Reducing the impacts of Neotropical oil palm development on functional diversity

Graham W. Prescott [a,*], James J. Gilroy [b,c], Torbjørn Haugaasen [c], Claudia A. Medina Uribe [d], William A. Foster [a], David P. Edwards [e]

[a] Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK
[b] School of Environmental Science, University of East Anglia, Norwich NR4 7JT, UK
[c] Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, 1430 Ås, Norway
[d] Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Calle 28A # 15-09, Bogotá, Colombia
[e] Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK

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ABSTRACT

Large-scale conversion of natural habitats to agriculture reduces species richness and functional diversity, with important implications for the provision of many ecosystem services. We investigated possible solutions to minimise loss of functional diversity: retaining forest fragments to enhance functional diversity within agricultural lands, and restricting future expansion of tropical crops to degraded lands or low-productivity farmlands to conserve functional diversity at a landscape level. We focused on birds, which play key functional roles and have well-known functional ecology, and oil palm, a rapidly expanding tropical crop. We did so in the Colombian Llanos, a region highlighted for the planting of sustainable oil palm, where plantations are currently replacing two main habitat types: forest remnants and improved cattle pasture. We found that levels of functional diversity (FD) and richness (FRic) were highest in remnant forests. Furthermore, levels of functional diversity and richness in oil palm and improved pasture were positively related to the proportion of forest in a 250 m radius surrounding each sample point. Frugivorous and canopy foraging species were particularly associated with remnant forests, while aquatic and terrestrial foragers were associated with pasture. This suggests that retaining forest remnants in agricultural landscapes is important in preventing large losses of functional diversity, and might also play a role in maintaining avifaunal functional richness within farmland.

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1. Introduction

We live in an era of rapid global change. One of the biggest changes is the rapid conversion of natural habitats, particularly forests, for agriculture (Ellis et al., 2010). The conversion of forest to farmland has led to large-scale declines in species richness and abundance (Foster et al., 2011; Gibson et al., 2011), and replacement of specialist species with widespread generalist species (Clavel et al., 2010; Sekercioglu, 2012). Given that many of the ecosystem services underpinning the production of food, such as pest control and pollination, are regulated by wild species (Garibaldi et al., 2013; Power, 2010), habitat loss could have important negative consequences not only for the survival of global biodiversity, but also for our ability to increase food production in line with rapidly increasing population and per capita consumption (Ehrlich and Ehrlich, 2013).

The importance of conserving species not only for what they are, but for what they do (Loreau et al., 2001; Tilman et al., 1997), has highlighted the need to assess communities in terms of the roles that their constituent species play in shaping ecological processes, rather than simply how many species they contain. Functional diversity is a concept developed to encapsulate the variety of functional roles played by the constituent species within a community (Magurran and McGill, 2010; Petchey and Gaston, 2002). It has the advantage over approaches that compare abundances of members of different functional guilds (Azhar et al., 2013; Gilroy et al., 2015a) in being less arbitrary and able to account for intra-guild differences between species (such as concurrent differences in body size and beak morphology; Edwards et al., 2013). Higher functional diversity is expected to increase the provision of ecosystem services via a variety of mechanisms (Cardinale et al., 2012; Hooper et al., 2005). For example, functional diversity was a better predictor of variation in above-ground biomass (and hence carbon storage) than species richness in a series of manipulative experiments in European grasslands (Petchey et al., 2004).

Previous studies have found a decline in functional diversity for an array of taxa following conversion of natural habitats to agriculture. For example, the functional diversity of dung beetles is reduced by conversion of forest to pasture (Barragán et al., 2011) or oil palm (F.A. Edwards et al., 2014a,b). Similarly, conversion of forest to oil palm in Sabah (Edwards et al., 2013) and to monocultures of *Eucalyptus camaldulensis* or exotic

* Corresponding author.
E-mail address: grahamprescott@gmail.com (G.W. Prescott).

pines in Australia (Luck et al., 2013) reduced the functional diversity of birds. Conversion of forest to coconut plantations and cattle pastures in the Solomon Islands reduced the functional diversity of understory plants (Katovai et al., 2012). Given the link between functional diversity and ecosystem services, it is important to understand how agriculture can be managed to prevent severe losses of functional diversity and to optimise functional diversity within farmed landscapes.

One potential method for conserving functional diversity within agricultural land is to retain areas of adjacent natural habitats to allow functionally important species to "spill-over" into farmland (Gilroy et al., 2014). Most of the work on functional spill-over from forest to farmland has so far focused on specific functions or services. For example, forest insect pollinators increased coffee yield by ~20% within ~1 km of contiguous forest (Ricketts et al., 2004), and proximity to forests has been correlated with increased levels of pollination in other studies (Blanche et al., 2006; Gemmill-Herren and Ochieng', 2008; Klein et al., 2003). Forest fragments in areas of coffee cultivation in Costa Rica doubled the levels of pest control (through insectivorous birds consuming coffee borer beetles *Hyothenemus hampei*), providing an ecosystem service worth $US75–$US310 per hectare per year (Karp et al., 2013). However, bird predation of model caterpillars (considered a proxy of natural pest control by insectivorous birds) was not affected by the presence of riparian forest reserves (Gray and Lewis, 2014). Despite these studies, there remains no assessment of the impacts of forest retention on functional diversity within farmland (Blitzer et al., 2012).

In addition to enhancing functional diversity within agricultural lands, we also need to look at ways to conserve functional diversity at the wider landscape level. The most damaging effects of agricultural expansion on species, phylogenetic, and functional diversity have been due to the conversion of high biodiversity habitats, especially tropical forest (Edwards et al., 2015; Flynn et al., 2009; Gibson et al., 2011; Laurance et al., 2014). Directing future conversion to lower biodiversity habitats—including degraded areas that previously lost their natural vegetation (e.g., burned) or areas already converted to less productive forms of agriculture (Garcia-Ulloa et al., 2012; Koh and Ghazoul, 2010; Smit et al., 2013)—could be a means of mitigating some of these negative impacts. While research indicates that such low-biodiversity habitats represent golden opportunities for farmland expansion at minimal cost to species (Gilroy et al., 2015b) and phylogenetic diversity (Prescott et al., 2016), there remains no assessment of the impacts of their conversion on functional diversity.

In this study, we focus on oil palm (*Elaeis guineensis*) cultivation, which is one of the most rapidly expanding tropical crops (now covering over 16 million hectares globally) as a result of increasing demand for vegetable oils for food, pharmaceuticals, and biofuels, with expansion largely at the expense of tropical forests (Gunarso et al., 2013). This conversion drives declines in species richness and abundance, and changes in community composition for most taxa (D.P. Edwards et al., 2014; Foster et al., 2011; Savilaakso et al., 2014), as well as loss of functional diversity of birds and dung beetles (Edwards et al., 2013; F.A. Edwards et al., 2014a,b). Spatial modelling for Indonesia (Koh and Ghazoul, 2010) and Colombia (Garcia-Ulloa et al., 2012) suggests that directing oil palm expansion to regions with degraded lands and less productive forms of agriculture could reduce biodiversity loss from forest conversion. In Colombia, the main form of agriculture suitable for conversion to oil palm is cattle pasture. In particular, the western Llanos has been highlighted for conversion (Garcia-Ulloa et al., 2012). This region contains a diverse mixture of improved cattle pasturelands and remnant forest patches and corridors, both of which have been converted to intensive cattle pasture in the past (Etter et al., 2008).

To determine the impacts of oil palm expansion and landscape configuration in the Colombian Llanos, we focus on the functional diversity of birds. Birds perform important functions as pollinators, seed dispersers, scavengers, and predators (Sekercioglu, 2006). Experimental exclusion of birds led to an increase in herbivory rates in young oil palms (Koh, 2008), and an increase in the abundance of herbivorous insects and a decrease in yield in cacao plantations (Maas et al., 2013). Their importance to ecosystem function and the widespread availability of functional trait information in the literature (del Hoyo et al., 2014; Dunning, 2007) makes them an excellent taxon with which to study functional diversity. Previous studies in the Llanos have revealed that the species richness (Gilroy et al., 2015b; see also D.P. Edwards et al., 2014) and phylogenetic diversity (Prescott et al., 2016) of birds was highest in forest but that the conversion of improved pasture to oil palm would result in minimal change. These studies also found that the amount of forest within a 250 m radius surrounding sampling points in oil palm and pasture increased the occupancy probability (Gilroy et al., 2015b) and the phylogenetic diversity (Prescott et al., 2016) of birds, suggesting the potential for spill-over of functional diversity from neighbouring forests.

In this study we therefore test the following hypotheses:

i) the conversion of forest to oil palm reduces functional diversity at the point and landscape level, but conversion of improved cattle pasture to oil palm does not.

ii) Retaining forest remnants close to agricultural land increases avian functional diversity in oil palm plantations and pasture.

2. Methods

2.1. Study sites

The study was based in the *Llanos Orientales* ecoregion of Colombia. This is a semi-natural open savanna system with a pronounced dry season from December–March. It contains a network of gallery forests along the rivers that ultimately drain into the Orinoco (Jiménez et al., 2012). Extensive cattle grazing has historically been the dominant agricultural land use (Etter et al., 2008; Van Ausdal, 2009). Agricultural production has intensified, and the region now has 2.5 million hectares of improved and intensive pastures (with *Brachiaria* sp. grasses introduced from Africa) and 140,000 ha of oil palm plantations (Romero-Ruiz et al., 2010). It is therefore a good place to test the relative biodiversity value of oil palm plantations and cattle pastures with a view to optimising future agricultural production in Colombia with regards to biodiversity conservation and the production of food and biofuels.

The study was conducted at three field sites — Palumea (4°20′15.2″ N, 73°11′47.8″W), La Carolina (4°17′44.9″N, 72°58′35.9″W), and Guaicaramo (4°27′34.8″N, 72°57′40.0″W) — in the municipalities of Medina (Cundinamarca), Cabuyaro (Meta), and Barranco de Upía (Meta) respectively. Each of these three sites contained a mixture of improved pasture, oil palm mature enough to produce fruit (5–28 years old), and forest fragments. The forest fragments included riparian forest strips, dry forest fragments, and wet forest fragments dominated by *moriche* palm (*Mauritia flexuosa*). These sites were sampled between January–March 2013.

2.2. Bird surveys

An experienced ornithologist (JJG) conducted ten-minute point counts on four successive days at each sampling point in our study sites (106 sampling points in total) (Gilroy et al., 2015b). Fixed radius (100 m) point counts were conducted between 05:45–11:00, and the order in which they were sampled was switched between days so that all points were visited during both the earlier and later parts of the sampling window. Sampling points were organised into transects with between one and four points per transect (transects only had fewer than four points if a forest fragment was too small to have more points), and 300 m between each sampling point within a transect. In total, we sampled 36 oil palm, 36 pasture, and 34 forest points. Unfamiliar vocalisations were recorded with a Sennheiser ME66 shotgun microphone and Olympus LS11, and compared to an online database (www.

xeno-canto.org). See Table A1 in the Appendix for the full list of species we recorded.

2.3. Functional traits

We used the *Handbook of the Birds of the World Alive* (del Hoyo et al., 2014); accessed from www.hbw.com) to collect functional trait data for each of the species recorded in the study, following Gilroy et al. (2015a). We collected data on size (selecting the upper end of the reported range for body length and mass, and using the mass reported for males if data were segregated by sex), foraging microhabitat (whether they foraged in aquatic, terrestrial, understorey, mid-strata, canopy, or grassland microhabitats), foraging substrate (aquatic, soil/litter, trunk/branches, foliage, aerial), and food type (aquatic arthropods, terrestrial arthropods, aquatic non-arthropod invertebrates, terrestrial non-arthropod invertebrates, fish, carrion, other vertebrate prey, nectar, fruit, seeds, or leaves). For species where mass and length data were not reported by del Hoyo et al. (2014), we used other sources (Dunning, 2007). Apart from body length and mass, which are continuous variables, all other traits were binary response variables. See Table A1 for the functional traits of all the species we recorded.

2.4. Landscape configuration

We used two measures of landscape configuration calculated for each point:

1) the minimum distance from a point to the nearest forest edge;
2) the proportion of forest in a 250 m radius surrounding the point.

All metrics were calculated by JJG using Landsat maps from Google Earth v. 7.1.2 (Gilroy et al., 2015b).

2.5. Statistical analysis

2.5.1. Calculating metrics of functional diversity

We used the *picante* (Kembel et al., 2010) and *FD* packages (Laliberté et al., 2014) in R version 3.03 (R Core Team, 2014) to calculate six functional diversity metrics: functional diversity (FD), the standard effect size of FD (sesFD), functional richness (FRic), functional evenness (FEve), functional divergence (FDiv), and functional dispersion (FDis).

FD and sesFD are tree-based measures of functional diversity. We first calculated a functional dendrogram for all species in our sites using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA), a standard method for hierarchical clustering (Swenson, 2014). FD for a point is calculated by summing the branch lengths of the functional dendrogram connecting all species occurring at a certain point (Petchey and Gaston, 2002). Since FD is known to be correlated with species richness, we also calculated sesFD, which adjusts FD for species richness by comparing the observed FD at each point to 999 scenarios in which the number of species at each point is held constant but species identity is randomly drawn from the community. Communities that are more functionally diverse than would be expected by chance (given their species richness) have positive values of sesFD, and those which are less functionally diverse than expected by chance have negative values.

The remaining four metrics (FRic, FEve, FDiv, FDis) are calculated by visualising species in multidimensional trait space, where each axis represents a different trait (or set of correlated traits). A convex hull can be created, the perimeter of which is defined by the most extreme values at each axis (i.e. a species at the perimeter of the convex hull on a given axis would have the most extreme value of the trait(s) represented by that axis) (Villéger et al., 2008). FRic is the volume of that convex hull and represents the total volume of trait space occupied by a community. A community with high FRic would be one with many traits (and potentially high utilisation of resources), whereas one with lower FRic might have some traits missing, suggesting that some niches are completely empty. FEve is a measure of the regularity of distribution of species and abundances throughout the trait space. A community with high FEve would have relatively equal abundances throughout trait space, which would theoretically mean resources are being used efficiently in the community. FDiv is a measure of the extent to which the most abundant species have the most extreme trait values (i.e. a measure of 'centre of gravity' within trait space). This gives a measure of niche differentiation in the community; if FDiv is high, then there are high levels of niche differentiation and potentially lower competition for resources. FRic, FEve, and FDiv were formalised by Villéger et al. (2008). FDis is the abundance-weighted mean distance of species from the centroid of trait space (Laliberté and Legendre, 2010). This measure incorporates both functional richness and divergence – it is influenced both by the range of trait values and the distribution of individuals within trait space – and can therefore be used as a standalone measure of functional diversity. A high value of FDis would imply that the community has high functional richness and/or divergence.

2.5.2. Levels of sampling

We calculated the six metrics of functional (FD, sesFD, FRic, FEve, FDiv, and FDis) diversity at four spatial levels at both the whole habitat and sample point (henceforth 'point') level. We then conducted our principal analysis at the point level, comparing each functional metric using linear mixed-effects models with maximum likelihood estimation (created in the *lme4* package (Bates et al., 2014)) with habitat as a fixed effect and site as a random effect against models containing only site as a random effect. FRic, FEve, FDiv, and FDis were log-transformed to normalise the model residuals. For each model we assessed the amount of variation in the data explained by the fixed and random effects using Nakagawa and Schielzeth's conditional and marginal R^2 (Nakagawa and Schielzeth, 2013) using the *MuMIn* package (Barton, 2014) in R. Where habitat was included as a term in the best model, we used the *multcomp* R package (Hothorn et al., 2008) to perform post-hoc Tukey tests.

2.5.3. Effects of landscape configuration in oil palm and pasture

For each of the six functional diversity metrics calculated at the point level, we then created two linear mixed effects models using maximum likelihood estimation (in the *lme4* package) to test for effects of the extent of nearby forest cover:

1) a null model containing only random effects (transect nested within site);
2) a model containing the same random effects, but also the proportion of forest within a 250 m radius surrounding the point.

Having created these models, we then compared the models by their AIC value (with the model with the lowest AIC value being the best). For each model we assessed the amount of variation in the data explained by the fixed and random effects using Nakagawa and Schielzeth's conditional and marginal R^2 (Nakagawa and Schielzeth, 2013) using the *MuMIn* package (Barton, 2014) in R.

2.5.4. Effect of habitat and landscape configuration on functional traits

To determine which functional traits were driving changes in avian functional diversity across habitat and landscape configurations, we used an RLQ analysis (Dolédec et al., 1996), implemented with the ade4 package (Chessel et al., 2004), This method uses a species x trait matrix (Q), a sample point x species matrix (L), and a sample point x environmental variables (R) to create a fourth matrix of traits x environmental variables. We then used a permutation test (with 50,000 permutations) to test which traits were significantly associated with each habitat, and with increased proportion of forest in a 250 m radius around each point.

2.5.5. Testing for spatial auto-correlation

To ensure that observed patterns were not artefacts of spatial auto-correlation, we performed Moran's I tests on the residuals of each of the models we tested using the *ape* package in R (Paradis et al., 2004).

3. Results

3.1. Effects of habitat on functional diversity metrics

At the whole habitat level, remnant forest had the highest levels of FD and FRic, but the lowest levels of sesFD and FDis (Table 1). Oil palm had the highest levels of sesFD, FEve and FDiv, while improved pasture had the highest levels of FDis (Table 1).

At the point level, for each of the functional diversity metrics (except functional divergence, FDiv), the best model was the linear mixed-effects model with habitat as a fixed effect, and transect and site as nested random effects (Table A2). For FDiv the null model (containing only the nested random effects of transect and site) was the best model. Post-hoc Tukey tests showed that both functional diversity (FD) and functional richness (FRic) were higher in forest than in both oil palm and pasture, but there was no significant difference between oil palm and pasture (Fig. 1a,c). Forest points, however, had significantly lower sesFD than oil palm and pasture (Fig. 1b). Point-level functional evenness (FEve) was not significantly different between forest and oil palm, but was significantly lower for pasture points than for both forest and oil palm points (Fig. 1d). There were no significant differences between any of the habitats for point-level functional divergence (FDiv) (Fig. 1e). Mean point-level functional dispersion (FDis) was significantly higher in pasture than in oil palm, and significantly higher in oil palm than in forest (Fig. 1f).

3.2. Effects of landscape configuration in oil palm

For point-level FD and FRic in oil palm, the best model contained the proportion of forest within a 250 m radius (Table A3). Points with a larger proportion of forest had higher FD and FRic (Fig. 2a-b). The best model for all other metrics was the null model containing only the nested random effects of transect and site (Table A3).

3.3. Effects of landscape configuration in improved pasture

For point-level FD, sesFD, FRic, FEve in pasture, the best model contained the proportion of forest within a 250 m radius (Table A4). Points with higher proportion of surrounding forest had higher levels of these four metrics (Fig. 2a-d). The null model was the best model of functional divergence (FDiv), suggesting that landscape configuration had no effect on this metric (Table A4).

3.4. Tests for spatial auto-correlation

Moran's I tests were run for all 36 models. None of the 18 best models for each of our metrics (Tables A2–4) showed evidence of spatial auto-correlation. However, two of the 18 null models — sesFD and FRic for the comparison between habitats — did show evidence of spatial autocorrelation ($p < 0.05$).

Table 1
Functional metrics at the whole habitat scale.

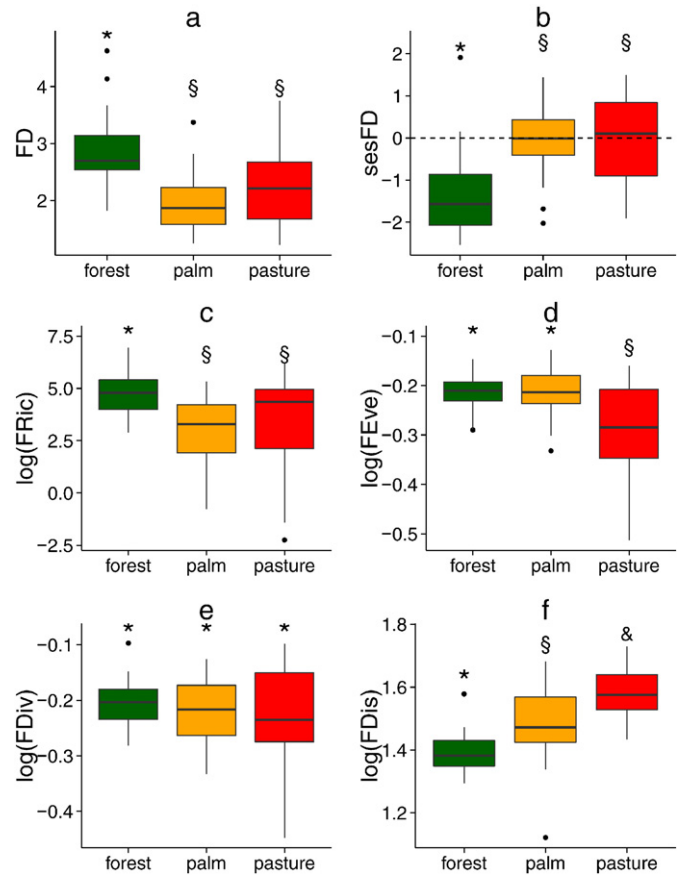| Metric	Remnant forest	Oil palm	Improved pasture
FD	9.05	6.63	7.51
sesFD	−1.88	0.63	0.10
FRic	3280.61	2096.50	3115.97
FEve	0.73	0.76	0.69
FDiv	0.79	0.82	0.81
FDis	4.33	4.53	5.27

Fig. 1. (a) Functional diversity (FD), (b) standard effect size of FD (sesFD), (c) functional richness (FRic), (d) functional evenness (FEve), (e) functional divergence (FDiv), and (f) functional dispersion (FDis) for sampling points in remnant forest, oil palm, and improved pasture. Different symbols above box plots (*, §, or &) indicate significant differences, and shared symbols indicate no significant difference.

3.5. Effect of habitat and landscape configuration on functional traits

Species that take prey from foliage and trunk or branches, species that forage in the understory, midstrata, and canopy strata, and frugivores were negatively associated with pasture points, but positively associated with points in forest (Fig. 3). For points in oil palm and pasture, a high proportion of surrounding remnant forest points was positively associated with the presence of frugivores. Meanwhile, larger species, and species that forage on the ground, in grassland, and in water, were positively associated with pasture, and negatively associated with points in forest or with high proportion of surrounding forest (Fig. 3). There were no significant associations between points in oil palm and any functional traits (Fig. 3).

4. Discussion

If we are to minimise the loss of functional diversity during agricultural expansion, we need to direct future expansion of crops to avoid forest loss and to explore the ways in which functional diversity might be enhanced by landscape configuration. We found that remnant forests had higher functional diversity (FD) and functional richness (FRic) than either of the agricultural habitats, which mirrors the trend seen with other taxa and in other regions (Edwards et al., 2013; F.A. Edwards et al., 2014a,b; Flynn et al., 2009). We also found that point-level FD and FRic in both pasture and oil palm were positively related to the proportion of forest in a 250 m radius around a sampling point. This suggests that maintaining forest fragments in these landscapes would
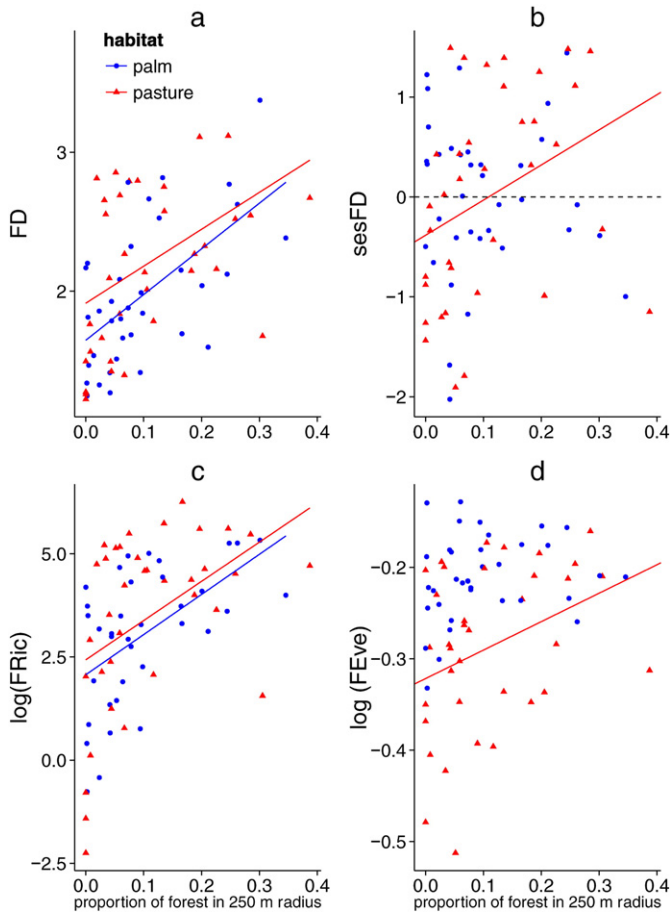
Fig. 2. (a) Functional diversity (FD), b) standard effect size of functional diversity (sesFD), (c) functional richness (FRic), and (d) functional evenness (FEve) for sampling points in oil palm and improved pasture, plotted against the proportion of remnant forest in a 250 m radius around each sampling point. Best fit lines only drawn for pasture points in (b) and (d) because the best model in oil palm was the null model.

Category	Trait	forest	palm	pasture	prop250
Size	length	-		+	
	mass			+	
Foraging stratum	aquatic	-		+	
	terrestrial	-		+	
	understorey	+		-	
	midstrata	+			
	canopy	+		-	
	grassland	-		+	
Foraging substrate	aquatic	-		+	
	soil/litter	-		+	
	trunk/branches	+		-	
	foliage	+		-	
	aerial				
Food	arthropods (non-aquatic)				
	arthropods (aquatic)	-		+	
	other invertebrates (aquatic)	-		+	
	other invertebrates (non-aquatic)	-		+	
	carrion				
	fish	-		+	
	other vertebrates				
	fruit	+		-	+
	nectar				
	seeds				
	leaves			+	

Fig. 3. Effects of habitat and landscape configuration (prop250 = proportion of forest in a 250 m radius around a point) on traits. Red boxes represent significant positive correlation, blue boxes represent significant negative correlation, and white boxes represent no significant correlation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

retain critical functional diversity, as they do for trees in the Brazilian Atlantic Forest (Magnago et al., 2014), and could help to enhance functional richness in farmland.

Our results suggest that remnant forests harbour a greater range of functional traits than improved cattle pasture and oil palm, and that resources are used more efficiently by forest than by farmland communities (Mason et al., 2005). Both FD and FRic are influenced by species richness, because each new species added increases the branch length of the functional dendrogram, especially if the new species is functionally dissimilar to the existing species (for FD), or may increase the volume of the convex hull (for FRic) if that species has a more extreme trait value than is present in the existing community (Mason et al., 2013; Poos et al., 2009; Swenson, 2014). Thus these patterns are partially confounded by the higher species richness of forest than oil palm or pasture.

When we adjusted FD for species richness (sesFD) we found that forest points had significantly *lower* sesFD (i.e. less FD than expected given their species richness) than oil palm and pasture, which contrasts with Edwards et al. (2013) who found equal avian sesFD between contiguous forest and oil palm in Borneo. This suggests that in the Llanos there are higher levels of functional redundancy in forests than in oil palm (Pavoine and Bonsall, 2011). This has important positive implications for the long-term maintenance of ecosystem processes, as the functional consequences of local species extinctions may be buffered if those functions are still provided by another remaining species (Hooper et al., 2005). It is unclear whether the reduced functional richness of oil palm and pasture relative to forest reflects a reduction in the range of available functional roles in structurally simpler habitats or, of

greater concern, whether there are unfilled functional roles in agricultural areas due to environmental filtering.

Pasture sampling points had significantly lower functional evenness than forest and oil palm points, but there was no significant difference between forest and oil palm. Previous studies found that habitat-level avian functional evenness was lower in oil palm than in unlogged or once-logged forest, but similar to that of twice-logged forest (Edwards et al., 2013), and that the conversion of forest to oil palm did not affect the functional evenness of dung beetles (F.A. Edwards et al., 2014a,b). An uneven distribution of individuals throughout trait space could imply less efficient utilisation of resources (and therefore lower levels of ecosystem functioning), although only if resources are evenly distributed (Mason et al., 2005). For example, a community may be uneven if it has a low relative abundance of frugivores compared to other guilds, but that would not necessarily translate into less efficient resource use in a landscape that lacks fruiting trees, such as pasture in our study.

Our results suggest that conversion of remnant forest or pasture to oil palm does not affect avian functional divergence (see also Edwards et al., 2013), indicating that the degree to which the most abundant species in each habitat had the most extreme trait values was similar across habitats (Mason et al., 2005), and meaning that communities had equally differentiated niches and similar resource competition. Functional dispersion is a metric which incorporates both functional richness and divergence (Laliberté and Legendre, 2010), both of which can impact upon ecosystem function. Ours is the first study to look at the impact of conversion of forest to oil palm on functional dispersion, and shows that forest loss increases avian functional dispersion. Theoretically this is predicted to lead to a reduction of ecosystem function in oil palm and pasture (Laliberté and Legendre, 2010), but since data are lacking on how functional dispersion relates to specific ecosystem functions and services provided by birds, it is difficult to make predictions about the functional relevance of this finding.

The retention of forest fragments was an important determinant of FD and FRic within oil palm and pasture, and was positively associated with both. Previous studies in the same sites showed that the forest fragments

also provided spill-over of species richness (Gilroy et al., 2015b) and phylogenetic diversity (Prescott et al., 2016). High proportions of surrounding forest in oil palm and pasture points were significantly and positively associated with frugivory, which further suggests that high proportions of forest allow spill-over of species that would otherwise be restricted to forest. Since sesFD in oil palm was not affected by the proportion of surrounding forest, the increase in FD in oil palm points close to forest is probably driven by increased species richness. However, sesFD increased in pasture points close to forest, which suggests that the forest is having an effect over and above that of spill-over in species richness, possibly through the addition of very functionally different species. Previous work has shown that the retention of forest fragments in coffee plantations in Costa Rica enhances the abundance of birds, predation by birds of coffee borers, and yield (Karp et al., 2013). We recommend the retention of forest fragments within oil palm and pasture landscapes in the Llanos, for the increases in avian functional diversity and for possible beneficial effects on ecosystem services.

Birds play key functional roles in many ecosystems (Sekercioglu, 2006), and a meta-analysis of exclosure experiments in Neotropical agroforestry systems found that higher species richness and functional group richness of birds were associated with higher levels of arthropod removal (Philpott et al., 2009). Whether or not lower avian functional richness in oil palm and pasture has a positive or negative effect on ecosystem services within these habitats remains to be tested. Higher functional richness could lead to beneficial ecosystem services (such as the control of insect or rodent pests) or to negative ecosystem services (in the oil palm context, this could include eating the oil palm fruit). An interesting avenue of research would be to explicitly test this in the Llanos, although studies in Malaysian Borneo suggest that forest remnants do not affect yield (F.A. Edwards et al., 2014a,b) or the rate at which caterpillar models are attacked (a proxy for predation on insects) (Gray and Lewis, 2014).

Research has begun to suggest that oil palm can expand sustainably in Colombia by converting existing areas of improved cattle pasture rather than forest (Garcia-Ulloa et al., 2012). Synthesising the results from this study and previous studies (Gilroy et al., 2015b; Prescott et al., 2016), we conclude that restricting landscape conversion to improved pastures is the best way to conserve the species richness, phylogenetic diversity, and important metrics of functional diversity (FD and FRic) of birds in the Colombian Llanos in the face of future oil palm expansion. Furthermore, retaining forest fragments will enhance the taxonomic, phylogenetic, and functional diversity of birds in surrounding agriculture. We now need to work towards economic incentives and legal safeguards to ensure that the last remaining forests in this region are spared from conversion, without incurring leakage of forest loss elsewhere (Arima et al., 2011).

Acknowledgements

Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx.doi.org/10.1016/j.biocon.2016.02.013.

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