


# Land-sparing agriculture sustains higher levels of avian functional diversity than land sharing

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## Abstract

The ecological impacts of meeting rising demands for food production can potentially be mitigated by two competing land-use strategies: off-setting natural habitats through intensification of existing farmland (land sparing), or elevating biodiversity within the agricultural matrix via the integration of “wildlife-friendly” habitat features (land sharing). However, a key unanswered question is whether sparing or sharing farming would best conserve functional diversity, which can promote ecosystem stability and resilience to future land-use change. Focusing on bird communities in tropical cloud forests of the Colombian Andes, we test the performance of each strategy in conserving functional diversity. We show that multiple components of avian functional diversity in farmland are positively related to the proximity and extent of natural forest. Using landscape and community simulations, we also show that land-sparing agriculture conserves greater functional diversity and predicts higher abundance of species supplying key ecological functions than land sharing, with sharing becoming progressively inferior with increasing isolation from remnant forest. These results suggest low-intensity agriculture is likely to conserve little functional diversity unless large blocks of adjacent natural habitat are protected, consistent with land sparing. To ensure the retention of functionally diverse ecosystems, we urgently need to implement mechanisms for increasing farmland productivity whilst protecting spared land.

## KEYWORDS

agroecosystems, conversion, defaunation, ecosystem function, habitat loss, land-use planning

## 1 | INTRODUCTION

Conversion of complex natural environments to increasingly homogenized agricultural systems poses the greatest threat to tropical biodiversity (Dobrovolski, Diniz-Filho, Loyola, & Marco, 2011; Laurance, Sayer, & Cassman, 2014). Occupying over 14 million km<sup>2</sup> of cropland and 33 million km<sup>2</sup> of pasture globally, agriculture now represents the single greatest land use (FAOSTAT, 2014; Foley et al., 2011). Recent expansion of farmlands has continued to exert wide-ranging negative impacts on global carbon emissions, natural environments

and ecosystem function (Fitzherbert et al., 2008; Flynn et al., 2009; Kotowska, Leuschner, Triadiati, Meriem, & Hertel, 2015). Two contrasting strategies have been proposed to meet growing agricultural demand, whilst alleviating their impacts on nature (Green, Cornell, Scharlemann, & Balmford, 2005). First, intensification of farming on existing lands to maximize per hectare yields, thereby “sparing” land elsewhere for nature (land sparing). Second, the integration of “wildlife-friendly” habitat features, such as riparian strips, hedgerows, patches of remnant forest and organic practices throughout farmland, elevating biodiversity within the agricultural landscape (land sharing).

The relative success of either land-use strategy varies considerably with contextual environment, depending on spatial scale and configuration of agricultural lands, institutional governance and existing social setting (Chaplin-Kramer et al., 2016; Law & Wilson, 2015; Phalan, 2018; Sayer et al., 2013; Tscharntke et al., 2012). Additionally, conclusions also appear dependent on study context, including the methodology used and researchers' focus. Whilst the majority of empirical studies support species conservation via land sparing, the evidence from modelling approaches is more evenly balanced, and the majority of reviews support land sharing (Luskin, Lee, Edwards, Gibson, & Potts, 2017).

Across tropical regions, low-intensity agriculture integrating "wildlife-friendly" features can harbour substantial biodiversity (Clough et al., 2011; Fischer et al., 2008; Ranganathan, Krishnaswamy, & Anand, 2010; Steffan-Dewenter et al., 2007), particularly when adjacent to blocks of contiguous forest (Edwards, Gilroy, Thomas, Uribe, & Haugaasen, 2015; Gilroy, Edwards, Medina Uribe, Haugaasen, & Edwards, 2014). In addition, such features can promote dispersal of organisms across agricultural landscapes through greater habitat connectivity (Anand, Krishnaswamy, Kumar, & Bali, 2010). However, despite evidence of elevated biodiversity benefiting agricultural production through enhanced ecosystem services, such as soil formation and pollination (Klein et al., 2007; Melo, Silva, Silva, Souza, & Neto, 2013; Perfecto & Vandermeer, 2010), low-intensity sharing landscapes always suffer some reduction in per hectare yields. Achieving necessary production can, therefore, come at the expense of remaining natural habitat (Edwards et al., 2010; Ewers, Scharlemann, Balmford, & Green, 2009). Thus, the intensification of agriculture, and protection of associated spared blocks of natural habitat, are increasingly advocated as the better strategies.

To date, empirical studies spanning regions and taxa have shown that more species are conserved at higher abundance within land-sparing than land-sharing farming (Chandler et al., 2013; Dotta, 2013; Edwards et al., 2010; Gilroy, Edwards et al., 2014; Hulme et al., 2013; Phalan, Onial, Balmford, & Green, 2011; Williams et al., 2017). Land sparing also appears to support ecological communities with higher phylogenetic diversity and more specialist species, potentially of greater conservation value (Edwards et al., 2015; Socolar, Gilroy, Kunin, & Edwards, 2016). Additionally, land-sparing landscapes can hold greater capacity for carbon storage (Gilroy, Woodcock et al., 2014; Williams et al., 2017). However, whether intensive agriculture does actively spare land for nature is still contentious (Carrasco, Larrosa, Milner-Gulland, & Edwards, 2014; Ewers et al., 2009; Hertel, Ramankutty, & Baldos, 2014) and land sparing can have negative ecological consequences arising from inappropriate application and unsustainable intensification (Angelsen & Kaimowitz, 2001; Tilman, Cassman, Matson, Naylor, & Polasky, 2002). However, many of the criticisms of land sparing are based on misconceptions of the sparing-sharing model and ignore its original purpose—to explain how wild species respond to agriculture, and how best to conserve their populations in the future without compromising food security (Phalan, 2018).

Previous studies have focused on quantifying the species richness and structure of communities conserved within extensive low-intensity agro-landscapes versus areas of high-yield farming which permit the retention of relatively large blocks of natural habitat (Edwards et al., 2015; Gilroy, Edwards et al., 2014; Phalan et al., 2011; Williams et al., 2017). A key gap in current knowledge is whether land-sparing or land-sharing strategies best conserve the functional structure of species' assemblages. Here, functional diversity (FD) quantifies the range of functionally important traits and ecological roles present within a community that are at least partially responsible for sustaining various ecological processes (Leitão et al., 2016; Petchey & Gaston, 2002; Tilman, 2001; Villéger, Mason, & Moullot, 2008). Alongside phylogenetic diversity, FD has been proposed to be a key metric of human impacts on biodiversity and ecosystem functioning (Chapman, Tobias, Edwards, & Davies, 2018; Flynn, Mirotnick, Jain, Palmer, & Naeem, 2011), with demonstrated links to the productivity of multiple wild ecosystems (Duffy, Godwin, & Cardinale, 2017). Evidence also suggests land-use change can have greater effects on FD than taxonomic diversity (Tinoco, Santillán, & Graham, 2018). Changes in environmental conditions following habitat disturbance and conversion consistent with a sparing or sharing strategy will likely drive environmental filtering, narrowing the range of ecological traits persisting within these altered landscapes (Cardinale et al., 2012; Fauset et al., 2012). In theory, this loss of functionally important species and their associated ecological roles can severely degrade the resilience and stability of communities to future conversion (Bregman et al., 2016; Elmqvist et al., 2003), and reduce the provision ecosystem services (Cardinale et al., 2012; Flynn et al., 2009; Hooper et al., 2005).

Previous work has shown that simplification of natural systems, such as conversion to agriculture, corresponds to varying declines in FD (Luck, Carter, & Smallbone, 2013; Tscharntke et al., 2008). For example, wholesale conversion of tropical forest to oil palm plantations in Borneo greatly reduced FD of both dung beetles (Edwards, Edwards, Larsen et al., 2013) and birds (Edwards, Edwards, Hamer, & Davies, 2013). Similarly, within the Neotropics, avian FD in groups of species involved in key ecological processes, including seed dispersal, undergoes catastrophic erosion when forest is converted to cropland or pasture (Bregman et al., 2016). Conversely, the retention of remnant forest patches is associated with the retention of higher FD in agricultural landscapes (Prescott et al., 2016), likely because natural forests enable "spill-over" of rare and functionally important species into farmland (Gilroy, Edwards et al., 2014). However, FD has not been empirically tested within land-sparing and land-sharing theory, limiting our understanding of how FD of communities is impacted in natural and agricultural landscape mosaics.

Here, we examine the relative performance of land-sparing and land-sharing agriculture in conserving FD of birds in the Chocó-Andes of Colombia, a threatened biodiversity hotspot (Jenkins, Pimm, & Joppa, 2013). To assess how agricultural landscapes shape avian communities, we use field survey data collected across forest and farmland habitats and along gradients of increasing distance from contiguous forest and increasing proportions of within-farm wooded

habitat cover. These habitat variables were then used to model species responses to varying natural and agricultural environments.

Birds are a useful system for assessing impacts of land-use change on ecosystem function because they are relatively easy to survey and have a number of measurable traits—including wing and beak shape—closely linked to key ecological or trophic processes (Bregman et al., 2016). In addition, they are widely acknowledged to play a vital role in key ecological processes, including seed dispersal, pollination, pest control, nutrient cycling and soil formation (see Lundberg & Moberg, 2003; Sekercioglu, 2006; Şekercioglu, Wenny, & Whelan, 2016). Previous research has shown that avian species and FD can significantly improve agricultural yields, particularly in the tropics (Karp et al., 2013; Maas, Clough, & Tschardtke, 2013), through services such as insect pest control and pollination (Classen et al., 2014; Martínez-Salinas et al., 2016; Milligan, Johnson, Garfinkel, Smith, & Njoroge, 2016). However, previous work has focused on agroforestry systems and current literature lacks empirical work demonstrating ecosystem service provision by birds specifically within open pasture systems. Despite the lack of current evidence, birds may provide important services within pasture via both provisioning services, including soil formation and nutrient cycling resulting from greater input of faeces and movement of nesting materials, and regulating services through the control of phytophagous (herbivorous) and parasitic pests.

We compiled a comprehensive dataset of functional traits for all bird species sampled and used this to calculate FD indices and abundance of key functional groups for observed and modelled communities. We then used these estimates to predict how FD varied across a range of land-sparing and land-sharing scenarios, varying in level of agricultural production and distance from adjacent forest. Our goal is to provide information critical to land-use planning exercises designed to optimize FD, with positive effects on the stability and resilience of natural systems, and potentially also of future agricultural production (Elmqvist et al., 2003; Karp et al., 2013).

## 2 | METHODS AND MATERIALS

### 2.1 | Study sites

We sampled three sites within the Colombian departments of Risaralda, Chocó and Antioquia (see Gilroy, Edwards et al., 2014; Figure S1). Ranging from 1,290 to 2,680 m above sea level and characterized by submontane and subtropical cloud forest (Armenteras, Gast, & Villareal, 2003), each study site spanned both farmland and contiguous blocks of predominantly primary forest, with some secondary forest (aged 6–30 years). Extensive cattle pasture represented the dominant agricultural form, covering around 10 million ha of the region and comprising >95% of agricultural lands within each study site (Etter, McAlpine, Wilson, Phinn, & Possingham, 2006; Giraldo, Escobar, Chará, & Calle, 2010).

Bird communities were sampled at 174 points distributed within 400 × 400 m squares apportioned to the relative cover of each of the three habitat types. A total of 58 squares were sampled, spanning

farmland and contiguous blocks of forest, 23 in primary, 15 in secondary (6 mature secondary, aged 15–30 and 9 younger secondary, aged 6–15) and 20 in agriculture (see Figure S1). Following previous studies, no distinction was made between forested habitats (Gilroy, Edwards et al., 2014). Squares were distributed randomly within habitats, with a minimum distance of 400 m between squares in the same habitat and 300 m between squares within different habitats. Within individual squares, sampling points were located at each corner of triangular transects, placed randomly within habitats to account for variation in microhabitat and spaced at least 200 m apart from one another to ensure community independence (Hill & Hamer, 2004; Pearman, 2002). Sampling was conducted during regional “dry seasons,” January to March and June to July 2012.

### 2.2 | Habitat variables

Squares located within cattle pasture spanned gradients of two habitat variables, the proportion of “wildlife-friendly” habitat cover, comprised of patches of remnant forest, isolated trees, riparian strips and hedgerows (<27 ha), and varying distance from contiguous blocks of forests (ranging from 50 to 1,550 m). We visually mapped the distribution of all “wildlife-friendly” features ( $F$ ), within a 100 m radius of each sampling point ( $r$ ), in addition to the extent of grazed pasture ( $P$ ) and areas of nonpasture habitat, using site walkovers where required. Maps were digitized and used to calculate an index of “wildlife-friendly” habitat within each sampling point relative to other land uses, termed  $W$  (Equation 1) (see Gilroy, Edwards et al., 2014). As to compare the proportion of habitat cover beneficial to biodiversity to that directly producing yield, we removed all other nonpasture habitats (farmland infrastructure, buildings and roads), before calculation of the index. Sampling points entirely composed of pasture (i.e. no “wildlife-friendly” habitat cover) and forest sampling points (i.e. no pasture cover) were assigned values of  $W = 0$  and  $W = 1$ , respectively.

$$W_r = \frac{F_r}{P_r + F_r} \quad (1)$$

To reduce inaccuracies, distances of each pasture sampling point from the nearest contiguous block of forest were measured via remote-sensed data (ALOS/PALSAR) (Shimada, Tadono, & Rosenqvist, 2010) and hand-held GPS devices. Additionally, where study sites remained largely inaccessible, visual mapping of forest edges was also used. Relative cover of each habitat from observations, excluding remnant forest fragments, was mapped by Gilroy, Edwards et al. (2014) (see Figure S1). Sampling points located entirely in either primary or secondary forest were assigned a distance of 0 m.

### 2.3 | Avifaunal sampling

Repeat visit point counts were used to sample bird communities (Gilroy, Edwards et al., 2014). Inside each square, three sampling

points were positioned 200 m apart at each corner of triangular transects, totalling 174 points across all habitats. Sampling occurred between 6:00 a.m. and 12:00 p.m. on four successive mornings, except in inclement conditions. Sampling order of points varied to ensure all points were sampled at different times throughout the morning. Point counts lasted 10 min, with all birds within a 100 m radius recorded, excluding transitory or highly mobile species. We selected a point count radius of 100 m ( $r$ ), based on previous evidence outlining spatial scales of community turnover in tropical forest birds (Hill & Hamer, 2004; Pearman, 2002). We identified species from unknown vocalizations by comparing field recordings (taken using Sennheiser ME66 microphones and Olympus LS11) with an online archive of preidentified calls ([www.xeno-canto.org](http://www.xeno-canto.org)).

## 2.4 | Constructing a functional trait matrix

We assessed avian FD by compiling a matrix of individual species' life history traits for every observed species ( $n = 318$ ) with respect to three broad categories, following previous studies highlighting functionally important traits (Edwards, Edwards, Hamer et al., 2013; Flynn et al., 2009; Luck et al., 2013). First, dietary traits, comprised of differing foraging guilds (nectarivore, insectivore, granivore, frugivore and carnivore). Second, behavioural traits split into foraging strata (canopy, mid-strata, understorey and terrestrial) and foraging mode (trunk/branch, aerial and foliage). Third, following previous studies (Bregman et al., 2016; Chapman et al., 2018), we compiled a suite of twelve morphological traits: body mass and length, tarsus length, tail length, wing length, Kipp's distance, hand-wing index, and bill width, depth, shape and length (both nares to tip and exposed culmen). Measurements of wing length and Kipp's distance—the distance from wing tip to the first (outermost) secondary feather—were not included directly in the matrix but used to calculate hand-wing index ( $\text{Kipp's} \times 100/\text{wing length}$ ), a measure of wing aspect ratio correlated with flight efficiency (Pigot, Tobias, & Jetz, 2016). Hand-wing index reflects the pointedness of a bird's wing, providing a widely used index of avian dispersal ability and ranging behaviour, with relevance to seed dispersal, pollination, gap-crossing ability and sensitivity to habitat fragmentation (Bregman et al., 2016; Pigot, Bregman et al., 2016). Additionally, information on basic life history traits, degree of territoriality and predominant habitat type, was also included (see Table S1 for full trait list and functional significance of each trait).

Information on individual species' traits was derived from both online sources and measurements from museum specimens. Dietary information, foraging strata, foraging mode and morphological traits (bill shape, body length and body mass) were obtained from an online source, *Handbook of Birds of the World Alive* (del Hoyo et al., 2014). Measurements of body length and mass represent averages across males and females. For all other morphological traits, we measured specimens from museum collections taking measurements from at least two female and two male specimens when possible. For further details of morphometric methods and sources of specimens, see Data S1 and Methods S1.

As many generalist species feed on multiple prey items or at multiple strata, we split trait categories—diet, foraging strata and foraging mode—into multiple independent binary traits, allowing species to possess multiple traits within the same category (e.g. to be frugivorous and insectivorous), following methods by Petchey, Evans, Fishburn, and Gaston (2007). Additionally, we checked that species traits had minimal correlation before inclusion in the final matrix from which measures of FD were calculated (see Figure S2 for correlation plot, and Table S1 for correlated traits).

## 2.5 | Measures of functional diversity

Having compiled information of individual species traits, we used the FD (Laliberté, Legendre, & Shipley, 2014) and *picante* packages (Kembel et al., 2010) to calculate five indices of FD. These included the complementary indices; functional richness (FRic), functional evenness (FEve), functional divergence (FDiv) (Villéger et al., 2008) and functional dispersion (FDis) (Laliberté & Legendre, 2010), in addition to the standalone measure of FD (Petchey & Gaston, 2002).

FRic, FEve, FDiv and FDis are measures of species ordination within multidimensional "trait space," with axes representing sets of correlated traits and species positioned in space by their individual traits, identifying each species ecological niche (Villéger et al., 2008). Each index gives specific information on the FD of communities based upon their ordination within trait space:

1. Functional richness (FRic) represents the total volume of space occupied by a set of species. Communities with greater FRic likely contain a greater range of functional traits potentially corresponding to greater utilization of resources. Loss of species at the edges of trait space, as a result of land-use change, will cause a reduction in functional richness potentially corresponding to a loss of specific functional roles.
2. Functional evenness (FEve) describes how evenly a community's species are distributed within trait space relative to their abundance. Communities with greater FEve have more efficient resource use, as species abundances are more evenly distributed within trait space. Communities whose constituent species occupy a similar region of trait space, and thus carry out similar functional roles, will be less evenly distributed, having lower FEve and higher functional redundancy.
3. Functional divergence (FDiv) measures the relative abundance of species with the most extreme functional traits (those furthest from the centre of trait space), indicating levels of niche differentiation. Thus, communities with greater FDiv likely have greater niche differentiation, correlating to reduced competition. Declining FDiv can, therefore translate to declining abundances of species with unique functional traits.
4. Functional dispersion (FDis) measures the distribution of species traits, measuring the mean distance of species from the centre of trait space and weighted by abundance (Laliberté & Legendre, 2010). Increases in FDis represent a greater representation of species with more unique functional traits.

Species were weighted by their abundance, with all traits weighted equally. Before calculation, we converted the trait matrix to a distance matrix using the Gower distance measure (Podani, 1999). Principle coordinate analysis (PCoA) was then used to calculate a transformed trait matrix, from which FD indices were calculated. Species were positioned within “trait space” via a multidimensional convex hull (Villéger et al., 2008).

To calculate the functional diversity index, FD, we used dendrogram-based methods following Petchey and Gaston (2002). Unweighted Pair Group Method with Arithmetic Mean (UPGMA) was used to calculate a functional dendrogram for all species within the regional species pool (Swenson, 2014), before calculating FD values by summing the total connecting branch lengths of all species within a community (Petchey & Gaston, 2002). Due to forested habitats having far greater species richness than pasture (Gilroy, Edwards et al., 2014) and a known correlation between species richness and FD, we also calculated the standardized effect size of FD (sesFD) for observed communities (see Text S2). Communities with positive values of sesFD hold greater FD than expected by chance, and relative to their species richness, whilst communities with negative sesFD hold lower levels of FD than expected by chance, and relative to their species richness. Communities with greater sesFD may be more susceptible to declining FD in response to species loss, as each constituent species contributes more to overall FD than those of a community with lower sesFD. Analysis of sesFD requires an abundance matrix (each species' abundance at each sample point). However, for model communities, a single abundance for each species is predicted for the entire hypothetical landscape, and not at the individual point scale. As a result, analysis of this index was limited to raw data (see Figure S3).

## 2.6 | Impacts of “wildlife-friendly” habitat and proximity to forest on FD in farmland

To examine variation in each FD metric in response to the two habitat variables, we controlled for the effects of imperfect detection on estimates of site level species occurrence using a Bayesian hierarchical occupancy model (Dorazio & Royle, 2005). For all 318 species detected, we modelled species occurrence probabilities in response to the proximity of contiguous forest, and the proportion of “wildlife-friendly” habitat cover, at each sampling site (following Gilroy, Edwards et al., 2014). The model accounts for large-scale spatial variation in occupancy via site-level random effects, as well as temporal and between-species variation in detection probabilities, including, for example, reduced detectability within dense forested or “wildlife-friendly” habitats relative to open farmland, and reduced vocal activity later in the day (Gilroy, Edwards et al., 2014). Prior to modelling, species were divided into those species detected in forested habitats (288 forest species) and species exclusively detected in cattle pasture (30 nonforest species), modelling each community separately. Parameters were estimated using WinBUGS version 1.4 (Spiegelhalter, Thomas, Best, & Lunn, 2003; see Gilroy, Edwards et al., 2014 for full details).

We used posterior-predictive samples of species occurrence probabilities to estimate the abundance of each species at each farmland sampling point, fully accounting for imperfect detection and model uncertainty (Dorazio & Royle, 2005). To calculate an abundance metric for each species at each site (necessary for some FD metrics), we took the sum of 30 Bernoulli trials with probability given by each of the 1,000 posterior-predictive samples of site-level species occurrence probability. Estimated communities are therefore equivalent to the relative prevalence (predicted occurrence and abundance) of each species in a hypothetical landscape composed of 30 sites (circles of 100 m radii) with identical habitat conditions to the sampled site in question. We then calculated each of the mean FD metrics for these 1,000 samples for each site.

## 2.7 | Simulating land-sparing and land-sharing scenarios

To assess the relative performance of land-sparing and land-sharing farming in conserving FD, a landscape simulation process was used to estimate species abundances under hypothetical land-sparing and land-sharing landscapes (see figure 1 in Gilroy, Edwards et al., 2014). Each hypothetical landscape consisted of management units, each made up of 30 “sites” with a set of habitat characteristics dictated by the scenario in question. For land-sharing scenarios, all units within a landscape consist of farmland sites, each containing a fixed proportion of “wildlife-friendly” habitat cover and located at a given distance from the nearest contiguous forest (with scenarios spanning 250–1,500 m, in increments of 250 m). To simulate land-sparing, landscapes are divided into farmland sites and “spared” sites, with farmland sites consisting entirely of pasture (i.e. no “wildlife-friendly” habitat), again located at a given distance from contiguous forest, and “spared” sites that are located within the contiguous forest block (i.e. the spared portion of the landscape is permitted to be “off-farm”).

Each scenario was simulated at two production levels of cattle pasture, consistent with upper and lower limits of pasture cover observed across sample sites: high production = 80% grazed land; low production = 20% grazed land. For instance, in a high-production simulation of land-sharing, 80% of each individual site was grazed and 20% designated as “wildlife-friendly” habitat, whereas in a high-production simulation of land-sparing, 80% of the sites were designated as fully grazed and 20% of sites designated as contiguous forest. Land-sparing and land-sharing scenarios, at a given production level, support the same aggregate level of cattle production, and thus examine the performance of each scenario in conserving FD, independent of production.

We then calculated our five measures of FD for 10,000 replicates for each simulated landscape scenario, again converting species occurrence probabilities to landscape-level abundance metrics via summed Bernoulli trials. Mean values of each FD measure were then produced from these 10,000 replicates under each land-sparing and land-sharing scenario. For each iteration, new parameter values were randomly drawn from their respective posterior distributions, thus fully exploring the uncertainty in model parameters.



## 2.8 | Estimating impacts of land-sparing and land-sharing agriculture on avian functional traits

Although functional indices provide important information about the functional structure of communities, they are insensitive to changes in the abundance of constituent species. In particular, FD and functional richness (FRic) are unaffected by changes in species abundance. To evaluate how the prevalence of key functional traits might be influenced by agricultural expansion under either land-use strategy, we estimated “trait abundances” for communities under land sparing and land sharing by summing the model-predicted abundances of species possessing each functional trait within 30-site simulated landscapes, derived using the method described above. We then calculated the change in the abundance of each trait relative to an all-forest baseline (i.e. a simulated landscape comprising 30 “sites” within forest) and repeat this for 1,000 replicates under each scenario. We compare changes in trait abundances for twelve categorical traits, spanning three trait categories (Dietary: frugivore, nectivore, carnivore, granivore and insectivore, Foraging mode: aerial, trunk/branch, and foliage, and Foraging strata: terrestrial, understorey, midstrata, and canopy).

## 3 | RESULTS

### 3.1 | Impacts of farming on FD

All FD indices, other than FDiv (Figure S4a), were affected by habitat type. Predicted values of FD and FRic were substantially lower within pasture than forest (Figure 1a,d). In contrast, FEve was predicted to peak within cattle pasture in comparison to forested habitat (Figure 1g). A similar effect of habitat was observed for FDis (Figure S4d). Within pasture sites, predicted responses of functional indices to the two habitat variables indicate strong effects of proximity to forest and proportion of “wildlife-friendly” habitat on FRic and FD (Figure 1). FRic and FD were predicted to peak in pasture containing a greater proportion of “wildlife-friendly” features and located closer to contiguous blocks of forest (Figure 1b,c,e and f). Contrastingly, functional evenness of pasture sites remained largely unaffected by either distance from forest or relative cover of “wildlife-friendly” habitat (Figure 1h,i), mirroring predicted responses of FDiv and FDis (Figure S4).

In addition to simulated communities, all functional indices and sesFD were calculated for observed communities, at the sample point and whole habitat level (see Table S2). In contrast to FD values of observed and simulated communities, sesFD was greater in cattle pasture than forest and was unaffected by both proportion of “wildlife-friendly” habitat cover and distance from contiguous forest (Figure S3).

### 3.2 | Impacts of land-sparing and land-sharing agriculture on FD

Predicted levels of FD conserved under simulated land-sparing and land-sharing scenarios varied considerably depending on production

level, distance from contiguous forest and functional indices. FRic and FD showed the most pronounced trends, with sparing scenarios conserving greater FD and richness than sharing at all distances and at both low and high production levels (Figure 2a–d).

Under low and high production land-sparing scenarios, predicted FD and FRic remained stable across all distances from contiguous forest (Figure 2a,b). In contrast, predicted FD and FRic under land-sharing scenarios progressively decreased with increasing distance from contiguous forest, with mean FD and FRic 26% and 30% lower, respectively, under high production sharing than sparing at the greatest distance from contiguous forest (1,500 m) (Figure 2d). Predicted values of FD and FRic were also affected by production level, with slightly lower FD and FRic occurring at high production for both strategies. Similar trends of land-use strategy and production, but not distance, were also predicted for functional divergence, with greater FDiv consistently predicted to occur under sparing than sharing, and at low rather than high production (see Figure S2).

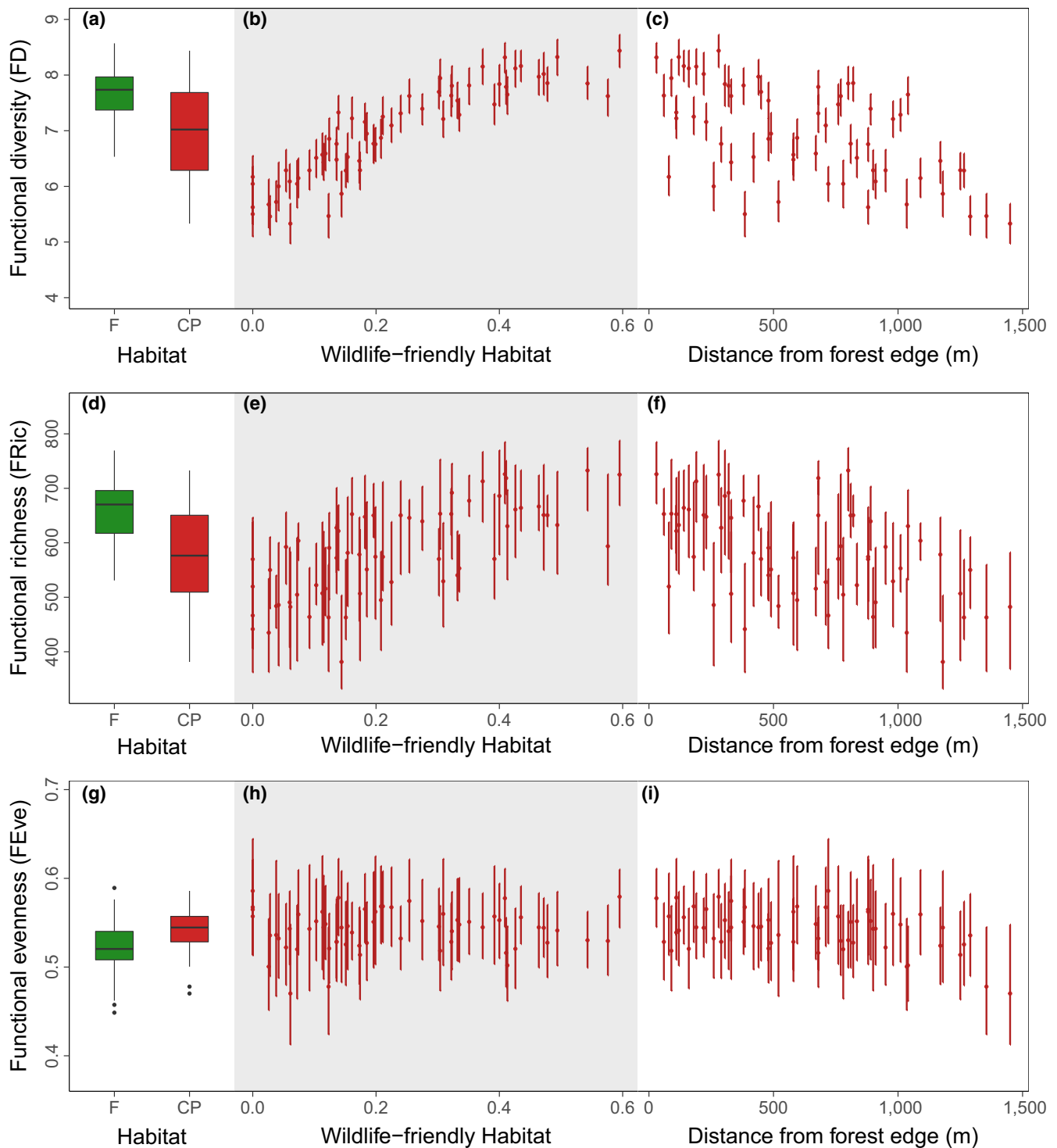
High production land-sparing scenarios were predicted to conserve consistently higher FEve than land sharing, with minimal effect of distance to contiguous forest (Figure 2f). By contrast, low production land-sharing scenarios were predicted to conserve slightly greater FEve than land sparing at close proximity to forest edge but to conserve less FEve furthest from forest edge (1,500 m; Figure 2e). Contrastingly FD and FRic, greater FEve was predicted under land-sparing and land-sharing scenarios at high rather than low production.

In contrast to all other indices, FDis was consistently predicted to be greater under land-sharing than land-sparing scenarios at all distances and at both production levels. Additionally, FDis was greater at high than low production (see Figure S5).

### 3.3 | Impacts of land-sparing and land-sharing agriculture on avian functional traits

As with overall FD, predicted trait abundances also varied considerably with level of production, land-use strategy and distance from contiguous forest. Of all twelve functional traits assessed, we predicted trait abundances of eleven to decline with agricultural expansion, irrespective of production level, distance from contiguous forest or whether farming via land-sparing or land-sharing strategy. The abundance of granivores was the only trait to increase under agricultural expansion, and only when farming under high production sharing scenarios.

Under low production, we predicted greater abundances of eleven traits (all but canopy) under land sparing than land sharing, including the abundances of all dietary traits (Figure 3). The greatest disparity in abundance between the two strategies was predicted for insectivores, with predicted declines in insectivore abundances over four times greater under land sharing than land sparing, across all distances from continuous forest. Under high production scenarios, differences in trait abundances between land-sparing and land-sharing landscapes were much less prominent. Abundances

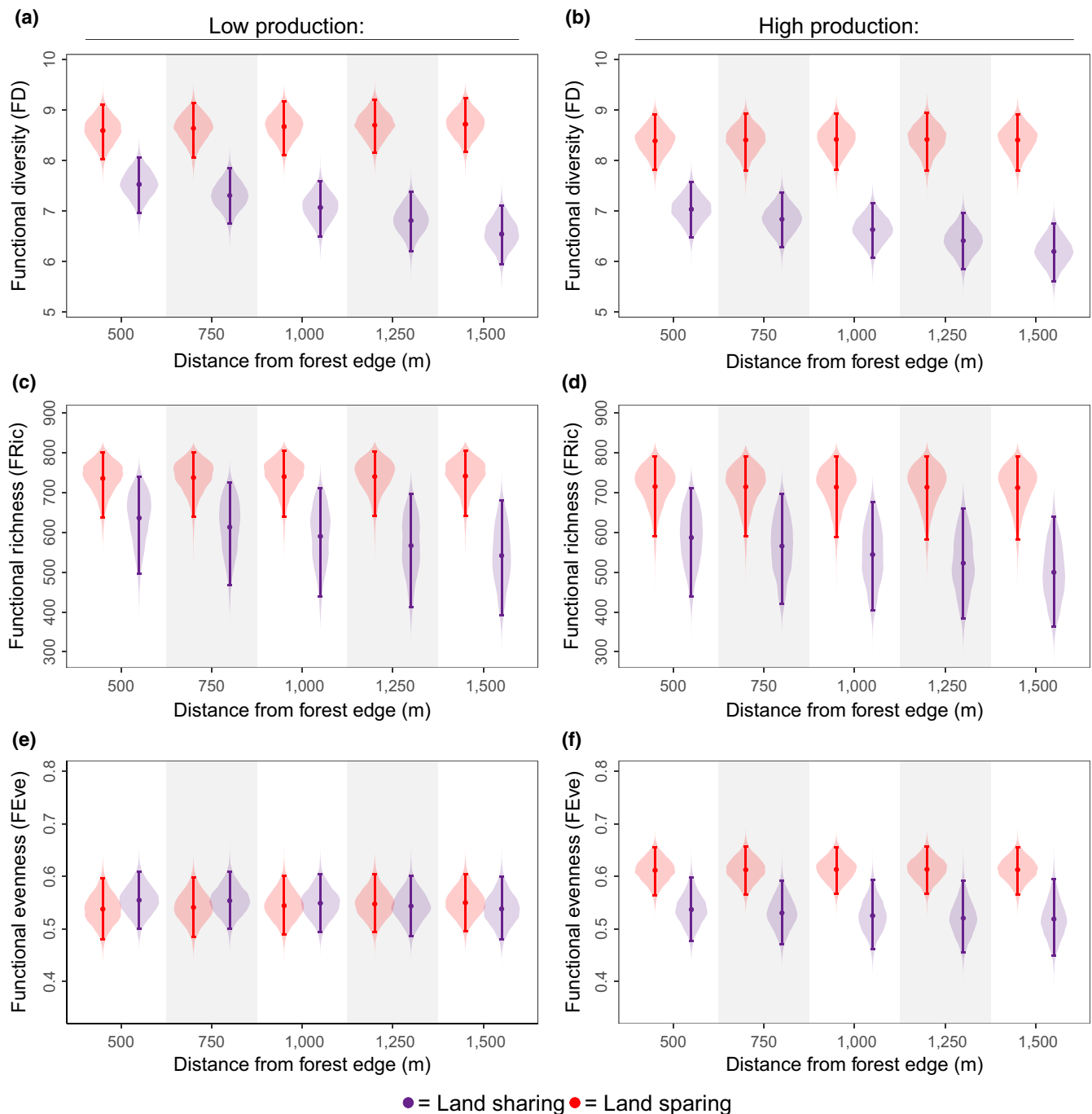


**FIGURE 1** Functional diversity indices for sample point-level model communities across habitat types (boxplots: F = forest; CP = cattle pasture) and plotted against the proportion of “wildlife-friendly” habitat and distance from forest blocks. Indices shown are mean FD (a–c), mean functional richness (d–f) and mean functional evenness (g–i). Error bars for each point represent 95th percentiles across 1,000 simulations (the variation in functional indices due to uncertainty in species occurrence probabilities at each sample point)

of insectivores, foliage, trunk/branch and midstrata feeding species were slightly greater under sparing, whilst the abundances of granivores, frugivores, nectivores, and aerial and terrestrial feeding species were slightly greater under land-sharing scenarios. Abundances of carnivores, and canopy and understorey feeding

species differed minimally between strategies (Figure 3, Figures S6 and S7).

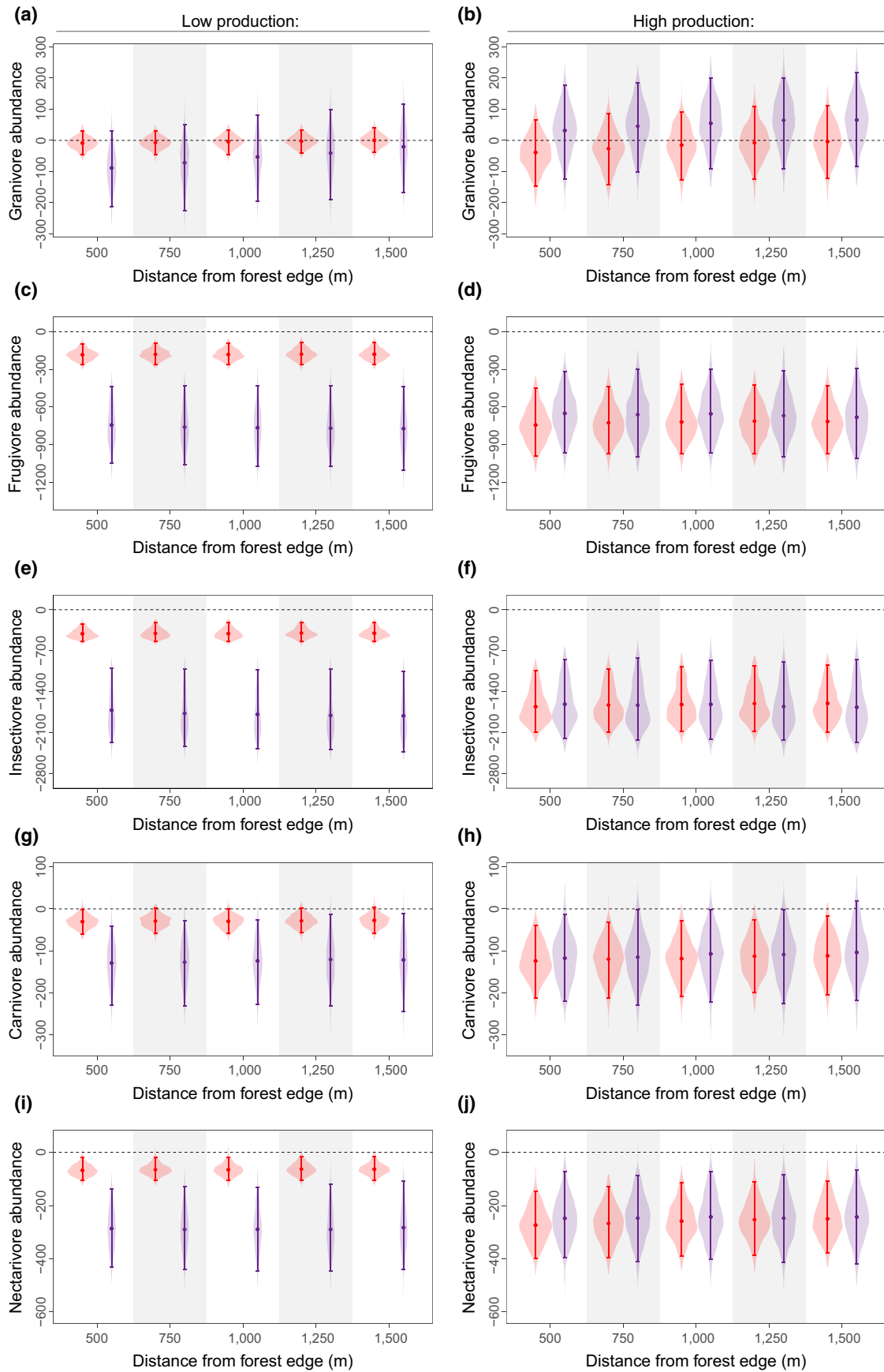
Trait abundances within land-sparing habitats were considerably more sensitive to production level than land sharing. Abundances of eleven functional traits (all other than granivores)



**FIGURE 2** (a, b) Functional diversity (FD), (c, d) functional richness (FRic), and (e, f) functional evenness (FEve) under simulated land-sparing (red) and land-sharing (purple) management units. Indices are generated for scenarios at two production levels: low – 20% land cover grazed (a, c, e), and high – 80% land cover grazed (b, d, f), and span increasing distance from contiguous forest blocks. Mean values from 10,000 randomizations under each scenario indicated by points, with error bars representing 95th percentiles. Surrounding violin plots display frequency distributions of indices from 10,000 randomizations of each scenario

**FIGURE 3** Changes in dietary trait abundance under simulated land-sparing (red) and land-sharing (purple) management units; (a, b) abundances of granivores, (c, d) frugivores, (e, f) insectivores, (g, h) carnivores and (i, j) nectivores. Abundance is generated for scenarios at two production levels; low – 20% land cover grazed (a, c, e, g and i), and high – 80% land cover grazed (b, d, f, h and j), and span increasing distance from contiguous forest blocks. Mean values from 1,000 randomizations under each scenario indicated by points, with error bars representing 95th percentiles. Surrounding violin plots display frequency distributions of indices from 1,000 randomizations of each scenario





● = Land sharing ● = Land sparing

were substantially lower under high production scenarios than low production. Contrastingly, trait abundances predicted to occur under land-sharing scenarios remained relatively unaffected by production level, with similar abundances conserved under sharing landscapes with a relatively small area of “wildlife-friendly” habitat as that of landscapes retaining much greater areas of forest amongst farmland.

## 4 | DISCUSSION

How best to limit the ecological impacts of expanding tropical agriculture is a key conservation question, and we uniquely investigate whether land-sparing or land-sharing farming would maximize the retention of FD. Functional indices represent variation in a wide range of biometric traits related to dietary guild, microhabitat niche, foraging strategy and locomotion. Functional indices thus reflect various dimensions of the ecological niche and provide information about the functioning of important ecological processes, such as seed dispersal and pollination (Pigot, Bregman et al., 2016). Our results indicate that high-yielding farming paired with blocks of protected natural habitat, consistent with land sparing, conserved greater overall FD than did land sharing, especially at increasing distance from contiguous forest. To ensure the retention of functionally diverse communities, we urgently need to better exploit mechanisms for increasing farmland productivity whilst protecting spared land.

Functional diversity under land-sharing scenarios was negatively affected by increasing distance from contiguous forest, with more isolated areas having lower FD and FRic. This trend mirrors those for species richness (Gilroy, Edwards et al., 2014) and phylogenetic diversity (Edwards et al., 2015), supporting suggestions that natural forests play important roles as population sources and provide resources necessary for species persisting in both forest and farmland (Gilroy & Edwards, 2017; Pereira & Daily, 2006; Şekercioğlu, Loarie, Oviedo, Ehrlich, & Daily, 2007). Beyond the intrinsic value of species, justification of low-intensity systems frequently highlights the benefits of enhanced ecosystem services from elevated biodiversity in offsetting potential yield losses caused by reduced crop cover (Melo et al., 2013; Schroth & McNeely, 2011; Tschamtket et al., 2008). However, we found that FD of land-sharing farming was tightly linked to proximity of contiguous forest, irrespective of “wildlife-friendly” habitat cover. Thus, as species fail to persist in increasingly isolated farmland, the loss of associated functional roles may also lead to declines in the provision of ecosystem services within agricultural systems. The greatest potential to protect FD within pasture landscapes therefore exists under land-sparing scenarios, where large blocks of natural habitat provide unparalleled conservation value (Barlow et al., 2016; Gibson et al., 2011). However, in tropical agroforestry, where biodiversity is high relative to pasture, ecosystem service provision can be more substantial (Karp et al., 2013) and may outweigh lost production from lower intensity practices.

Both FD and FRic are positively related to species richness (Petchey & Gaston, 2002; Villéger et al., 2008). Accounting for this confounding influence, we found lower sesFD within forested habitats than cattle pasture; communities with low sesFD and high species richness can occur when multiple constituent species perform similar functional roles, and thus appear functionally redundant. Greater functional redundancy can be beneficial for long-term ecosystem functioning, as loss of functionally important species does not necessarily translate to degradation of ecosystem processes when other functionally similar species continue to persist (Pavoine & Bonsall, 2011). These results are consistent with studies of avian FD in an oil palm-forest matrix in the Colombian Llanos (Prescott et al., 2016), and that of avian dispersal traits between forest and pasture in Amazonia (Bregman et al., 2016). Furthermore, we predict lower FEve under land sharing than land sparing, particularly at greater distances from forest. Declines in FEve and overall species richness indicate greater overlap in specific functional groups, suggesting declines or potential loss of species in specific functional groups in extensive low-intensity farmlands. Additionally, under land sharing, we predict declines in the abundance of the vast majority of traits, further supporting suggestions that the ecological functions provided by birds are degraded within sharing relative to sparing landscapes.

Predicted values of FDis contrast those of all other functional indices, with greatest FDis predicted to occur under land-sharing scenarios at the greatest distances from contiguous forest. Our results suggest land-sharing communities contain a greater proportion of species that possess functionally unique traits, and therefore appear further from the centre of trait space. This response is likely a result of how FDis is calculated. Functional dispersion measures the mean distance of constituent species within trait space from an abundance-weighted centroid (Laliberté & Legendre, 2010). In this way, loss of species at the centre of trait space can result in greater values of FDis. Given predicted declines in the majority of trait abundances under land sharing, this further demonstrates a lack of functional redundancy within these landscapes, with FD supported by a few functionally unique species.

We predict lower abundances of nearly all functional traits under low-production land sharing, than land sparing, including significant declines in the abundances of frugivores and nectivores. Given the importance of frugivorous and nectivorous birds in seed dispersal and pollination, particularly in the tropics (Şekercioğlu, 2006), their reduced abundances may lead to reductions in the provision of these important ecological processes. This could impact the long-term stability of natural habitats dispersed within agriculture, as well as the potential for restoration of abandoned pasture to secondary forests (Carlo & Morales, 2016; Martínez-Garza, Palmas-Pérez, Rivas-Alonso, & Howe, 2014).

In terms of ecosystem service provision, the impacts of declining trait abundances are unlikely to be confined to natural landscapes. Both the abundances of carnivores and insectivores are also predicted to be lowest under land-sharing scenarios, suggesting limited benefits of avian pest control services within sharing

landscapes. However, empirical studies demonstrating yield or production benefits from increases in ecological processes are greatly needed. In particular, evidence of enhanced soil formation, nutrient cycling and insect predation within pasture are currently lacking. In addition, the link between increased FD and greater provision of ecosystem services requires further attention, particularly in pasture, given that it represents the most prominent anthropogenic land-use throughout much of the tropics (FAOSTAT). However, our simulations of sparing landscapes constitute “off-farm” sparing, where protected lands exist in separation from intensive pasture. Thus, in our sparing systems, the flow of potential services from “spared” land to pasture may be severely impeded due to lack of forest directly adjacent to farmland (Mitchell et al., 2015). Furthermore, trait abundances conserved under land sparing declined markedly under high production scenarios, where spared lands represent only a small proportion of the landscape. This result supports findings of other studies, emphasizing the importance of sparing large blocks of natural habitat for effective biodiversity conservation via land sparing (Edwards et al., 2015; Gilroy, Woodcock et al., 2014; Lamb, Balmford, Green, & Phalan, 2016).

An important caveat is that our landscape scenarios did not account for fragmentation of spared lands, with all sparing management units pairing intensified agriculture with “off-farm” protected areas in contiguous forest. Greater fragmentation of natural habitats can result in dramatic increases in edge, isolation and area effects (Ewers & Didham, 2007; Ferraz et al., 2003; Gibson et al., 2013; Hagen et al., 2012) that will likely diminish the conservation value of protected lands (Laurance et al., 2014). Additionally, if agricultural intensification is accompanied by unsustainable farming practices, immigration of people, and greater land use due to localized economic growth, then elevated edge and deforestation effects will likely degrade biodiversity benefits of adjacent spared forest (Angelsen & Kaimowitz, 2001; Tilman et al., 2002).

Lamb et al. (2016) showed that for Ghanaian birds the relative benefits of sparing versus sharing are partially influenced by habitat quality, with land sharing marginally outperforming land sparing when spared lands constitute severely fragmented landscapes and suffer acute edge effects. Because rare and disturbance-sensitive species are most likely to be affected by fragmentation (Banks-Leite, Ewers, & Metzger, 2010) and contribute disproportionately to FD by possessing unique traits necessary for ecosystem function (Leitão et al., 2016), fragmentation effects could be especially important in degrading the value of sparing for FD. However, fragmentation will likely also affect the long-term persistence of species under land-sharing farming, given that biodiversity values are evidently contingent on spill-over from adjacent forest (see also Gilroy, Woodcock et al., 2014; Edwards et al., 2015).

The superiority of land sparing compared to land sharing in conserving FD remains, as it does so in similar studies of species richness and phylogenetic diversity, partly dependent on the assumption that agricultural production increases in line with pasture cover (Edwards et al., 2015; Gilroy, Edwards et al., 2014). Realized production of

intensified agriculture can, however, be substantially lower than expected when practices are not tailored to local social dynamics, as is the case for much of the smallholder-dominated tropics (Chappell & LaValle, 2011). Furthermore, high-yielding sharing systems can occur when aspects of biodiversity are used to improve beneficial ecosystem services, such as pest control and pollination (Schroth & McNeely, 2011; Tscharntke et al., 2012). Additionally, even when intensification results in greater yields, intensification may not necessarily translate to increased spared land for nature (Ewers et al., 2009; Ramankutty & Rhemtulla, 2012). Conversely, fears of further conversion and rising conservation costs as a result of stimulated demand, and regional and local leakage remain substantial obstacles to successful land sparing (Carrasco et al., 2014; Hertel et al., 2014; Phelps, Carrasco, Webb, Koh, & Pascual, 2013). Nonetheless, the apparent necessity for large tracts of natural habitat to sustain maximum levels of biodiversity under land sharing lends further support to the integral role that land sparing must play in future conservation.

In conclusion, our results suggest that avian FD will be best protected via conserving large blocks of contiguous natural habitat through the intensification of agriculture on existing lands. Achieving such optimized landscapes requires steps to discourage further expansion and ensure sparing of natural habitats as a direct result of intensification. Maximization of conservation benefits resulting from prioritization of spared lands will likely occur when applied in combination with policies advocating sustainable intensification practises, minimizing negative ecological impacts to natural environments (Phalan et al., 2016). In addition, directing inevitable future agricultural expansion to areas of low biodiversity, especially recently abandoned agricultural land, offers considerable opportunity to reduce biodiversity losses while maintaining secure food systems (Chazdon, 2014; Gilroy, Woodcock et al., 2014; Prescott et al., 2016). Such opportunities are particularly apparent in Central and South America, where phases of land abandonment have already yielded substantial expanses of potentially productive lands (Aide et al., 2013). Our results provide important inferences about how the functional structure of ecosystems and associated ecosystem services are likely to be affected across agricultural and natural landscapes, lending further support to biodiversity conservation via land sparing.

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## SUPPORTING INFORMATION

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