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Avian Functional Diversity across Agroforest Landscape Tree-cover Gradient in Cameroon: Implications for the Conservation of Avian Communities

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Declaration

This thesis is the result of my own work with the following help:

I was provided with the Cameroonian bird point count data from Luck Powell and Crinan Jarrett, who carried out the fieldwork. Whereas the bird morphometric trait data was supplied by Joseph Tobias. I did all the clearing and analysis of the data and modelling with support from Adam Devenish.

Abstract

Tropical forests are among the most diverse and complex ecosystems on Earth. They provide critical habitats for biodiversity, and a wide range of ecosystems services that are important to human well-being. Loss of forest, through the conversion to agricultural land is a major global driver of biodiversity loss and threatens integrity of our environment. Agroforestry systems have been suggested as a viable wildlife friendly strategy to reconcile human needs while conserving a significant portion of tropical forest diversity. Here, we investigated the effects of landscape tree-cover change on avian assemblages in agroforestry cocoa farms in Cameroon, Africa. By looking at the impacts on avian species richness and functional diversity across a range of trophic guilds, we found evidence to suggest that insectivores and frugivores are sensitive to landscape tree-cover change. With both avian guilds showing significant declines in species richness and functional diversity in more disturbed and lower tree-cover landscapes. By contrast, granivores and omnivores were found not to be significantly impacted by landscape tree-cover change. Additionally, functional redundancy increased with increasing insectivores and omnivores species richness, a trend which was reversed in granivores. Overall, while there was some variation across the different trophic guilds, high landscape tree-cover cocoa farms (50-70%) scored the highest in terms of species richness and functional redundancy, suggesting that these systems may be able to maintain local avian biodiversity to some degree.

Keywords: *avian community, functional diversity, landscape tree-cover, trophic niche, agroforest*

Contents

1. Introduction

The growing global demand for natural resources, driven by rapid population growth and changing consumption patterns is threatening the Earth's ecosystems and their life-supporting services (Godfray *et al*., 2010). Human disturbance through urbanisation can everlastingly damage the natural environment like habitat fragmentation and consequently cause a severe threaten toward wildlife (Markovchick-Nicholls *et al*., 2008). Land-use change, such as conversion of forests to agriculture, is recognised as one of the leading drivers of global biodiversity loss (Sala *et al*., 2000). Besides contributing to a substantial loss of wildlife (Green *et al*., 2005), the conversion of forest to agricultural land has been shown to negatively affect human well-being by reducing the availability of ecosystem services, such as natural pest control and pollination (Foley *et al*., 2005; Cardinale *et al*., 2012). Mitigating the effects of habitat loss and land-use change, so as to manage the land in such a way that it works for both humans and wildlife requires a more detailed understanding of the consequences of land-use change for ecosystem functioning.

Conversely, not all land-use systems have the same negative consequence for the local environment. Rather, some land-use systems may help to meet the needs of humans (e.g. food and energy), while at the same time conserving a significant proportion of the local biodiversity. For example, amphibians and reptiles which were found to be negatively associated with increased cultivation, were less impacted in plantations, which share some structural aspects with natural forests (Trimble and van Aarde, 2014). Likewise, Hervé B. and Vidal (2008) found that the diversity, biomass, and carbon storage potential in cocoa plantation in Cameroon declined with higher land-use intensity, but more diverse species were found in traditional cocoa plantation with smallholder farming systems. As such, a mixed land use type may benefit both biodiversity and human activities. Furthermore, the influence on local species biodiversity can also be determined by specific farming strategies. For example, Maitima *et al*. (2009) found that croplands in areas with less tree-cover enhanced the local biodiversity due to the fact that it attracted birds with increased tree cover and recovered soil quality with conjoint livestock rearing. Therefore, farm management, in some cases, can be another approach to enhance the biodiversity and replenish the loss. Since the biodiversity change appears to be the conspicuous response to the impact on ecosystem processes (Hooper *et al*., 2012), the trade-off between increasing human desire for natural resources and conservation for ecosystem should be investigated based on wildlife communities.

Tropical forest, despite covering less than 10% of the Earth's land surface, support at least two-thirds of the world's biodiversity (Bradshaw, Sodhi and Brook, 2009). These biodiverse regions, especially in Africa, are being increasingly threatened by a range of human activities, such as agricultural development (Lambin, Geist and Lepers, 2003), human settlements (Maitima *et al*., 2009), logging and hunting (Ahrends *et al*., 2010; Effiom *et al*., 2013). To date, while numerous studies have been conducted in Africa to assess the impact of land-use change on biodiversity. Agroforests in Africa, which are able to conserve organisms with abundant tree cover compared with croplands, have attracted the attention of ecologists. Previous studies demonstrated

that agroforestry system in Africa could encourage carbon storage and reduce soil degradation (Dixon *et al*., 1994). Agroforest can be a shelter for organisms escaping from the condition of insensitive agriculture activities (Tadu *et al*., 2014). Therefore, evaluations for agroforest may be a practical way to achieve conservation in Africa. Also, determining the critical point of biodiversity can be necessary to sustainably achieve the maximum benefit, as a stable ecosystem would be maintained with more precious biodiversity (Ibarra and Martin, 2015).

Avian communities, which include a variety of diets and foraging strategies, play an integral role in many ecological processes (Sekercioglu, 2006). Birds not only provide services important to maintaining ecological function (e.g. seed dispersal), but also many ecosystem services which are a benefit to human society. For example, insectivorous birds can provide pest control services in agriculture land (Philpott *et al*., 2009), whereas granivores may be regarded as a pest in some croplands (Sekercioglu, 2012). However, bird assembles in Africa are being increasingly threatened due to deforestation (de Coster, Banks-Leite and Metzger, 2015). Previous studies that have looked at the effect of land-use change on bird assemblages have tended to focus on measures of species richness and abundance; however, these indices alone often fail to capture the true extent of the impact. More recently, measures of functional diversity are being used to estimate the ecological niches of bird assembles. Based on a multidimensional space characterised by functional traits, these indices provide a potentially more robust means to understand the impacts of land-use change on avian communities (Petchey, O'Gorman and Flynn, 2009; Pigot, Trisos and Tobias, 2016). Additionally, other information like functional redundancy can be assessed by combining the functional diversity and species richness (Cadotte, Carscadden and Mirotchnick, 2011). In a complex bird community, the responses to the changed environment may differ in functional groups, which requires an application of different functional indices (Hidasi-Neto, Barlow and Cianciaruso, 2012)

Despite our increased understanding of the impacts of land-use change on avian diversity, relatively few studies have been conducted in Cameroon. This paper aims to fill this knowledge gap by investigating the effects of landscape tree-cover change on the species richness and functional diversity of avian assembles in the agroforest and natural forest systems of Cameroon. In addition, by linking the functional diversity indices with species richness, we also assess the functional redundancy across different trophic guilds, which may be associated with particular ecosystem functions. It is hypothesised that both species richness and functional diversity may decline with dwindling landscape tree cover, and the correlations may differ across the different avian trophic guilds. Also, we suppose that more redundant functional traits may be found in high tree-cover sites. To test the hypothesis, bird communities collected were identified into trophic guild groups, and functional traits were gathered to calculate the functional diversity indices.

2. Materials and Methods

(a)   Study area

Our study area is in a region of southwest Cameroon (Figure 1a). This previously forested region of Cameroon is fairly representative of other human-dominated tropical areas in sub-Saharan Africa and is comprised of sparsely shaded cocoa plantations and small-scale subsistence mixed crop farmlands. The area has two distinct dry and wet seasons originally driven by the wind. The dry season, accompanied by the appearance of the north-east trade wind, stars from October, and may last for six months in the south (Molua and Lambi, 2014). Likewise, the southwest wind intensively grows from the Atlantic Ocean, bringing the substantial rainfall in about mid-March, which is also the beginning of the wet season (Molua and Lambi, 2014). The annual precipitation in south Cameroon varies between 1500mm close to the coast and 3000mm in the interior, and the mean annual temperature is around 25°C (Ngomanda *et al*., 2009). The vegetation in south Cameroon is a mix of evergreen forest and patches of semi-deciduous forests, as well as the natural savanna filling the gaps of forests (Maley and Brenac, 1998; Hervé B. and Vidal, 2008). Plantations with different trees, home gardens and croplands also compose the landscapes close to the human settlement (Hervé B. and Vidal, 2008). For bird communities, there are endemic birds and some avian birds, consisting of multiple guilds (Kupsch *et al*., 2019; Tchoumbou *et al*., 2020).
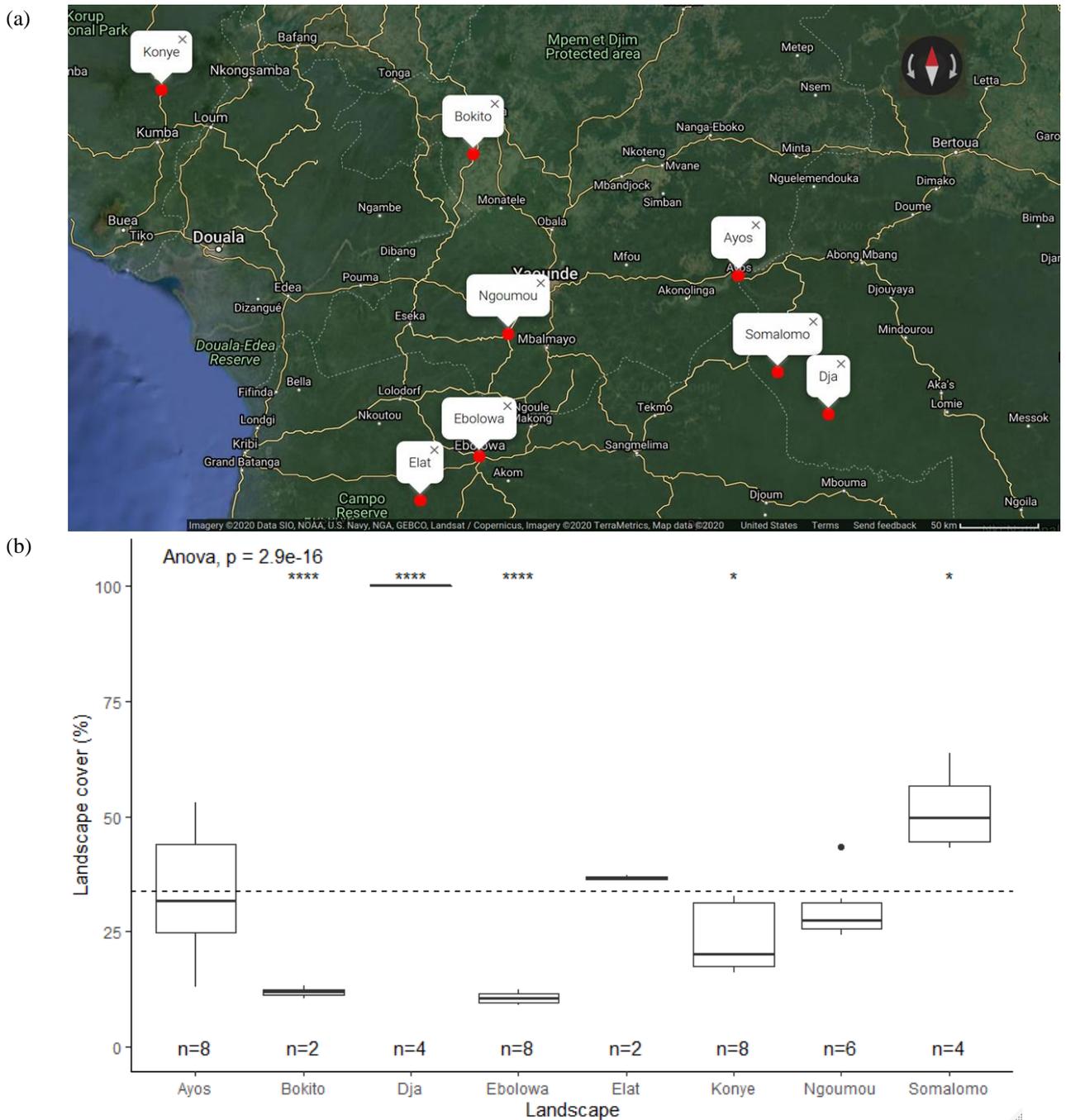
Figure 1. Locations of eight landscapes sampled in Cameroon (a) and the mean and variations of landscape tree-cover in each landscape. n represents the number of cocoa plantations (sites) sampled. The reference line shows the average landscape tree-cover across all sites. The asterisk shows the significance of the difference between each landscape and the mean landscape tree-cover.

(b) Data collection

This study was conducted between 2017 and 2020, spanning both wet (August to September) and dry (January to February) seasons. Data on bird community structure was collected across 42 individual sites, from eight distinct geographical areas (hereafter landscapes; Figure 1a) and representing two distinct habitat types: natural forest and plantation forest (agroforest). The natural forest sites (n = 4, Figure 1b) were found within the Dja

Biosphere reserve close to UCLA's Bouamir research station and were selected on the basis that they are undisturbed primary dense forest (controls). Whereas the remaining plantation forest sites (n = 38) were comprised of 1.5 ha smallholder cocoa farms; with each farm separated by a minimum distance of 500 m. To establish a land use gradient, each site was characterised by the percentage of tree cover around it (5km buffer) using MODIS satellite data.

In each site, the birds were counted using a fixed-radius point count method (Sedláček *et al.*, 2015). Samplings were conducted in the morning from 6-8:00 am using audio recorders in each coca farm. Then the records were broken into two 10-minute intervals as each minute was one record. In total, 142 species were detected across all sites. Bird species encounter rates (number of times a species was detected within two 10-minute intervals) were calculated for each site, as a surrogate to relative abundance methods, which are highly sensitive to variable species detection rates (Nalwanga *et al.*, 2012; Marsden *et al.*, 2016). Birds were identified to species level and assigned to one of eight dietary guilds (aquatic predator, frugivore, granivore, herbivore terrestrial, invertivore, nectarivore, omnivore and vermivore) based on the Pigot *et al.* (2020) classification system.

Morphological trait data for each species were taken from the unpublished Tobias *et al.* (2020) dataset. Which comprises of 10 trait measurements, including: beak length from tip to skull along the culmen, beak length to the nares, beak width at the nares, beak depth at the nares, tarsus length, Kipp's distance, Hand-wing index (HWI) wing chord length, first secondary length, tail length, gape width, and body weight. To avoid the potential biasing of the analysis due to the high correlative nature of bird biometric traits with overall body size (Supplementary Figure A2; Trisos, Petchey and Tobias, 2014), a two-step principal component analysis (PCA) was applied to the biometric traits (Bregman *et al.*, 2016; Chapman *et al.*, 2018), detailed processes can be found in supplementary (a). Biometric traits were separated into trophic traits (bill-related traits) and locomotory traits (tarsus, wing-related traits and till) for PCA, respectively. The first principal component (PC1) scores of the two PCA were extracted to generate a second PCA, which is correlated with the body size. Then the PC2 of trophic and locomotory traits and the PC1 of the body size traits were extracted as the independent variables served for the functional matrix. Dietary information and foraging strategies were also additionally supplied for the functional matrix.

(c)   Data analysis

Indices used for functional diversity measures are functional richness, functional evenness, functional divergence, and functional dispersion. These indices are independent of each other and can demonstrate functional diversity in different facets that deeply assess how biodiversity interacts with the ecosystem functioning (Mason *et al.*, 2005). Functional richness (FDpg), which is commonly used for functional diversity measures (Luck, Carter and Smallbone, 2013), was derived from the sum of the brunch length of the functional dendrogram based on the presence or absence of bird species (Supplementary Figure A3; Petchey and Gaston,

2002; Petchey and Gaston, 2006). The functional evenness (FEve) represent the evenness in abundance distributed across species in the multidimensional trait space; functional divergence (FDiv) measures the divergence of the abundance distribution in the multidimensional space of functional traits (Mason *et al.*, 2005). FEve and FDiv were calculated according to Villéger, Mason and Mouillot (2008). Functional dispersion (FDis) was a distance-based index proposed to investigate the functional dissimilarity in terms of the average distance between each species and the centroid of all species in a multivariate space of functional traits (Laliberté and Legendre, 2010).

The FDpg was calculated by the function *FD_dendro* from the package "fundiv" (Bartomeus, 2018). The function dbFD in the package "FD" was used to measure FEve, FDiv and FDis for bird communities, and the three indices are weighted by the encounter rate (Laliberté, Legendre and Maintainer, 2014). The trait distance matrix was generated based on Gower's dissimilarity distance to account for the variables of mixed type. The Hierarchical clustering was derived from the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) to build the functional dendrogram, which returned a high Cophenetic correlation coefficient (r = 0.806). The high correlation suggests an appropriate proxy of the functional dendrogram for the functional traits. Besides, FDpg, FEve and FDiv were constrained between zero and one.

Functional mean pairwise distance (fMPD) means the mean distance of individuals across the functional dendrogram, suggesting the functional dissimilarities among species. Functional mean nearest taxon distance (fMNTD) is the mean distance between individuals and their nearest taxon in the functional dendrogram. fMPD and fMNTD were measured by function *mpd* and *mntd* in package "picante" (Kembel *et al.*, 2010).

The general linear model was used for all the analysis of the correlations between variables. The general linear mixed model was used to exam the importance of landscape as the random effects. I used the function *glm* in package "states" for GLM model and the functional *glmer* in package "lme4" for GLMM (Bates et al., 2015). The correlation between species richness and tree-cover change was measured across all sites and then separately measured for each guild. Guilds whose richness is highly associated with landscape tree-cover change or contain more than three species were selected for further analysis. The response of functional diversity indices to the landscape tree-cover change was investigated for all species as well as for major guilds. The functional redundancy was finally assessed by measuring the correlation between functional indices and species richness. I did all the modelling and data wrangling in R studio 3.6.3 (RStudio Team, 2020).

3. Results

(a)   Species richness across landscape tree-cover gradient

Overall, we found that decreasing landscape tree-cover is associated with a significant decline in bird species richness (GLM: $p < 0.001$, $n = 42$; Table 1, Figure 2a). A similar pattern was also found in the species overall richness and diversity indices as shown in supplementary (c-d). Of the eight avian guilds present within our study system, only two (frugivores and insectivores) were found decline significantly with decreasing landscape tree-cover (GLM: $p < 0.01$ for frugivores, $p < 0.001$ for insectivores, Figure 2b). However, the values of the correlation coefficient for both frugivores and insectivores are relatively low ($r = 0.15$ for both), suggesting a weak agreement for the correlations between species richness and tree-cover.

By including landscape type as an additional explanatory factor (random effect) within our models, we were able to improve their fit (measured using the AIC; Table 1). However, landscape type still only accounted for a relatively small portion of the detected species richness variance in our models (0.05) and did not change the overall significance of our findings (GLMM: $F = 3.42$, $p > 0.05$; Table 1) or the correlation coefficient values. The variance of the correlation explained by landscape types is relatively higher in granivores and omnivore.

Table 1. The correlation between species richness and landscape tree-cover change across 42 sites using GLM and GLMM under Poisson distribution. The number of species in each trophic niche is shown brackets. P-values, F statistics, correlation coefficient (r) and Akaike information criterion (AIC) values are displayed. The landscape is a random effect in GLMM, and the variance occupied is displayed. Asterisk marks out the significant correlations.

Trophic niche	GLM			GLMM				
	p-value	*r*	AIC	p-value	F value	*r*	AIC	Variation explained by landscapes
Aquatic predator (3)	0.052945	0.39	64.996	0.05295	3.7456	0.39	67	0
Frugivore (24)	0.00402*	0.15	195.98	0.0378*	4.3044	0.15	195	0.02343
Granivore (16)	0.348	-0.06	212.76	0.432	0.6159	-0.09	197	0.1251
Herbivore terrestrial (1)	0.8658	-0.11	25.804	0.8658	0.0286	-0.11	27.8	0
Invertivore/insectivores (79)	9.86E-07*	0.15	287.67	0.0108*	6.5003	0.16	267	0.03899
Nectarivore (3)	0.5645	-0.15	72.916	0.5646	0.3319	-0.15	74.9	0
Omnivore (15)	0.589	0.03	195.34	0.926	0.0085	0.00943	187.2	0.07361
Vermivore (1)	0.6213	-0.52	19.857	0.794	0.0441	-0.42	21.2	4.026
Total Richness (142)	3.79E-06*	0.11	371.87	0.0644	3.419	0.1	300.3	0.05161

This variation could, in part, be explained by the fact that the sampling intensities were not equal across the eight landscapes (Supplementary, Figure B1), and therefore may have failed to sufficiently capture the avian community species richness in some of our landscapes. This is perhaps best illustrated by the fact that in some landscapes (e.g. Bokito) the species accumulation curves did not approach asymptote.

Overall, more bird species (on average) were detected in landscapes with a forest cover of between 50-75% (ANOVA: $p < 0.001$; Figure 2a). This pattern was broadly consistent across our four most abundant avian guilds, with the exception of granivores, which had the highest detected species richness in landscapes with a forest cover of between 25-50% (ANOVA: $p < 0.001$; Figure 2b). Interestingly, while fewer species were detected in forested sites (>75% tree cover), the most substantial effect was observed in omnivores. The variation of species richness also more dispersed under lower landscape tree-cover, especially in insectivores when the range was even more than 20. Therefore, tree-cover may have a significant effect on the distribution of bird species. Similarly, this finding was also reflected in the Shannon-weaver and Simpson's diversity indices, which showed a strong negative correlation with landscape tree-cover (Supplementary Table A2).
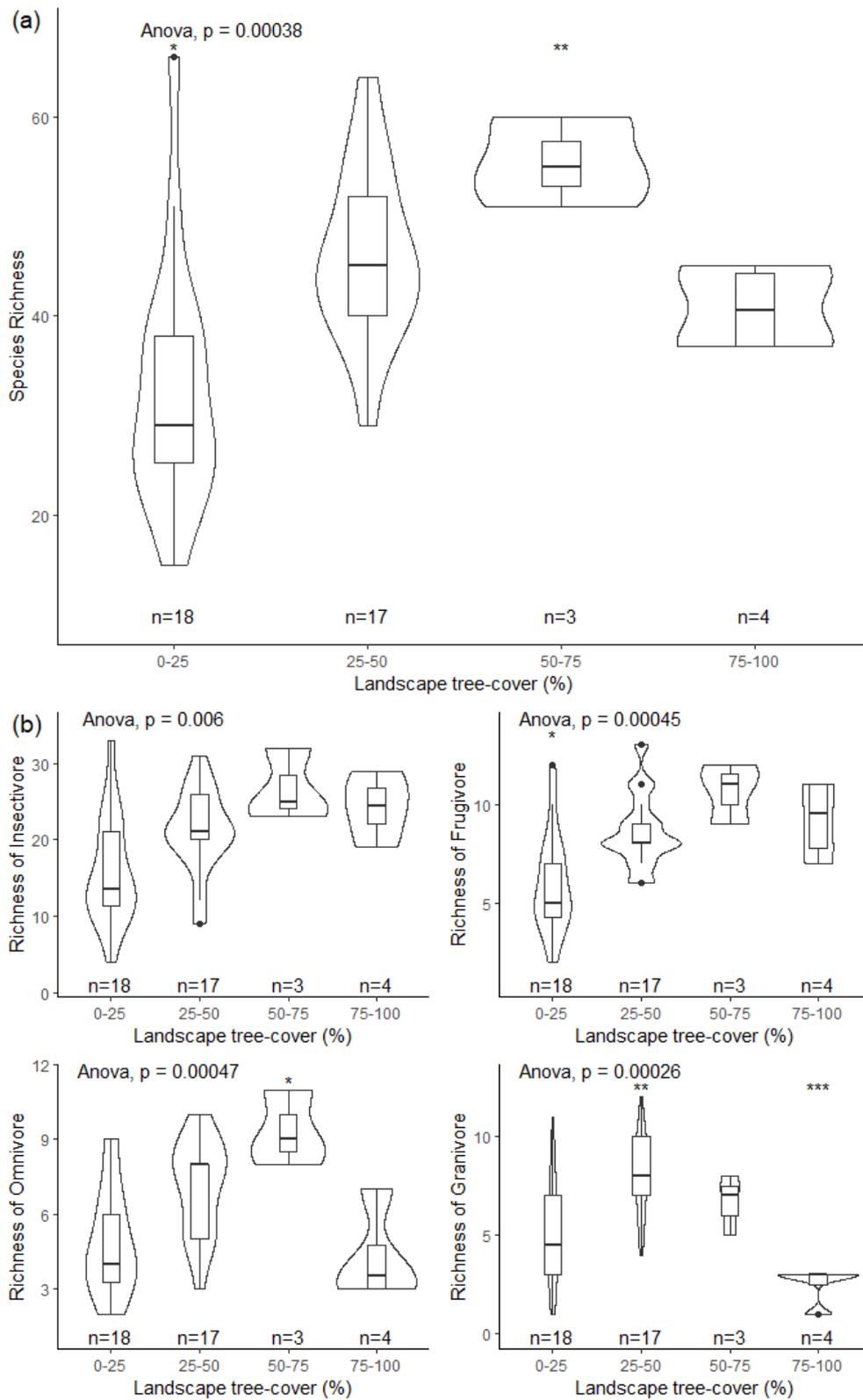
Figure 2. Species richness of all species (a) and four dietary guilds including insectivores, frugivores, omnivores and granivores (b) across landscape tree-cover gradient. The number of sites in each landscape tree-cover groups is shown in the bottom when the four forest sites have 100% tree cover. The green square denotes the mean richness. The p-values of ANOVA show the significance of the difference among groups, and asterisks shows the difference between the group and the average richness.

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(b)   Responses of functional diversity indices

Functional diversity (FDpg) showed similar patterns to that of the species richness, with increased functional diversity for invertivores and frugivores with increasing landscape tree-cover (Figure 3a). By contrast, the FDpg of omnivores and granivores was not statistically affected by increasing landscape tree-cover (Figure 3a). A notable decline of functional diversity in forest site was also found in all the four guilds especially granivores. Although the FDpg patterns are similar, there is a slight difference in the functional similarities among different trophic guilds. In insectivores, more functional similar species or functionally complementary species involved with increasing landscape tree-cover according to markedly declined fMNTD within higher landscape tree-cover (Figure 3b-c). However, the unchanged fMPD was detected in insectivores across landscape tree-cover, indicating that new species were not added in the previous assemblages. Functionally dissimilar species of frugivores appeared with elevated tree-cover based on both increased fMNTF and fMPD. However, no remarkable response of fMNTD and fMPD was detected in omnivores and granivores, which is consistent with the FDpg patterns. Other functional indices were mostly not associated with tree-cover change as shown in supplementary (e). Seasonality effect was also estimated using GLM. There was no interaction between season and landscape tree-cover for species richness and functional diversity (supplementary Table F1; Table F2); however, they were both higher in dry season (supplementary Figure F1)
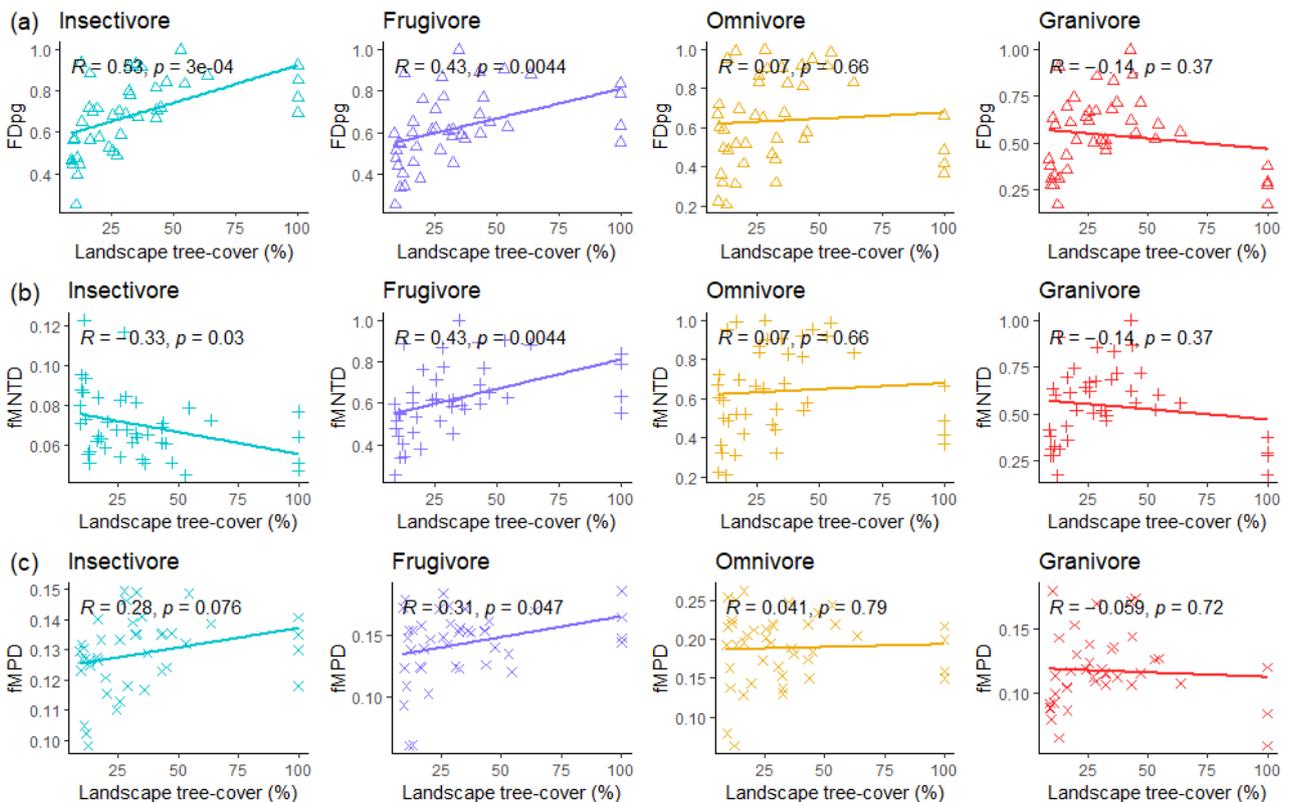

Figure 3. Changes of (a) FDpg, (b) fMNTD and (c) fMPD across landscape tree-cover gradient in four dietary guilds (blue for insectivores, purple for frugivores, yellow for omnivores and red for granivores). The correlation coefficient (R) and p-values for correlations are provided.

(c) Correlations between functional diversity indices and species richness

The correlations between Functional diversity indices and species richness would further reveal the different aspect of functional diversity in bird communities. We found that functional composition and dispersion varied according to different trophic guilds.

The functional diversity was significantly linearly associated with species richness in the four bird guilds (i.e. more species-rich sites were more functionally diverse), since the FDpg was calculated based on the species richness (presence or absence; Figure 4a). Figure 4b shows that only insectivores have a decreasing functional evenness with increasing species, suggesting the involvement of functionally unique species with richer species. The decline of functional divergence in granivores displayed in Figure 4c illustrates that abundant species have extreme functional trait values, then divergence is high. Interestingly, both frugivores and granivores, trait space decreases with decreasing species richness (Figure 4d).
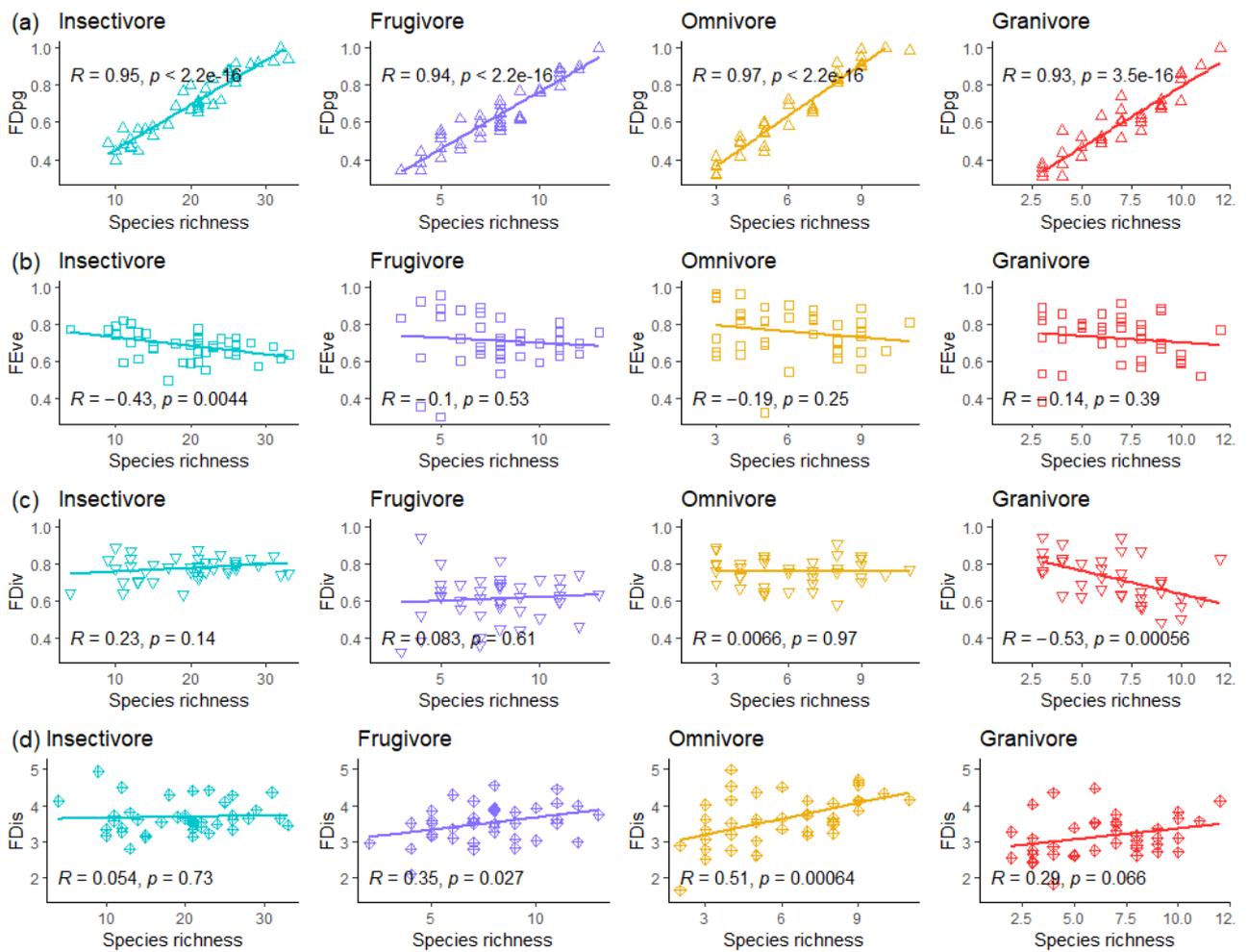

Figure 4. Correlations between functional diversity indices and species richness in four dietary guilds (blue for insectivores, purple for frugivores, yellow for omnivores and red for granivores). (a) FDpg; (b) FEve; (c) FDiv; (d) FDis. The correlation coefficient (R) and p-values are provided.

4. Discussion

Overall, I found that decreasing landscape tree cover is negatively associated with bird species richness and functional diversity. In particular, decreasing landscape tree cover was found to be disproportionally affecting insectivorous and frugivorous bird species, both in terms of their overall species richness and functional diversity. These finding, while not novel by themselves, corroborate some of the earlier findings that habitat loss and fragmentation are negatively affecting avian diversity in the tropics (Flynn *et al*., 2009; Bregman *et al*., 2016; Hatfield, Harrison and Banks-Leite, 2018). More importantly, to my knowledge this is one of the first studies from this region, that has shown this relationship, and this indicates that local cocoa farms with coterminous forest edge would be beneficial for maintaining the diversity of bird communities.

Insectivores were the most dominate avian guild (in terms in the number of species), forming approximately half of species detected in our study system; followed by frugivores, omnivores and granivores. The rare appearance of other avian guilds in our study system is consistent with other studies, showing different biodiversity in high land-use intensity areas compared with natural forest (Flynn *et al*., 2009; Luck, Smallbone and Sheffield, 2013; Mestre *et al*., 2020). The strong correlation between species richness and functional diversity of insectivores and landscape tree-cover is possibly due to the evidence that their species richness was positively associated with overhead canopy cover (Sekercioglu, 2012), supporting that tropical insectivores were sensitive to habitat loss (Sekercioglu *et al*., 2002). Despite the relatively high number of insectivorous species present in most of the sites (as compared with other guilds), which may indicate a degree of resilience to agricultural development. Bregman *et al*. (2016) observed that forest insectivores were more sensitive to land cover change (i.e. from agroforest to natural forests), as compared to non-forest insectivores, which were less impacted by the change in habitat type. Therefore, some kinds of insectivores have adapted to the environment in agroforest, perhaps keeping the relatively high species richness. Additionally, I found that decreasing landscape tree cover was associated with a reduction in the functional redundancy of the insectivorous bird community (measured in terms of fMNTD), which may affect the ecological stability and stability of the community. However, given that the fMNTD and fMPD measures the mean functional dissimilarity with relative abundance (Mestre *et al*., 2020), the relatively insignificant change reflects that some functional correlations added with increasing tree-cover may not belong to the existing functional clustering. Therefore, there are some spare niche spaces for more insectivores to settle down in the agroforest.

Similarly, for frugivores, the reduction of richness seems to be more rapid in low landscape tree-cover sites. One possible reason can be the less available food that frugivores can obtain in low tree-cover lands. A similar pattern was also found in the Amazonian trophic forest that the FDpg and FDis of frugivores rapidly declined with high land-use intensity, resulting from the disappearance of fruiting trees (Bregman *et al*., 2016). Clough *et al*. (2009) stated that frugivores consist of a large number of forest specialists, thus, were more

negatively affected by reduced forest and a distance to natural forest. As the seed size is positively related with the body size of frugivores, the decrease of seed size in agriculture land under strong human disturbance appears to eliminate to the occurrence of large seed dispersers (Galetti *et al*., 2013). Besides, the smaller seed size may negatively impact plant growth and dynamics (Moles *et al*., 2005), such as seed germination and mortality (Pizo, von Allmen and Morellato, 2006) and seeding biomass (Aparicio *et al*., 2002). Therefore, restricted quality and quantity of food resources may drive the disappearance of frugivores. The strong increased fMNTD and fMPD along to the elevated landscape tree-cover in frugivores means a higher functional dissimilarity across species in higher tree-cover sites, suggesting that richer species with unique functions occurred in high tree-cover agroforest approaching the forest edge.

The relatively weaker change of species richness and FDpg across tree-cover change was found in omnivores and granivorous, suggesting that they appear to be less impacted by reduced tree-cover. Banks-Leite, Ewers and Metzger (2013) proposed that the species richness of omnivores are more likely to be affected in small local scales but was less varied among large scale, supporting stable conditions found across all agroforests. There was also evidence revealing that omnivores were also a big fruit consumer; therefore, they would be attracted by the abundant food resource in agroforests (Peters *et al*., 2010). Likewise, Tscharntke *et al*. (2008) found that granivorous became richer with decrease landscape tree cover, especially in agriculture land, within which the richness can reach even four-five times richer than in the forest. Clough *et al*. (2009) added that there was more available food such as crop seeds in coterminous farmland as well as herb seeds from agroforest for granivorous in low tree-cover sites. Also, given that granivorous were more likely to forage on the ground (Waltert *et al*., 2005), the higher accessibility to food resources may be responsible for the richer granivorous detected in sites with more ground area.

However, the lower species richness of insectivores, as well as frugivores in the natural forest compared to high tree-cover sites, was opposite to previous work that insectivores were more abundant in the forest than agroforest (Waltert *et al*., 2005; Tscharntke *et al*., 2008). The positive edge effect may account for the enhanced species richness and diversity for varied guilds (Kahana, Malan and Sylvina, 2013; Neate-Clegg, Morshuis and Banks-Leite, 2016), since the increasing landscape tree-cover contributes to a closer distance to the forest edge. Barbaro *et al*. (2014) interpreted that the positive edge effect towards insectivores might be attributed to the richer available larvae at forest edge with higher tree productivity and the higher prey detectability as well as efficiency. Regarding frugivores, Saavedra *et al*. (2014) proposed that richer frugivores, accompanied with higher fruit–bird interactions and seed dispersion, were found at the forest edge rather than in the interior forest since frugivores were attracted by both quality and quantity of available resources such as fruit crops, the high quality of fruits in sunnier condition and more unobstructed visibility at the forest edge.

Overall, the species richness of total bird community and the four guilds reaches the peak in high landscape tree-cover farmlands (around 75%), but sharply decreases in forest sites. Similarly, a relatively lower FDpg was also found in forest sites. There was evidence supporting that the composition of bird assemblages

strikingly shifted from agriculture land to natural forest (Waltert *et al.*, 2005; Lindenmayer *et al.*, 2015), since some vulnerable species fail to survive in modified habitat and the abundance of different species can vary in habitat types (Karp *et al.*, 2019). Faria *et al.* (2006) investigated that forest specialists appear to have difficulties in surviving in agroforest without surrounding remnant forest. The loss of forest specialist species in higher human-disturbed lands can be complemented by the habitat generalists, contributing to rising or unchanged species richness (Faria *et al.*, 2006; Burivalova, Şekercioğlu and Koh, 2014). This replacement of avian species represented an alteration of bird communities to habitat change and was corroborated to exist in Cameroon (Waltert *et al.*, 2005). Although the ecological functions and ecosystem services are affected by the turnover of bird communities, the agroforest was still able to maintain a degree of avian diversity.

Generally, the reflections of different guilds to the landscape tree-cover change demonstrate the potential ability of high tree-cover cocoa agroforest for maintaining ecosystem functions. The agroforest is not only able to provide fruit resources (Peters *et al.*, 2010), but also can be an alternative shelter for bird communities owing to the shade canopies (Hernandez *et al.*, 2013). Most of the avian guilds would benefit from the shade canopies offered by agroforest, especially near the forest edge where the shade cover was the key factor; however, it would be independent of shade cover when birds deviated from forest edge (Clough *et al.*, 2009). Besides, forest species can be supplemented from the neighbouring agroforest, which is one approach to maintain the local biodiversity (Pino *et al.*, 2000). Also, higher species richness is more likely to contain birds that have particularly ecological functions as the functional diversity showed a similar trend as the species richness. Therefore, the agroforest may play an important role in protecting regional biodiversity. Besides, the shift of avian communities can be considered into cocoa farm management since functionally unique birds would provide an extra service for the pest control (Tscharntke *et al.*, 2008).

(a)   Functional diversity indices

The assessment for environmental change on avian communities on the basis of merely functional composition and species richness may not adequately explore the implications for ecosystem functioning (Gagic *et al.*, 2015). The relationships between functional diversity indices and species richness have significant meaning for ecosystem functioning, which were able to quantify the functional redundancy in different aspects in terms of the tendency of the correlation across species richness. The FDpg was almost exactly proportional to the species richness respectively in guilds, demonstrating that the change of species richness dominates the change in functional richness/diversity within the bird community. This strong relationship also suggests that FDpg may not be used to predict the functional redundancy because the FDpg was not independent of species richness (Mouchet *et al.*, 2010; Luck, Carter and Smallbone, 2013).

Generally, the functional evenness declines with the increasing species richness, but the decline was only significant in insectivores. Therefore, with new insectivore species added, the distribution of abundance tends to fluctuate among different functional clustering (Luck, Carter and Smallbone, 2013), if there was a space

for new functional niches (Ibarra and Martin, 2015). This pattern in insectivores supports the assertion above that with denser landscape tree cover in agroforest, more functional clustering groups occurred. Also, the unchanged other functional diversity indices in low species richness conditions are in agreement with the conclusion that some insectivore species have a potential resilience to reduced tree cover. Likewise, the flat trend of functional evenness with added species richness in frugivores, omnivores and granivores revealed a potentially low functional redundancy or the even functional traits within the bird communities, which is accordance with previous work that omnivores and granivores were less impacted (Luck, Carter and Smallbone, 2013).

Interestingly, functional divergence was not significantly affected by the change of species richness, with the exception being granivores. Since the functional divergence demonstrates the niche difference among most abundant functional characters in bird communities (Mason *et al*., 2005), the dwindling functional divergence indicated that biometric features of abundant granivore species become more functionally similar with increased species richness. It possibly shows a functional redundancy in abundant granivore species, but overlook the minor granivores (Mason *et al*., 2005). The strong positive correlation of functional dispersion against species richness was only found in omnivores. The functional dispersion measures the average distance to the centre of the multidimensional functional space of the avian community (Laliberté and Legendre, 2010); therefore, more functional unique omnivores appeared with rising species richness. These findings supported that both omnivores and granivorous were able to adapt to tree-cover change; however, they would differ in the abundance of functional clustering groups. More granivore generalists with a potentially fierce competition (Cooke, Bates and Eigenbrod, 2019) were detected in agroforest, accompanied by more omnivore specialists.

The different aspects of functional diversity are able to reveal the affected local biodiversity not only by the presence or absence of avian species but also by the relative abundance. The four functional diversity indices were designed to be complementary (Villéger, Mason and Mouillot, 2008), and functional evenness, divergence and dispersion were more sensitive to functional redundancy in different means. Therefore, it was reasonable that though the major trend of FDpg was similar among bird guilds, the trends of other functional indices still differ in trophic guilds. The information characterised by decomposed functional diversity would benefit researchers to hold further insight into the influence on avian ecosystem functioning (Mouchet *et al*., 2010).

(b)   Limitations and future recommendations

Despite these findings, this study has several key limitations. The first limitation concerns the uneven sampling conducted in each landscape, contributing to a potential loss of the species richness in some area — as seen by the species accumulation curve in Figure B1 (which illustrates the unsaturated species richness in Bokito). This may affect the correlations between species richness and landscape tree-cover due to the fact that there were insufficient samples to accurately capture bird species richness. On the other hand, since the abundance

in this study was encounter rates and measured based on the audio record, rather than through capture data, it is possible that the same individuals were sampled multiple times, or the sound of other individuals was not distinguished from similar individuals. Therefore, it can be a fake abundance that may not precisely represent the abundance of the real situation. Ultimately, it would affect the calculation of functional diversity indices as they were built to be sensitive to abundance.

Also, there was a gap of the sampling sites between the highest tree cover with around 70% in agroforest and the 100% tree cover in forest sites; therefore, the result reported here should be elaborated cautiously as there would be missing information within the gap, and remaining to be explored in further studies. The other issue is the 5km buffer used to estimate the landscape tree cover. Since the distance between cocoa farms was at least 500m, a 5km buffer may contribute to an overlap of landscapes, and ultimately causes a similar tree-cover. Besides, the forest fragments counted within the buffer could be either close to the farm or distant from the farm (near the buffer edge), which would mask the result.

It is always a key point to discover the trade-off between anthropogenic exploitation and conservation for the ecosystem, which drives the attention to the ability of agroforests to sustain the local ecosystem. There was a global trend of functional homogenisation from specialists to generalists (Clavel, Julliard and Devictor, 2011); however, the effects on functionally similar or functionally unique species vary in bird guilds in this study. Therefore, future work can detailly focus on one niche group to see the change of specialists or generalists. Also, functional diversity indices can be applied for deeply learning the response of bird communities. Other indices like phylogenetic diversity, which was proven to be a suitable surrogate for functional diversity, can also be considered to further estimate the bird functions (Chapman *et al*., 2018). It may also be interesting to investigate the effects of neighbouring vegetation types on bird guilds, as the food resources seem to be one of the main drivers for different trophic niches.

5. Conclusion

To conclude, reduced landscape tree-cover can negatively impact the species richness and functional diversity of avian communities. However, the extent of impact seems to differ across the different trophic guilds. Insectivores and frugivores were more prone to being affected, possibly due to the large number of specialists in frugivores and sensitivity of insectivores to canopy cover. The high species richness of insectivores and frugivores suggested the high capacity of high tree-cover agroforest as well as vacant niches for specialized species. Granivores and omnivores were less restricted by the changed landscape tree-cover, basically due to the abundant food resources from both agroforest and surroundings. However, the functional redundancy varied in guilds based on multiple functional diversity indices. The results of this study highlighted the utilization of high tree-cover agroforest for maintaining the avian diversity. Also, using multiple functional diversity indices to assess biodiversity can provide a deeper understanding for the impact of environments, which can be promoted in further studies.

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7. Data and Code Availability

The code applied in this thesis can be found in the following link:

https://drive.google.com/drive/folders/1Brpr_YNhefsCu6cI_Ex2pFqnqnrFFnv0?usp=sharing

The data used in the thesis are from the unpublished database of my supervisors, and therefore are currently not available.

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9. Supplemental Material

(a)   Two-step PCA of functional traits

Figure 1 illustrates the processes of two step PCA. As demonstrated in methods, finally, three PC scores were used to replace biometric data. Tow-step PCA was used to reduce the redundancy of traits corresponding to similar functions, within which three relatively independent indexes can be extracted to represent different aspects of the foraging niche. Original biometric traits were separated into two groups: trophic traits and locomotory traits. The second principal components (PC2) of each group were extracted to represent foraging/trophic traits and locomotory traits. Overall body-size was calculated based on the first principal components (PC1) of two groups. The loading of traits in PC1 of both trait groups is relatively similar among all traits. However, in PC2 the difference of loading of traits is much more distinct.

Figure A2 shows the clustering of trophic niche groups in functional trait space. It is clear that without two-step PCA it can be difficult to distinguish the trophic guilds from functional traits. The functional dendrogram in Figure A3 was used to calculate the FDpg, which sums up the brunch length of species found in the field.
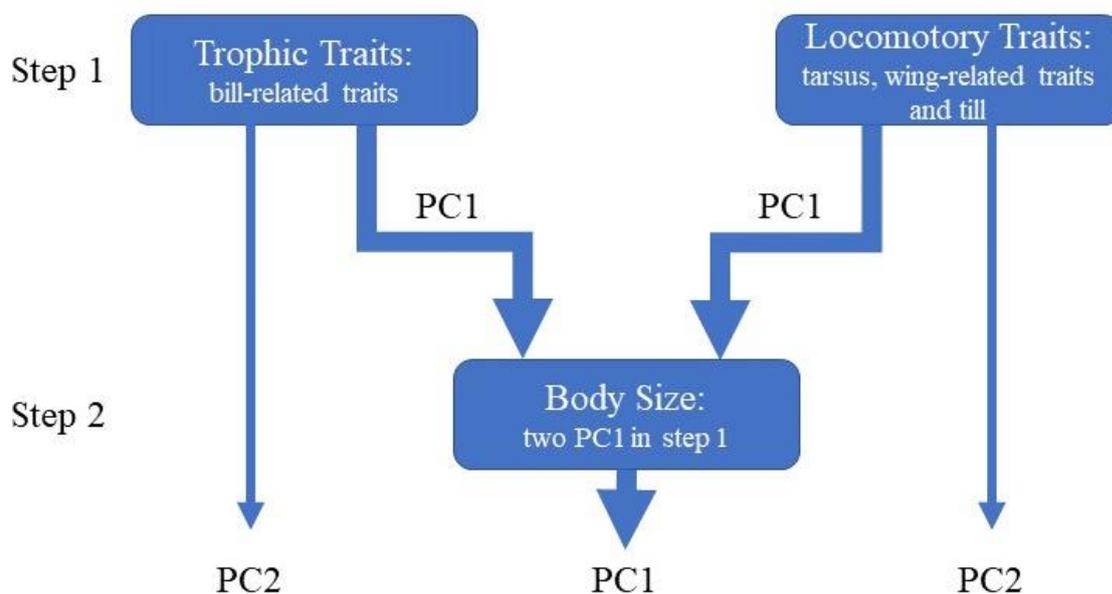

Figure A1. Processes of two-step PCA. Functional traits used in this thesis were shown in this Figure, detailed traits could be found in the methods part in the main content.

Table A1. Factors loadings and percentage of total variance explained for principal components from PCA including all traits.

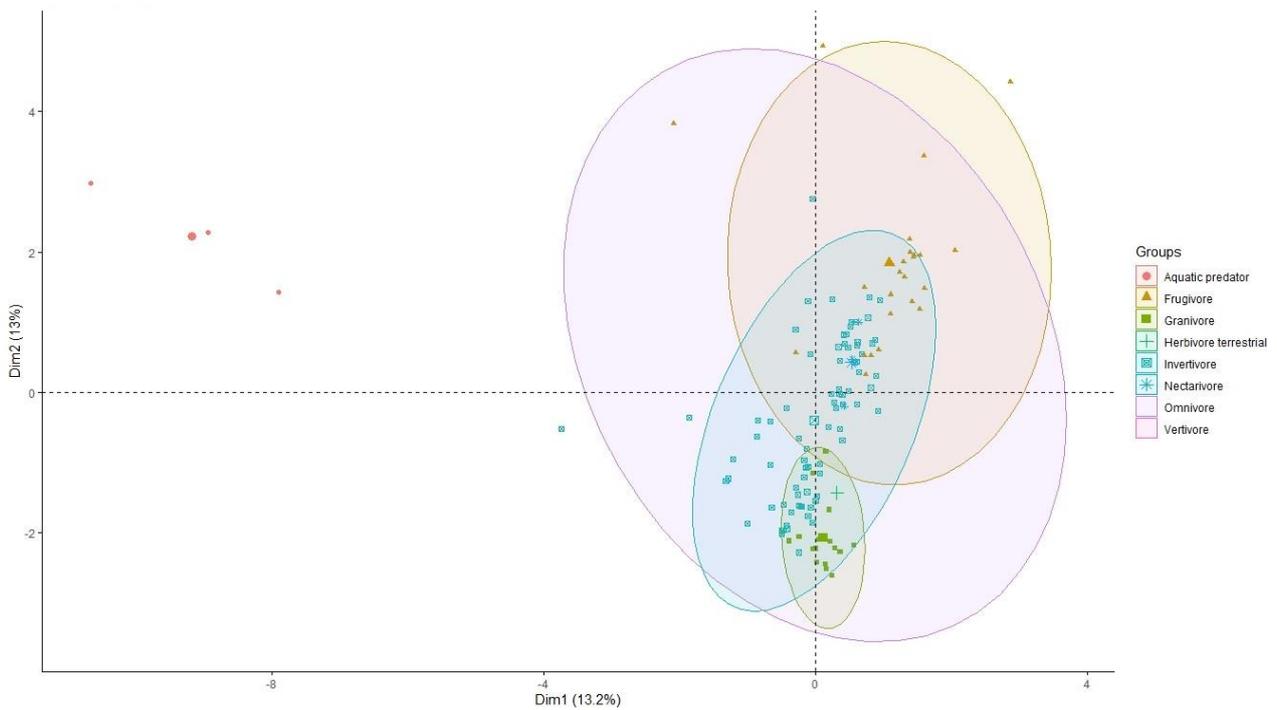| PC	Variance	Loadings					
Trophic		Bill Total Culmen	Bill Nares	Bill Width	Bill Depth		
1	0.95	-0.50	-0.50	-0.50	-0.49		
2	0.03	0.47	0.44	-0.20	-0.73		
Locomotory		Tarsus Length	Kipps's Distance	Secondary1	Wing Chord	Hand Wing Index	Tail Length
1	0.71	0.43	0.40	0.46	0.48	0.17	0.43
2	0.23	0.30	-0.45	0.23	0.00	-0.79	0.18
Body size		Trophic	Locomotory				
1	0.84	0.71	-0.71				

Figure A2. Morpho-space plot using PCA of trait matrix used for functional diversity. Four major niche groups can be easily observed.
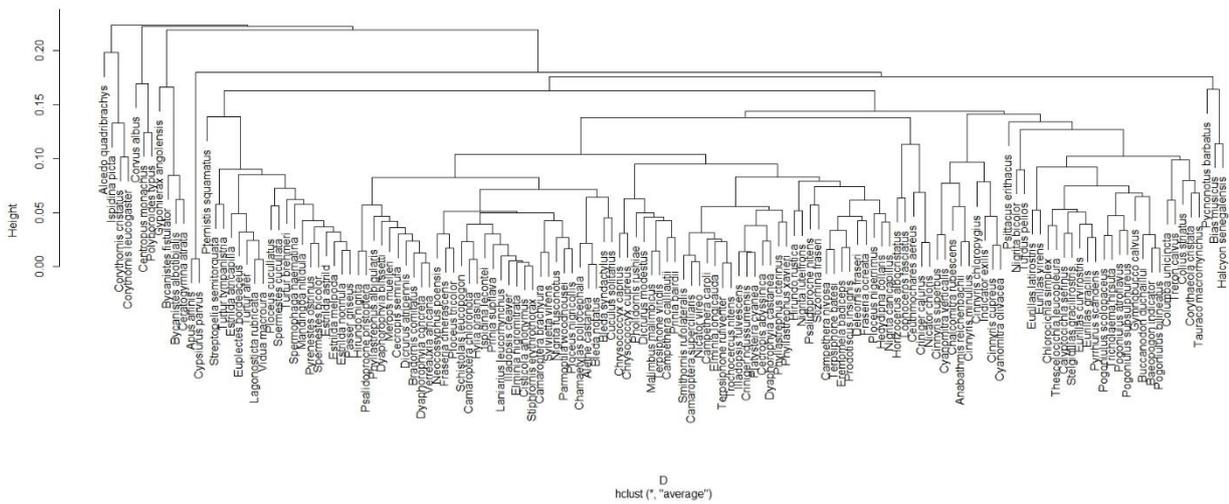
Figure A3. Dendrogram for functional traits of all 142 species.

(b) Species accumulation curve

Given that the sampling intensity was not equal across the eight landscapes, it is plausible that there has been insufficient sampling in some landscapes. The species accumulation curve shown in Figure B1 illustrates the accumulated species richness with increasing sampling times in eight landscapes. There was an explicitly fewer sampling times in Bokito but a more substantial amount of sampling times in Ayos according to the number of the error bars. In consequences, the total number of species found as well as the trend of the curve differs in landscapes. A strong linear correlation of accumulation species richness was observed in Bokito, indicating that the unsaturated species richness detected in Bokito may not reach the real total species richness.
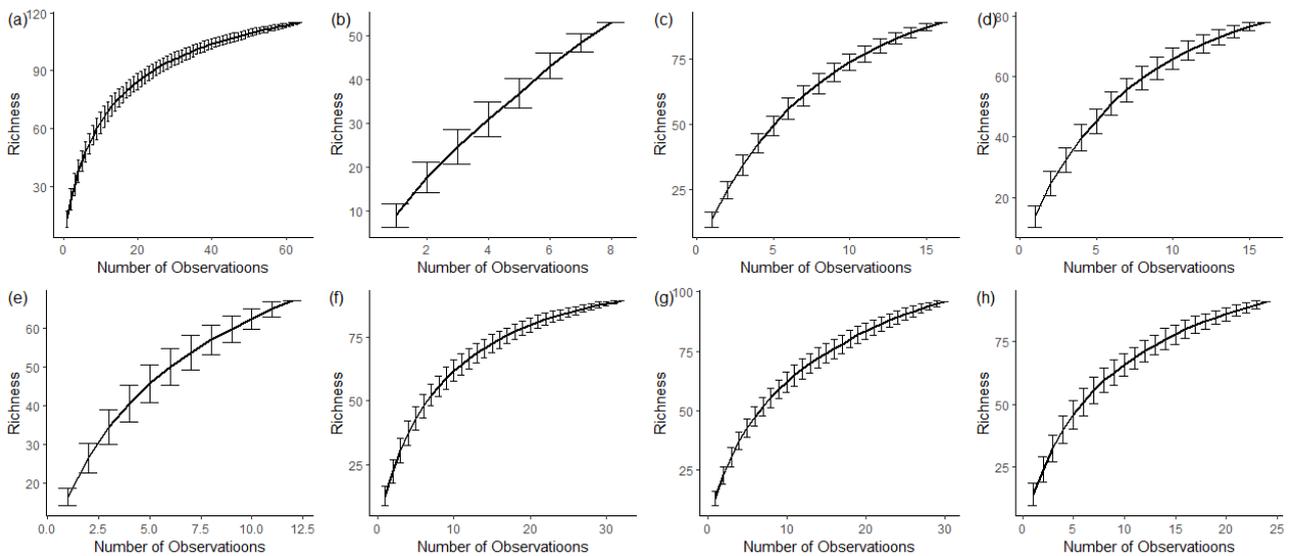

Figure B1. Species accumulation curve in different landscapes. (A) Ayos; (B) Bokito; (C) Ebolowa; (D) Elat; (E) Konye; (F) Ngoumou; (G) Somalomo. Observations were counted based on hours. The error bar for each observation was given from random permutations of data.

(c)   Species diversity indices

I tried to calculate the abundance of avian in each site by collapse data in different ways. Then I used diversity indices to test the potential difference of the collapse ways. However, few differences between the result derived from the three collapse ways were found. Table C1 shows the correlations between diversity indices and landscape tree-cover change for the whole avian communities. Similarly, the correlation is as significant as the correlation of the species richness.

Table C1. Diversity indices (Shannon Weaver and Simpson's) against landscape tree-cover change.

Index	GLM			GLMM			
	p-value	r	AIC	p-value	r	AIC	Variance of landscape
Shannon	0.000526	0.51	7.6447	0.0084	0.55	10.54656	0.03345
Simpsons	0.00293	0.45	-227.98	0.0148	0.44	-200.5885	0.0000342

The difference in diversity indices in three collapse ways is shown in Figure C1. In all the three diversity indexes, diversity indexes become higher when more data were collapsed. A few differences are observed between the diversity with data collapsed by day or hour in both Shannon and Simpson's indexes. However, since the sampling times in each site were different, finally relative abundance was used to generate functional diversity indices, which avoids the issues from uneven sampling times.

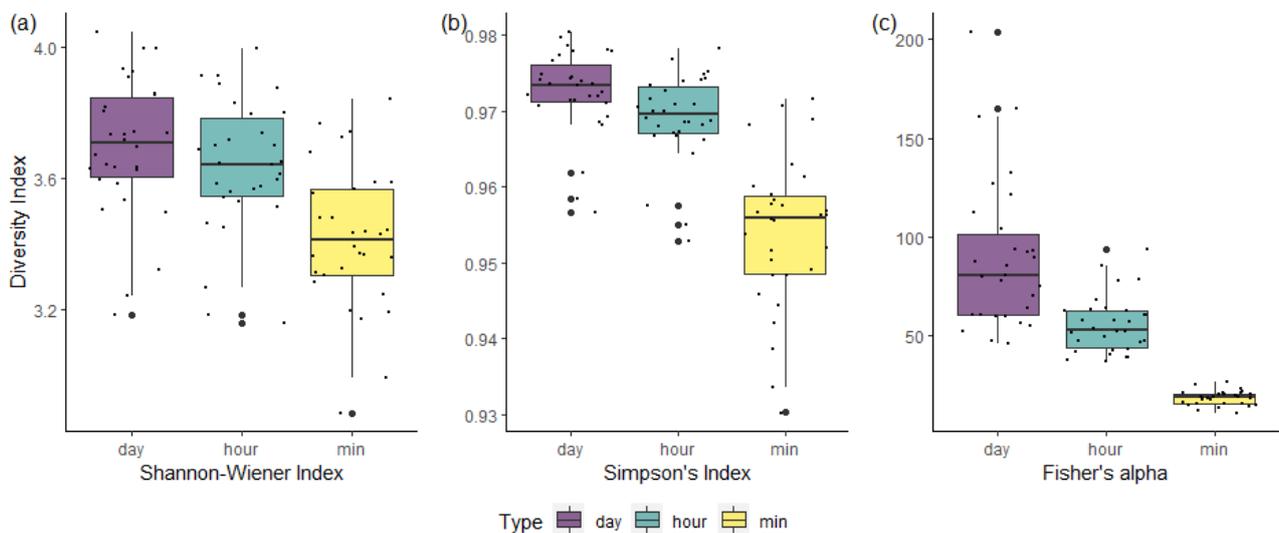Figure C1. Mean of diversity indexes using three ways of collapsing data (day, hour, and original records (min)). Three diversity indexes include (A) Shannon-Wiener index; (B) Simpson's index; (C) Fisher's alpha.

(d)   Overall richness

I also tried overall richness calculated by the following equation:

$$Overall\ Richness = species\ richness + \frac{species\ counted\ once}{2 \times species\ counted\ twice} \quad (1)$$

However, the result in Table D1 suggests that there was no difference in using the real specie richness or using overall richness. As the distribution of species richness of trophic guilds is mostly not normal

Table D1. The correlations between species richness and overall richness against landscape change.

Index	GLM				GLMM/LMM			
	p-value	F-value	r	AIC	p-value	F-value	r	AIC
Total Richness	0.0143	6.5663	0.38	328.19	0.0947	2.96014	0.35	301.7215
Overall Richness	0.0146	6.5114	0.37	328.24	0.097	2.91756	0.35	301.8255

(e)   The response of functional indices against landscape tree-cover change

Table E1 shows the response of functional indices against landscape tree-cover change. However, functional evenness, divergence and dispersion are not associated with landscape tree-cover change.

Table E1. The general linear model of each trophic niches for functional indexes and landscape using Gaussian distribution. The number of species in each trophic niche is shown in the brackets.

Trophic niche	Index	p-value	F value	r	AIC
Invertivore (79)	FDpg	0.000302*	15.666	0.53	-35.459
	FEve	0.00542*	8.6482	-0.42	-103.5
	FDiv	0.686	0.1655	-0.06	-113.15
	FDis	0.724	0.1264	0.06	56.297
	fMNTD	0.0302*	5.0499	-0.33	-222.64
	fMPD	0.0757	3.3252	0.28	-249.93
Frugivore (25)	FDpg	0.00441*	9.1079	0.43	-32.68
	FEve	0.74	0.1115	-0.05	-43.074
	Fdiv	0.732	0.1193	-0.06	-48.123
	FDis	0.148	2.1798	0.23	77.343
	fMNTD	0.000623*	13.793	-0.51	-180.97
	fMPD	0.0471	4.1982	0.31	-178.89
Omnivore (15)	FDpg	0.661	0.1956	0.07	0.79681
	FEve	0.791	0.0713	0.04	-43.718
	Fdiv	0.13	2.3994	0.24	-91.621
	FDis	0.986	0.0003	-0.00277	94.213
	fMNTD	0.478	0.5134	0.11	-150.63
	fMPD	0.795	0.0685	0.04	-137.29
Granivore (16)	FDpg	0.375	0.8055	-0.14	-10.872
	FEve	0.243	1.4087	0.19	-46.582
	Fdiv	0.699	0.1515	0.06	-48.511
	FDis	0.791	0.071	-0.04	112.59
	fMNTD	0.578	0.3149	-0.09	-160.62
	fMPD	0.716	0.1346	-0.06	-168.01

(f)   Seasonality in species richness and functional diversity

Table F1 demonstrates the species richness against landscape tree-cover change with seasonality as the fixed effect. No interaction was discovered between seasonality and tree-cover. A similar result was detected in functional diversity as shown in Table A6. Figure A6 also supports the above statement that the regression lines of the two seasons were parallel. However, the significantly higher abundant species was found in the dry season.

Table F1. Correlations between species richness and landscape tree-cover change with the impact of seasonality.

Groups		GLM			
		p-value		r	AIC
Season	Interaction	Landscape tree-cover	0.247	0.17	
		Season	0.0274*	-0.82	553.97
		Interaction	0.9393	0.02	
	No interaction	Landscape tree-cover	0.10363	0.18	551.97
		Season	0.00025*	-0.82	

Table F2. Correlations between functional richness and landscape tree-cover change with the impact of seasonality.

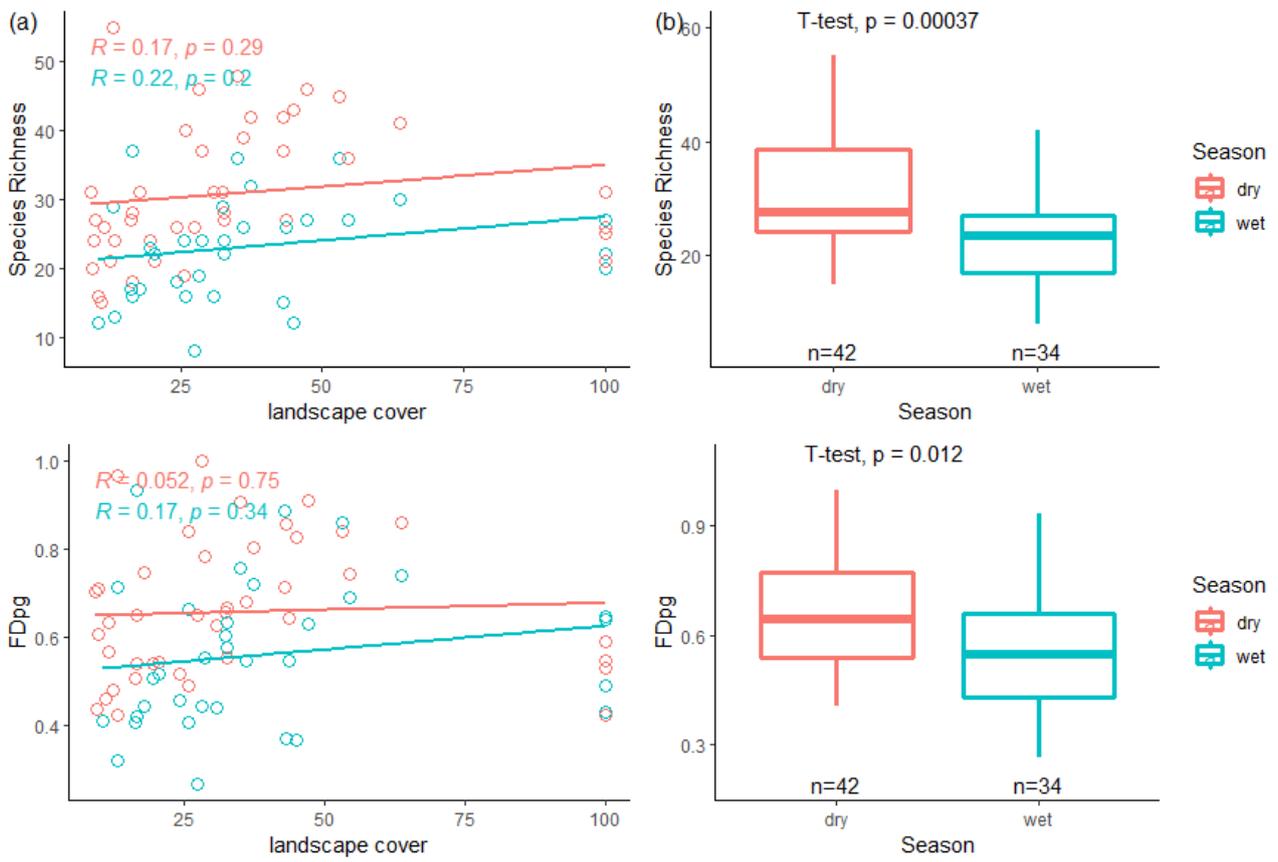| Index	p-value		r	AIC
FDpg	Landscape tree-cover	0.36978	0.1	-56.212
	Season	0.00928*	-0.6	
fMNTD	Richness	7.65E-05*	-0.42	-442.71
	Season	0.000225*	0.77	
fMPD	Richness	0.05	-0.23	-492.95
	Season	0.15	0.33	
FDpg	Richness	<2e-16*	0.97	-211.65
	Season	0.0399*	0.18	
FEve	Richness	0.0109*	-0.31	-205.28
	Season	0.7643	0.07	
FDiv	Richness	0.892	-0.02	-208.63
	Season	0.491	-0.18	
FDis	Richness	0.1219	0.19	97.432
	Season	0.0102*	0.64	

Figure F1. The correlation between species richness, FDpg and landscape tree-cover change (a). The difference of the species richness and FDpg between the two seasons was shown in (b).