570

Allaire, J., Ushey, K., Tang, Y., & Eddelbuettel, D. (2017). *reticulate: R interface to python*. https://github.com/rstudio/reticulate

Balmford, A. (2021). Concentrating vs. spreading our footprint: How to meet humanity's needs at least cost to nature. *Journal of Zoology*, *315*(2), 79–109. https://doi.org/10.1111/jzo.12920

Balmford, B., Green, R. E., Onial, M., Phalan, B., & Balmford, A. (2019). How imperfect can land sparing be before land sharing is more favourable for wild species? *Journal of Applied Ecology*, *56*(1), 73–84. https://doi.org/10.1111/1365-2664.13282

Barlow, J., Gardner, T. A., Araujo, I. S., Avila-Pires, T. C., Bonaldo, A. B., Costa, J. E., Esposito, M. C., Ferreira, L. V., Hawes, J., Hernandez, M. I., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. B., Mestre, L. A., Miranda-Santos, R., Nunes-Gutjahr, A. L., Overal, W. L., … Peres, C. A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. *Proceedings of the National Academy of Sciences of the United States of America*, *104*(47), 18555–18560. https://doi.org/10.1073/pnas.0703333104

Birch, B. D. J., Mills, S. C., Socolar, J. B., Martínez-Revelo, D. E., Haugaasen, T., & Edwards, D. P. (2024). Data from: Land sparing outperforms land sharing for Amazonian bird communities regardless of surrounding landscape context. *Zenodo Digital Repository*, https://doi.org/10.5281/zenodo.10501055

BirdLife International. (2021). Birdlife International IUCN Red List for birds website: http://www.birdlife.org/datazone

Braun, A., Van Dijk, S., & Grulke, M. (2016). *Upscaling silvopastoral systems in South America*. http://publications.iadb.org/handle/11319/7928

Busscher, N., Parra, C., & Vanclay, F. (2020). Environmental justice implications of land grabbing for industrial agriculture and forestry in Argentina. *Journal of Environmental Planning and Management*, *63*(3), 500–522. https://doi.org/10.1080/09640568.2019.1595546

Cannon, P. G., Gilroy, J. J., Tobias, J. A., Anderson, A., Haugaasen, T., & Edwards, D. P. (2019). Land-sparing agriculture sustains higher levels of avian functional diversity than land sharing. *Global Change Biology*, *25*(5), 1576–1590. https://doi.org/10.1111/gcb.14601

Clough, Y., Barkmann, J., Juhrbandt, J., Kessler, M., Wanger, T. C., Anshary, A., Buchori, D., Cicuzza, D., Darras, K., Putra, D. D., Erasmi, S., Pitopang, R., Schmidt, C., Schulze, C. H., Seidel, D., Steffan-Dewenter, I., Stenchly, K., Vidal, S., Weist, M., … Tscharntke, T. (2011). Combining high biodiversity with high yields in tropical agroforests. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(20), 8311–8316. https://doi.org/10.1073/pnas.1016799108

Dambros, C., Zuquim, G., Moulatlet, G. M., Costa, F. R. C., Tuomisto, H., Ribas, C. C., Azevedo, R., Baccaro, F., Bobrowiec, P. E. D., Dias, M. S., Emilio, T., Espirito-Santo, H. M. V., Figueiredo, F. O. G., Franklin, E., Freitas, C., Graça, M. B., D'Horta, F., Leitão, R. P., Maximiano, M., … Magnusson, W. E. (2020). The role of environmental filtering, geographic distance and dispersal barriers in shaping the turnover of plant and animal species in Amazonia. *Biodiversity and Conservation*, *29*(13), 3609–3634. https://doi.org/10.1007/s10531-020-02040-3

Dorazio, R. M., & Royle, J. A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. *Journal of the American Statistical Association*, *100*(470), 389–398.

Edwards, D. P., Gilroy, J. J., Thomas, G. H., Uribe, C. A. M., & Haugaasen, T. (2015). Land-sparing agriculture best protects avian phylogenetic diversity. *Current Biology*, *25*(18), 2384–2391. https://doi.org/10.1016/j.cub.2015.07.063

Edwards, D. P., Magrach, A., Woodcock, P., Ji, Y., Lim, N. T., Edwards, F. A., Larsen, T. H., Hsu, W. W., Benedick, S., Khen, C. V., Chung, A. Y. C., Reynolds, G., Fisher, B., Laurance, W. F., Wilcove, D. S., Hamer, K. C., & Yu, D. W. (2014). Selective-logging and oil palm: Multitaxon impacts, biodiversity indicators, and trade-offs for conservation planning. *Ecological Applications*, *24*(8), 2029–2049. https://doi.org/10.1890/14-0010.1

Edwards, F. A., Massam, M. R., Cosset, C. C. P., Cannon, P. G., Haugaasen, T., Gilroy, J. J., & Edwards, D. P. (2021). Sparing land for secondary forest regeneration protects more tropical biodiversity than land sharing in cattle farming landscapes. *Current Biology*, *31*(6), 1284–1293.e4. https://doi.org/10.1016/j.cub.2020.12.030

Feniuk, C., Balmford, A., & Green, R. E. (2019). Land sparing to make space for species dependent on natural habitats and high nature value farmland. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1909), 20191483. https://doi.org/10.1098/rspb.2019.1483

Fischer, J., Abson, D. J., Butsic, V., Chappell, M. J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H. G., & von Wehrden, H. (2014). Land sparing versus land sharing: Moving forward. *Conservation Letters*, *7*(3), 149–157. https://doi.org/10.1111/conl.12084

Fischer, J., Brosi, B., Daily, G. C., Ehrlich, P. R., Goldman, R., Goldstein, J., Lindenmayer, D. B., Manning, A. D., Mooney, H. A., Pejchar, L., Ranganathan, J., & Tallis, H. (2008). Should agricultural policies encourage land sparing or wildlife-friendly farming? *Frontiers in Ecology and the Environment*, *6*(7), 380–385. https://doi.org/10.1890/070019

Ford, S. A., Jepsen, M. R., Kingston, N., Lewis, E., Brooks, T. M., MacSharry, B., & Mertz, O. (2020). Deforestation leakage undermines conservation value of tropical and subtropical forest protected areas. *Global Ecology and Biogeography*, *29*(11), 2014–2024. https://doi.org/10.1111/geb.13172

Gilroy, J. J., & Edwards, D. P. (2017). Source-sink dynamics: A neglected problem for landscape-scale biodiversity conservation in the tropics. *Current Landscape Ecology Reports*, *2*(1), 51–60. https://doi.org/10.1007/s40823-017-0023-3

Gilroy, J. J., Edwards, F. A., Medina Uribe, C. A., Haugaasen, T., & Edwards, D. P. (2014). EDITOR'S CHOICE: Surrounding habitats mediate the trade-off between land-sharing and land-sparing agriculture in the tropics. *Journal of Applied Ecology*, *51*(5), 1337–1346. https://doi.org/10.1111/1365-2664.12284

Gorelick, N., Hancher, M., Dixon, M., Ilyushchenko, S., & Thau, D. (2017). Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, *202*, 18–27. https://doi.org/10.1016/j.rse.2017.06.031

Grass, I., Loos, J., Baensch, S., Batáry, P., Librán-Embid, F., Ficiciyan, A., Klaus, F., Riechers, M., Rosa-Schleich, J., Tiede, J., Udy, K., Westphal, C., Wurz, A., & Tscharntke, T. (2019). Land-sharing/–sparing connectivity landscapes for ecosystem services and biodiversity conservation. *People and Nature*, *1*(2), 262–272. https://doi.org/10.1002/pan3.21

Green, R. E., Cornell, S. J., Scharlemann, J. P. W., & Balmford, A. (2005). Farming and the fate of wild nature. *Science*, *307*(5709), 550–555. https://doi.org/10.1126/science.1106049

Hamer, K. C., Sasu, M. A., Ofosuhene, L., Asare, R., Ossom, B., Parr, C. L., Scriven, S. A., Asante, W., Addico, R., & Hill, J. K. (2021). Proximity to forest mediates trade-offs between yields and biodiversity of birds in oil palm smallholdings. *Biotropica*, *53*(6), 1498–1509. https://doi.org/10.1111/btp.12997

Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., Thau, D., Stehman, S. V., Goetz, S. J., Loveland, T. R., Kommareddy, A., Egorov, A., Chini, L., Justice, C. O., & Townshend, J. R. G. (2013). High-resolution global maps of 21st-century forest cover change. *Science*, *342*(6160), 850–853. https://doi.org/10.1126/science.1244693

Hill, J. K., & Hamer, K. C. (2004). Determining impacts of habitat modification on diversity of tropical forest fauna: The importance of spatial scale. *Journal of Applied Ecology*, *41*(4), 744–754. https://doi.org/10.1111/j.0021-8901.2004.00926.x

Kamp, J., Urazaliev, R., Balmford, A., Donald, P. F., Green, R. E., Lamb, A. J., & Phalan, B. (2015). Agricultural development and the conservation of avian biodiversity on the Eurasian steppes: A comparison of land-sparing and land-sharing approaches. *Journal of Applied Ecology*, *52*(6), 1578–1587. https://doi.org/10.1111/1365-2664.12527

Karp, D. S., Rominger, A. J., Zook, J., Ranganathan, J., Ehrlich, P. R., & Daily, G. C. (2012). Intensive agriculture erodes β-diversity at large scales. *Ecology Letters*, *15*(9), 963–970. https://doi.org/10.1111/j.1461-0248.2012.01815.x

Kremen, C. (2015). Reframing the land-sparing/land-sharing debate for biodiversity conservation. *Annals of the New York Academy of Sciences*, *1355*(1), 52–76. https://doi.org/10.1111/nyas.12845

Lamb, A., Balmford, A., Green, R. E., & Phalan, B. (2016). To what extent could edge effects and habitat fragmentation diminish the potential benefits of land sparing? *Biological Conservation*, *195*, 264–271. https://doi.org/10.1016/j.biocon.2016.01.006

Lerner, A. M., Zuluaga, A. F., Chará, J., Etter, A., & Searchinger, T. (2017). Sustainable cattle ranching in practice: Moving from theory to planning in Colombia's livestock sector. *Environmental Management*, *60*(2), 176–184. https://doi.org/10.1007/s00267-017-0902-8

Lessmann, J., Fajardo, J., Bonaccorso, E., & Bruner, A. (2019). Cost-effective protection of biodiversity in the western Amazon. *Biological Conservation*, *235*, 250–259. https://doi.org/10.1016/j.biocon.2019.04.022

Lim, F. K. S., Carrasco, L. R., McHardy, J., & Edwards, D. P. (2017). Perverse market outcomes from biodiversity conservation interventions. *Conservation Letters*, *10*(5), 506–516. https://doi.org/10.1111/conl.12332

Morante-Filho, J. C., Arroyo-Rodríguez, V., & Faria, D. (2016). Patterns and predictors of β-diversity in the fragmented Brazilian Atlantic forest: A multiscale analysis of forest specialist and generalist birds. *Journal of Animal Ecology*, *85*(1), 240–250. https://doi.org/10.1111/1365-2656.12448

Moura, N. G., Lees, A. C., Aleixo, A., Barlow, J., Berenguer, E., Ferreira, J., Mac Nally, R., Thomson, J. R., & Gardner, T. A. (2016). Idiosyncratic responses of Amazonian birds to primary forest disturbance. *Oecologia*, *180*(3), 903–916. https://doi.org/10.1007/s00442-015-3495-z

Murgueitio, E., Cuellar, P., Ibrahim, M., Gobbi, J., Cuartas, C. A., Naranjo, J. F., Zapata, A., Mejía, C., Zuluaga, A. F., & Casasola, F. (2006). Adoption of agroforestry systems for animal production. *Pastos y Forrajes*, *29*(4), 235–250.

Northrup, J. M., & Gerber, B. D. (2018). A comment on priors for Bayesian occupancy models. *PLoS ONE*, *13*, e0192819. https://doi.org/10.1371/journal.pone.0192819

Pebesma, E. (2018). Simple features for R: Standardized support for spatial vector data. *R Journal*, *10*(1). https://doi.org/10.32614/rj-2018-009

Phalan, B., Balmford, A., Green, R. E., & Scharlemann, J. P. W. (2011). Minimising the harm to biodiversity of producing more food globally. *Food Policy*, *36*(Suppl. 1), S62–S71. https://doi.org/10.1016/j.foodpol.2010.11.008

Phalan, B., Green, R. E., Dicks, L. V., Dotta, G., Feniuk, C., Lamb, A., Strassburg, B. B., Williams, D. R., zu Ermgassen, E. K., & Balmford, A. (2016). How can higher-yield farming help to spare nature? *Science*, *351*, 450–451. https://doi.org/10.1126/science.aad0055

QGIS Association. (2021). *QGIS geographic information system*. http://www.qgis.org

Reider, I. J., Donnelly, M. A., & Watling, J. I. (2018). The influence of matrix quality on species richness in remnant forest. *Landscape Ecology*, *33*(7), 1147–1157. https://doi.org/10.1007/s10980-018-0664-6

Samberg, L. H., Gerber, J. S., Ramankutty, N., Herrero, M., & West, P. C. (2016). Subnational distribution of average farm size and smallholder contributions to global food production. *Environmental Research Letters*, *11*(12). https://doi.org/10.1088/1748-9326/11/12/124010

Sánchez-Cuervo, A. M., Aide, T. M., Clark, M. L., & Etter, A. (2012). Land cover change in Colombia: Surprising forest recovery trends between 2001 and 2010. *PLoS ONE*, *7*(8), e43943. https://doi.org/10.1371/journal.pone.0043943

Schulenberg, T. S., Stotz, D. F., Lane, D. F., O'Neill, J. P., & Parker, T. A. (2010). *Birds of Peru*. Christopher Helm London.

Socolar, J. B., & Mills, S. C. (2022). *flocker: Flexible occupancy estimation in R*. Flocker. https://jsocolar.github.io/flocker/index.html

Socolar, J. B., Mills, S. C., Haugaasen, T., Gilroy, J. J., & Edwards, D. P. (2022). Biogeographic multi-species occupancy models for large-scale survey data. *Ecology and Evolution*, *12*(10), 1–11. https://doi.org/10.1002/ece3.9328

Socolar, J. B., & Wilcove, D. S. (2019). Forest-type specialization strongly predicts avian responses to tropical agriculture. *Proceedings of the Royal Society B: Biological Sciences*, *286*(1913), 20191724. https://doi.org/10.1098/rspb.2019.1724

Solar, R. R., Barlow, J., Ferreira, J., Berenguer, E., Lees, A. C., Thomson, J. R., Louzada, J., Maués, M., Moura, N. G., Oliveira, V. H., Chaul, J. C., Schoereder, J. H., Vieira, I. C., Mac Nally, R., & Gardner, T. A. (2015). How pervasive is biotic homogenization in human-modified tropical forest landscapes? *Ecology Letters*, *18*(10), 1108–1118. https://doi.org/10.1111/ele.12494

Stan Development Team. (2021). *Stan modelling language users guide and reference manual*. https://mc-stan.org

Valente, J. J., Bennett, R. E., Gómez, C., Bayly, N. J., Rice, R. A., Marra, P. P., Ryder, T. B., & Sillett, T. S. (2022). Land-sparing and land-sharing provide complementary benefits for conserving avian biodiversity in coffee-growing landscapes. *Biological Conservation*, *270*(March), 109568. https://doi.org/10.1016/j.biocon.2022.109568

Van Schmidt, N. D., & Beissinger, S. R. (2020). The rescue effect and inference from isolation–extinction relationships. *Ecology Letters*, *23*, 598–606. https://doi.org/10.1111/ele.13460

Vehtari, A., Gelman, A., Simpson, D., Carpenter, B., & Burkner, P. C. (2021). Rank-normalization, folding, and localization: An improved (formula presented) for assessing convergence of MCMC (with discussion)*†. *Bayesian Analysis*, *16*(2), 667–718. https://doi.org/10.1214/20-BA1221

Williams, D. R., Alvarado, F., Green, R. E., Manica, A., Phalan, B., & Balmford, A. (2017). Land-use strategies to balance livestock production, biodiversity conservation and carbon storage in Yucatán, Mexico. *Global Change Biology*, *23*(12), 5260–5272. https://doi.org/10.1111/gcb.13791

Winkler, K., Fuchs, R., Rounsevell, M., & Herold, M. (2021). Global land use changes are four times greater than previously estimated. *Nature Communications*, *12*(1), 1–10. https://doi.org/10.1038/s41467-021-22702-2

Wu, J. J. (2018). Landscape ecology. *Encyclopedia of Ecology*, *July*, 527–531. https://doi.org/10.1016/B978-0-12-409548-9.10919-4

Zabel, F., Delzeit, R., Schneider, J. M., Seppelt, R., Mauser, W., & Václavík, T. (2019). Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. *Nature Communications*, *10*(1), 1–10. https://doi.org/10.1038/s41467-019-10775-z

SUPPORTING INFORMATION

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

Figure S1: Map showing the locations of three study regions across Colombia (red pins).

Figure S2: Displays the mapped distribution of forest cover in 1000 m radius from the centre of each pasture point, using Landsat data from 2019 (Hansen et al., 2013).

Figure S3: Shows the proportional distribution of landscape WF for 500–5000 m radii of each point.

Table S1: List of all species detected during sampling.

How to cite this article: Birch, B. D. J., Mills, S. C., Socolar, J. B., Martínez-Revelo, D. E., Haugaasen, T., & Edwards, D. P. (2024). Land sparing outperforms land sharing for Amazonian bird communities regardless of surrounding landscape context. *Journal of Applied Ecology*, *00*, 1–11. https://doi.org/10.1111/1365-2664.14596