

Current Biology

Land-Sparing Agriculture Best Protects Avian Phylogenetic Diversity

Highlights

- Forest conversion to farming drives massive losses of avian phylogenetic diversity
- Land-sparing farming would save more avian phylogenetic diversity than land sharing
- Under land sharing, phylogenetic diversity declines at larger distance from forest
- Evolutionarily distinct bird species benefit more from land sparing than sharing

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In Brief

Appropriate management of farming is critical to slowing the biodiversity extinction crisis. Edwards et al. show that farming intensively while offsetting large natural reserves will save more phylogenetic diversity and evolutionarily distinct species of bird than low-intensity farming, especially when farmland is isolated from contiguous forests.



Land-Sparing Agriculture Best Protects Avian Phylogenetic Diversity

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SUMMARY

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 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 cloud forest landscapes threatened by cattle pastures. Using landscape simulations, we find that land sharing would protect lower community-level 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 evolutionarily 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 without the simultaneous protection of larger blocks of natural habitat, which is most likely to be achieved via land-sparing measures.

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 (PD) 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 (pink and lilac “winners” 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 Suboscine families (e.g., Thamnophilidae, Grallariidae, Cotingidae), by contrast, were primarily associated with forest (red and blue “losers” in Figure 1; for species names, see Figure S2).

Using a complete avian phylogeny [12], we found a severe depletion of 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 PD (Figures S3A and S3B), as farmland communities showed lower than expected levels of phylogenetic diversity (expPD) after accounting for richness [13, 14], unlike forest communities (Figures 2C and 2D). The average number of years of evolutionary history separating species in a community (mean pairwise distance), standardized against a null expectation (standardized mean pairwise distance [sesMPD]) was greater in forests than farmland (Figures 2E and 2F). 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 (Figures S3C and S3D).

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

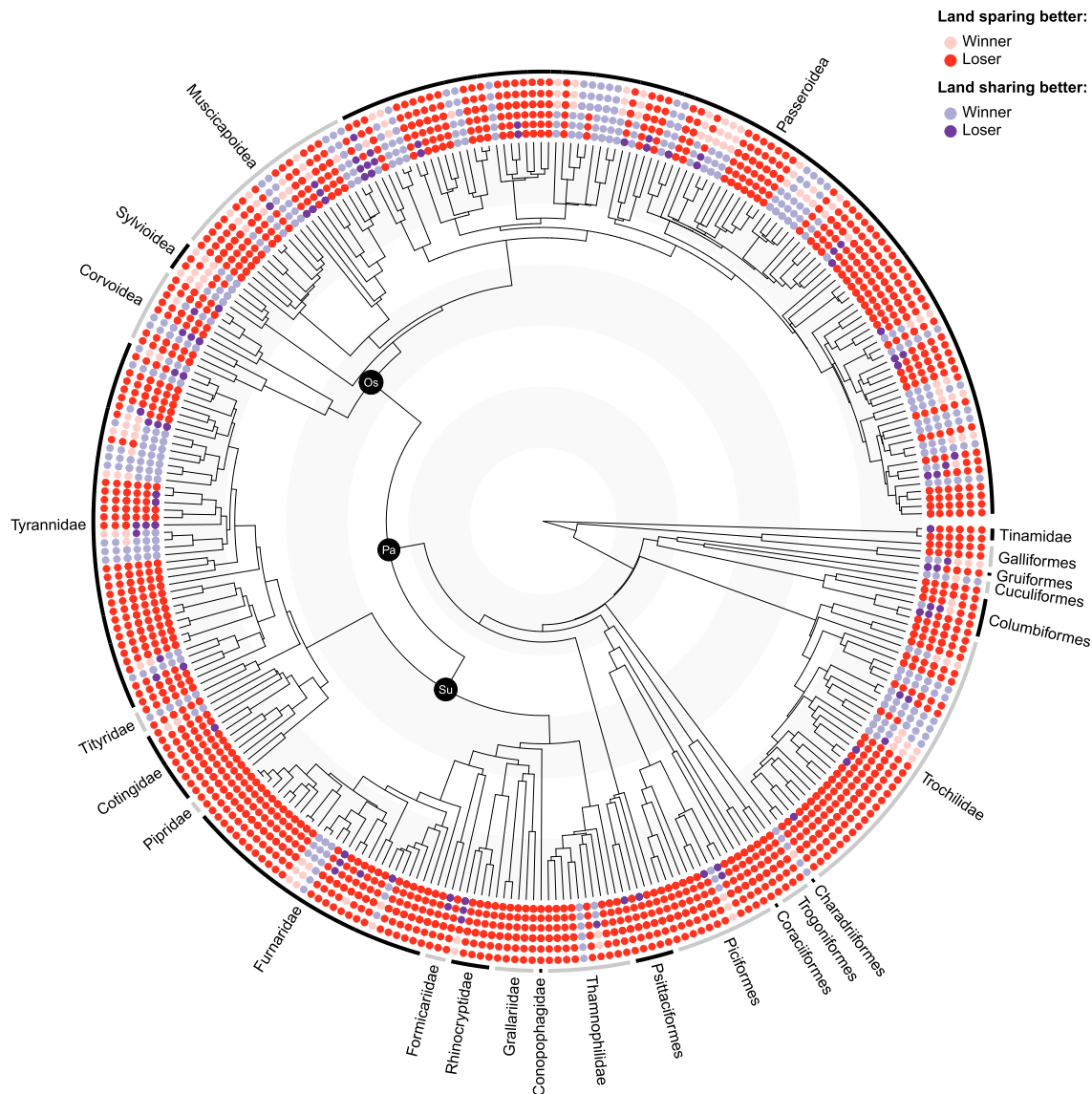


Figure 1. The Distribution of Chocó-Andean Birds

Species are categorized as follows: winners from farming that do best in land sparing (pink); winners from farming that do best in land sharing (lilac); losers from farming that do best in land sparing (red); or losers from farming that do best in land sharing (purple). Six alternative scenarios are shown, from inner to outer colored ring: high productivity (20% concession to conservation), 500 m from forest; high productivity, 1,000 m; high productivity, 1,500 m; low productivity (80% concession to conservation), 500 m from forest; low productivity, 1,000 m; low productivity, 1,500 m. Major nodes indicate Passerines (Pa), Suboscines (Su), and Oscines (Os).

contiguous forest [22, 23]. An important question is whether a land-sharing approach to agriculture outperforms the alternative land-sparing strategy in conserving PD.

Does Land-Sparing or Land-Sharing Farming Best Protect PD?

We evaluated how these strategies influence PD 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 (Figures 1 and S2, lilac and purple), but these are heavily outnumbered by those benefitting more from land sparing (Figures 1 and S2, pink and red). Of particular note are several hyperdiverse families that are predicted to depend strongly on land-sparing strategies,

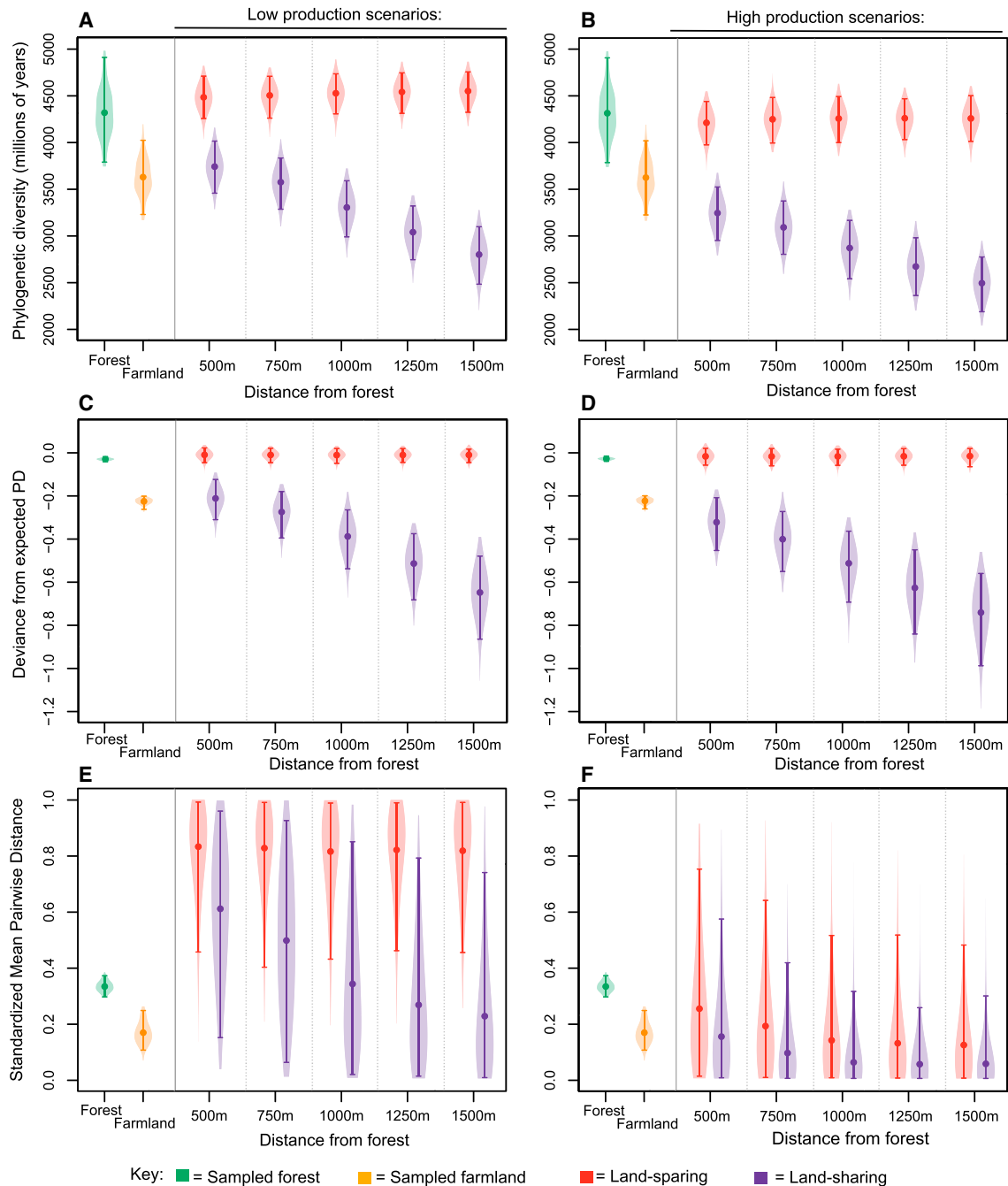


Figure 2. Phylogenetic Diversity in Forest, in Farmland, and under Land-Sparing and Land-Sharing Simulations

(A–F) The total phylogenetic diversity (PD) present in a community (A and B) is higher in contiguous forests (green) than farmland landscapes (orange). Landscape simulations suggest that land-sparing strategies (red) retain more PD than land-sharing strategies (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 PD is measured as the deviance from a null expectation (C and D), suggesting that land sparing retains more PD than land sharing even after accounting for differences in species richness. Land-sparing landscapes also have higher mean pairwise evolutionary distances between species (E and F, standardized to account for richness effects) relative to land-sharing landscapes, particularly in low production scenarios (E). This suggests that land sparing retains communities with more distantly related species. Points show means, bars show 95th percentile ranges, and polygons show smoothed frequency distributions of 1,000 randomizations under each land allocation scenario.

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 (Figures 2A and 2B), expPD (Figures 2C and 2D), and species richness (Figures S3A and S3B) relative to land

sharing. The relative benefits of land sparing for PD 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 billion years at 1,500 m in the low production scenario) (Figures 2A–2D). There was high uncertainty in predicted patterns of sesMPD across the two strategies, although land sparing was consistently predicted to conserve greater mean pairwise distance than land sharing (Figures 2E and 2F). When farmland was more isolated from forest, predicted sesMPD tended to decline under both strategies (Figures 2E and 2F), 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 (Figures S3A and S3B). Mean pairwise distances (sesMPD) were predicted to decline at higher production levels under both strategies (Figures 2E and 2F). 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 (Figures S3C and S3D). Predicted sesMNTD was slightly higher on average under land sharing at low production levels (Figure S3C) but higher under land sparing at high production levels (Figure S3D).

Overall, these results suggest that community PD 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 PD 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 species with larger global ranges and hence lower “evolutionary distinctiveness rarity” (EDR), a metric that apportions ED evenly across a species’s occupied range [5]. Both metrics showed little correlation with species occurrence probabilities in forest (Figures 3A and 3B) but a weak negative correlation with species occurrence probabilities in farmland (Figures 3C and 3D). Correspondingly, we found a substantial decline in both mean ED and EDR in farmland communities relative to forest (Figure 4), indicating a loss of evolutionarily distinct species, in particular for those species with ED concentrated within small global areas [15, 30]. Our results also suggest that species with higher diversification rates (DRs) in the recent evolutionary past tend to benefit more from expansion of farming into contiguous forest (Figures S4A and S4B). The proliferation of these recently diversified clades does not, however, counterbalance the overall loss of PD with agricultural conversion (Figures 2A–2D).

Our simulations predict higher mean ED and EDR on average under land sparing than land sharing (Figures 4A and 4C), particularly at high production levels (Figures 4B and 4D). 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 4). At the same time, mean DR tended to increase with distance from contiguous forest in land-sharing landscapes, regardless of production level (Figures S4C and S4D). Land-sparing strategies tended to support lower mean DR than land sharing across all scenarios (Figures S4C and S4D), 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 PD and evolutionarily unique species could be reduced (but see [13], who found no such impact on PD 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 PD. 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 (e.g., export pests and weeds, or shade) impacts 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 PD and distinctive evolutionary lineages under land sharing would still be contingent on the presence of surrounding forest.

Our results underline the critical importance of halting the conversion of contiguous forests to farmland, predicting major

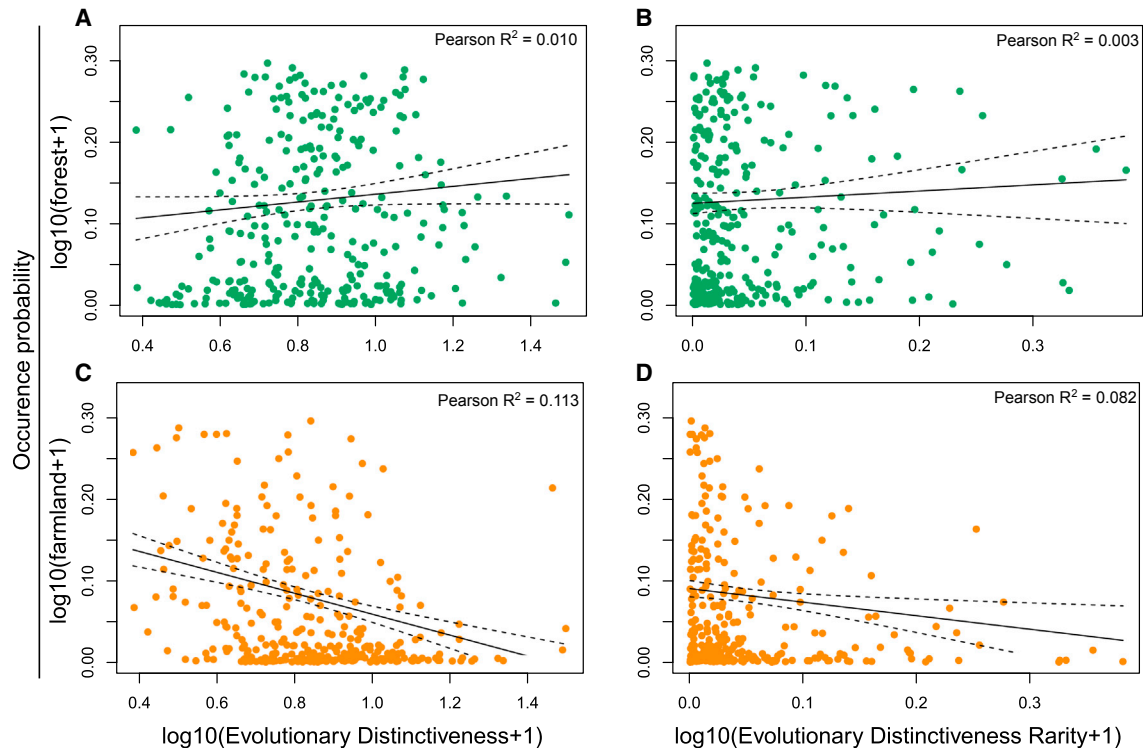


Figure 3. Species Occurrences in Forest and Farmland Related to Evolutionary Distinctiveness

(A–D) Species occurrence probabilities in contiguous forest (A and B) and farmland (C and D) related to a species's evolutionary distinctiveness (ED; A and C) or evolutionary distinctiveness rarity (EDR; B and D). Lines indicate slopes and 95% confidence interval (CI) from univariate linear regressions.

losses of PD and ED 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 PD, 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].

EXPERIMENTAL PROCEDURES

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 cloud forest (>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 × 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-min 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 $W = 1$ (Supplemental Experimental Procedures). Farmland squares also spanned a continuum of distances from contiguous forest (50–1,550 m; Figure S1; [22]). We estimated the distance 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 (Supplemental Experimental Procedures). Forest sampling locations were assigned a distance of zero.

Statistical Analyses

We used four metrics to examine patterns of PD (evolutionary history) across communities and land-use scenarios: PD, deviation from expPD, sesMPD,

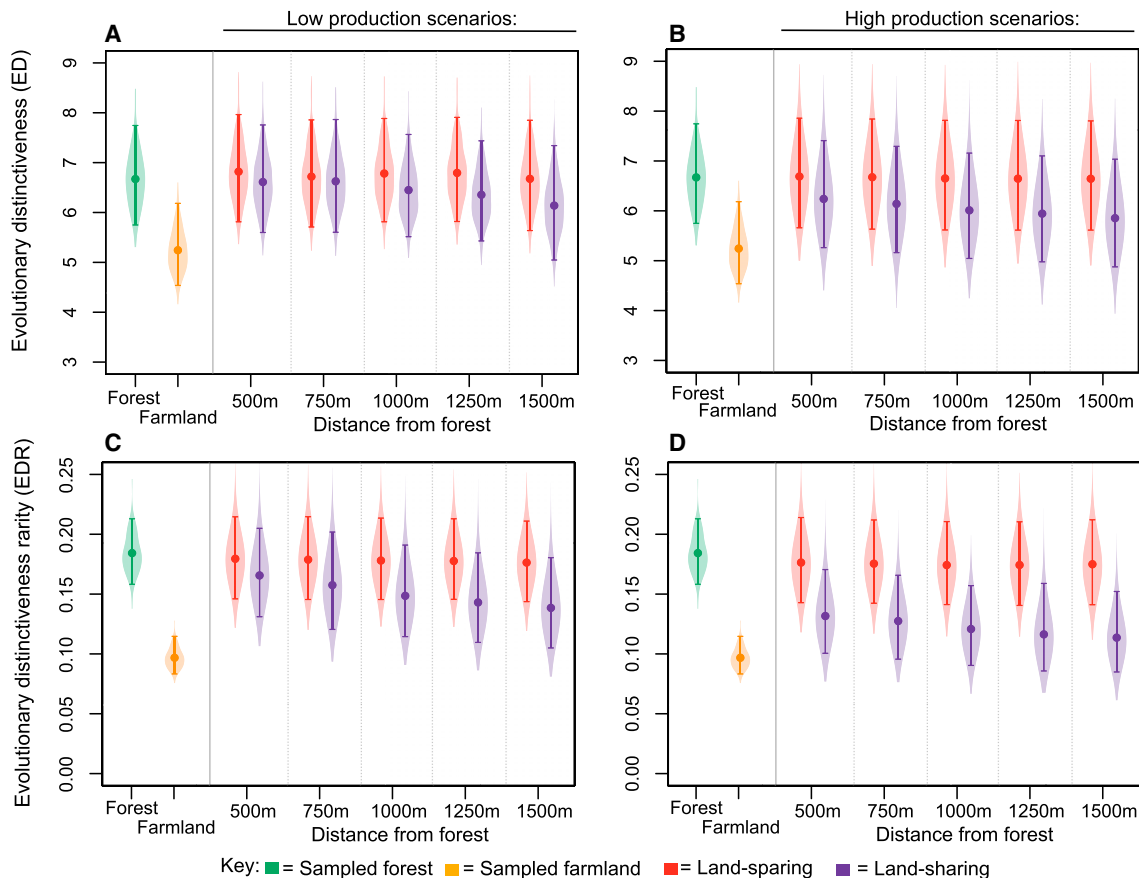


Figure 4. ED in Forest, in Farmland, and under Land-Sparing and Land-Sharing Simulations

(A–D) The mean ED of species present in a community (A and B) is higher in contiguous forests (green) than farmland landscapes (orange). Land-sparing (red) and land-sharing (purple) strategies retain similar ED in scenarios with low food production (A), but ED is higher in land-sparing scenarios at higher production (B), particularly when farmed areas are more isolated from contiguous forest. These differences are more marked when ED is apportioned across the global range size of species (EDR; C and D), with higher EDR in land-sparing than land-sharing landscapes, particularly at increasing distances from forest and at higher production levels (D). Points show means, bars show 95th percentile ranges, and polygons show smoothed frequency distributions of 1,000 randomizations under each land allocation scenario.

and sesMNTD, following [12–14] (Supplemental Experimental Procedures). We also examined mean ED following [13], mean EDR following [5], and mean DR following [12, 15] (Supplemental 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

We calculated each metric of PD 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

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 (Supplemental 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 farmland spaced at increasing distance from the edge of the remaining contiguous forest and under low and high production levels [22] (Supplemental Experimental Proce-

dures). We predicted species occurrence probabilities for 1,000 replicates under each scenario to generate simulated communities from which we calculated each PD metric, ED, EDR, and DR (Supplemental Experimental Procedures).

SUPPLEMENTAL INFORMATION

Supplemental Information includes Supplemental Experimental Procedures and four figures and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2015.07.063>.

AUTHOR CONTRIBUTIONS

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. analyzed the data. J.J.G. and G.H.T. produced the figures. D.P.E. wrote the first draft of the manuscript, and all authors contributed substantially to revisions.

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