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RESEARCH ARTICLE

Limited evidence of biodiversity spillover from forest fragments into oil palm plantations in the Amazon

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Abstract

1. Oil palm expansion is a major driver of the biodiversity extinction crisis. Emerging frontiers of oil palm development in the Amazon risk major biodiversity loss. Spillover of biodiversity from adjacent forest fragments into plantations may reduce the loss of functional and phylogenetic diversity, but the extent of this effect remains unclear.
2. We surveyed bird communities in large forest fragments and oil palm plantations in the Brazilian Amazon during the dry seasons of 2012 and 2016. We assessed the loss of avian functional and phylogenetic diversity due to forest conversion, its impact on community structure and whether the percentage of forest and proximity to fragments in oil palm points mitigate losses.
3. Compared to forest fragments, oil palm plantations exhibited lower phylogenetic and functional diversity. Conversion had a strong negative effect on functional structure, shifting communities from overdispersed to clustered, while phylogenetic structure remained largely unchanged. Trait composition also differed significantly between habitats, with shifts in the distribution of traits related to foraging behaviour, movement and flight efficiency.
4. Surrounding forest cover did not mitigate the loss of functional and phylogenetic diversity in plantations. Although bird communities closer to forest edges showed higher mean nearest taxon distance (MNTD) and its standardized value (sesMNTD), the spillover effect was weak, as indicated by the low R^2 in our models.
5. *Synthesis and applications*. Converting primary forest into oil palm plantations results in substantial biodiversity losses, highlighting the urgent need to preserve the few remaining large forest fragments in the area. Measures that enhance matrix permeability are essential to conserving the evolutionary and

functional integrity of Amazonian landscapes and mitigating the negative effects of oil palm expansion.

KEYWORDS
birds, forest cover, landscape management, patch configuration, set-asides, species composition, spillover, trait composition

1 | INTRODUCTION

The expansion of agricultural activities is one of the main drivers of the biodiversity extinction crisis and is responsible for the loss of at least 30% of species richness worldwide (Newbold et al., 2015). In the tropics, the production of oil palm (*Elaeis guineensis* Jacq.) is an important driver of deforestation (Lim et al., 2024; Meijaard et al., 2020), and its continued expansion could potentially affect 54% of threatened bird species worldwide (Meijaard et al., 2018).

One potential mechanism for reducing the negative impacts of agriculture expansion on biodiversity is the retention of set-asides, that is forested areas within an agricultural landscape (Bicknell et al., 2023). In landscapes dominated by oil palm production, evidence indicates that forest fragments support a diverse community of birds (Edwards, Edwards, et al., 2014; Edwards, Gilroy, et al., 2014; Mitchell et al., 2018), mammals (Azhar et al., 2013), ants and dung beetles (Edwards, Gilroy, et al., 2014; Edwards, Edwards, et al., 2014; Gilroy et al., 2015). Furthermore, forest fragments serve as natural repositories that conserve evolutionary history (Cardoso et al., 2021; Prescott et al., 2016a) and functionally diverse bird communities (Almeida et al., 2016; Prescott et al., 2016b) in oil palm-dominated landscapes in Colombia and Brazil. However, the extent to which forest fragments act as sources of avian communities with higher ecosystem functions or evolutionary history in oil palm plantations is less understood (Foster et al., 2011; Koh, 2008).

Biodiversity spillover is characterized by the movement of organisms from a suitable habitat, often referred to as the 'source', to a less hospitable matrix or 'recipient' habitat (Gray & Lewis, 2014; Sperry et al., 2019). This dispersal can enhance species richness and provide ecosystem services in recipient areas (Dislich et al., 2017; Lucey et al., 2014), but the extent of these benefits depends on factors such as the size and quality of the source habitat and matrix permeability (Montealegre-Talero et al., 2021). For example, oil palm trees produced larger fruits when naturally pollinated closer to forest fragments (Li et al., 2022), yet the spillover of dung beetles from set-asides to oil palm plantations in Borneo did not increase functional diversity within the plantation (Gray & Lewis, 2014). Similarly, the phylogenetic diversity of orchid bees in oil palm declines with increasing distance from forest fragments (Livingston et al., 2013). These findings underscore the lack of consensus on whether spillover improves functional and phylogenetic diversity within recipient agricultural habitats effectively, given that its effects are context dependent.

The total amount of evolutionary history (phylogenetic diversity) and the diversity and distribution of functional traits (functional diversity) in natural communities provide valuable information about the community assembly processes, community resilience (Cadotte et al., 2011; Schmitt et al., 2020) and ecosystem functioning (Cadotte, 2013). For example, more functionally diverse plant communities are capable of using resources more efficiently, ultimately presenting higher biomass, maximum diameter and height (Coelho et al., 2024). On the contrary, the phylogenetic structure of bird communities tends to change from clustered to overdispersed with increased fragmentation and landscape heterogeneity (Adorno et al., 2021; Morante-Filho et al., 2018). Therefore, quantifying functional and phylogenetic diversity is essential for conservation priorities and planning landscape management actions (Cadotte et al., 2011; Rolland et al., 2012; Thuiller et al., 2015).

In Latin America, most oil palm expansion occurs on previously used land (Furumo & Aide, 2017) mainly impacted by logging, cattle ranching and agricultural expansion (deAlmeida et al., 2020). In this context, oil palm plantations emerge as an additional contributing factor, not only displacing old-growth/secondary forests but also causing significant changes in landscape structure, for example by reducing the size and connectivity of forest remnants (da Silva et al., 2023). In Amazonia, mature oil palm plantations are characterized by trees 15 to 20 m high, spaced 5 m apart, with persistent clearance of understorey vegetation. This configuration drastically reduces habitat complexity (Foster et al., 2011), restructures landscapes and lowers carbon stocks (Almeida et al., 2020), with significant consequences for biodiversity (Almeida et al., 2016; Cardoso et al., 2021; Lees et al., 2015; Mendes-Oliveira et al., 2017). Understanding how bird communities respond to set-asides within oil palm plantations—and whether they can access production areas—is crucial for refining conservation efforts in this highly threatened region (Moraes et al., 2020). This provides essential evidence for improved landscape management strategies (Grass et al., 2019) that enhance not only the number of species present, but also the functional and phylogenetic diversity of communities in agricultural landscapes (Prescott et al., 2016a, 2016b).

In this study, we focus on the impacts that oil palm expansion and forest fragment retention have on birds in the eastern Brazilian Amazon. We addressed three main questions: (1) How much functional and phylogenetic diversity is lost when mature forest is converted into oil palm plantations? (2) Does the functional and phylogenetic structure of bird communities change following conversion? (3) Are these effects mitigated by the distance to the nearest forest fragment and/or the amount of forest cover in the landscape? We focus on birds because of the availability of complete phylogenies (Jetz et al., 2012), morphological, ecological and geographical traits database (Tobias et al., 2022) for all extant bird species. The group is also a good indicator taxon (Birch et al., 2024), providing a number of ecosystem services (Sekercioglu, 2006). By addressing these questions, we expect to demonstrate that: (1) The conversion of forest fragments into oil palm plantations drastically reduces bird functional and phylogenetic diversity; (2) alters the functional and phylogenetic structure of Amazonian bird communities; and (3) oil palm samples with higher forest cover and closer to forest fragments will present higher functional and phylogenetic diversity due to spill-over effect.

2 | MATERIALS AND METHODS

2.1 | Study area

We sampled two large-scale oil palm producers located in the eastern Amazon within the municipalities of Mojú, Tailandia and Tomé-Açu (Figure S1). The agro-industry properties contain 159,000 ha of *terra firme* primary forest set aside and 95,000 ha of oil palm plantations. The eastern Amazon region has lost more than 75% of its natural forest cover, the landscape of the region is composed of a mosaic of agriculture and pastures, agroforests, secondary forests of varying ages and primary forest fragments (da Silva et al., 2023) and has a high number of threatened species (Moraes et al., 2020). The regional climate is classified as tropical humid (*Af*) according to the Köppen system (Peel et al., 2007), with no defined winter and high levels of rainfall throughout the year. The mean annual rainfall is 2300 mm^3, the dry season normally happens from June to November and the rainy season between December and May.

2.2 | Bird sampling

In the dry seasons of 2012 and 2016, we conducted bird sampling along 22 transects (2 km long). Of these 22 transects, eleven were established within primary forest fragments (i.e. fragments larger than 1000 ha) without the presence of selective logging or fire and at least 500 m away from the edge of the forest. The remaining 11 transects were placed within a minimum distance of 2 km from each other, in mature oil palm (*Elaeis guineenses*, Jacq.) monoculture and within different distances from the forest edge. As required by Brazilian environmental law, the oil palm plantations in our study retained natural vegetation on most riverbanks; more information on the width of these riparian strips are given by Cardoso et al. (2021). To avoid registering species that did not occur in oil palm, our transects in plantation areas were never crossed by riparian reserves.

Along each transect, two experienced observers conducted a total of 220 fixed point counts. At 10 points located at 200 m intervals along each transect, observers conducted 10-min, 50 m-radius point counts (Vielliard et al., 2010). The points were visited once during the data collection process, surveys took place between 06:00 and 11:00 and were not conducted on days with continuous rain and/or strong winds. Species vocalizations not recognized during the point count survey were recorded for later identification. No fieldwork permission or ethical approval was required for this study.

2.3 | Oil palm landscape design and metrics

We used the 'patch-landscape' approach (Galán-Acedo et al., 2019; McGarigal & Cushman, 2002) to investigate the effect of landscape characteristics on bird diversity. (i) The linear distance from each point to the nearest forest fragment larger than 1000 ha (range from 0 to 6000 m). Higher values indicate higher levels of isolation, while lower values imply the opposite. (ii) Percentage of forest cover in a circular buffer of 1 km radius around the central point count of each transect (ranging from 1% to 37%), resulting in a total of 22 buffers. Higher values suggest greater levels of forest cover, while lower values suggest the opposite. This buffer scale was adopted because it represents an important scale for different ecological processes in birds (Birch et al., 2024), trees (Matos et al., 2019) and bats (Put et al., 2019). For detailed information on how the metrics were obtained, see Supporting Information: Methods.

2.4 | Phylogenetic construction and diversity metrics

To calculate phylogenetic distances, we obtained 500 phylogenetic trees from the global phylogenetic tree of birds BirdTree—250 trees based on the Hackett backbone and 250 trees based on the Ericson backbone (Jetz et al., 2012). Each tree represents hypothetical species evolutionary relationships. Some recorded bird species were absent from BirdTree or had updated nomenclature; in these cases, we considered the closest relative species available (Table S1).

We computed six abundance-weighted phylogenetic diversity indices for our communities:

1 The phylogenetic diversity index (PD) measures the total evolutionary history by summing the branch lengths from the root to the tips of the phylogenetic tree for all species present in a community (Faith, 1992).
2 The Mean Pairwise Distance (MPD) calculates the average phylogenetic distance between all pairs of species within a community, highlighting the longer branches within the tree (Webb, 2000).
3 Mean Nearest Taxon Distance (MNTD) refers to the average phylogenetic distance between each species and its closest nonconspecific relative, providing a terminal measure of phylogenetic relationships among co-occurring species (Webb, 2000).
4 to 6 The standardized effect sizes (ses) of PD (sesPD), MPD (sesMPD) and MNTD (sesMNTD) evaluate the phylogenetic relatedness of species within each sample while controlling for

species richness (Swenson, 2014). These values were obtained using the formula: $X_{ses}=(X_{obs}$ mean $(X_{null}))/SD\ (X_{null})$, X_{obs} corresponds to the observed value, the mean (X_{nul}) is the mean of null communities with equivalent species richness and (sdX_{null}) the standard deviation of 999 random values. Positive ses values indicate higher than expected PD, MPD or MNTD values for a given richness, suggesting phylogenetic overdispersion. On the contrary, negative values indicate phylogenetic clustering. Null communities were created using an independent swap algorithm, which maintains species richness by randomly selecting species from the regional pool (Gotelli, 2000).

We calculated PD, MPD and MNTD metrics, along with null model randomizations using the *picante* package (Kembel et al., 2010) within the R environment (R Core Team, 2020). To address the phylogenetic uncertainty, the mean values for each diversity metric were calculated from 500 phylogenetic trees for each sample point.

2.5 | Functional diversity metrics

We built a functional trait matrix composed of seven functional morphological characteristics Culmen length, beak width and depth, tarsus length, tail length, body mass and hand-wing index (HWI)—obtained for each species from the AVONET database (Tobias et al., 2022). These traits are typically associated with diet, habitat preferences and dispersal ability and are directly related to ecosystem services (Luck et al., 2012; Tobias et al., 2022). Prior to functional analysis, we accounted for the influence of differences in species body mass on beak length, beak width, beak depth, tail length and tarsus length, which induce allometry in these traits. This was achieved by dividing each trait value by the cube root of the body mass of the respective species (West et al., 1997).

We estimate functional diversity using the same indices used for phylogenetic diversity in the picante package. However, instead of a phylogenetic tree, we used a functional dendrogram to calculate functional indices. To do this, we used the trait matrix to calculate a dissimilarity matrix using Euclidean distance and then used the UPGMA clustering approach to construct the functional dendrogram. The six functional diversity indices are referred to as FD, MPD.func, MNTD.func and their respective standardized effect sizes. Furthermore, we assessed the trait composition through a principal component analysis (PCA) of the community-weighted mean (CWM) for each functional trait (Supporting Information: Methods).

2.6 | Statistical analyses

To compare the metrics of phylogenetic and functional diversity between habitats (that is, large primary forest fragments and oil palm plantations), we performed generalized linear mixed effects models (GLMM) at the point count level. By using GLMMs, we addressed potential violations of independence that could arise from the spatial clustering of sample points (Zuur et al., 2009). The habitat type was included in the model as a fixed effect, while the transect was included as a random effect. GLMM models were built using the function 'lmer' in the package *lmerTest*, with Gaussian error and an identity link (Kuznetsova et al., 2017). Functional Diversity (FD) and Phylogenetic Diversity (PD) were highly correlated with species richness ($R=0.78$, $p<0.001$; $R=0.94$, $p<0.001$, respectively, Figures S2 and S3), therefore, we did not test models for species richness.

We then fit GLMM to evaluate how landscape composition and patch configuration metrics affect the phylogenetic and functional diversity of birds in oil palm plantations. We tested multicollinearity between predictor variables using Spearman correlation analysis. The proportion of forest cover and distance to forest fragments exhibited a low correlation index (<0.30, Figure S4), and for this reason, both variables were included in the model as fixed effects. We used the 'transect' as a random effect in our model. The amount of variation explained by the fixed and random effects of each model was obtained by the values of R^2 from the package *rsq* in R (Zhang, 2023). Furthermore, we tested spatial autocorrelation in the model residuals using Moran's *I* statistic using the *spdep* package (Bivand & Piras, 2015) with 1000 repetitions. The residuals were checked for normality and homoscedasticity for all fitted models. All statistical analyses were performed in R, version 4.0.2 (R Core Team, 2020).

3 | RESULTS

We registered 2055 individuals of 224 bird species, with 187 species occurring in forest fragments and 53 species in oil palm plantations; 17 species occurred in both habitats; they were predominantly generalists and associated with the edge of the forest (Figure 1 and Figure S5). The CWM showed that forest fragments and oil palm plantation presented distinct trait composition (Pseudo-$F=42.47$, $p=0.001$, Figure S6). We did not detect spatial autocorrelation for any of the residuals for phylogenetic diversity and functional diversity models (Moran's *I* test: all $p>0.05$).

3.1 | Effects of habitat on phylogenetic and functional diversity

Including habitat type as a fixed effect improved the fit for our PD, MPD and MNTD, as well as sesPD models (Table S2). Oil palm plantations exhibited significantly lower phylogenetic richness (PD, $p<0.001$), evolutionary diversity of older groups (MPD; $p<0.0001$) as well as lower diversity of closely related species (MNTD; $p<0.05$) when compared to forest fragments (Figure 2a,c,e). Of the phylogenetic structure metrics, only sesPD differed significantly between habitats, with lower values in oil palm plantations than in forest fragments ($p<0.0001$, Figure 2b).

Including habitat type as a fixed effect improved the model fit for most functional diversity metrics (Table S2). Oil palm plantations

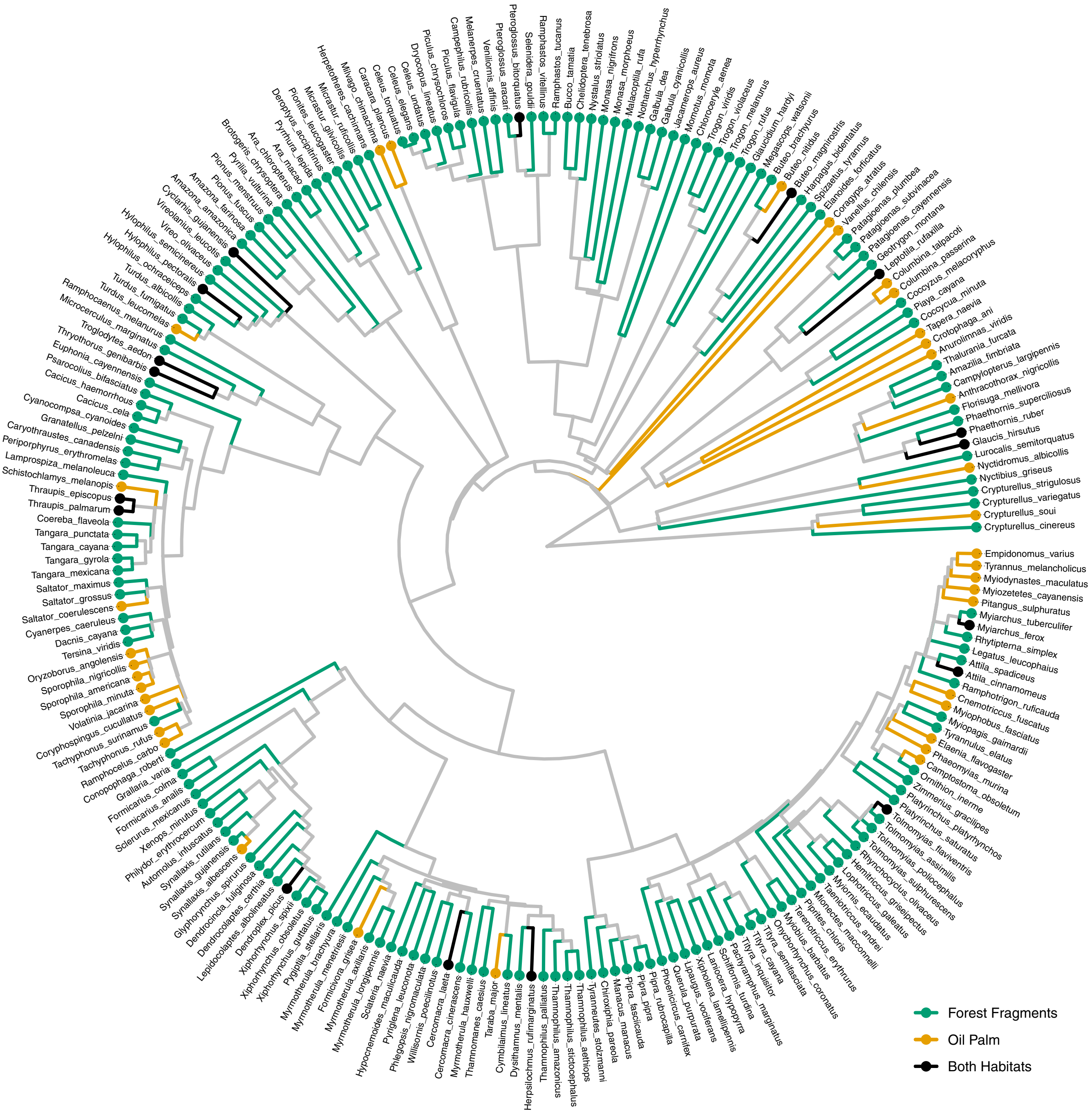

FIGURE 1 Circular phylogenetic tree of the bird community found in forest fragments (green), oil palm plantations (yellow) and in both habitats (black). The phylogenetic distances were plotted based in Jetz et al. (2012).

had significantly lower values for all six functional diversity metrics ($p < 0.001$ in all cases, Figure 3).

3.2 | Effects of landscape metrics on phylogenetic and functional diversity in oil palm

Our models showed that the distance to the nearest forest fragment has a significant impact on the diversity of closely related species (MNTD) and its standardized metric (sesMNTD) within oil palm (Table 1). We observed that MNTD and sesMNTD decrease in oil palm samples far from forest fragments (Figure 4). However, our models presented a low explanation power, explaining 25.73% (R^2 fixed = 10.73%, R^2 random = 15.00%) of the variance of MNTD and 4.45% of sesMNTD (R^2 fixed = 4.45%, R^2 random = 0). We then removed outliers post hoc and re-analysed the models, but our results only marginally changed ($p = 0.054$ for MNTD and $p = 0.060$ for sesMNTD; Figure S7), with no impact on the explanation of the models. The distance to the nearest forest fragment had no impact on phylogenetic richness (i.e. PD and sesPD) or the mean pairwise distance (i.e. MPD and sesMPD). The

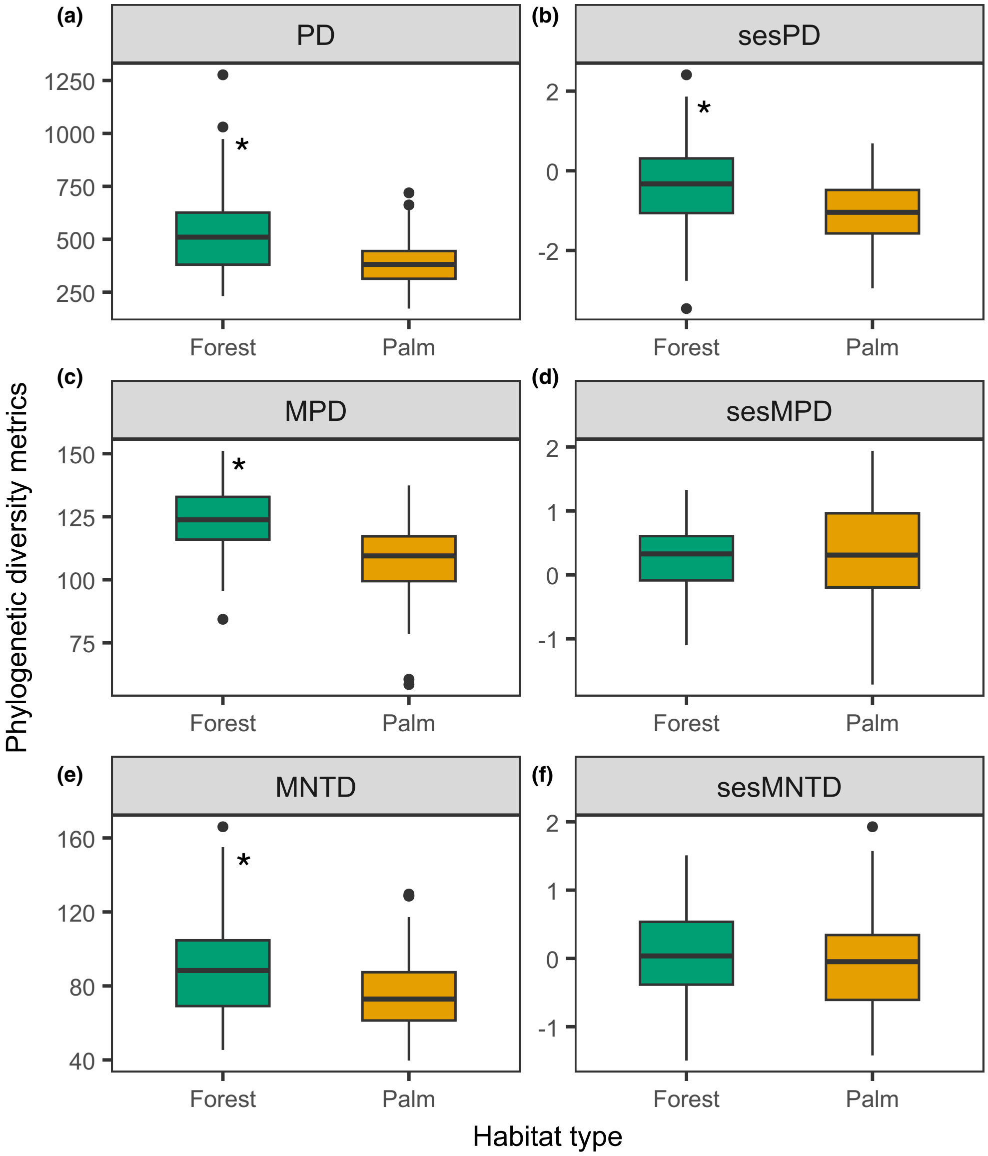

FIGURE 2 Habitat effects on phylogenetic diversity measures of bird communities in the eastern Amazon. PD, Phylogenetic diversity (a); sesPD, standard effect size of PD (b); MPD, mean pairwise distance (c); sesMPD, standard effect size of MPD (d); MNTD, mean nearest taxon distance (e) and sesMNTD, standard effect size of MNTD (f). The middle line represents the median, while the lower and upper bounds of the box plots represent the first and third quartiles, respectively; vertical lines show the minimum and maximum values, and the individual points represent outliers. Asterisks (*) indicate a significant difference ($p < 0.05$).

distance to the nearest forest fragment did not significantly affect any of the six functional metrics in oil palm plantations (Table 2). Landscape composition had no significant effect on any phylogenetic or functional diversity metric (Tables 1 and 2).

4 | DISCUSSION

Our results confirm that the conversion of Amazonian Forest into oil palm plantations leads to drastic losses in bird functional and phylogenetic diversity. While this loss translated into significant changes in functional structure, the phylogenetic structure of bird communities remained largely unchanged. The percentage of forest cover within agricultural landscapes did not improve functional diversity nor any metric based on deep phylogenetic relationships in oil palm plantations. However, we found that landscape configuration might have a marginal influence on phylogenetic diversity and structure, as indicated by a decrease in mean pairwise distance (MNTD and sesMNTD) at oil palm sites farther from the forest edge. Although large forest fragments serve as reservoirs of evolutionary history and ecosystem functions, we found little evidence of substantial spillover of functional and phylogenetic diversity into the oil palm-dominated matrix. This suggests that oil palm plantations in Amazonia remain largely inhospitable to most bird species, despite the presence of riparian reserves and adjacent forest fragments within plantation sites.

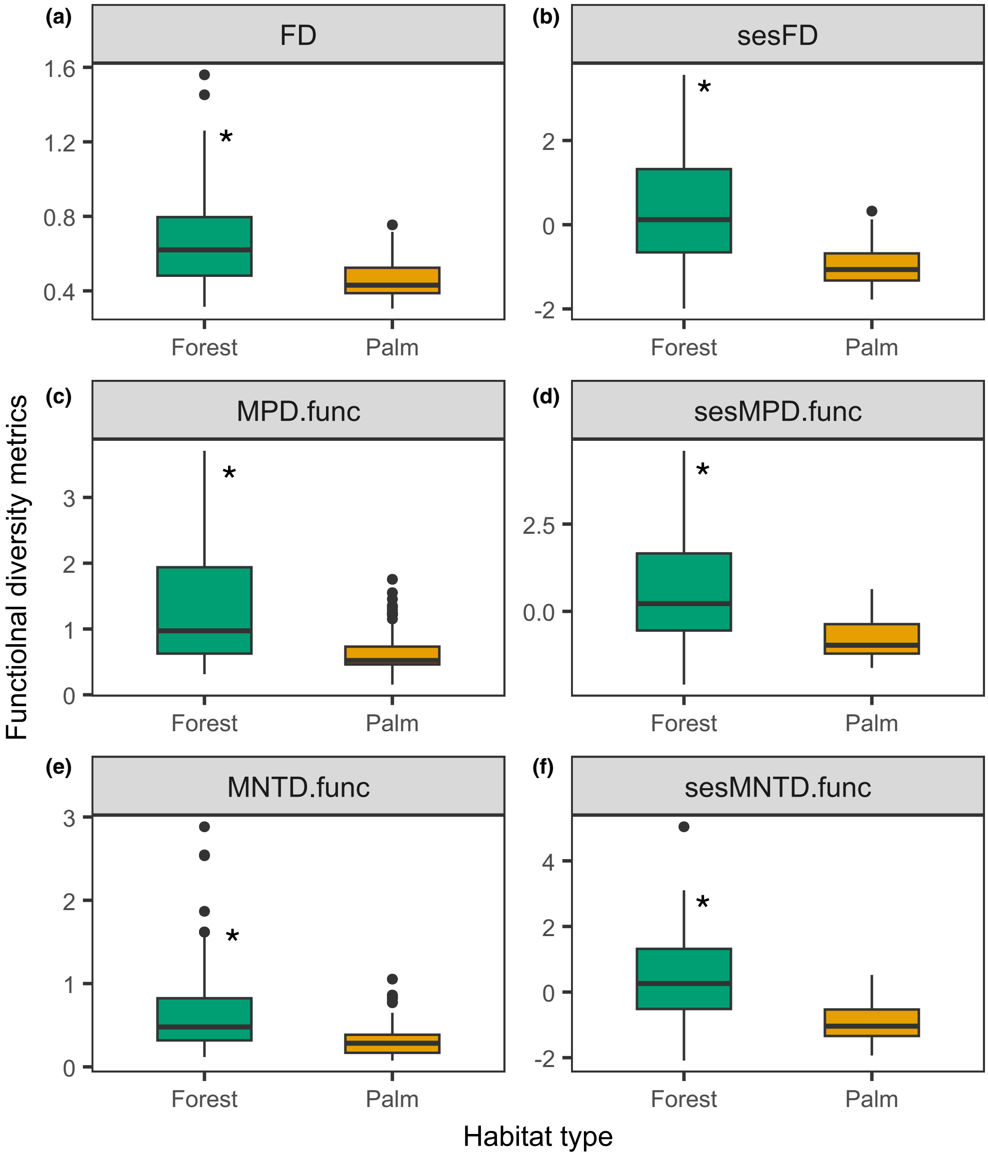

FIGURE 3 Habitat effects on functional diversity metrics of bird communities in the eastern Amazon. FD, Functional Diversity (a); sesFD, standard effect size of FD (b); MPD.func, mean functional distance (c); sesMPD.func, standard effect size of MPD.func (d); MNTD.func, mean functionally nearest species distance (e)and sesMNTD.func, standard effect size of MNTD.func (f) The middle line represents the median, while the lower and upper bounds of the box plots represent the first and third quartiles, respectively; vertical lines show the minimum and maximum values, and the individual points represent outliers. Asterisks (*) indicate a significant difference ($p < 0.05$).

4.1 | Effects of habitat in phylogenetic and functional diversity

The conversion of forest into oil palm plantations strongly reduced the phylogenetic diversity (PD, MPD and MNTD) of bird communities in Amazonia. Our findings corroborate other studies that show the high value of forest compared to oil palm (Cardoso et al., 2021; Edwards et al., 2013; Mitchell et al., 2018; Morante-Filho et al., 2018; Prescott et al., 2016a, 2016b), and underscore the importance of protecting forests, especially in larger reserves (Edwards et al., 2010; Gibson et al., 2011).

The forest fragments exhibited higher sesPD values (standardized values of the total phylogenetic history in the community) than the oil palm, but the phylogenetic composition of the older lineages (sesMPD) and younger clades (sesMNTD) did not differ between the two habitats. Standardized values of phylogenetic diversity provide insights into patterns of community structure (Arroyo-Rodríguez et al., 2012), and no difference in sesMPD and sesMNTD between habitats indicates that oil palm has a homogeneous impact on community phylogenetic history instead of targeting entire clades (Adorno et al., 2020; Arroyo-Rodríguez et al., 2012). Studies suggest that communities in highly fragmented areas can show a compensatory dynamic in phylogenetic structure, such that bird communities retain phylogenetic structure comparable to forest remnants despite losses in phylogenetic diversity (Arroyo-Rodríguez et al., 2012; Morante-Filho et al., 2018). In this sense, we

TABLE 1 Estimated values, standard error and *t* value of the generalized mixed-effect model for the landscape metrics on phylogenetic diversity of bird community on oil palm points.

Response variable	Predictors	Estimate	Std. error	df	*t* value	*p*	R^2 fixed; random
PD	(Intercept)	387.13	23.789	8.355	16.27	<0.0001***	0.006; 0.43
	Distance from forest (m)	12.128	20.965	15.17	0.578	0.571	
	Proportion of forest (%)	−5.024	23.634	8.635	−0.21	0.837	
sesPD	(Intercept)	−0.983	0.1134	8.24	−8.67	<0.0001***	0.05; 0.11
	Distance from forest (m)	−0.1721	0.112	9.909	−1.54	0.156	
	Proportion of forest (%)	0.045	0.1142	8.609	0.394	0.703	
MPD	(Intercept)	107.56	2.46	8.106	43.72	<0.0001***	0.03; 0.21
	Distance from forest (m)	2.089	2.357	10.82	0.886	0.395	
	Proportion of forest (%)	1.092	2.462	8.411	0.444	0.668	
sesMPD	(Intercept)	0.3232	0.1195	8.154	2.705	0.0264*	0.02; 0.18
	Distance from forest (m)	−0.0275	0.1158	10.45	−0.24	0.8172	
	Proportion of forest (%)	0.09	0.1198	8.478	0.751	0.4729	
MNTD	(Intercept)	75.885	3.2285	8.055	23.51	<0.0001***	0.10; 0.15
	Distance from forest (m)	−6.8284	3.1456	10.13	−2.17	**0.0548***	
	Proportion of forest (%)	0.1439	3.2398	8.386	0.044	0.9656	
sesMNTD	(Intercept)	−0.0741	0.0717	98	−1.03	0.304	0.045; 0
	Distance from forest (m)	−0.1577	0.0729	98	−2.16	**0.033***	
	Proportion of forest (%)	−0.0253	0.0729	98	−0.35	0.73	

Note: All models include the transect as a random factor. Symbol (*) and boldface indicate a significant difference (*p<0.05, ** p< 0.001, ***p< 0.0001).

Abbreviations: MNTD, mean nearest taxon distance; MPD, mean pairwise distance; PD, Phylogenetic diversity; sesMNTD, standard effect size of MNTD; sesMPD, standard effect size of MPD; sesPD, standard effect size of PD.

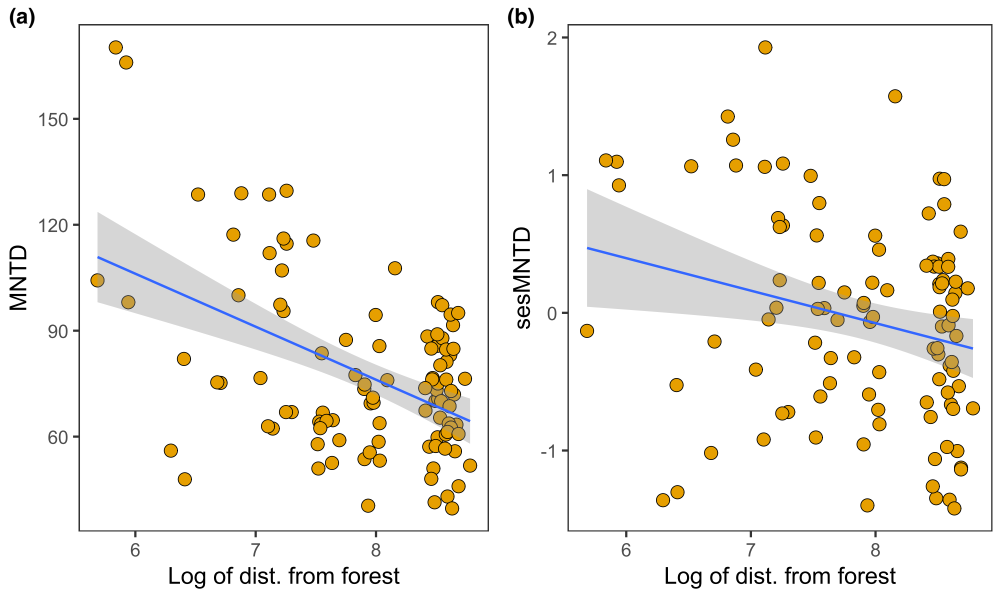

FIGURE 4 Relationships between phylogenetic and functional diversity metrics and the log of the distance to the nearest forest fragment (m) selected by the Generalized Mixed Models. MNTD, mean nearest taxon distance (a) and sesMNTD, standard effect size of MNTD (b).

found that oil palm impacts in the phylogenetic structure of bird communities is not directional, affecting the whole phylogenetic tree without altering its width.

Oil palm plantations strongly reduced the functional diversity of the bird communities (FD, MPD.func and MNTD.func), and changed the functional structure (sesFD, sesMPD.func, sesMNTD.func) from overdispersed in forest fragments to clustered in oil palm plantations. This change in the functional structure of the bird community suggest the replacement of forest by oil palm plantations can cause the loss of entire functional groups. Our findings mirror the results

TABLE 2 Estimated values, standard error and *t* value of the generalized mixed-effect model for the landscape metrics on functional diversity of bird community on oil palm points.

Response variable	Predictors	Estimate	Std. error	*t* value	*p*	R^2 fixed;random
FD						0.02; 0.28
(Intercept)	0.459197	0.019161	8.102702	23.97	<0.0001***	
Distance from forest (m)	0.016883	0.017935	11.76257	0.941	0.365	
Proportion of forest (%)	−0.003901	0.019126	8.388429	−0.204	0.843	
sesFD						0.06; 0.12
(Intercept)	−0.972	0.07012	8.36054	-13.86	<0.0001***	
Distance from forest (m)	−0.10159	0.06894	10.19858	−1.474	0.171	
Proportion of forest (%)	0.03667	0.0705	8.72242	0.52	0.616	
MPD.func						0; 0.08
(Intercept)	0.653041	0.04286	7.791093	15.24	<0.0001***	
Distance from forest (m)	0.031332	0.042712	9.132132	0.734	0.482	
Proportion of forest (%)	−0.008475	0.04324	8.166085	−0.196	0.849	
sesMPD.func						0.02; 0.18
(Intercept)	0.32321	0.1195	8.15393	2.705	0.0264*	
Distance from forest (m)	−0.02745	0.11577	10.45013	−0.237	0.817	
Proportion of forest (%)	0.08999	0.1198	8.47762	0.751	0.473	
MNTD.func						0.003; 0.05
(Intercept)	0.323864	0.023926	7.997916	13.54	<0.0001***	
Distance from forest (m)	−0.007309	0.02402	9.191756	−0.304	0.768	
Proportion of forest (%)	0.008645	0.024197	8.401267	0.357	0.73	
sesMNTD.func						0.07; 0.16
(Intercept)	−0.91514	0.09477	8.23925	−9.656	<0.0001***	
Distance from forest (m)	−0.12375	0.09219	10.41318	−1.342	0.208	
Proportion of forest (%)	0.06521	0.09508	8.57321	0.686	0.511	

Note: All models include the transect as a random factor. Symbol (*) indicate a significant difference (*$p < 0.05$, **$p < 0.001$, ***$p < 0.0001$).
Abbreviations: FD, Functional diversity; MNTD.func, mean functionally nearest species distance (e); MPD.func, mean functional distance (c); sesFD, standard effect size of FD; sesMNTD.func, standard effect size of MNTD.func; sesMPD.func, standard effect size of MPD.func.

of other studies focusing on birds in Amazonia (Almeida et al., 2016), Colombia (Prescott et al., 2016b) and Malaysia (Azhar et al., 2013; Edwards et al., 2013), and more broadly, of functional losses for dung beetles (Davies et al., 2021; Edwards, Edwards, et al., 2014; Edwards, Gilroy, et al., 2014) and ants (Senior et al., 2013). These results suggest a loss of species and functional strategies, which could be attributable to environmental filtering effects (Luck et al., 2013) driven by changes in resources, structure and microclimate of oil palm plantations (Dislich et al., 2017) that reduce the ability of sensitive species to inhabit plantation habitats (Lees et al., 2015).

In fact, the filtering effect of oil palm plantations can be observed by the distinct composition of functional traits that reflects differences in resource use by birds in the two habitats (Figure S6). In our study, the habitat-related differences in trait composition were evident across all traits, including body size, beak dimensions, tarsus, tail length and hand-wing index, traits related to foraging behaviour, movement and flight efficiency (Luck et al., 2012; Tobias et al., 2022). Forested areas are capable of supporting large birds that depend on a greater amount of resources and large prey (Barros et al., 2022; Luck et al., 2012), while disturbed habitats are, in general, positively associated with birds of small body size and small beaks, the latter being a characteristic of granivorous bird species frequently observed in monoculture areas (Barros et al., 2021; Vaccaro & Filloy, 2022). Ultimately, the loss of functional groups caused by the replacement of forest can have negative implications for food web stability, invasion resistance and ultimately ecosystem functioning (Dislich et al., 2017; Foster et al., 2011; Sekercioglu, 2006).

4.2 | Effects of landscape metrics on phylogenetic and functional diversity in oil palm

The distance to the nearest forest fragments did not improve the functional diversity (FD, sesFD, MPD.func, sesMPD.func, MNTD.func and sesMNTD.func) nor most of phylogenetic diversity metrics (PD, sesPD, MPD and sesMPD) within oil palm plantations points. Retaining forest patches close to production areas can increase the species richness of mammals (Mendes-Oliveira et al., 2017; Pardo et al., 2018), birds, dung beetles (Barros et al., 2019; Gilroy et al., 2015; Lees et al., 2015), ants and butterflies (Lucey et al., 2014; Lucey & Hill, 2012) in oil palm plantations through spillover. In our study, only ~10% of the species occurred in both habitats (17 species, Figure 1), which were predominantly generalists species (Tobias et al., 2022), and their abundance was not directly associated with the distance from the forest fragments (Figure S5) or the percentage of forest cover within 1 km buffer (Tables 1 and 2).

The lower number of shared species between habitats may reflect the low permeability of oil palm plantations: one of the main factors determining the spillover is the matrix permeability (Montealegre-Talero et al., 2021). Previous studies conducted in the study area suggest that insectivorous birds are unlikely to cross oil palm plantations when translocated from forest fragments to nearby riparian reserves (Knowlton et al., 2017), reinforcing the low permeability of this environment. In contrast, Prescott et al. (2016a, 2016b) found that the spillover of edge-tolerant species was related to the percentage of forest cover and was reflected in the phylogenetic and functional richness of birds found in oil palm plantations in Colombian Llanos.

The proximity of oil palm points to the forest fragments increased the MNTD and sesMNTD compared to the oil palm points far from the forest fragments. These results suggest that the bird community in oil palm closer to the forest fragments are more phylogenetically diverse, composed by both species typical from forest edge and from disturbed areas. In our study, we sampled oil palm points at a range of distances to forest fragments (0 to 6000 m from the forest edge), yet only one species (*Cercomacra laeta*) occurred exclusively in oil palm points closer to forest—within 600 m of the forest edge. Additionally, all hummingbirds registered in oil palm (*Phethornis ruber*, *Glaucis hirsutus* and *Anthracothorax nigricollis*) were found within 1500 m from the forest edge, and these species were probably driving the differences in MNTD and sesMNTD found in our study. In the Atlantic Forest, Adorno et al. (2020) found a positive relationship between nearest taxon distance (MNTD and sesMNTD) and landscape heterogeneity; this result might reflect the spectrum of species associated with different habitats and land-use intensity co-occurring. Similarly, in our study, oil palm points closer to the forest edge could present higher MNTD and sesMNTD through the occurrence of both species from the forest edge and oil palm plantations, although the low R^2 suggests this effect is weak.

The percentage of forest cover in the landscape had no impact on any metrics of phylogenetic and functional diversity despite the fact that many studies report that the amount of forest cover in oil palm plantations influences taxonomic, phylogenetic and functional diversity (Carvalho et al., 2018; Gilroy et al., 2015; Mendes-Oliveira et al., 2017; Prescott et al., 2016a, 2016b). A possible explanation for the absence of a significant effect of landscape composition in our diversity metrics could be due to the fact that forest cover ranged from 1% to 37% in our oil palm landscapes. Evidence suggests that landscapes with less than 60% forest cover led to population extinction thresholds (Driscoll et al., 2013; Lindenmayer et al., 2005; Radford et al., 2005). For example, Pardo et al. (2018) found that oil palm landscapes with less than 55% forest cover exhibit an impoverished mammalian community. However, Birch et al. (2024) showed that wildlife-friendly agricultural landscapes failed to support forest-dependent species, independent of the amount of forest remnants in the surroundings. This result highlights that the preservation of set-asides within agricultural landscapes has only a limited benefit to the conservation of Amazonian wildlife.

In conclusion, our study shows that the amount of forest cover around plantation areas only minimally reduces the negative impacts of Amazonian oil palm plantations on birds. Therefore, while there is some spillover of phylogenetically related species in oil palm sites closer to the forest, these species did not affect the functional diversity of plantation areas. Converting forests to oil palm drives substantial losses in the majority of phylogenetic and functional diversity metrics of bird communities, indicating the need to conserve the biodiversity present in the few remaining fragments in the region. Therefore, bird communities could benefit from measures that increase landscape heterogeneity, permeability of oil palm plantations and connectivity of forest fragments, such as restoring forested riparian corridors and second-growth forest. Such measures could support the maintenance of healthy forest fragments and might increase inter-habitat movements of a larger range of species (Arroyo-Rodríguez et al., 2020; Grass et al., 2019).

AUTHOR CONTRIBUTIONS

David P. Edwards, Maira R. Cardoso, Fabio A.R. Matos and Marcos P. D. Santos conceived the ideas and designed the methodology. Maira R. Cardoso, Sara M. Almeida and Marcos P. D. Santos collected the data. Maira R. Cardoso and Sara M. Almeida analysed the data. Maira R. Cardoso led the writing of the manuscript. All authors contributed substantially to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.c59zw3rm6 (Cardoso et al., 2025).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Map of study area.

Figure S2. Spearman correlation between Functional diversity metrics and species richness (sp_rich)—FD, functional diversity; MNTD.func, mean functionally nearest species distance; MPD.func, mean functional distance; sesFD, standard effect size of FD; sesMNTD.func, standard effect size of MNTD.func; sesMPD.func, standard effect size of MPD.func. Significance level: $^{**}p < 0.001$; $^{***}p < 0.0001$.

Figure S3. Spearman correlation between Phylogenetic diversity metrics and species richness (spe_rich). MNTD, mean nearest taxon distance; MPD, mean pairwise distance; PD, phylogenetic diversity; sesMNTD, standard effect size of MNTD; sesMPD, standard effect size of MPD; sesPD, standard effect size of PD. Significance level: $^{**}p < 0.001$; $^{***}p < 0.0001$.

Figure S4. Spearman correlation between landscape configuration variables. Dist_fonte.m. = distance to the nearest forest fragment; Pland_for. = proportion of forest cover in 1 km buffer. $^{**}p \leq 0.01$.

Figure S5. Abundance of bird species registered in a gradient of distance from the forest edge. Dots colour and size indicate higher abundance.

Figure S6. Principal Component Analysis (PCA) of the community-weighted traits mean (CWM) showing the relationship between composition of traits and habitats (forest fragments and oil palm plantations).

Figure S7. Relationships between phylogenetic diversity metrics and the log of the distance to the nearest forest fragment (m) selected by the Generalized Mixed Models. MNTD, mean nearest taxon distance (a) and sesMNTD, standard effect size of MNTD (b).

Table S1. Birds species registered in forest fragments and oil palm points in the eastern Amazon that are absent from the BirdTree phylogeny. These species were substituted by either its corresponding nomenclature or the closest relative.

Table S2. Results of generalized mixed-effect models for the effect of habitat type on phylogenetic and functional diversity.

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