RESEARCH ARTICLE

Journal of Applied Ecology | BRITISH ECOLOGICAL SOCIETY

Contrasting impacts of land-use change on phylogenetic and functional diversity of tropical forest birds

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Abstract

1. Biodiversity conservation strategies increasingly target maintaining evolutionary history and the resilience of ecosystem function, not just species richness (SR). This has led to the emergence of two metrics commonly proposed as tools for decision making: phylogenetic diversity (PD) and functional diversity (FD). Yet, the extent to which they are interchangeable remains poorly understood.

2. We explore shifts in and relationships between FD and PD of bird communities across a disturbance gradient in Borneo, from old-growth tropical forest to oil palm plantation.

3. We show a marked decline in PD, and an increase in phylogenetic mean nearest taxon distance from forest to oil palm, in line with declining SR across the gradient. However, phylogenetic mean pairwise distance is constrained by forest logging more than by conversion to oil palm, taking account of SR.

4. The decline in FD across the gradient is less severe than in PD, with all metrics indicating relatively high trait diversity in oil palm despite low SR, although functional redundancy is much reduced. Accounting for SR, levels of functional over- or under-dispersion of bird communities are strongly coupled to habitat disturbance level rather than to any equivalent phylogenetic metric.

5. *Policy implications*. We suggest that while phylogenetic diversity (PD) is an improvement on species richness as a proxy for functional diversity (FD), conservation decisions based on phylogenetic diversity alone cannot reliably safeguard maximal functional diversity. Thus, phylogenetic diversity and functional diversity are related but still complementary. Priority setting exercises should use these metrics in combination to identify conservation targets.

KEYWORDS
biodiversity indices, birds, disturbance, functional diversity, oil palm, phylogenetic diversity, selective logging, species richness, tropical rainforest

1 | INTRODUCTION

Biodiversity assessments are an important component of conservation planning and are increasingly used to identify land-use management practices that maximise both evolutionary value and ecosystem function (Bregman et al., 2016; Ribeiro et al., 2016). Key requirements are to maintain community resilience to environmental disturbance and to preserve ecosystem functions and services across time and space (Socolar, Gilroy, Kunin, & Edwards, 2016). Consequently, it is often proposed that we need to look beyond merely conserving species richness (SR) towards maintaining the maximum diversity of evolutionary lineages and associated ecological functions (Bregman et al., 2016;

Jarzyna & Jetz, 2016). To achieve these goals, it is becoming standard practice to capitalise on extensive phylogenetic or functional trait data-sets to generate community-level phylogenetic and functional diversity (FD) indices and capture the breadth of evolutionary history and ecological functions, respectively (Jarzyna & Jetz, 2016; Srivastava, Cadotte, Macdonald, Marushia, & Mirotchnick, 2012). Phylogenetic metrics are also often proposed as surrogates for functional metrics (Lopez et al., 2016; Srivastava et al., 2012), where relevant trait data are lacking. However, the extent to which phylogenetic and functional metrics provide interchangeable or contrasting types of information remains unclear (Lopez et al., 2016; Pigot, Trisos, & Tobias, 2016).

Although many FD indices exist, a popular and conceptually simple measure is FD, the sum of branch lengths in a dendrogram generated from functional trait differences (Petchey & Gaston, 2002). Greater differences between species result in higher FD, which, therefore, provides an index of niche complementarity and the diversity of ecological interactions present within communities (Petchey & Gaston, 2002; Srivastava et al., 2012). The idea that FD or functional complementarity performs better than SR as predictors of ecosystem functions is supported by a range of empirical studies (e.g. Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011; Fründ, Dormann, Holzschuh, & Tscharntke, 2013; Mokany, Ash, & Roxburgh, 2008; Petchey, Hector, & Gaston, 2004; Tilman et al., 1997). However, estimation of FD relies on the subjective choice of a defined set of traits, measurable across a range of taxa, representing a limited subset of possible ecological interactions and functions (Petchey & Gaston, 2002).

An alternative metric, phylogenetic diversity (PD) estimates cumulative evolutionary history by totalling the branch lengths in a community-wide phylogenetic tree (Faith, 1992). Communities with greater PD are predicted to be more resilient to environmental change and to better preserve unique lineages (Faith, 1992; Srivastava et al., 2012; Vane-Wright, Humphries, & Williams, 1991). PD has also been proposed as an improvement on FD because: (1) PD is considered a more synthetic estimate of community-wide trait diversity (Wiens et al., 2010), hence more effectively summarising phenotypic and functional similarity (Srivastava et al., 2012); (2) PD captures unknown interactions that influence ecosystem functions (Srivastava et al., 2012); and (3) PD may outperform FD in predicting ecosystem functions, while complementing FD in the components of ecosystem function accounted for (e.g. Cadotte, Cardinale, & Oakley, 2008; Cadotte, Cavender-Bares, Tilman, & Oakley, 2009; Flynn et al., 2011).

With the increasing ease of applying molecular tools, community-wide PD is arguably more tractable than FD for all but the best-known taxa with comprehensive available functional trait data (Srivastava et al., 2012; Voskamp, Baker, Stephens, Valdes, & Willis, 2017). In addition, phylogenetic metrics might provide a suitable surrogate for functional metrics according to the concept of phylogenetic niche conservatism (Peterson, 2011), which predicts that phylogenetic distance between lineages is correlated with the difference in their ecological or functional niches. Nevertheless, the extent to which niches and associated traits are phylogenetically conserved is likely to vary substantially with taxon, biogeographic context and spatial scale, as well as the functional traits selected, leading to *a priori* uncertainty over the strength and form of FD–PD relationships (Srivastava et al., 2012; Wiens et al., 2010). Empirical tests are, therefore, needed to explore this relationship, since any lack of congruence could indicate the need for a trade-off approach to the application of PD and FD to guide land-use management strategies.

In this study, we applied PD and FD metrics to bird communities sampled across a forest disturbance gradient in Sabah, Malaysian Borneo, a region facing intense pressure on forest biodiversity (Wilcove, Giam, Edwards, Fisher, & Koh, 2013). The gradient spanned unlogged forest, through forest subject to one or two rounds of selective logging, to oil palm plantation. We then compared patterns in local-scale PD and FD in response to land-use change, capitalising on the fact that both PD and FD are dendrogram-derived estimates based on an equivalent concept of summing across branch lengths.

Birds are a well-established indicator taxon across tropical forest disturbance gradients (Edwards, Magrach, et al., 2014) and make an ideal study system for testing PD–FD relationships for three main reasons. First, comprehensive ecological information now exists for almost all species, even in tropical systems (e.g. del Hoyo, Elliott, Sargatal, Christie, & de Juana, 2017). Second, the link between morphological traits and ecological function is relatively well established, as the avian beak is an index of trophic niche, and other biometric measurements are related to foraging strategy, microhabitat and substrate use (Miles & Ricklefs, 1984; Trisos, Petchey, & Tobias, 2014). Third, a global phylogeny is available spanning the majority of extant bird species (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012).

In this study, we first examined how PD metrics, and their level of over- or under-dispersion, vary across the disturbance gradient, in comparison with equivalent FD metrics. Second, by modelling each functional metric against the equivalent phylogenetic metric and habitat disturbance level, we: (1) examined evidence for variation in functional redundancy, or lack thereof, for a given amount of change in each phylogenetic metric; and (2) tested the assumption that measures of PD and phylogenetic clustering are good proxies for equivalent FD measures.

2 | MATERIALS AND METHODS

2.1 | Study area

We sampled bird communities in unlogged (old-growth) lowland dipterocarp rainforest and selectively logged production forests in the 1,000,000 ha Yayasan Sabah logging concession in Sabah, Malaysian Borneo, and in neighbouring oil palm plantations. Specifically, we focused on 45,200 ha of unlogged forest at the Danum Valley Conservation Area and Palum Tambun Watershed Reserve, and forests that have been selectively logged once or twice in the contiguous 238,000 ha Ulu Segama-Malua Forest Reserve (US-MFR). We also sampled unlogged forest in the 28,000 ha Tawau Hills Park, *c.* 60 km to the south-east.

Once-logged locations (41% of US-MFR) were logged in 1987–1991 using a modified uniform system which removed all commercial stems >0.6 m diameter and yielded an average 120 m³/ha of timber. Twice-logged locations (59% of US-MFR) were logged again in

2001–2007, employing the same techniques but with minimum diameter reduced to ≈0.4 m, yielding an additional 15–72 m^3/ha (Edwards et al., 2011; Fisher, Edwards, Giam, & Wilcove, 2011). We sampled mature oil palm plantations (20–30 years old, 100 trees per ha) to the north, east and south of the US-MFR (total area >1,000,000 ha, Edwards et al., 2010).

2.2 | Sampling protocol

We sampled bird communities between 2008 and 2011, with five transects each in unlogged and once-logged forest, and seven each in twice-logged forest and oil palm plantations (Figure S1 and Table S1). Within habitat types, transects averaged 37.8 ± 3.8 km apart, and between habitat types, they averaged 40.3 ± 1.8 km apart. Minimum inter-transect distance was 1.7 km. Along each transect, we sampled birds using 12 unlimited-radius point counts (total n = 288 communities). Points were spaced 250 m apart to ensure statistical independence (Hill & Hamer, 2004). Each point was visited by the same experienced observer (DPE) for 15 min on three consecutive days between 05.45 and 10.00 hr. Given that many tropical forest birds have low dispersal and high site fidelity, we assume that movement of individuals between points is negligible. Hence, we took the final count for species i at point j as the highest number of individuals recorded on any of the three visits.

2.3 | Functional trait data

We collected biometric trait data for all 206 species in the community dataset by measuring museum specimens at the Natural History Museum, Tring, UK. In all cases, we measured seven traits, including beak, wing, tail and tarsus measurements, following established procedures (see Bregman et al., 2016; Pigot, Bregman, et al., 2016; Pigot, Trisos, et al., 2016; Ulrich, Lens, Tobias, & Habel, 2016). Where possible, all biometric measurements were averaged across ≥3 repeat measurements taken by the same person from each of four individuals (two males and two females). The final mean values were entered into the trait matrix. For further details of methods and justification of the choice of traits, see Appendix S1.

Biometric trait measurements are strongly dependent on body size, so we separated size- and shape-associated variation using principal components analysis (PCA). Using a two-stage PCA process (see Bregman et al., 2016; Trisos et al., 2014), we extracted three principal components (PCs): two that partitioned shape variation between dispersal-linked traits and trophic-linked traits and one that partitioned overall size variation (Table S2, Appendix S1). We added these three PCs as variables to the final trait matrix in place of the original biometric data. We complemented the biometric data with foraging stratum and dietary information, comprising a series of binary variables for different diets and feeding strata (compiled from Edwards, Edwards, Hamer, & Davies, 2013). Finally, we also included an ordinal index of the primary habitat for each species from literature (Tobias et al., 2016; Table S2). For further explanation and rationale, see Appendix S1.

2.4 | Phylogenetic data

We obtained phylogenetic trees for our species pool of Bornean birds using the subsetting algorithm provided by Jetz et al. (2012). We generated a distribution of 100 randomly selected permutations of the global avian phylogeny (Hackett backbone; downloaded from Birdtree website, www.birdtree.org, accessed 14/03/2017). We then used Maximum Clade Credibility analysis (MCCA, programme "BEAST 2," Bouckaert et al., 2014) to reduce the 100 subset trees to one tree with maximal phylogenetic support.

2.5 | Phylogenetic and FD metrics

We used closely equivalent tree-based approaches to the computation of phylogenetic and functional metrics for each community, in all cases using R version 3.0.3 (R Core Team, 2016, see Appendix S2). We derived Faith's PD (hereafter PD_F; Faith, 1992); phylogenetic Mean Pairwise Distance (pMPD; Webb, Ackerly, McPeek, & Donoghue, 2002); and phylogenetic Mean Nearest Taxon Distance (pMNTD; Webb et al., 2002) from the MCCA consensus tree, using functions *pd*, *mpd* and *mntd*, respectively (package "picante," Kembel et al. 2010). pMPD is the average pairwise phylogenetic distance between species in a community; pMNTD is the average distance between a species and the most closely related species. Because some species tips in our phylogeny are placed using taxonomic inference rather than genetic data, we re-ran sensitivity analyses based solely on genetic data to investigate the effects of taxonomic uncertainty. We found that results were qualitatively unchanged (our two measures of PD_F were correlated with R^2 = .997, see Appendix S1, Table S3) and thus present the results using the full phylogeny.

We computed the equivalent functional metrics derived from a functional dendrogram, hence FD (hereafter FD_{PG}; Petchey & Gaston, 2002), functional Mean Pairwise Distance (fMPD), and functional Mean Nearest Taxon Distance (fMNTD). We derived FD_{PG} using function *FD_dendro* in package "fundiv" (Bartomeus, 2016), using a Gower's dissimilarity distance matrix for the species pool to account for ordinal and binary variables (Borcard, Gillet, & Legendre, 2011; Podani & Schmera, 2006). Hierarchical clustering used the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) algorithm, which returned the highest Cophenetic correlation coefficient (=0.79), suggesting that the functional dendrogram is a good representation of the distance matrix. Using functions *mntd* and *mpd* in "picante," we calculated fMNTD and fMPD from the functional dendrogram. We standardised FD_{PG} and PD_F values between zero and one by dividing by the same metric computed for all species in the regional species pool. However, we did not standardise MNTD and MPD, since the regional species pool does not necessarily have the highest values of these indices.

2.6 | Standard effect size and null models

To estimate the extent to which communities are over- or under-dispersed in PD and FD, we used a null model approach, calculating

the standard effect sizes (SES) of each of our three pairs of phylogenetic and functional metrics for every community (function *sespd*; package "picante," Kembel et al. 2010). We calculated SES as

$$(\text{observed value} - \text{mean expected value})/SD(\text{expected value})$$

where expected values for the metric are calculated for 1,000 draws of a random community from the species pool, each with equal SR to the observed community. SES, therefore, measures the difference between the observed values and null expectation, indicating the extent of underdispersion (negative values) or overdispersion (positive values). We calculated SES using an independent swap algorithm (Gotelli, 2000), which weights the probability of drawing a species from the species pool by its overall abundance in the dataset.

2.7 | Analyses

For all analyses, we ran linear mixed models (package "nlme," Pinheiro et al., 2016), treating sampling transect as a random factor with individual point counts nested within it. First, we investigated how phylogenetic and functional metrics varied across the habitat disturbance gradient, using models fitting habitat type as the predictor. Next, for each of our three pairs of metrics, we tested how well the phylogenetic metric predicted the corresponding functional metric. Starting with simple metric–metric models, we then constructed multi-predictor models in two stages: (1) additionally fitting habitat type to each model and (2) fitting the habitat type × phylogenetic metric interaction where there was a significant main effect of habitat type. We checked at each stage to see whether adding terms improved model fit (i.e. lower Akaike information criterion [AIC]). The raw fMNTD data were not normally distributed, so we log-transformed this variable before analysis.

We constructed an equivalent set of models using the standard effect size (SES) of each metric as response variables to: (1) explore which communities are over- or under-dispersed in phylogeny and function across the disturbance gradient; and (2) assess whether dispersion in a given phylogenetic metric is a good predictor of dispersion in the equivalent functional metric, and whether this interacts with the land-use gradient. Finally, to complete our assessment of the relative value of phylogenetic metrics as proxies for functional metrics, we tested the importance of SR, and SR and habitat type combined, as predictors of our three pairs of PD and FD metrics, and the SES of each metric.

There is potential for spatial autocorrelation in model residuals to bias our results. Specifically, this can cause inflation of type I error rates and biasing of independent variable parameter estimates (and their perceived relative fit), when using regression methods that assume independent model errors (Clifford, Richardson, & Hemon, 1989). The 250-m spacing apart of point counts largely addresses this issue. Additionally, we used a nested mixed model design to account for non-independence arising from the nested structure of the sampling (points contained within transects). In all cases, we compared the performance of models with and without the random factor "transect," by performing a univariate correlogram function (*correlog*, package "NCF," Bjørnstad, 2013) on the residuals of each model to test for autocorrelation at multiple lag distances. For all response–predictor combinations, correlograms demonstrated that the mixed model design effectively removed spatial autocorrelation (e.g. using FD_{PG}, see Figure S3). Thus, we present only the mixed models. We report marginal and conditional R^2 (Nakagawa & Schielzeth, 2013), describing variance explained by fixed effects only, and by fixed and random effects combined, respectively. We focus our discussion of model explanatory power on marginal R^2 (R^2_{mar}).

3 | RESULTS

3.1 | Habitat effects on FD and PD metrics

Habitat type was a weak predictor of FD_{PG} and a highly significant predictor of PD_F (Table 1). Habitat type was also highly significant in predicting

Dependent variable	Predictor Habitat type	Fit statistics R^2_{mar}	R^2_{con}	AIC
FD_{PG}	$F = 3.02, p = .05$	.11	.36	−1,019.5
PD_F	$F = 40.39, p < .0001$	.58	.66	−1,078.1
fMNTD	$F = 105.19, p < .0001$	.74	.78	19.8
pMNTD	$F = 11.86, p = .0001$	.26	.38	2,100.0
fMPD	$F = 27.47, p < .0001$	.47	.56	−1,236.0
pMPD	$F = 3.51, p = .03$	.08	.21	2,186.9
SES-FD_{PG}	$F = 61.27, p < .0001$	.50	.52	309.4
SES-PD_F	$F = 2.34, p = .10$	.06	.19	337.3
SES-fMNTD	$F = 25.28, p < .0001$	.31	.35	463.7
SES-pMNTD	$F = 1.32, p = .29$	.03	.17	477.4
SES-fMPD	$F = 40.70, p < .0001$	.45	.49	354.5
SES-pMPD	$F = 5.41, p = .007$	.11	.19	359.9

TABLE 1 Mixed models for each functional and phylogenetic diversity metric and their SES values, using habitat type as a predictor. Fixed effects (*F*-statistics and *p*-values) of habitat type, marginal (R^2_{mar}) and conditional (R^2_{con}) R^2 values; Nakagawa & Schielzeth, 2013), and AIC values are displayed

FD, functional diversity; PD, phylogenetic diversity; fMNTD, functional mean nearest taxon distance; pMNTD, phylogenetic mean nearest taxon distance; fMPD, functional mean pairwise distance; pMPD, phylogenetic mean pairwise distance; SES, standard effect sizes, AIC, Akaike information criterion.

fMNTD, pMNTD and fMPD, but a weak predictor of pMPD (Table 1). Both mean FD_{PG} and PD_F did not differ between unlogged, once-logged and twice-logged forest types (all $p > .05$). FD_{PG} was significantly lower in oil palm plantations compared with unlogged and twice-logged forest, but did not differ between oil palm and once-logged forest. PD_F was significantly lower in oil palm than in all forest types (Figure 1a,b). Neither functional nor phylogenetic MNTD differed between unlogged and logged forest but were both significantly higher in oil palm than in all forest types (Figure 1c,d). Functional MPD did not differ between unlogged and logged forest but was significantly higher in oil palm (Figure 1e). In contrast, pMPD did not differ between logged forest and oil palm but was significantly higher in unlogged forest (Figure 1f).

Patterns of SES variation across habitat type differed markedly for phylogenetic and functional metrics. Habitat type was a strongly significant predictor of SES of all functional metrics, showing substantial explanatory power for both SES FD_{PG} and SES fMPD, but was not a

significant predictor of SES of phylogenetic metrics with the exception of pMPD for which explanatory power was quite low (Figure 2, Table 1). Mean SES FD_{PG} was significantly higher in oil palm than for unlogged or logged forest, with twice-logged forest also being significantly higher than once-logged forest (Figure 2a). In contrast, SES PD_F did not differ significantly between any habitat types although it showed highest mean levels in oil palm (Figure 2b). Oil palm also had significantly higher SES fMNTD than all forest types, but SES pMNTD did not differ between any land use (Figure 2c,d). SES fMPD was also significantly higher in oil palm than all forest types, as well as being lower in once-logged forest than unlogged forest (Figure 2e). SES pMPD did not differ between unlogged forest and oil palm, but was significantly lower in logged than unlogged forest (Figure 2f). SES differences between land-use types broadly corresponded with tests of departure from null expectation: functional metrics tended towards net overdispersion in oil palm and underdispersion in forest, while
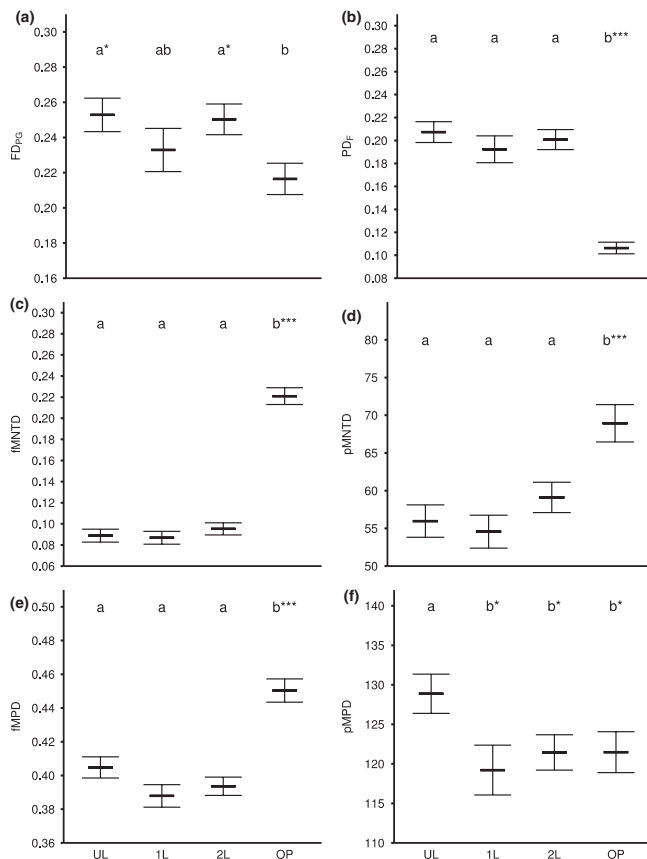

FIGURE 1 Mean functional and phylogenetic metrics across the habitat disturbance gradient covering unlogged forest (UL), once-logged forest (1L), twice-logged forest (2L), and oil palm (OP). (a) FD_{PG}; (b) PD_F; (c) fMNTD; (d) pMNTD; (e) fMPD; (f) pMPD. Short thick bars are means, and error bars represent 95% confidence intervals. Letters denote significance groups, with significantly different means not sharing letters. Asterisks denote significance levels: $^*p \leq .05$; $^{**}p \leq .01$; $^{***}p \leq .001$. FD, functional diversity; PD, phylogenetic diversity; fMNTD, functional mean nearest taxon distance; pMNTD, phylogenetic mean nearest taxon distance; fMPD, functional mean pairwise distance; pMPD, phylogenetic mean pairwise distance
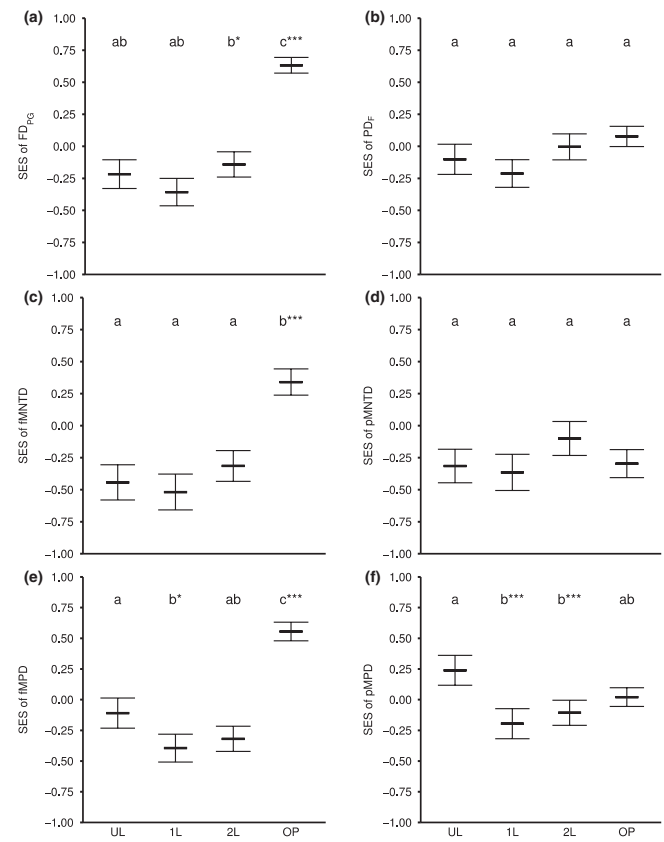
FIGURE 2 Standard effect sizes of functional and phylogenetic metrics across the habitat disturbance gradient covering unlogged forest (UL), once-logged forest (1L), twice-logged forest (2L) and oil palm (OP). (a) FD_{PG}; (b) PD_F; (c) fMNTD; (d) pMNTD; (e) fMPD; (f) pMPD. Short thick bars are means, and error bars represent 95% confidence intervals. Letters denote significance groups, with significantly different means not sharing letters. Asterisks denote significance levels: $^*p \leq .05$; $^{**}p \leq .01$; $^{***}p \leq .001$. FD, functional diversity; PD, phylogenetic diversity; fMNTD, functional mean nearest taxon distance; pMNTD, phylogenetic mean nearest taxon distance; fMPD, functional mean pairwise distance; pMPD, phylogenetic mean pairwise distance

phylogenetic metrics mostly showed underdispersion or no difference from zero, with the exception of overdispersion of PD_F in oil palm and of pMPD in logged forest (Table S4).

3.2 | Relationships between phylogenetic and functional metrics and effect of habitat type

All three phylogenetic metrics were highly significant positive predictors of their equivalent functional metrics. However, while PD_F explained a substantial amount of variation in FD_{PG} (R^2_{mar} = .67), pMNTD and pMPD showed low R^2_{mar} values (Table 2, Figure 3). In all cases, habitat type showed a significant effect when added to models, increasing explanatory power (R^2_{mar}) and overall model fit (lower AIC), substantially in the case of fMNTD and fMPD. The phylogenetic metric × habitat type interaction was significant in all cases, but model AICs indicated improved fit only for the FD_{PG} model, with a decrease in fit for both fMNTD and fMPD (Table 2). The importance of the interaction term for the FD_{PG}–PD_F relationship can be attributed mostly to a steeper slope in oil palm compared with unlogged and logged forests, indicating that changing land use alters the slope of the relationship (Figure 3a). For fMPD, the slope for oil palm was also steeper than for unlogged and logged forests; however, for fMNTD, oil palm showed a similar slope to forest habitats (Figure 3b,c).

For all three pairs of SES metrics, each phylogenetic metric was a significant positive predictor of its corresponding functional metric; however, explanatory power (R^2) was consistently weak (Table 2). In all cases, the addition of habitat type was highly significant, greatly increasing explanatory power and overall model fit. The interaction terms for SES phylogenetic metric × habitat type was non-significant, with the exception of the SES fMPD model which indicates a steeper slope with SES pMPD in oil palm plantations (Table 2, Figure S4). Nevertheless, for all three metrics, fitting the interaction term resulted in negligible increase in R^2 and a decrease in overall model fit (increase in AIC).

3.3 | Prediction of phylogenetic and functional metrics using SR

Species richness was a strong significant predictor of FD_{PG}, PD_F, fMNTD, and pMNTD, but a weak predictor of both fMPD and pMPD (Table S4, Figure S5). FD_{PG}, PD_F and pMPD increased with increasing SR, while fMNTD, pMNTD and fMPD decreased. SR was a strongly significant negative predictor of the SES of all functional metrics and showed substantial explanatory power. SR was also a weakly significant negative predictor of SES PD_F, but was not significantly associated with SES of pMNTD or pMPD (Table S4, Figure S6). Finally, in the case of fMNTD, models fitting SR and habitat type combined (Table

TABLE 2 Mixed models for each functional diversity metric (FD_{PG}, fMNTD, fMPD) and its SES value, showing slope, F-statistic and p-value for the corresponding phylogenetic diversity metric (PD_F, pMNTD and pMPD, and their SES values, respectively) fitted as a predictor. F-statistics and p-values are also shown for models with additional stepwise fitting of habitat type and the phylogenetic metric × habitat type interaction. Marginal (R^2_{mar}) and conditional (R^2_{con}) R^2 values (Nakagawa & Schielzeth, 2013) and model AIC values are displayed

	Predictor	Additional fixed effects		Fit statistics		
Metric relationship	Phylogenetic metric	Habitat type	Interaction	R^2_{mar}	R^2_{con}	AIC
FD_{PG}–PD_F	0.844, F = 511.97, p < .0001	—	—	.67	.87	−1,318.1
	0.912, F = 540.23, p < .0001	F = 27.03, p < .0001	—	.71	.76	−1,328.0
	0.832, F = 651.62, p < .0001	F = 40.06, p < .0001	F = 19.67, p < .0001	.78	.81	−1,366.6
fMNTD–pMNTD	0.012, F = 70.06, p < .0001	—	—	.09	.78	17.6
	0.011, F = 177.75, p < .0001	F = 72.49, p < .0001	—	.78	.82	−23.3
	0.017, F = 181.20, p < .0001	F = 73.63, p < .0001	F = 4.35, p = .005	.79	.83	−1.8
fMPD–pMPD	0.001, F = 54.29, p < .0001	—	—	.09	.63	−1,260.5
	0.001, F = 65.44, p < .0001	F = 49.49, p < .0001	—	.58	.62	−1,277.1
	0.001, F = 69.92, p < .0001	F = 54.33, p < .0001	F = 7.00, p = .0002	.61	.65	−1,248.8
SES-FD_{PG}–SES-PD_F	0.402, F = 54.92, P = .0001	—	—	.10	.58	302.1
	0.371, F = 83.63, p < .0001	F = 50.60, p < .0001	—	.57	.60	268.8
	0.503, F = 84.81, p < .0001	F = 52.21, p < .0001	F = 1.33, p = .26	.58	.60	277.4
SES-fMNTD–SES-pMNTD	0.265, F = 20.83, p < .0001	—	—	.05	.41	471.2
	0.254, F = 19.91, p < .0001	F = 24.95, p < .0001	—	.35	.40	449.7
	0.150, F = 20.00, p < .0001	F = 24.58, p < .0001	F = 1.22, p = .30	.36	.41	458.2
SES-fMPD–SES-pMPD	0.362, F = 40.82, p < .0001	—	—	.08	.54	352.0
	0.374, F = 64.85, p < .0001	F = 54.39, p < .0001	—	.53	.55	317.3
	0.284, F = 69.99, p < .0001	F = 63.13, p < .0001	F = 3.20, p = .02	.54	.56	320.4

FD, functional diversity; PD, phylogenetic diversity; fMNTD, functional mean nearest taxon distance; pMNTD, phylogenetic mean nearest taxon distance; fMPD, functional mean pairwise distance; pMPD, phylogenetic mean pairwise distance; SES, standard effect sizes.
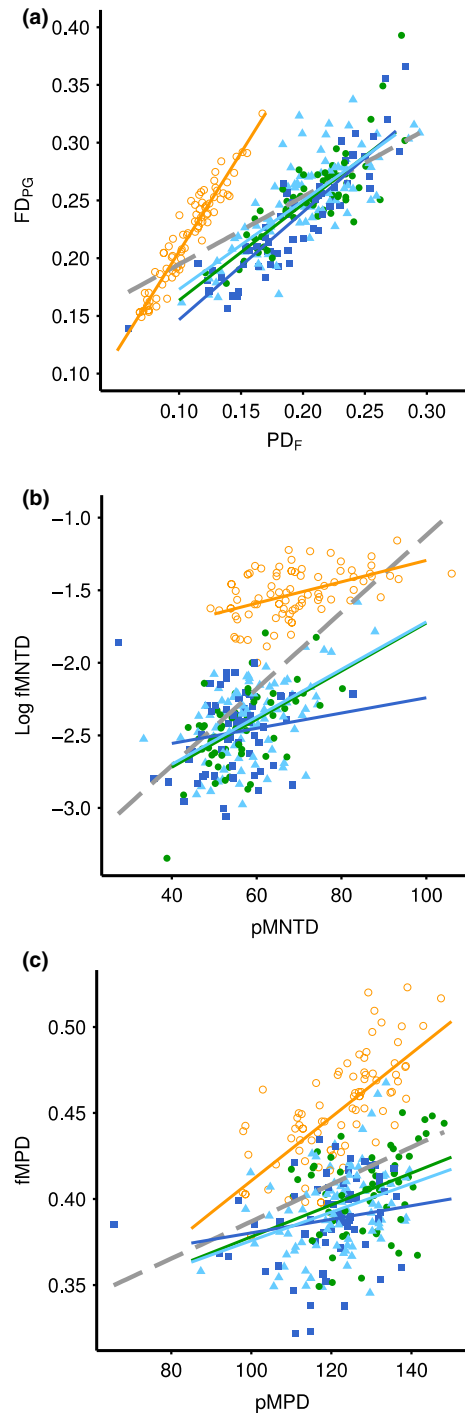
FIGURE 3 Bivariate relationships for (a) FD_{PG} with PD_F, (b) fMNTD and pMNTD, and (c) fMPD and pMPD, split by habitat type. Green circles = unlogged forest; dark blue squares = once-logged forest; light blue triangles = twice-logged forest; yellow open circles = oil palm plantations; grey dashes = overall fit. All slopes fitted show predicted values from a linear mixed model of *Functional metric–phylogenetic metric × habitat type* (the third model for each metric pair in Table 2). FD, functional diversity; PD, phylogenetic diversity; fMNTD, functional mean nearest taxon distance; pMNTD, phylogenetic mean nearest taxon distance; fMPD, functional mean pairwise distance; pMPD, phylogenetic mean pairwise distance

S4) performed better than models fitting phylogenetic metrics and habitat type combined (Table 2).

4 | DISCUSSION

Our results reveal that the marked decline in avian SR between forest habitat and oil palm plantation accompanies not only a loss in FD_{PG} but also a marked decline in PD_F. While the broadly concordant response to land-use intensification between metrics is to be expected, further exploration using metrics to determine patterns of clustering (MNTD and MPD) and dispersion (SES) revealed important differences between phylogenetic and functional community structure in response to land use, including different levels of functional redundancy and resilience among habitat types. Overall, these findings suggest that the use of phylogenetic metrics as proxies for functional metrics is neither straightforward nor unequivocal, and that a combined approach integrating both phylogenetic and functional trait data is advisable.

4.1 | Responses of phylogenetic and functional clustering and dispersion to land use

The dramatic loss in PD_F with conversion to oil palm closely echoes patterns in SR, both here and in other studies (Edwards, Magrach, et al., 2014; Edwards et al., 2011). Indeed, there is no significant difference between habitat types once SR is accounted for (SES PD_F). One notable effect is that phylogenetic tip clustering markedly decreases (pMNTD increases) after conversion to oil palm, suggesting that closely related species assemblages (e.g. understorey babblers, Timaliidae) are disproportionately reduced to just one or two representative species, as has been observed elsewhere (Prescott et al., 2016). In contrast, tree-wide phylogenetic clustering increases (pMPD decreases) markedly after selective logging, suggesting that logging has a phylogenetic filtering effect across the whole tree.

The decline in FD with oil palm conversion is relatively small given declines in SR, suggesting that species occurring in oil palm plantations remain fairly evenly dispersed across trait space. Indeed, once SR is accounted for, SES FD_{PG} is much higher in oil palm than all forest types and significantly over-dispersed compared to null expectations (Table S5). This suggests that FD_{PG} is disproportionately high in species-poor oil palm communities, with a few species dispersed across a wider breadth of functions (Figure 2 and Figure S6). Consistent with this were marked increases in fMNTD and fMPD, suggesting decreased functional clustering of species in oil palm. Increase in fMNTD confirms that concomitant loss of phylogenetic tip clustering (increased pMNTD) reflects a thinning out of functionally similar species. Similarly, the concomitant decline in fMPD and pMPD from unlogged to logged forest indicates that tighter ecological filtering accompanies tree-wide phylogenetic filtering. However, the loss and turnover of

species after conversion to oil palm drives a relaxation of tree-wide clustering (fMPD increase) leading to overdispersion of functional traits once SR is accounted for (Figure 2, Table 1 and Table S4).

4.2 | Land use and functional redundancy

Phylogenetic metric × habitat type interaction effects revealed that conversion to oil palm steepens the relationship between FD_{PG} and PD_F and (to a lesser extent) between fMPD and pMPD, supporting the idea of reduced functional redundancy and greater distinctness of species in oil palm (e.g. a greater increase in FD_{PG} relative to PD_F). Hence, the most species-rich oil palm sites have disproportionately high FD_{PG} and fMPD, and these decline more steeply with decreasing SR, PD_F and pMPD than in forest habitats (Figure 3 and Figure S5). Controlling for SR using SES resulted in consistently weaker relationships between functional and phylogenetic metrics, and the weakening or disappearance of slope differences (interactions) among habitat types. Nevertheless, significant positive relationships remain for all indices, so even accounting for SR, functionally diverse communities clearly have an underlying tendency to have greater evolutionary diversity.

4.3 | Phylogenetic and taxonomic proxies for functional metrics

We found a widespread positive association between phylogenetic and functional metrics, although with greatly varying strength. Our results indicate that PD_F strongly predicts FD_{PG} and outperforms SR as a predictor, both in explanatory power and model fit, and is, therefore, the best proxy of FD_{PG}. This finding accords with previous studies in birds (Devictor et al., 2010) and grassland plants (Flynn et al., 2011). However, examination of community clustering metrics (pMNTD and pMPD) revealed that they are relatively poor proxies for their equivalent functional metrics, and outperformed by SR, at least for fMNTD. Moreover, it is notable that habitat type is a much better predictor of functional over- or under-dispersion (SES) than any corresponding phylogenetic metric, and SR and habitat type combine to give the best prediction for fMNTD. Taken together, these results suggest that metrics for functional trait clustering (fMNTD) and dispersion (SES) tend to be more tightly coupled to the ecological conditions (i.e. habitat) driving community structure than are equivalent phylogenetic metrics. This may be because nearest taxon distance and functional dispersion are more directly dependent on ecological drivers than phylogenetic metrics, at least when functional traits have been well selected.

Focusing on species-level diversity, our results indicate that SR serves as a very strong proxy of PD_F in tropical forest bird communities, in line with findings reported in other study systems (Flynn et al., 2011; Rodrigues & Gaston, 2002; Tucker, Cadotte, Davies, & Rebelo, 2012; Tucker et al., 2017). However, SR is a relatively poor proxy of the phylogenetic clustering metrics pMNTD and pMPD, and an even weaker proxy of phylogenetic over- or under-dispersion. The very strong PD_F-SR correlation, on one hand, and the fact that SES metrics

largely control for SR, on the other hand, may partly explain the poor association with phylogenetic SES metrics. While habitat type does not compete with SR as a predictor of phylogenetic metrics overall, it performs better than SR in explaining variation in the dispersion of such metrics.

4.4 | Study limitations

Choice of traits is likely to influence FD results strongly, although broadly similar patterns of FD with land use were reported by Edwards et al. (2013) using a different trait matrix. We selected a standard set of traits with a long history of usage in avian eco-morphological studies, but future work should explore whether trait choice mediates PD–FD relationships. Moreover, given likely variation in the strength of niche conservatism influencing levels of congruence between functional and phylogenetic metrics, our finding that PD_F can serve as a proxy for FD_{PG} should be verified with additional studies before it can be generalised to avian assemblages worldwide.

4.5 | Conclusions and management implications

Our results indicate that avian assemblages in logged forests retain high levels of phylogenetic and FD, albeit with the loss of some evolutionarily distinct species, and thus support the growing consensus that protecting logged tropical forest is a conservation priority (Edwards, Magrach, et al., 2014). We also found that while bird communities in oil palm plantations contain few species, they are disproportionately diverse in phylogeny and functional traits. Some of this diversity reflects a surprisingly broad range of ecosystem functions and services, including predators of plantation pests such as rodents and invertebrates. We, therefore, recommend that plantation management supports key bird species, with measures such as artificial nest site provision, and curbing persecution for the cagebird trade. We also recommend retention of yield-neutral landscape features such as relict tree stumps, ponds, vegetated gullies and riparian zones. Nevertheless, our results highlight the overall low value of oil palm for avian biodiversity, suggesting that land-sparing remains the optimal approach to conservation in this system. They also raise the question of whether plantations support sufficient functional redundancy to withstand further environmental perturbations (Edwards, Edwards, et al., 2014; Edwards et al., 2011, 2013).

Focusing on the utility of diversity metrics, our results suggest that that PD_F is a more useful proxy for FD_{PG} than SR in cases where functional trait data are not available, and therefore, any survey results restricted to SR are likely to perform poorly in identifying areas of high FD_{PG}. However, the spatial dissimilarities we detected in phylogenetic and functional structuring demonstrate that a focus on PD alone will not safeguard all areas of maximal FD, or clades with high functional redundancy. We also note that SR and habitat type combine to give a better prediction of functional clustering (fMNTD) than any phylogenetic metric.

These findings highlight that there is no silver-bullet metric that captures all components of biodiversity value, and instead provide further evidence that a range of different biodiversity metrics are required to inform conservation decision making, at least when the target is preserving not only species but also their evolutionary history, adaptive potential and ecological function (Devictor et al., 2010; Lopez et al., 2016). We propose that, where possible, impact assessments and prioritisation exercises should rely on a combination of phylogenetic and functional trait data, perhaps integrating them using established methods (Cadotte, Albert, & Walker, 2013). Of these two key dimensions of biodiversity, quantitative functional traits are perhaps the most informative and least accessible, suggesting that the compilation and publication of ecologically relevant trait datasets is an urgent priority to facilitate effective management. However, as the performance of all biodiversity metrics may vary with context, more research is needed at the interface between phylogenetic and functional ecology across a variety of environmental and human land-use gradients.

AUTHORS' CONTRIBUTIONS

D.P.E. and R.G.D. initially conceived the study, with all authors contributing to designing the conceptual framework and analyses. D.P.E. carried out fieldwork; J.A.T. compiled trait data. P.M.C. conducted all analyses. P.M.C. and R.G.D. wrote the manuscript with substantial inputs from J.A.T. and D.P.E. All authors approved the final version of the manuscript for publication.

DATA ACCESSIBILITY

Data are made available in Dryad Digital Repository https://doi.org/10.5061/dryad.3tk7g (Chapman, Tobias, Edwards, & Davies, 2017).

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