

# Land-sparing agriculture best protects avian phylogenetic diversity

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15 Short title: Land-sparing farming and phylogenetic diversity

## Summary

20 The conversion of natural habitats to farmland is a major driver of the global extinction crisis [1, 2]. Two strategies are promoted to mitigate the impacts of agricultural expansion on biodiversity: land-sharing integrates wildlife-friendly habitats within farmland landscapes, and land-sparing intensifies farming to allow the offset of natural reserves [3]. A key question is which strategy would protect the most phylogenetic diversity—the total evolutionary history shared across all species within a community [4]. Conserving phylogenetic diversity decreases  
25 the chance of losing unique phenotypic and ecological traits [5], and provides benefits for ecosystem function and stability [6, 7]. Focusing on birds in the threatened Chocó-Andes hotspot of endemism [8], we tested the relative benefits of each strategy for retaining phylogenetic diversity in tropical cloudforest landscapes threatened by cattle pastures. Using landscape simulations, we find that land-sharing would protect lower community-level  
30 phylogenetic diversity than land-sparing, and that with increasing distance from forest (from 500 to >1,500 m), land-sharing is increasingly inferior to land-sparing. Isolation from forest also leads to the loss of more evolutionary distinct species from communities within land-sharing landscapes, which can be avoided with effective land-sparing. Land-sharing policies that promote the integration of small-scale wildlife-friendly habitats might be of limited benefit  
35 without the simultaneous protection of larger blocks of natural habitat, which is most likely to be achieved via land-sparing measures.

**Keywords:** conservation farming, agroecosystems, biodiversity conservation, evolutionary distinctiveness rarity, cloud forest, food security, Tropical Andes, habitat loss.

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## Results and Discussion

### Impacts of farming on phylogenetic diversity

Conversion of tropical forest to farmland causes dramatic species loss [9] and a reduction in the diversity of functions played by communities [10, 11], but impacts of land-use change on phylogenetic diversity are poorly understood. Across three study areas, each containing both contiguous forest and cattle farming (Figure S1, 174 sampling locations), we recorded 318 bird species from across the avian phylogeny (Figure 1). We found representatives of many clades thriving in farmland (pale pink in Figure 1) with numerous Oscines (Passeroidea, Sylvioidea and Corvoidea), and clusters of Tyrannidae and Trochilidae being particularly associated with farmed habitats. Several non-passerine orders (e.g. Psittaciformes, Piciformes, Trogoniformes), and Sub-Oscine families (e.g. Thamnophilidae, Grallariidae, Cotingidae), by contrast, were primarily associated with forest (for species names, see Figure S2).

Using a complete avian phylogeny [12], we found a severe depletion of phylogenetic diversity (PD) in low-intensity farmland communities relative to forest (Figure 2A), equating to the loss of over 650 million years of evolutionary history. Species loss alone did not account for this erosion of phylogenetic diversity (Figure S3), as farmland communities showed lower than expected levels of phylogenetic diversity after accounting for richness (expPD; [13, 14]), unlike forest communities (Figure 2C & D). The average number of years of evolutionary history separating species in a community (mean pairwise distance), standardized against a null expectation (sesMPD) was greater in forests than farmland (Figure 2E & F). Communities with higher sesMPD tend to have species that are distributed across clades that diverged from each other a long time ago (i.e., more phylogenetically even), whereas communities with sesMPD approaching 0 tend to consist of species that are distributed within clades with relatively recent common ancestors (i.e., more phylogenetically clustered). The average number of years separating each species from its closest relative in the community (standardized mean nearest taxon distance, sesMNTD) also showed greater deviation from a null expectation in forest than farmland (Figure S4).

A recent study found that the conversion of tropical forest to diversified farmland, which incorporates features such as forest fragments, riverine strips and isolated trees, retains more evolutionary history than conversion to intensive monocultures [15] (see also [16, 17]). However, such ‘land-sharing’ practices reduce per hectare food production, and therefore potentially increase pressure to convert remaining natural habitats to agriculture [3, 18, 19], but see [20, 21]. Importantly, their value for many species tends to diminish with increasing distance from contiguous forest [22, 23]. An important question is whether a land-sharing approach to agriculture outperforms the alternative land-sparing strategy in conserving phylogenetic diversity.

### Does land-sparing or land-sharing farming best protect phylogenetic diversity?

We evaluated how these strategies influence phylogenetic diversity via a simulation approach [22]. We used Bayesian hierarchical methods to model the relationship between species occurrence probability and point-level habitat characteristics, including cover of wildlife-friendly habitat and distance from contiguous forest. The resulting models were used to simulate species occurrence patterns across hypothetical landscapes representing each strategy [22]. We used mean occurrence probabilities from replicated simulations for each scenario to evaluate whether species were ‘winners’ or ‘losers’ from forest conversion to agriculture, and

whether they were more likely to persist under land-sharing or land-sparing strategies.

We predict that species from across the bird phylogeny would benefit more from land-sharing (Figure 1 & S5, pale pink and red), but these are heavily outnumbered by those benefitting more from land-sparing (Figure 1 & S5, pale and dark blue). Of particular note are several hyperdiverse families that are predicted to depend strongly on land-sparing strategies, including the ovenbirds (Furnariidae), antbirds (Thamnophilidae) and cotingas (Cotingidae), all of which are limited to the Neotropics.

Our models predict land-sparing landscapes to conserve higher PD (Figure 2A & B), expPD (Figure 2C & D) and species richness (Figure S3) relative to land-sharing. The relative benefits of land-sparing for phylogenetic diversity became more marked with increasing isolation of farmland from forest: whereas land-sparing farming retained similar PD and expPD regardless of farmland distance from contiguous forest, land-sharing resulted in a substantial reduction in PD and expPD when farmland was further from contiguous forest (mean = 3.52 billion years at 500 m to 2.75 at 1500 m in the low production scenario) (Figure 2A-D). There was high uncertainty in predicted patterns of standardized mean pairwise distance (sesMPD) across the two strategies, although land-sparing was consistently predicted to conserve greater mean pairwise distance than land-sharing (Figure 2E & F). When farmland was more isolated from forest, predicted sesMPD tended to decline under both strategies (Figure 2E & F), reflecting an increasing dominance of farmland species within simulated communities, which tend to be more closely related (see below).

We considered two food production levels, simulated by varying the proportion of land that is grazed (low = 20% pasture, high = 80% pasture) [22]. Increased food production led to declines in predicted PD for both land-sparing and land-sharing strategies, relative to the low production scenario (Figure 2B). After accounting for relative species richness (sesPD), these differences were no longer apparent (Figure 2D), suggesting that the effect of production level on PD is largely driven by richness effects (Figure S3). Mean pairwise distances (sesMPD) were predicted to decline at higher production levels under both strategies (Figure 2E & F). Differences between strategies in sesMPD were also more marked under low production scenarios (Figure 2E) than high production (Figure 2F). Similarly, mean nearest-neighbor distances (sesMNTD) decreased at higher food production levels under both strategies (Figure S3). Predicted sesMNTD was slightly higher on average under land-sharing at low production levels (Figure S4A), but higher under land-sparing at high production levels (Figure S4B).

Overall, these results suggest that community phylogenetic diversity would be best conserved by farming intensively, provided that this allows for the protection of spared contiguous forests (see also [24]). A common criticism of land-sparing is that widespread intensification—via removal of small non-farmed features such as forest patches, isolated trees and hedgerows (this study), or replacing mixed-cropping with monoculture—may restrict landscape-level connectivity and dispersal between spared habitat patches [20, 25]. Our models, by contrast, highlight the importance of proximity to contiguous forest for the conservation of phylogenetic diversity in land-sharing landscapes. This suggests that many species with higher-than-average contributions to community PD tend to persist only in ‘wildlife-friendly’ agricultural landscapes when large forest tracts are adjacent [10, 26], potentially due to source-sink dynamics [27] or periodic movements between natural and farmed habitats [28]. Consequently, although wildlife-friendly features can provide high connectivity across farmland, our results indicate that many species are unlikely to persist in larger land-sharing landscapes that lack areas of contiguous forest. Birds are considered to be good indicators of wider biodiversity responses to environmental change [29], representing a broad range of dispersal abilities. In

tropical landscapes, it thus appears that forest protection remains an essential requirement for the conservation of evolutionary history. Given society's increasing food demands, forest protection will perhaps be best ensured via the intensification of production within existing farmland.

### **Managing farming to retain evolutionary distinctiveness**

Agricultural expansion could favor species with lower evolutionary distinctiveness (ED) [15], as well as those with larger global ranges and hence lower 'evolutionary distinctiveness rarity' (EDR), a metric that apportions ED evenly across a species' occupied range [5]. Both metrics showed a weak negative correlation with species occurrence probabilities in farmland (Figure 3A & B), but little correlation with species occurrence probabilities in forest (Figure 3C). Correspondingly, we found a substantial decline in both mean ED and EDR in farmland communities relative to forest (Figure 4), indicating a loss of evolutionary distinct species, and in particular those with ED concentrated within small global areas [15, 30]. Our results also suggest that species with higher diversification rates (DR) tend to benefit more from expansion of farming into contiguous forest (Fig. SX). The proliferation of these recently diversified clades does not, however, counterbalance the overall loss of phylogenetic diversity with agricultural conversion (Figure 2A-D).

Our simulations predict higher mean ED and EDR on average under land-sparing than land-sharing (Figure 4A & C), particularly at high production levels (Figure 4B & D). Evolutionarily distinct species, and those with ED concentrated within a smaller global area, are therefore predicted to be lost from land-sharing landscapes as food production levels increase. At both production levels, predicted mean ED and EDR tended to decline with increasing distance from contiguous forest for land-sharing communities (Figure 4A & B). At the same time, mean DR tended to increase with distance from contiguous forest in land-sharing landscapes, regardless of production level (Figure SXA & B). Land-sparing strategies tended to support lower mean DR than land-sharing across all scenarios (Figure SXA & B), indicating an increased dominance of species from more rapidly-diverging clades in land-sharing landscapes.

Our simulations assume that spared land designations fall exclusively within large contiguous tracts of forest, rather than forests that have been fragmented. If spared lands are subject to edge effects or other fragmentation impacts [31], the relative benefits for phylogenetic diversity and evolutionarily unique species could be reduced (but see [13] who found no such impact on phylogenetic diversity of trees). Fragmentation could also disrupt the flow of benefits from natural habitat into land-sharing farmland over time [31], further diminishing the value of farmland for evolutionarily distinct species and phylogenetic diversity. We have also assumed that food production increases in direct proportion to pasture cover, although in reality wildlife-friendly habitats may have positive (e.g., export pest predators or nutrients) or negative impacts (e.g., export pests and weeds, or shade) on pasture productivity, as they do in other agricultural systems [32–34]. Land-sparing could also negatively affect some social dynamics and ecosystem services [19, 32, 33, 35]. While such issues could favor land-sharing, protection of phylogenetic diversity and distinctive evolutionary lineages under land-sharing would still be contingent on the presence of surrounding forest.

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Our results underline the critical importance of halting the conversion of contiguous forests to farmland, predicting major losses of phylogenetic diversity and evolutionary distinctiveness if forested landscapes are converted wholesale to low-intensity agriculture, even when significant wildlife-friendly habitat cover is retained. Provided that land-sparing policies can genuinely deliver protection for contiguous blocks of habitat, pairing spared forest reserves with intensively-managed (and thus highly productive) farmland might best serve conservation interests [24]. Such reserves are likely to be ‘off-farm’ sparing schemes, and their development is an urgent priority for tropical conservation [22, 25, 35]. Land-sharing practices, in turn, can provide important targeted benefits in preserving community-level phylogenetic diversity, particularly in areas with surrounding forests in close proximity, facilitating the dispersal of forest taxa between tracts [1, 36]. However, these benefits may be short-lived if the land-sharing approach ultimately results in the wholesale replacement of remaining contiguous forests [25].

## Materials and Methods

### 190 Study sites

We sampled three study sites in the departments of Antioquia, Risaralda and Chocó, Colombia (1,290-2,680 m above sea level; Figure S1, Table S1). Each site straddled the interface between cattle pasture (>95% of farmed land, mirroring land-use patterns throughout the Colombian Andes; [37]) and contiguous tracts of subtropical and submontane cloudforest (>1,000,000 ha; Figure S1), dominated by old-growth with some secondary forest cover (6-30 years old). We sampled bird communities at points arrayed within 400 m x 400 m squares, summing to 38 squares in contiguous forest and 20 squares in farmland (see Figure S1). We made no distinction between primary and secondary forests in our analyses. We applied a minimum spacing of 300 m for squares in different habitats and 400 m for squares within the same habitat, with sampling points within squares spaced at 200 m to allow community independence [38]. All sampling was conducted from January to March and June to July 2012 [22], corresponding with the relatively dry period in the region.

### Bird surveys

We sampled bird communities using repeat-visit point counts [22] on four consecutive mornings each of 10-minute duration (06:00 to 12:00), avoiding rain or high winds. We varied the routes taken by experienced observers (D.P.E. and J.J.G.) each day, thus visiting each point early and late. We recorded unknown vocalizations using Sennheiser ME66 microphones and Olympus LS11 recording devices, allowing subsequent identification using online reference material. We restricted analyses to detections within a 100 m radius, excluding highly mobile or transient species (e.g. non-breeding migrants, large raptors, and swifts).

### Habitat variables

Farmland squares incorporated varying levels of remnant woodland habitat, including fragments (0.1 ha - 27 ha), riparian corridors, and hedgerows, which we classed collectively as ‘wildlife-friendly habitat’ and visually mapped within a 100 m radius around each farmland sampling point [24, 39]. From digitized copies of these maps, we calculated an index of wildlife-friendly habitat cover  $W$  at each point, with forest sampling points assigned  $W=1$  (Supporting Experimental Procedures). Farmland squares also spanned a continuum of distances from contiguous forest (50 - 1,550 m, Figure S1; [22]). We estimated the distance

220 from each farmland sampling point to the nearest contiguous forest edge using a ground-truthed  
map based on ALOS/PALSAR pantropical cloud-free forest cover data (Supporting  
Experimental Procedures). Forest sampling locations were assigned a distance of zero.

### **Statistical analyses**

225 We used four metrics to examine patterns of phylogenetic diversity (evolutionary history)  
across communities and land-use scenarios—Phylogenetic diversity (PD), deviation from  
expected Phylogenetic Diversity (expPD), standardized Mean Pairwise Distance (sesMPD),  
and standardized Mean Nearest Taxon Distance (sesMNTD), following [12-14] (Supporting  
Experimental Procedures). We also examined mean evolutionary distinctiveness (ED)  
following [13], mean evolutionary distinctiveness rarity (EDR) following [5] and mean  
230 diversification rate (DR) following [12, 15] (Supporting Experimental Procedures). For each  
metric, we calculated means across 250 randomly selected trees from Jetz et al. ([12], Hackett  
backbone).

#### *Comparing sampled communities in forest and farmland*

235 We calculated each metric of phylogenetic diversity for communities observed at each sampling  
point in contiguous forest and farmland. To do this, we used abundance estimates taken as the  
maximum count observed on any single point count.

#### *Comparing simulated communities under land-sharing and land-sparing*

240 To generate simulated communities under each strategy, we first estimated relationships  
between species occurrence probability and habitat characteristics (variation in the degree of  
wildlife-friendly habitat and distance from contiguous forest), using a state-space model  
formulation to control for detection probability and site-level random effects [39, 40]. We  
incorporated hierarchical structuring at the community level by specifying all model parameters  
as random effects, fitting the models using WinBUGS version 1.4 (Supporting Experimental  
Procedures). Next, we used these models to predict species occurrence across hypothetical  
landscapes representing land-sparing and land-sharing strategies. We considered scenarios with  
245 farmland spaced at increasing distance from the edge of the remaining contiguous forest, and  
under low and high production levels [22] (Supporting Experimental Procedures). We predicted  
species occurrence probabilities for 1,000 replicates under each scenario to generate simulated  
communities from which we calculated each phylogenetic diversity metric, evolutionary  
distinctiveness and diversification rate (Supporting Experimental Procedures).

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### **Author contributions**

255 D.P.E. and J.J.G. conceived the study, D.P.E., J.J.G. and T.H. designed the field protocols,  
D.P.E. and J.J.G. collected the data, J.J.G. analysed the data, D.P.E wrote the first draft of the  
manuscript and all authors contributed substantially to revisions.

### **Acknowledgements**

We thank staff at the Instituto de Investigación de Recursos Biológicos Alexander von  
Humboldt, particularly F. Forero for logistical support. For field access permissions we thank  
Fundación Colibri (Reserva Mesenia-Paramillo), Fundación ProAves (Reserva Las Tangaras),

260 National Parks (Parque Nacional Natural Tatamá) and L. Tapasco (Cerro Montezuma). We  
thank Y. Tapasco, O. Cortes, F. Prada, G. Suarez and many local assistants for help with data  
collection. We thank three anonymous Reviewers for comments that improved the article.  
Simulations were run on the High Performance Computing Cluster supported by the Research  
and Specialist Computing Support service at the University of East Anglia. Funding was  
265 provided to T.H. and D.P.E. by the Research Council of Norway, grant number 208836. This  
is publication #7 of the Biodiversity, Agriculture and Conservation in Colombia /  
Biodiversidad, Agricultura, y Conservación en Colombia (BACC) project. The authors declare  
no conflicts of interest.



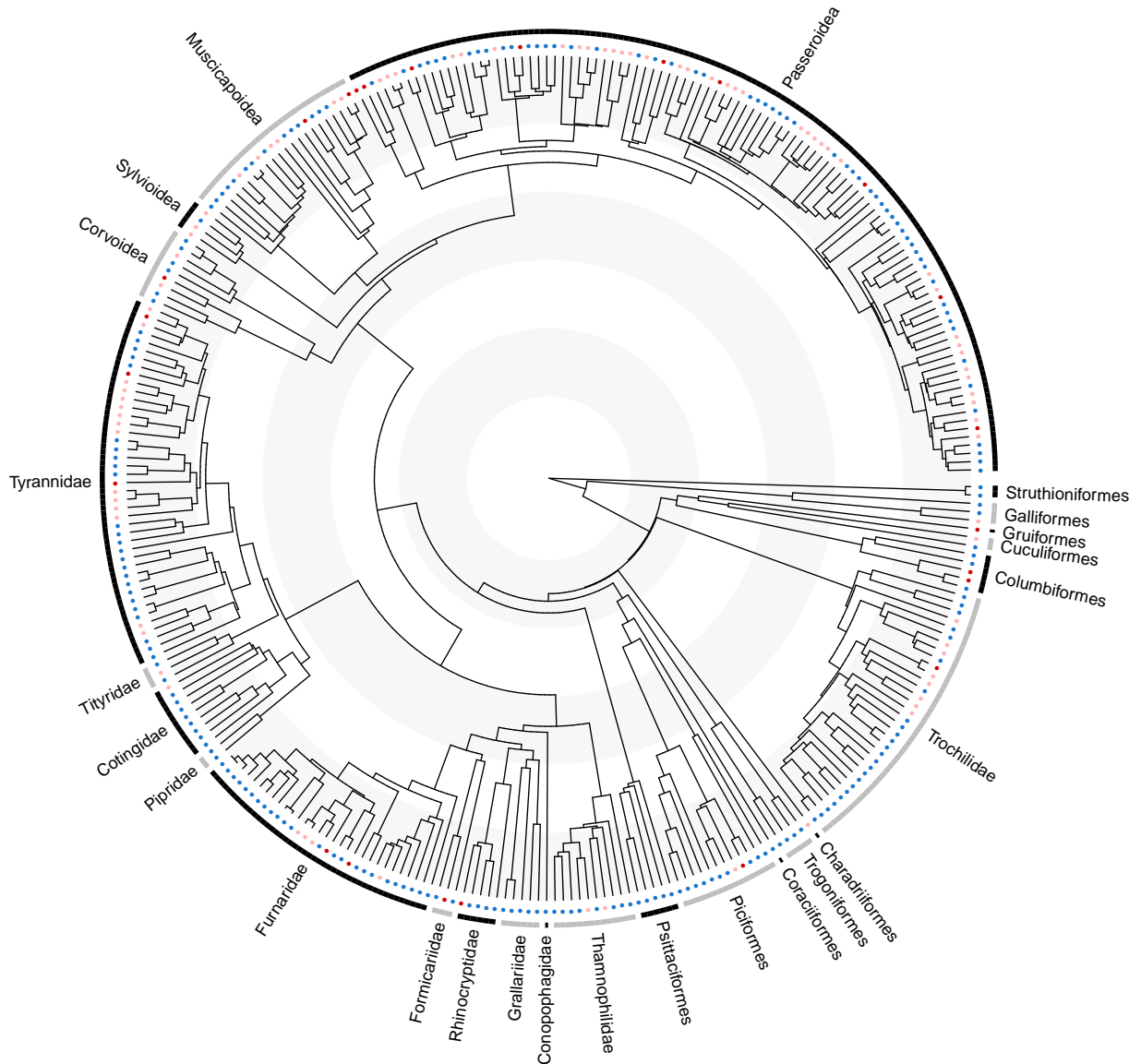
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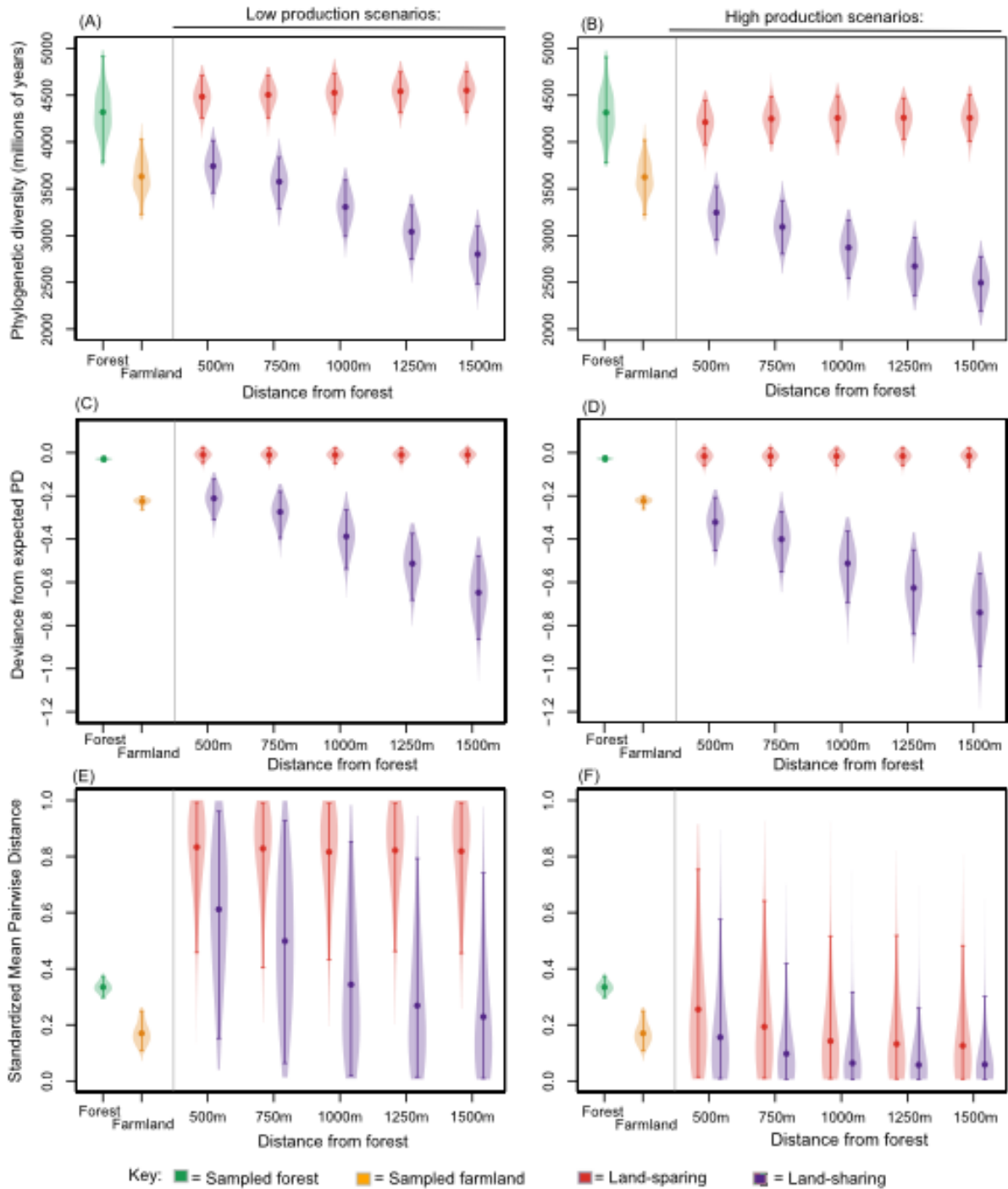
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**Figure 1.** The distribution of Chocó-Andean birds. The species categorisations are derived from a high productivity scenario (80% land concession to conservation) at 1000 metres from the forest. Labeling: Pale pink = species that are winners from farming and do best in land-sharing; blue = species that are losers from farming and do best in land-sparing; red = species that are losers from farming and do best in land-sharing. There are no winners from farming that do best with land-sparing.

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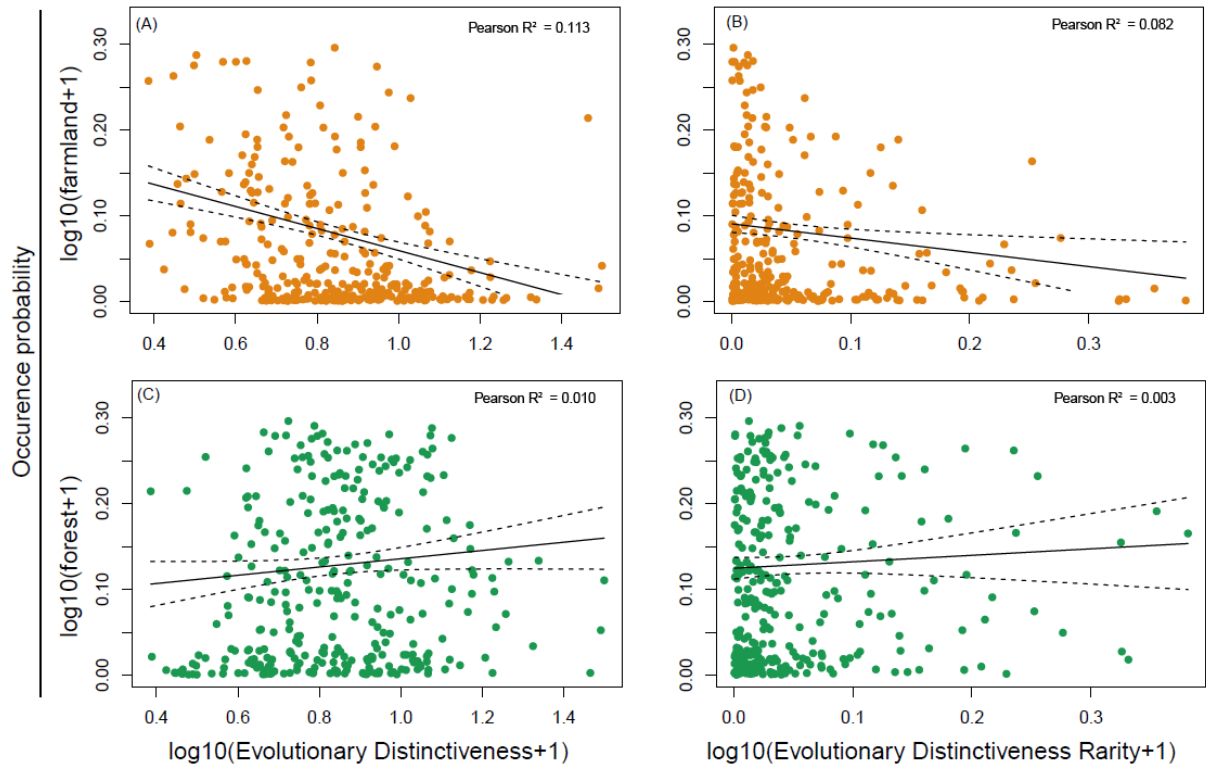
**Figure 2.** The total phylogenetic diversity present in a community (A & B) is higher in contiguous forests (green) than farmland landscapes (orange). Landscape simulations suggest that land-sparing strategies (red) retain more phylogenetic diversity than land-sharing (purple), particularly when farmed areas become increasingly isolated from contiguous forest. This is true in scenarios of both low food production (A, 80% concession to conservation) and high food production (B, 20% concession to conservation). These patterns remain consistent when phylogenetic diversity is measured as the deviance from a null expectation (C & D), suggesting that land-sparing retains more phylogenetic diversity than land-sharing even after accounting for differences in species richness. Land-sparing landscapes also have higher mean pairwise evolutionary distances between species (E & F, standardized to account for richness effects) relative to land-sharing, particularly in low production scenarios (E). This suggests that land-sparing retains communities with more distantly-related species. Points show means, bars show

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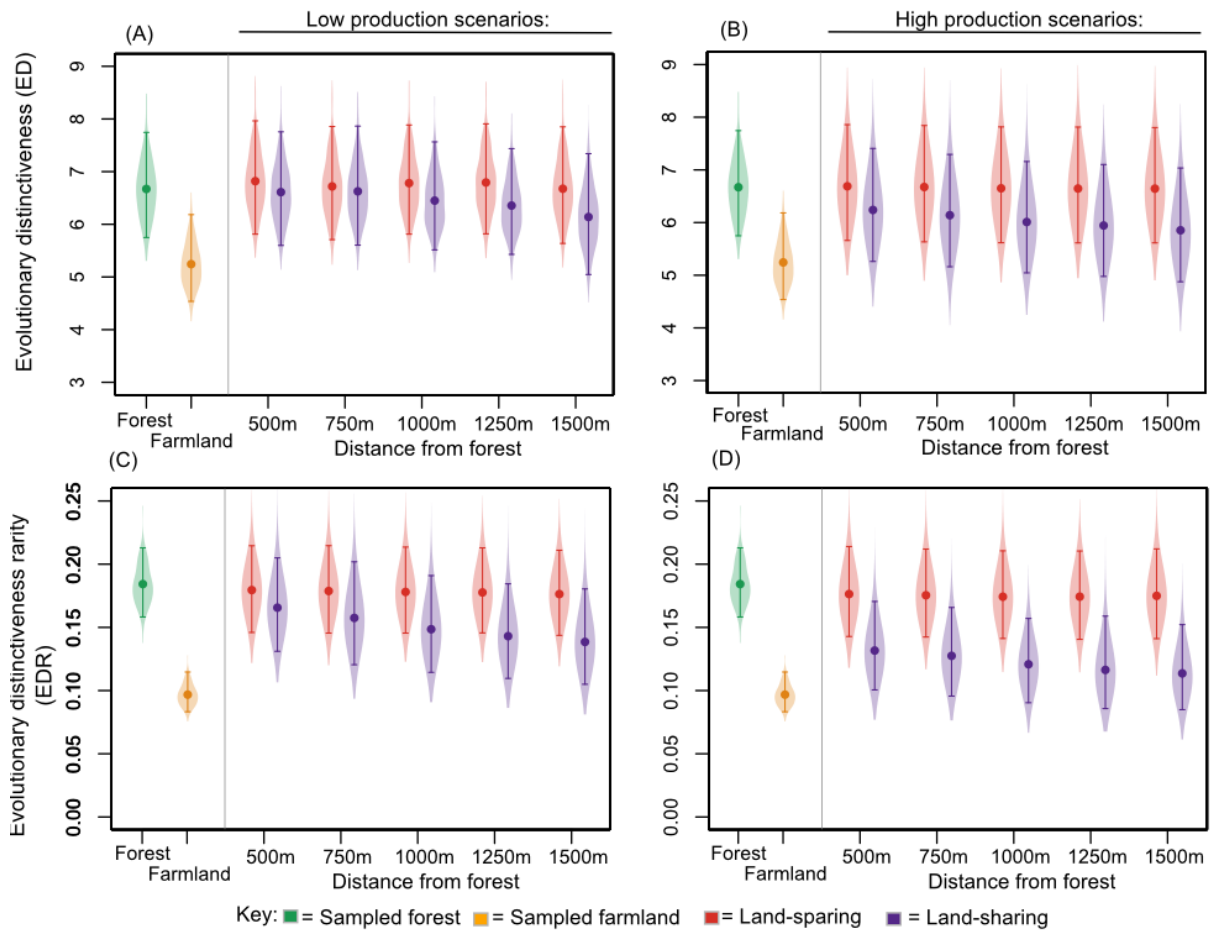
95<sup>th</sup> percentile ranges and polygons show smoothed frequency distributions of 1000 randomizations under each land allocation scenario.

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**Figure 3.** Species occurrence probabilities in farmland (A & B) and contiguous forest (C & D) related to a species' evolutionary distinctiveness (A & C) or diversification rate (B & D). Lines indicate slopes and 95% CI from univariate linear regressions.

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415 **Figure 4.** The mean evolutionary distinctiveness (ED) of species present in a community (A & B) is higher in contiguous forests (green) than farmland landscapes (orange). Land-sparing (purple) and land-sharing strategies (red) retain similar ED in scenarios with low food  
 420 production (A), but ED is higher in land-sparing scenarios (purple) at higher production (B), particularly when farmed areas are more isolated from contiguous forest. These differences are even more marked when ED apportioned across the global range size of species (EDR), (C & D), with higher EDR in land-sparing landscapes than land-sharing particularly at increasing distances from forest and at higher production levels (D). Points show means, bars show 95<sup>th</sup> percentile ranges and polygons show smoothed frequency distributions of 1000 randomizations under each land allocation scenario.

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