Managing Neotropical oil palm expansion to retain phylogenetic diversity

Graham W. Prescott[1*], James J. Gilroy[2,3], Torbjørn Haugaasen[3], Claudia A. Medina Uribe[4], William A. Foster[1], David P. Edwards[5]

[1]*Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK;*

[2]*School of Environmental Science, University of East Anglia, Norwich NR4 7JT, UK;*

[3]*Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, 1430 Ås, Norway;*

[4]*Instituto de Investigación de Recursos Biológicos Alexander von Humboldt, Calle 28A # 15-09, Bogotá, Colombia;*

[5]*Department of Animal and Plant Sciences, University of Sheffield, Sheffield S10 2TN, UK.*

[*]E-mail: grahamprescott@gmail.com

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Summary

1. The expansion of tropical agriculture is a major driver of the extinction crisis. A key question is whether biodiversity losses may be minimised by restricting future expansion to low-productivity farmland and retaining forest fragments, especially in rapidly changing Neotropical landscapes.
2. We investigated these methods in the context of avian phylogenetic diversity, which summarises the evolutionary history preserved within communities. Evidence suggests that phylogenetic diversity plays an important role in maintaining key ecosystem functions.
3. We collected data on avian communities in the Colombian Llanos, a region highlighted as being optimal for the expansion of oil palm, at the expense of existing habitats including forest remnants and improved cattle pastures.
4. PD, a measure of phylogenetic richness, and MPD, a measure of the phylogenetic distance between individuals in a community in deep evolutionary time, were significantly higher in forest than in oil palm or pasture, but did not differ significantly between oil palm and pasture. MNTD, a measure of distance between individuals in a community at the intra-familial and intra-generic level, was significantly higher in oil palm and pasture than in forest. However, median evolutionary distinctiveness (ED) was highest in pasture, partly due to the abundance of distinct waterbirds, but did not differ between oil palm and forest. PD in oil palm and pasture increased with the extent of remnant forest cover.

5. *Synthesis and applications.* The PD and MPD of bird communities in this region can best be conserved by ensuring that new oil palm plantations replace pasturelands rather than forest. A secondary benefit of preserving forest would be the enhancement of PD in the surrounding agricultural landscape. This strategy will need to be coupled with measures to either reduce demand for beef or to intensify existing cattle production to ensure that forest is not replaced by pasture elsewhere.

Keywords: Phylogenetic diversity, oil palm, pasture, Colombian Llanos, tropical agriculture, landscape configuration, birds

Introduction

Humans have transformed the biosphere by converting natural habitats into agricultural lands (Smil 2013). The majority of agricultural expansion between 1980-2000 occurred at the expense of tropical forests (Gibbs *et al.* 2010), and future expansion is likely to be concentrated in the tropics (Laurance, Sayer & Cassman 2014). Tropical forests are the habitats with the highest biodiversity (Brown 2014), and their conversion to agriculture is a major source of biodiversity loss (Gibson *et al.* 2011). If biodiversity loss continues we face an extinction crisis on par with some of the biggest mass extinction events in the history of life on Earth (Barnosky *et al.* 2011).

We must urgently find ways to avert this crisis, not only to protect species for their intrinsic value, but because biodiversity underpins important ecosystem functions, including many that influence food production (Millenium Ecosystem Assessment 2005). Incorporating measures of evolutionary distinctiveness — the extent to which a species is not closely related to any other extant species (note that this differs from measures of phylogenetic diversity, which relate to communities rather than species) — into conservation planning can help us to preserve as much of the tree of life as possible (Redding & Mooers 2006). Placing particular emphasis on the conservation of evolutionarily distinct species will mean that a greater proportion of evolutionary history is preserved, decreasing the chance of unique phenotypic and ecological traits being lost forever (Jetz *et al.* 2014).

Phylogenetic diversity — the amount of evolutionary history present, and the way in which evolutionary relationships are patterned in a site or community — is increasingly understood to be extremely relevant to both ecology and conservation (Webb *et al.* 2002; Rolland *et al.* 2012; Winter, Devictor & Schweiger 2013). Measures of phylogenetic diversity provide insights into patterns of community assembly (Pavoine & Bonsall 2011) and high levels of phylogenetic diversity are associated with higher levels of ecosystem function (Cadotte, Cardinale & Oakley 2008). For example, in a long-term biodiversity-ecosystem function experiment in North America, phylogenetically diverse plant communities had more temporally constant above-ground biomass production (Cadotte, Dinnage & Tilman 2012). High levels of phylogenetic diversity may enhance the resilience and evolutionary potential of communities in an era of rapid environmental change (Mouquet *et al.* 2012), but the evidence for this remains inconclusive (Winter, Devictor & Schweiger 2013).

Given the importance of phylogenetic diversity for conservation and its likely importance for ecosystem functioning, there are two questions we need to answer in order to identify best management practices:

(1) Can concentrating new crop expansion to areas of existing low productivity agriculture reduce losses of phylogenetic diversity? The conversion of tropical forest to agriculture greatly reduces taxonomic and functional diversity (Flynn *et al.* 2009; Gibson *et al.* 2011; Moura *et al.* 2013). However, many regions have large areas of land that have already lost their native vegetation, and are

used for low-productivity agriculture, such as extensive cattle pasture. Directing future crop expansion to such areas instead of towards existing areas of natural habitat could potentially mitigate biodiversity loss (Garcia-Ulloa *et al.* 2012; Gilroy *et al.* 2014b), although forest succession on these lands could be another beneficial pathway for biodiversity and carbon sequestration (Gilroy *et al.* 2014c). The extent to which this strategy could also help preserve phylogenetic diversity remains unknown.

(2) Can retaining forest fragments increase phylogenetic diversity in surrounding agriculture? Avian phylogenetic diversity is higher in diversified agriculture than in intensive monocultures across a range of agricultural systems in Costa Rica (Frishkoff *et al.* 2014), but it is unclear which features of diversified agricultural landscapes help to promote phylogenetic diversity. Large blocks of contiguous forest are needed to support the persistence of bird and dung beetle species in wildlife-friendly cattle pastures in the Colombian Andes (Gilroy *et al.* 2014a), but it remains unclear whether the presence of nearby forest habitats also contributes to the preservation of phylogenetic diversity in farmland communities.

In this study, we address these questions in the context of oil palm expansion in Colombia. Oil palm cultivation is currently concentrated in Southeast Asia, where most recently established plantations have replaced forest (Gunarso *et al.* 2013), reducing species richness and functional diversity in several taxa (Foster *et al.* 2011; Edwards *et al.* 2014a; b). Oil palm cultivation is likely to increase in South America (Butler & Laurance 2009). We ultimately need to reduce demand for vegetable oils and crop-based biofuels and thus the need to cultivate vegetable oil crops (and the environmental damage associated with their cultivation). However, assuming that demand continues to rise as projected (Corley 2009), biodiversity loss could be minimized by converting less productive types of agriculture (rather than natural habitats) to oil palm plantations (Garcia-Ulloa *et al.* 2012; Gilroy *et al.* 2014b). In Colombia, the agricultural habitat most available for conversion to oil palm is cattle pasture (Garcia-Ulloa *et al.* 2012). The western part of the Colombian Llanos, which contains a mixture of intensive and semi-natural cattle pastures and forest remnants, is an area in which oil palm expansion could have a relatively low environmental impact (Garcia-Ulloa *et al.* 2012; Gilroy *et al.* 2014b).

We focused on the phylogenetic diversity of birds to determine the impacts of oil palm expansion and the retention of forest fragments in the Colombian Llanos. Complete phylogenies of all extant bird species are available (Jetz *et al.* 2012) and birds are functionally important (Sekercioglu 2006) and a good indicator taxon – they are cost-effective to survey (Gardner *et al.* 2008) and their responses to land-use change is a good predictor of that in other taxa, including dung beetles, scavenging mammals, hymenoptera, and hemiptera (Edwards *et al.* 2014b). Previous studies have shown that avian species richness and functional diversity was highest in forest (Edwards *et al.* 2014a), but that replacing existing cattle pastures with oil palm in this region would lead to minimal biodiversity loss (Gilroy *et al.* 2014b; Lees *et al.* 2015). Here, we aim to determine whether impacts on phylogenetic diversity are likely to differ if oil palm expansion occurs at the expense of remnant forests, rather than existing cattle pastures. We also examine whether the preservation of forest fragments within oil palm landscapes can help to conserve phylogenetic diversity within oil palm plantations.

Methods

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, which contains a network of riparian forests along the rivers that ultimately drain into the Orinoco (Jiménez, Decaëns & Rossi 2012). The main agricultural land use has historically been extensive cattle grazing (Etter, McAlpine & Possingham 2008). Agricultural production in the region has intensified, and the region now has 2.5 million hectares of intensive pastures (with *Brachiaria sp.* grasses introduced from Africa) and 140,000 hectares of oil palm plantations (Romero-Ruiz *et al.* 2010), with oil palm area predicted to expand rapidly over the coming decade (Garcia-Ulloa *et al.* 2012; Castiblanco, Etter & Aide 2013).

We conducted the study at three field sites — Palumea (4°20’15.2”N, 73°11’47.8”W), Carolina (4°17’44.9”N, 72°58’35.9”W), and Guaycaramo (4°27’34.8”N, 72°57’40.0”W) — in the municipalities of Medina (Cundinamarca), Cabuyaro (Meta), and Barranco Upía (Meta) respectively (Figure S1). These sites were separated from each other by 11-24 km. Each of these three sites contained a mixture of intensive 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 *Mauritia flexuosa* (*moriche* palm). Forest fragments in this region are small patches or fairly narrow riparian strips, which means that there is a high edge to interior ratio, and most points in a forest are therefore edge-affected and close to agricultural habitats. We sampled these sites in the dry season, between January and March 2013.

In total we sampled 36 oil palm, 36 pasture, and 34 forest points. We arranged these points into transects (four points per transect in oil palm and pasture, 1-5 points (median 2) per forest transect), with at least 300 m separating each point. We calculated the proportion of forest in a 250 m radius around each point in ArcGIS, using Landsat maps from Google Earth v. 7.1.2 (imagery from 2012) which we ground-truthed during fieldwork. Site choice was constrained by accessibility. Site choice was constrained by accessibility. Transect locations were chosen a priori and at random, within constraints of habitat type and distance to other transects. Transects that later proved inaccessible in the field were moved to the nearest suitable location.

BIRD SURVEYS

A single experienced observer (J. J. Gilroy) conducted ten-minute, fixed radius (100 m) point counts between 05:45–11:00 on four successive days at each sampling point. Sampling order was switched between days so that all points were visited during both the earlier and later parts of the morning. Unfamiliar vocalisations were recorded with a Sennheiser ME66 shotgun microphone and Olympus LS11, and compared to an online database (www.xeno-canto.org). We excluded flying individuals not observed to settle within the point count radius.

PHYLOGENETIC TREES

We used 500 phylogenies downloaded from http://birdtree.org/ (Jetz *et al.* 2012) - 250 of them based on the Hackett *et al.* (2008) backbone (used to constrain deep-level relationships among major clades), and 250 of them using the Ericson *et al.* backbone (2006). Each tree is a different hypothesis about the evolutionary relationships between species, and we calculated six metrics of phylogenetic diversity (as listed below) for each of the 500 trees. Having checked that the 500 values were normally distributed, we took the mean value for each metric at each sample point to ensure that our results were robust to phylogenetic uncertainty.

MEASURES OF PHYLOGENETIC DIVERSITY AND EVOLUTIONARY DISTINCTIVENESS

We calculated six abundance-weighted measures of phylogenetic diversity and one measure of evolutionary distinctiveness for each sampling point (see also Supplementary Methods):

i) *PD* (phylogenetic diversity) – the total sum of phylogenetic history in a community;

ii) *sesPD* (the standard effect size (SES) of PD) – PD is positively correlated with species richness (Swenson 2014). These variables can be disentangled by comparing the PD values of the observed community with that of communities of equal species richness created by null models which randomly draw species from the regional species pool. Communities with greater PD than expected given the species richness have positive values of sesPD, and those with less than expected have negative values;

iii) *MPD* (mean pairwise distance) – the average phylogenetic distance between individuals in a community. This is influenced by relationships in deep evolutionary time. Higher values suggest that species are distributed across a wide range of clades, and low values suggest phylogenetic clustering;

iv) *sesSMPD* – MPD adjusted for species richness. Communities with greater MPD than expected given the species richness have positive values, and those with less than expected have negative values;

v) *MNTD* (mean nearest taxon distance) – the average distance between an individual and the most closely related (non-conspecific) individual. High levels of MNTD suggest that closely related individuals do not co-occur in the community, and low levels suggest that they do;

vi) *sesMNTD* – MNTD adjusted for species richness. Communities with greater MNTD than expected given the species richness have positive values, and those with less than expected have negative values;

vii) *Evolutionary Distinctiveness (ED)* – a measure of how much unique evolutionary history a species contributes to a phylogenetic tree. A species with no extant close relatives have high values of ED, and species with closely related extant species have low values.

We calculated these seven metrics using the *picante* package (Kembel *et al.* 2010) in R version 3.0.3 (R Core Team 2014). To calculate SES, we used null models with an independent swap algorithm that constrains species richness at each point but randomly draws species from the regional species pool to generate 999 null communities against which to compare the observed community. We did this for each metric (PD, MPD, and MNTD), and for all 500 trees. For abundance-weighted metrics we used the highest recorded number of individuals of a species at a given point (i.e., spanning the four point count repeats) as that species' abundance. We obtained a single measure of ED for each species from a global phylogeny of birds from species.mol.org (Jetz *et al.* 2014), revealing the distinctiveness of each species at a global level rather than within our samples. We then calculated the median ED of the species recorded at each point in our study. See Supplementary Methods for further details.

STATISTICAL ANALYSIS

We analysed the effect of habitat (forest, oil palm, or pasture) on each of the metrics using linear mixed effects models to account for potential spatial auto-correlation between points in the same transect and/or site. For the subset of points in oil palm and pasture, we also analysed whether each metric was influenced by the proportion of forest in a 250 m radius around each point. All models included sampling transect and site as nested random effects, and were estimated using Maximum Likelihood in the *lme4* R package (Bates *et al.* 2014). We checked model residuals for normality and homoscedasticity. Apart from median ED (which we log-transformed), we did not transform any of the metrics. We compared model fit using AIC (Anderson 2008). We used Nagakawa and Schielzeth's R^2 (Nakagawa & Schielzeth 2013), calculated using the *MuMIn* R package (Barton 2014) to calculate how much of the data were explained by fixed and random effects in each of the linear mixed effects models. Where habitat was included in the best model, we performed Tukey post-hoc tests using the *multcomp* R package (Hothorn, Bretz & Westfall 2008). To ensure that our results were not affected by spatial auto-correlation, we performed Moran's I test, implemented using the *ape* package in R (Paradis, Claude & Strimmer 2004).

Waterbirds in our study area are generally associated with pasture/grassland habitats, which can be waterlogged or flooded, and tend to be more evolutionarily distinctive than other birds (Table S1). To test whether their inclusion in our analyses were biasing the results, we repeated the analyses without water-dependent species, following species descriptions from the Handbook of the Birds of the World Alive (del Hoyo *et al.* 2014).

Species counts in points near the agriculture-forest interface could be elevated by edge-specialist species. We therefore tested whether our analyses were affected by edge effects by repeating the analysis excluding all study points in oil palm and pasture that were less than 100 m away from forest. For forest points, we also compared models of PD, MPD, and MNTD including distance to nearest forest edge or the proportion of forest cover in 250 m surrounding the point and comparing them to null models containing only the random effects of transect nested within site.

Results

PHYLOGENETIC DIVERSITY

We recorded 244 species of bird, of which 31 species were classified as waterbirds (Table S1). For each of the six metrics of phylogenetic diversity we measured, including habitat as a fixed effect improved model fit (Table 1). PD (Figure 1a) and MPD (Figure 1c) were significantly higher in forest than in both oil palm and pasture, but not significantly different between pasture and oil palm. Both sesPD (Figure 1b) and sesMPD (Figure 1c), which control for the effects of species richness, did not differ significantly among habitats. Finally, MNTD was significantly higher in oil palm and pasture than in forest, but did not differ significantly between oil palm and pasture (Figure 1e).

sesMNTD was significantly higher in oil palm than in forest, but there was no significant difference between pasture and the other two habitats (Figure 1f).

These results did not change when we repeated the analysis excluding waterbirds (Table S2, Figure S2) or oil palm and pasture points less than 100 m away from forest (Table S3, Figure S3). Furthermore, for forest points, distance to nearest forest edge or the proportion of forest cover in 250 m surrounding a point did not improve model fit over a null model containing only the random effects of transect nested within site (Table S4).

We did not detect spatial auto-correlation for any of the model residuals (p>0.05 for all Moran's I tests).

EVOLUTIONARY DISTINCTIVENESS

Pasture had significantly higher median ED than oil palm and forest, but ED did not differ significantly between oil palm and forest (Figure 2). When we excluded waterbirds from the analysis, pasture had significantly higher median evolutionary distinctiveness than oil palm, but there were no other significant differences between habitats (Figure S4). There was no impact of the exclusion of points less than 100 m away from forest on our results (Figure S5).

EFFECTS OF RETAINING FOREST FRAGMENTS WITHIN OIL PALM AND PASTURE

Including proportion of remnant forest cover within 250 m improved model fit for PD in both oil palm and pasture (Tables 2 and 3, respectively) and for MNTD in pasture (Table 3); PD increased and MNTD decreased with increasing proportion of remnant forest cover (Figure 3). For all other metrics, the best models were the null models containing only the random effects of transect and site. We did not detect spatial auto-correlation for any of the model residuals (p>0.05 for all Moran's I tests). Results for PD and MNTD in oil palm and pasture were similar when excluding waterbirds (Tables S5 & S6, Figures S6 & S7) and points less than 100 m away from forest (Tables S7 & S8, Figure S8 & S9). Additionally, when excluding points less than 100 m away from forest, MPD in oil palm (Figure S10) and sesMNTD in pasture (Figure S11) both increased with proportion of forest in a 250 m radius around a point.

Discussion

Our results suggest that directing future expansion of intensive oil palm monocultures towards existing improved cattle pastures, avoiding forest loss and preserving forest fragments within agricultural landscapes, would minimize losses of avian phylogenetic diversity in the Llanos ecoregion. PD and MPD were higher in forest than in oil palm (Figure 1), whereas pasture did not differ significantly from oil palm in either metric (Figure 1), suggesting that oil palm could replace pastures without significant loss of avian phylogenetic diversity. PD increased with extent of remnant forest cover (Figure 3a), showing the importance of remnant forests for the maintenance of phylogenetic diversity in agricultural landscapes.

PD is affected by both species richness and branch topology – adding species to a community increases the sum of branch lengths, and a community comprised of close relatives will have a lower branch length sum than one comprised of an equal number of distantly related species (Swenson 2014). After controlling for species richness (sesPD), PD in the three habitats did not differ significantly (Figure 1b), suggesting that on a per species basis, oil palm and pasture conserve similar levels of evolutionary history to forest, but that different avian clades are not more or less likely to survive in agriculture. A caveat to this interpretation is that historic forest loss and fragmentation may have already extirpated the most sensitive forest species.

The higher MPD in forests suggests that that the bird species recorded in our forest sites are distributed across a wider range of clades than those recorded in oil palm or pasture sites (Figure 1c). Conversion of forest to various types of agriculture (heart-of-palm, banana, pineapple, sugar cane, coffee, melon, rice, cattle pasture, and aquaculture) similarly resulted in a reduction in bird PD and MPD in Costa Rica (Frishkoff et al. 2014), suggesting that there is a general pattern of PD and MPD loss with conversion of forests to farmland. Forest, pasture and oil palm did not differ in sesMPD, suggesting that each habitat has similar MPD to that expected given the number of species (Figure 1d).

In contrast to the other metrics we studied, the mean distance between a species and its most closely related species (MNTD; for example, the evolutionary distance between species within families and genera) was significantly higher in oil palm than in forest (Figure 1e). Forest points had lower sesMNTD than oil palm points, which suggests that forest communities are more phylogenetically clustered in their terminal branches (i.e. at the intra-familial or intra-generic level, Figure 1f). Pasture communities did not differ significantly from either forest or oil palm in this regard. Together with the finding that pasture and oil palm points have low MPD, this suggests that pasture communities represent relatively few clades but contain many species within those clades, whereas oil palm communities tend to have a broader representation of clades, but fewer occurrences of closely related species. Forest points have higher MPD and lower MNTD than oil palm and pasture (see also Frishkoff et al. 2014), which suggests that there is a broader representation of clades in forest points, but with many closely related species co-existing.

Pasture had significantly higher median evolutionary distinctiveness (ED; the phylogenetic uniqueness of a species) than oil palm and forest (Figure 2). The significant difference between forest and pasture disappeared when we repeated the analysis without waterbird species. This suggests that higher ED in pasture is partly driven by the occurrence of waterbirds, which tend to have higher ED values than other species and greater affinity for pasture/grassland environments that can be flooded or waterlogged (Table S1). Directing oil palm development towards existing pastures may therefore help to protect overall phylogenetic diversity, although this strategy could have negative impacts on some evolutionarily distinct species (including waterbirds) that require grassland habitats. None of the species we detected are IUCN red-listed (BirdLife International 2014), although this might reflect historical local extinctions due to forest-loss or planting of non-native grasses, and Colombia still has large expanses of improved cattle pasture – approximately 4.5 MHa of pasture in areas bioclimatically suitable for oil palm (Garcia-Ulloa *et al.* 2012). Populations of evolutionarily distinct waterbirds may be best protected by conserving remaining areas of semi-natural savannah and wetlands in the Llanos ecoregion.

The persistence of nearby forest cover was an important predictor of PD in both oil palm and pasture (Figure 3a). It was not, however, an important predictor of sesPD (Table 3). Together with the findings of a previous study that avian species richness increases with enhanced forest cover (Gilroy *et al.* 2014b), this suggests that higher remnant forest cover increases PD through increased avian species richness, rather than an increased tendency for species that contribute disproportionately to PD to persist near forest. Increased proportion of forest cover in pasture was, however, associated with a decline in MNTD (Figure 3b). Since forest points had lower MNTD than pasture points, this may be further evidence that points near forest have more forest bird species. Higher levels of phylogenetic diversity have been linked to higher levels of ecosystem function in plants (Cadotte, Cardinale & Oakley 2008; Cadotte, Dinnage & Tilman 2012). If birds follow similar patterns, then it is possible that spill-over of PD might lead to a spill-over of ecosystem services provided by birds, such as pest control in oil palm. However, we need data on the links between different metrics of avian phylogenetic diversity (such as the relative influence of PD and MNTD, which follow opposite patterns in our data) and ecosystem services before we can confidently predict functional implications.

Our study area contains a patchy matrix of land-uses, including small forest fragments and riparian strips surrounded by oil palm and pasture (Fig. S1). The forests and farmland we sampled are therefore vulnerable to edge-effects, and it is possible that species totals at the border between forest and agricultural habitats could be inflated by edge-specialists. However, we found that PD, MPD, and MNTD in forest points were not impacted by proximity to edge (Table S4) and that excluding points in oil palm and pasture less than 100 m away from forest did not alter our main conclusions. Consequently, we are confident that edge effects are not explaining our results, and thus that forest fragments are valuable for the conservation of avian phylogenetic diversity in this landscape. While birds are a good indicator taxon (Barlow *et al.* 2007; Edwards *et al.* 2014b), it will be interesting and important to confirm whether or not the same patterns are found in other taxa when phylogenies are developed for them.

POLICY RECOMMENDATIONS

We recommend that forest fragments be conserved, and that oil palm expansion be restricted to areas already used for low-productivity agriculture, such as cattle pasture. To ensure that this does not cause deforestation through indirect land-use change elsewhere (Arima *et al.* 2011) this will need to be part of a broader policy of 'land-neutral agricultural expansion' in which the total area allocated to different types of agriculture can change, but the total area allocated to agriculture does not (Strassburg *et al.* 2012). Intensification of cattle ranching is a feasible and necessary part of this strategy (Garcia-Ulloa *et al.* 2012; Calle *et al.* 2013; Strassburg *et al.* 2014).

Legal restrictions on future forest conversion and financial incentives for intensifying beef production and restricting future cultivation of oil palm to existing agricultural areas may be needed to implement these policies. Controlling demand for meat and biofuels will also reduce the pressure for agricultural expansion. While we have focused on oil palm and cattle ranching, broad scale agricultural policies will also need to incorporate other types of agriculture, such as small-holder subsistence agriculture (UNCTAD 2013). Policies will also need to be sensitive to the needs and rights of 2.7-4.3 million people displaced by internal conflict in Colombia, many of whom were rural smallholder farmers forced to migrate to cities and may want to reclaim their land when conditions become more peaceful (Carrillo 2009).

Unchecked oil palm expansion has the potential to diminish avian phylogenetic diversity in the Colombian Llanos. It is essential that we find ways to protect remaining forest fragments in the region, and ensure that future oil palm expansion occurs at the expense of improved cattle pasture instead of forest.

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Table 1. Comparison of linear mixed effects models for point-level phylogenetic metrics. Null model contains transect and site as nested random effects. Best model in bold. Marginal R^2 describes the amount of variation explained by the fixed effects, and conditional R^2 represents the total amount of variation explained by the model.

Response variable	Model	AIC	∆AIC	Marginal R^2	Conditional R^2
PD	**Habitat**	**1494.10**	**0.00**	**0.47**	**0.55**
	Null	1527.60	33.50	0.00	0.58
sesPD	**Habitat**	**268.50**	**0.00**	**0.06**	**0.19**
	Null	269.59	1.09	0.00	0.19
MPD	**Habitat**	**804.80**	**0.00**	**0.18**	**0.22**
	Null	817.61	12.81	0.00	0.20
sesMPD	**Habitat**	**253.62**	**0.00**	**0.05**	**0.15**
	Null	254.08	0.46	0.00	0.14
MNTD	**Habitat**	**942.07**	**0.00**	**0.18**	**0.31**
	Null	954.21	12.14	0.00	0.29
sesMNTD	**Habitat**	**248.71**	**0.00**	**0.09**	**0.25**
	Null	251.66	2.95	0.00	0.25
ED	**Habitat**	**-88.32**	**0.00**	**0.11**	**0.19**
	Null	-81.81	6.52	0.00	0.17

Table 2. Comparison of linear mixed effects models for point-level phylogenetic diversity metrics for points in oil palm plantations. Null model contains transect and site as nested random effects; ‘radius(250)’ is the proportion of forest cover within a 250 m radius around the point. Best models in bold. Marginal R^2 describes the amount of variation explained by the fixed effects, and conditional R^2 represents the total amount of variation explained by the model.

Response variable	Model	AIC	ΔAIC	Marginal R^2	Conditional R^2
PD	**Radius(250)**	**488.84**	**0.00**	**0.41**	**0.53**
	Null	504.20	15.36	0.00	0.04
sesPD	**Null**	**101.12**	**0.00**	**0.00**	**0.13**
	Radius(250)	102.77	1.65	0.01	0.13
MPD	**Null**	**284.63**	**0.00**	**0.00**	**0.09**
	Radius(250)	285.87	1.24	0.02	0.10
sesMPD	**Null**	**100.46**	**0.00**	**0.00**	**0.08**
	Radius(250)	101.93	1.47	0.02	0.12
MNTD	**Null**	**339.96**	**0.00**	**0.00**	**0.10**
	Radius(250)	341.12	1.16	0.02	0.12
sesMNTD	**Null**	**100.56**	**0.00**	**0.00**	**0.07**
	Radius(250)	102.56	2.00	0.00	0.07

Table 3. Comparison of linear mixed effects models for point-level phylogenetic diversity metrics for points in pasture. Null model contains transect and site as nested random effects; 'radius(250)' is the proportion of forest cover within a 250 m radius around the point. Best model in bold. Marginal R^2 describes the amount of variation explained by the fixed effects, and conditional R^2 represents the total amount of variation explained by the model.

Response variable	Model	AIC	ΔAIC	Marginal R^2	Conditional R^2
PD	**Radius(250)**	**505.58**	**0.00**	**0.21**	**0.42**
	Null	511.93	6.35	0.00	0.11
sesPD	**Null**	**82.77**	**0.00**	**0.00**	**0.26**
	Radius(250)	84.43	1.66	0.01	0.30
MPD	**Null**	**284.18**	**0.00**	**0.00**	**0.06**
	Radius(250)	285.37	1.19	0.03	0.05
sesMPD	**Null**	**74.67**	**0.00**	**0.00**	**0.33**
	Radius(250)	76.50	1.83	0.00	0.34
MNTD	**Radius(250)**	**320.13**	**0.00**	**0.05**	**0.50**
	Null	320.77	0.64	0.00	0.42
sesMNTD	**Null**	**81.94**	**0.00**	**0.00**	**0.29**
	Radius(250)	83.43	1.49	0.01	0.29

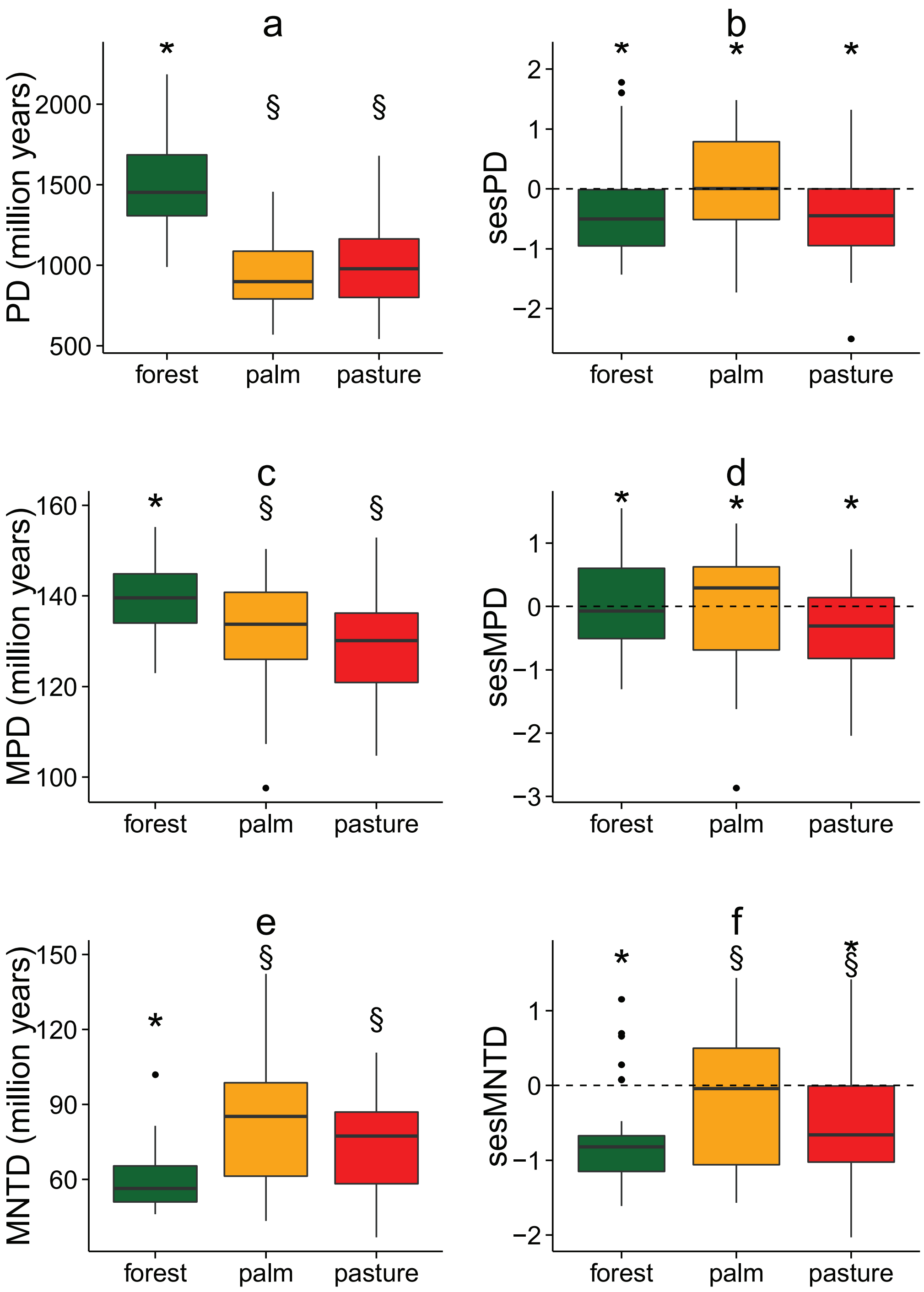

Figure 1 – a) Phylogenetic diversity (PD) b) sesPD (PD adjusted for species richness) c) mean pairwise difference (MPD) d) sesMPD e) mean nearest taxon difference (MNTD) f) sesMNTD. Shared symbols indicate no significant difference, different symbols indicate significant difference.

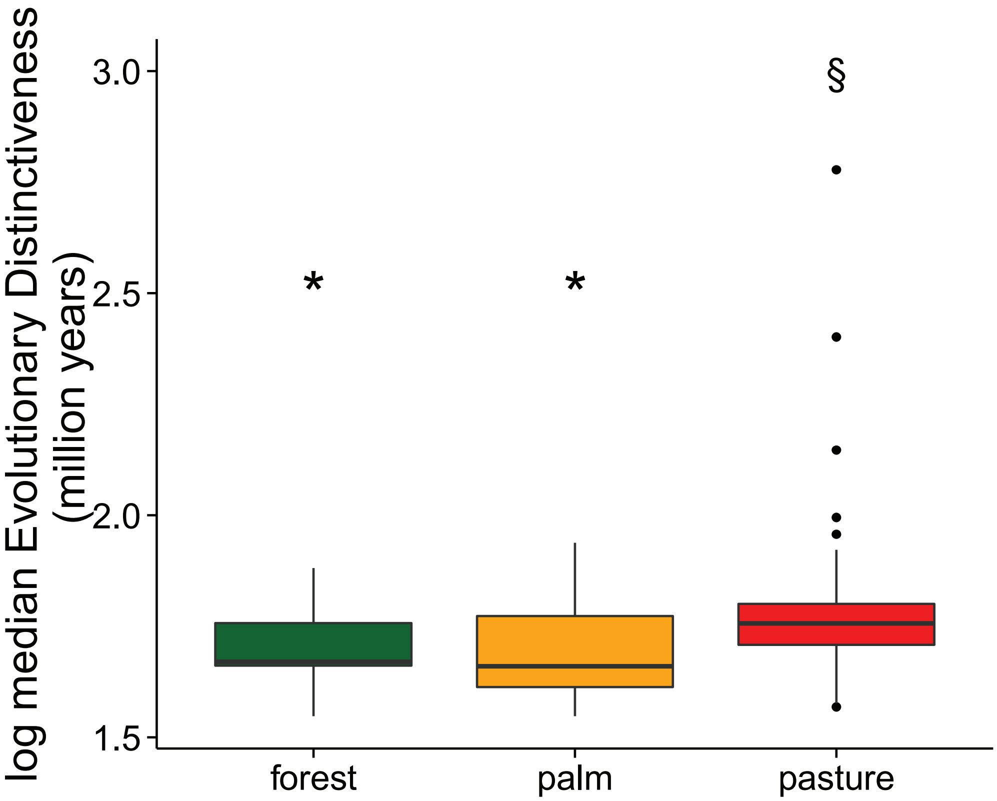

Figure 2 – logged median evolutionary distinctiveness (ED) in forest, oil palm, and pasture points. Shared symbols indicate no significant difference, different symbols indicate significant difference.

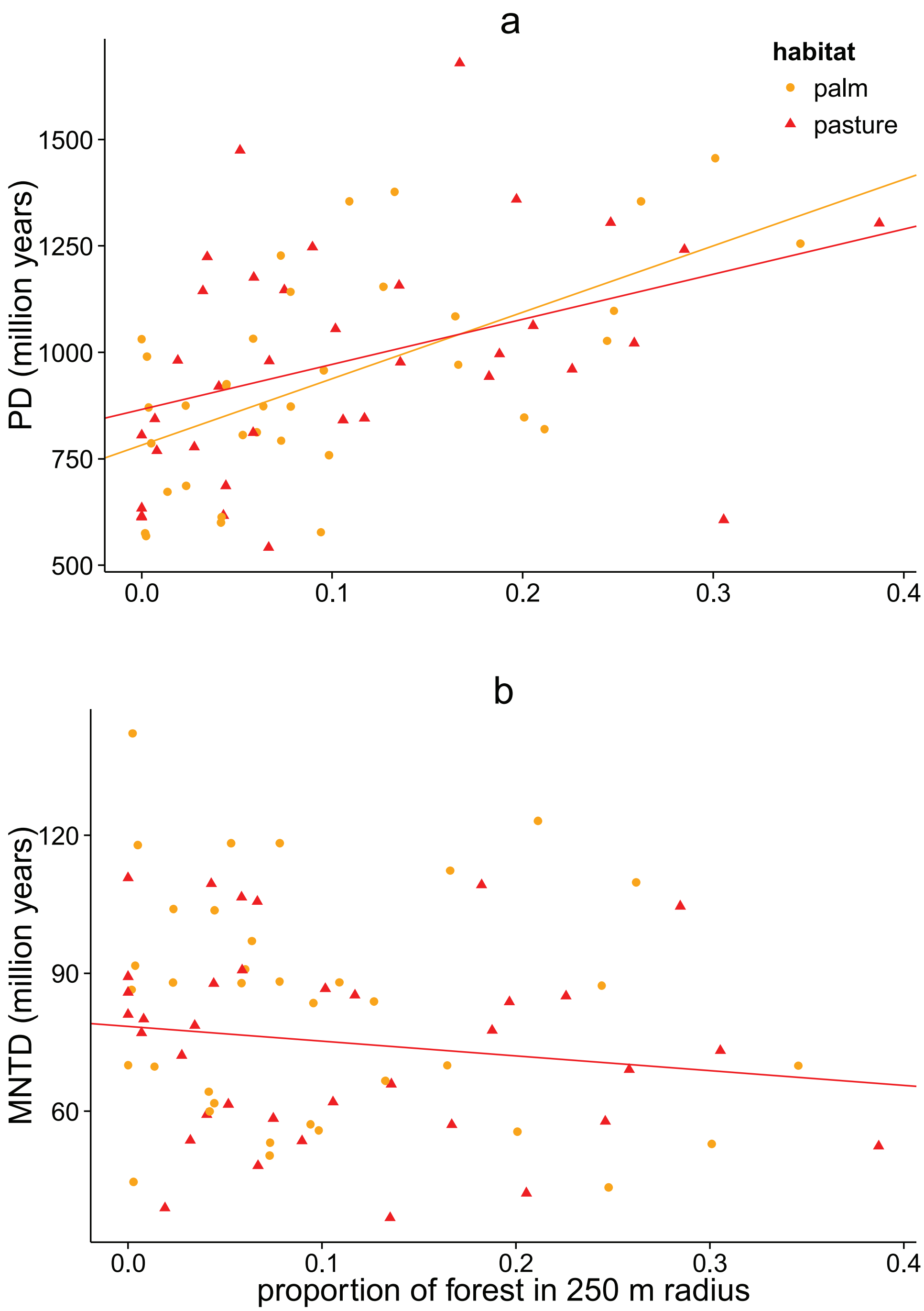

Figure 3 – effect of proportion of forest in a 250 m radius around a point on a) phylogenetic diversity (PD) in oil palm and pasture points; and b) MNTD (mean nearest taxon distance) in oil palm and pasture points. We have not plotted a best fit line for oil palm points because the best model of MNTD in oil palm points was the null model.