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

Running head: Functional diversity of forest and farmland

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Keywords: agroecosystems; defaunation; ecosystem function; conversion; habitat loss; land-use planning.

Type of paper: Primary Research Article

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.

Introduction

Conversion of complex natural environments to increasingly homogenised agricultural systems poses the greatest threat to tropical biodiversity (Dobrovolski et al., 2011; Laurance et al., 2014). Occupying over 14 million km^2 of cropland and 33 million km^2 of pasture globally, agriculture now represents the single greatest land use (FAOSTAT, 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; Kotowaska et al., 2015). Two contrasting strategies have been proposed to meet growing agricultural demand, whilst alleviating their impacts on nature (Green et al., 2005). First, intensification of farming on existing lands to maximise 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 (Tscharntke et al., 2012; Sayer et al., 2013; Chaplin-Kramer et al., 2015; Law & Wilson, 2015; Phalan 2018). 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 et al., 2017).

Across tropical regions, low-intensity agriculture integrating 'wildlife-friendly' features can harbour substantial biodiversity (Steffan-Dewenter, 2007; Fischer et al., 2008; Ranganathan et al., 2010; Clough et al., 2011), particularly when adjacent to blocks of contiguous forest (Gilroy et al., 2014a; Edwards et al., 2015). In addition, such features can

promote dispersal of organisms across agricultural landscapes through greater habitat connectivity (Anand et al., 2010). However, despite evidence of elevated biodiversity benefiting agricultural production through enhanced ecosystem services, such as soil formation and pollination (Klien et al., 2007; Perfecto & Vandermeer, 2010; Melo et al., 2013), 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 (Ewers et al. 2009; Edwards et al. 2010). Thus, the intensification of agriculture, and protection of associated spared blocks of natural habitat, is increasingly advocated as the better strategy.

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 (Edwards et al., 2010; Phalan et al., 2011; Chandler et al., 2013; Dotta et al., 2013; Hulme et al., 2013; Gilroy et al., 2014a; 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 et al., 2016). Additionally, land-sparing landscapes can hold greater capacity for carbon storage (Gilroy et al., 2014b; Williams et al., 2017). However, whether intensive agriculture does actively spare land for nature is still contentious (Ewers et al., 2009; Carrasco et al., 2014; Hertel et al., 2014) and land sparing can have negative ecological consequences arising from inappropriate application and unsustainable intensification (Angleson & Kaimowitz, 2001; Tilman et al., 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 (Phalan et

al., 2011; Gilroy et al., 2014a; Edwards et al., 2015; 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 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 (Tilman, 2001; Petchey & Gaston, 2002; Villéger et al., 2008; Leitão et al., 2016). Alongside phylogenetic diversity, functional diversity has been proposed to be a key metric of human impacts on biodiversity and ecosystem functioning (Flynn et al., 2011, Chapman et al., 2018), with demonstrated links to the productivity of multiple wild ecosystems (Duffy et al., 2017). Evidence also suggests land-use change can have greater effects on functional diversity than taxonomic diversity (Tinoco et al., 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 (Elmqvist et al., 2003; Bregman et al., 2016), and reduce the provision ecosystem services (Hooper et al., 2005; Flynn et al., 2009; Cardinale et al., 2012).

Previous work has shown that simplification of natural systems, such as conversion to agriculture, corresponds to varying declines in functional diversity (Tscharntke et al., 2008; Luck et al., 2013). For example, wholesale conversion of tropical forest to oil palm plantations in Borneo greatly reduced functional diversity of both dung beetles (Edwards et al., 2013a) and birds (Edwards et al., 2013b). Similarly, within the Neotropics, avian functional diversity 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 functional diversity in agricultural landscapes (Prescott et al., 2016), likely because natural

forests enable ‘spill-over’ of rare and functionally important species into farmland (Gilroy et al., 2014a). However, functional diversity has not been empirically tested within land-sparing and land-sharing theory, limiting our understanding of how functional diversity 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 functional diversity 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 and Moberg 2003; Şekercioğlu 2006; Şekercioğlu et al., 2016). Previous research has shown that avian species and functional diversity can significantly improve agricultural yields, particularly in the tropics (Karp et al., 2013; Maas et al., 2013), through services such as insect pest control and pollination (Classen et al., 2014; Martínez-Salinas et al., 2016; Milligan et al., 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 functional diversity indices and abundance of key functional groups for observed and modelled communities. We then used these estimates to predict how functional diversity 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 optimise functional diversity, 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).

Methods and materials

Study sites

We sampled three sites within the Colombian departments of Risaralda, Chocó and Antioquia (see Gilroy et al., 2014a; Fig. S1, Supporting information). Ranging from 1290-2680 m above sea level and characterised by sub-montane and sub-tropical 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 et al., 2006, Giraldo et al., 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 Fig. S1, Supporting information). Following previous studies, no distinction was made between

forested habitats (Gilroy et al., 2014a). 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 (Pearman, 2002; Hill & Hamer, 2004). Sampling was conducted during regional 'dry seasons', January-March and June-July 2012.

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 50-1550 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 non-pasture habitat, using site walkovers where required. Maps were digitised 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 et al., 2014a). As to compare the proportion of habitat cover beneficial to biodiversity to that directly producing yield, we removed all other non-pasture 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.

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

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

189 remained largely inaccessible, visual mapping of forest edges was also used. Relative cover of
190 each habitat from observations, excluding remnant forest fragments, were mapped by Gilroy
191 et al., (2014a) (see Fig S1, Supporting information). Sampling points located entirely in either
192 primary or secondary forest were assigned a distance of 0 m.

193 **Avifaunal sampling**

194 Repeat visit point counts were used to sample bird communities (Gilroy et al., 2014a). Inside
195 each square, three sampling points were positioned 200 m apart at each corner of triangular
196 transects, totalling 174 points across all habitats. Sampling occurred between 6:00 am and
197 12:00 pm on four successive mornings, except in inclement conditions. Sampling order of
198 points varied to ensure all points were sampled at different times throughout the morning. Point
199 counts lasted 10 minutes, with all birds within a 100 m radius recorded, excluding transitory or
200 highly mobile species. We selected a point count radius of 100 m (r), based on previous
201 evidence outlining spatial scales of community turnover in tropical forest birds (Pearman,
202 2002; Hill & Hamer, 2004). We identified species from unknown vocalisations by comparing
203 field recordings (taken using Sennheiser ME66 microphones and Olympus LS11) with an
204 online archive of pre-identified calls (www.xeno-canto.org).

205 **Constructing a functional trait matrix**

206 We assessed avian functional diversity by compiling a matrix of individual species' life history
207 traits for every observed species (n = 318) with respect to three broad categories, following
208 previous studies highlighting functionally important traits (Flynn et al., 2009; Luck et al., 2012;
209 Edwards et al., 2013b). First, dietary traits, comprised of differing foraging guilds (nectarivore,
210 insectivore, granivore, frugivore, and carnivore). Second, behavioural traits, split into foraging
211 strata (canopy, mid-strata, understorey and terrestrial) and foraging mode (trunk/branch, aerial
212 and foliage). Third, following previous studies (Bregman et al. 2016; Chapman et al. 2018),
213 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 (Kipp's ×100 ⁄ wing length), a measure of wing aspect ratio correlated with flight efficiency (Pigot et al., 2016b). 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 et al., 2016a). Additionally, information on basic life history traits, degree of territoriality and predominant habitat type, were 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, Supporting information.

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 et al. (2007). Additionally, we checked that species traits had minimal correlation before inclusion in the final matrix from which measures of functional diversity were calculated (see Fig S2, Supporting information for correlation plot, and Table S1 for correlated traits).

Measures of functional diversity

Having compiled information of individual species traits, we used the *FD* (Laliberté et al., 2014) and *picante* packages (Kembel et al., 2010) to calculate five indices of functional diversity. 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 functional diversity, 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 functional diversity 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 utilisation 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 (Pondanni, 1999). Principle coordinate analysis (PCoA) was then used to calculate a transformed trait matrix, from which functional diversity 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 dendogram 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 et al., 2014a) and a known correlation between species richness and FD, we also calculated the standardised effect size of FD (sesFD) for observed communities (see Text S2, Supporting information). Communities with positive values of sesFD hold greater functional diversity than expected by chance, and relative to their species richness, whilst communities with negative sesFD hold lower levels of functional diversity than expected by chance, and relative of their species richness. Communities with greater sesFD may be more susceptible to declining functional diversity in response to species loss, as each constituent species contributes more to overall functional diversity 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 Fig S3).

Impacts of 'wildlife-friendly' habitat and proximity to forest on functional diversity in farmland

To examine variation in each functional diversity metric in response 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 et al. 2014a). 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 et al. 2014a). Prior to modelling, species were divided into those species detected in forested habitats (288 forest species) and species exclusively detected in cattle pasture (30 non-forest species), modelling each community separately. Parameters were estimated using WinBUGS version 1.4 (Spiegelhalter et al. 2003; see Gilroy et al., 2014a 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 functional diversity metrics), we took the sum of 30 Bernoulli trials with probability given by each of the 1000 posterior-predictive samples of site-level species occurrence probability. Estimated communities are therefore equivalent to

316 the relative prevalence (predicted occurrence and abundance) of each species in a hypothetical
317 landscape composed of 30 sites (circles of 100m radii) with identical habitat conditions to the
318 sampled site in question. We then calculated each of the mean functional diversity metrics for
319 these 1000 samples for each site.

320 **Simulating land-sparing and land-sharing scenarios**

321 To assess the relative performance of land-sparing and land-sharing farming in conserving
322 functional diversity, a landscape simulation process was used to estimate species abundances
323 under hypothetical land-sparing and land-sharing landscapes (see Fig 1. in Gilroy et al., 2014a).
324 Each hypothetical landscape consisted of management units, each made up of 30 'sites' with a
325 set of habitat characteristics dictated by the scenario in question. For land-sharing scenarios,
326 all units within a landscape consist of farmland sites, each containing a fixed proportion of
327 'wildlife-friendly' habitat cover and located at a given distance from the nearest contiguous
328 forest (with scenarios spanning 250-1500 m, in increments of 250 m). To simulate land-
329 sparing, landscapes are divided into farmland sites and 'spared' sites, with farmland sites
330 consisting entirely of pasture (i.e. no 'wildlife-friendly' habitat), again located at a given
331 distance from contiguous forest, and 'spared' sites that are located within the contiguous forest
332 block (i.e. the spared portion of the landscape is permitted to be 'off-farm').

333 Each scenario was simulated at two production levels of cattle pasture, consistent with
334 upper and lower limits of pasture cover observed across sample sites: high production = 80%
335 grazed land; low production = 20% grazed land. For instance, in a high-production simulation
336 of land-sharing, 80% of each individual site was grazed and 20% designated as 'wildlife-
337 friendly' habitat, whereas in a high-production simulation of land-sparing, 80% of the sites
338 were designated as fully-grazed and 20% of sites designated as contiguous forest. Land-sparing
339 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 functional diversity, independent of production.

We then calculated our five measures of functional diversity 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 functional diversity 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.

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, functional diversity (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 categorial 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).

Results

Impacts of farming on functional diversity

All functional diversity indices, other than FDiv (Fig S4. A), were affected by habitat type. Predicted values of FD and FRic were substantially lower within pasture than forest (Fig. 1A, D). In contrast, FEve was predicted to peak within cattle pasture in comparison to forested habitat (Fig. 1G). A similar effect of habitat was observed for FDis (Fig S4. D). 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 (Fig. 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 (Fig. 1B and 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 (Fig. 1H and I), mirroring predicted responses of FDiv and FDis (Fig 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, Supporting information). 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 (Fig S3, Supporting information)**.**

Impacts of land-sparing and land-sharing agriculture on functional diversity

Predicted levels of functional diversity 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 functional diversity and richness than sharing at all distances and at both low and high production levels (Fig. 2A, B, and C, D).

Under low and high production land-sparing scenarios, predicted FD and FRic remained stable across all distances from contiguous forest (Fig. 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 (1500 m) (Fig. 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 Fig S2, Supporting information).

High production land-sparing scenarios were predicted to conserve consistently higher FEve than land sharing, with minimal effect of distance to contiguous forest (Fig. 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 (1500 m; Fig. 2E). Contrasting 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, functional dispersion (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 Fig S5, Supporting information).

Impacts of Land-sparing and Land-sharing agriculture on avian functional traits

As with overall functional diversity, 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

414 via land-sparing or land-sharing strategy. The abundance of granivores was the only trait to
415 increase under agricultural expansion, and only when farming under high production sharing
416 scenarios.

417 Under low production, we predicted greater abundances of eleven traits (all but canopy)
418 under land sparing than land sharing, including the abundances of all dietary traits (Fig 3). The
419 greatest disparity in abundance between the two strategies was predicted for insectivores, with
420 predicted declines in insectivore abundances over four times greater under land sharing than
421 land sparing, across all distances from continuous forest. Under high production scenarios,
422 differences in trait abundances between land-sparing and land-sharing landscapes were much
423 less prominent. Abundances of insectivores, foliage, trunk/branch and midstrata feeding
424 species were slightly greater under sparing, whilst the abundances of granivores, frugivores,
425 nectivores, and aerial and terrestrial feeding species were slightly greater under land-sharing
426 scenarios. Abundances of carnivores, and canopy and understorey feeding species differed
427 minimally between strategies (Fig 3, S6 and S7).

428 Trait abundances within land-sparing habitats were considerably more sensitive to
429 production level than land sharing. Abundances of eleven functional traits (all other than
430 granivores) were substantially lower under high production scenarios than low production.
431 Contrastingly, trait abundances predicted to occur under land-sharing scenarios remained
432 relatively unaffected by production level, with similar abundances conserved under sharing
433 landscapes with a relatively small area of 'wildlife-friendly' habitat as that of landscapes
434 retaining much greater areas of forest amongst farmland.

435 Discussion

436 How best to limit the ecological impacts of expanding tropical agriculture is a key conservation
437 question, and we uniquely investigate whether land-sparing or land-sharing farming would
438 maximise the retention of functional diversity. 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 et al., 2016a). Our results indicate that high-yielding farming paired with blocks of protected natural habitat, consistent with land sparing, conserved greater overall functional diversity 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 et al., 2014a) 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 (Pereira & Daily 2006; Sekercioglu et al. 2007; Gilroy & Edwards 2017). 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 (Tscharntke et al., 2008; Schroth & McNeely 2011; Melo et al., 2013). However, we found that functional diversity 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 functional diversity within pasture landscapes therefore exists under land-sparing scenarios, where large blocks of natural habitat provide unparalleled conservation value (Gibson et al., 2011; Barlow et al. 2016). 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 functional diversity 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 Functional dispersion (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

490 the centre of trait space can result in greater values of FDis. Given predicted declines in the
491 majority of trait abundances under land sharing, this further demonstrates a lack of functional
492 redundancy within these landscapes, with functional diversity supported by a few functionally
493 unique species.

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

502 In terms of ecosystem service provision, the impacts of declining trait abundances are
503 unlikely to be confined to natural landscapes. Both the abundances of carnivores and
504 insectivores are also predicted to be lowest under land-sharing scenarios, suggesting limited
505 benefits of avian pest control services within sharing landscapes. However, empirical studies
506 demonstrating yield or production benefits from increases in ecological processes are greatly
507 needed. In particular, evidence of enhanced soil formation, nutrient cycling and insect
508 predation within pasture are currently lacking. In addition, the link between increased
509 functional diversity and greater provision of ecosystem services requires further attention,
510 particularly in pasture given that it represents the most prominent anthropogenic land-use
511 throughout much of the tropics (FAOSTAT). However, our simulations of sparing landscapes
512 constitute 'off-farm' sparing, where protected lands exist in separation from intensive pasture.
513 Thus, in our sparing systems, the flow of potential services from 'spared' land to pasture may
514 be severely impeded due to lack of forest directly adjacent to farmland (Mitchell et al., 2015).
515 Furthermore, trait abundances conserved under land sparing declined markedly under high

516 production scenarios, where spared lands represent only a small proportion of the landscape.
517 This result supports findings of other studies, emphasising the importance of sparing large
518 blocks of natural habitat for effective biodiversity conservation via land sparing (Gilroy et al.,
519 2014; Edwards et al., 2015; Lamb et al. 2016).

520 An important caveat is that our landscape scenarios did not account for fragmentation
521 of spared lands, with all sparing management units pairing intensified agriculture with 'off-
522 farm' protected areas in contiguous forest. Greater fragmentation of natural habitats can result
523 in dramatic increases in edge, isolation, and area effects (Ferraz et al., 2003; Ewers & Didham,
524 2007; Hagen et al., 2012; Gibson et al., 2013) that will likely diminish the conservation value
525 of protected lands (Laurance et al., 2011). Additionally, if agricultural intensification is
526 accompanied by unsustainable farming practices, immigration of people, and greater land-use
527 due to localised economic growth, then elevated edge and deforestation effects will likely
528 degrade biodiversity benefits of adjacent spared forest (Angelsen and Kaimowitz 2001; Tilman
529 et al., 2002).

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

The superiority of land sparing compared to land sharing in conserving functional diversity 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 (Gilroy et al., 2014a; Edwards et al., 2015). Realised 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 (Phelps et al., 2013; Carrasco et al., 2014; Hertel et al., 2014). 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 functional diversity will be best protected via conserving large blocks of contiguous natural habitat through the intensification of agriculture on existing lands. Achieving such optimised landscapes requires steps to discourage further expansion and ensure sparing of natural habitats as a direct result of intensification. Maximisation of conservation benefits resulting from prioritisation of spared lands will likely occur when applied in combination with policies advocating sustainable intensification practises, minimising 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 et al., 2014; Gilroy et al., 2014b; 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.

Acknowledgements

For field access permissions, we thank Fundación Colibri (Reserva Mesenia-Paramillo), Fundación ProAves (Reserva Las Tangaras) and L. Tapasco (Cerro Montezuma). For assistance with data collection, we thank O. Cortes, F. Prada, G. Suarez Y. Tapasco, and many local assistants. We also wish to thank the staff of the Museum of Natural History of London for their kind permission to access bird reference collections for the compiling of the functional trait matrix. Similarly we thank staff at the Instituto Alexander von Humboldt at Villa De Leyva, Colombia, in particular Claudia Alejandra Medina Uribe, Beatrix Salgado and Fernando Forero, for access to their extensive collection, logistical support and their kind support in connecting us to the curators of other important Colombian collections, including at The University of Valle in Cali, The University Of Cauca in Popayán, the University of Antioquia in Medellin, The Museum of Natural History San Jose de la Salle in Medellin, and the Institute of Natural Sciences in Bogotá, to each of who's staff we are also indebted. Juan Pablo López Ordóñez also provided invaluable support, expertise, and measurements of rare taxa. Further thanks go to Angela Chira, Emma Hughes, Catherine Sheard and many others for assistance with compiling functional trait data. Felix Lim improved the manuscript with constructive comments. Finally, we thank David Williams and an anonymous reviewer for comments that greatly improved the manuscript. Funding was provided to T.H. and D.P.E. by the Research Council of Norway (grant number 208836). This is publication #16 of the Biodiversity, Agriculture, and Conservation in Colombia (Biodiversidad, Agricultura, y Conservación en Colombia [BACC]) project. Authors declare no conflicts of interest.

Supporting Information captions

Figure S1. Map of study sites and habitat squares.

Methods S1. Sampling of morphometric traits.

Table S1. List of traits and functional significance.

Figure S2. Correlation of species traits

Methods S2. Calculation of sesFD.

Figure S3. sesFD between habitat types & against site level habitat variables (Observed communities).

Table S2. Habitat and point level functional diversity indices for observed communities.

Figure S4. Point level simulated community values of FDiv and FDis.

Figure S5. FEve, FDiv and FDis for simulated land-sparing vs. land-sharing scenarios.

Figure S6. Changes in feeding strata trait abundances for simulated land-sparing vs. land-sharing scenarios.

Figure S7. Changes in foraging mode trait abundances for simulated land-sparing vs. land-sharing scenarios.

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Figure legends

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, B, C), mean functional richness (D, E, F) and mean functional evenness (G, H, I). Error bars for each point represent 95th percentiles across 1000 simulations (the variation in functional indices due to uncertainty in species occurrence probabilities at each sample point).

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 randomisations under each scenario indicated by points, with error bars representing 95th percentiles. Surrounding violin plots display frequency distributions of indices from 10,000 randomisations 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 1000 randomisations under each scenario indicated by points, with error bars representing 95th percentiles. Surrounding violin plots display frequency distributions of indices from 1000 randomisations of each scenario.