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Research Article

The impact of plantation establishment on avian ecological and functional diversity

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Abstract

Conversion of tropical and sub-tropical forest to plantation agriculture poses a significant threat to Madagascar's unique biodiversity and ecosystem functioning, yet little research effort has been dedicated to studying its effects. By comparing avian diversity, community composition, and functional diversity metrics between secondary forest and plantation habitats in the Sambirano eco-region of Madagascar, this study simultaneously explored the impact of plantation establishment on forest communities and the conservation value of low-intensity, closed-canopy fruit plantations. Plantation habitats were found to maintain ecologically and functionally rich assemblages of birds. However, these assemblages were highly modified compared to the secondary forest and with significantly lower functional evenness. Closed-canopy plantations acted as a middle ground between open-canopy plantation and secondary forest. These results suggest that preservation of secondary forest will be essential to conservation efforts, but closed-canopy plantation may present a viable compromise between conservation and human development objectives.

Keywords: Agroforestry, birds, community composition, ecosystem functioning, land-use change

Introduction

A wealth of literature exists detailing the negative impacts of plantation agriculture on avian communities within tropical and sub-tropical forest systems (Foley *et al.* 2005, Waltert *et al.* 2005, Barlow *et al.* 2007, Flynn *et al.* 2009, Philpott *et al.* 2008, Tscharntke *et al.* 2008, Phalan *et al.* 2013, Clough *et al.* 2016). Conversion of tropical forest to agriculture plantations is consistently accompanied by a loss of structural diversity and tree cover, changes to understory and ground cover plant composition, forest 'edges', and a loss of connectivity, which result in altered micro-climates and resource availability. (Foley *et al.* 2005, Fischer *et al.* 2007, Steffan-Dewenter *et al.* 2007, Gardner *et al.* 2010). These changes introduce new constraints and opportunities to the system and alter inter-specific interactions, providing some species, usually generalists, with a competitive advantage. The resulting biased loss of bird species creates profoundly modified avifaunal communities dominated by limited functional guilds and traits (Fischer *et al.* 2007, Philpott *et al.* 2008, Tscharntke *et al.*

2008, Clough *et al.* 2009, Maas *et al.* 2009, Poch and Simonetti 2013).

Loss of functional groups is associated with the erosion of functional diversity, ecosystem resilience, and functioning (Hooper *et al.* 2005, Cardinale *et al.* 2006, Fischer *et al.* 2007, Philpott *et al.* 2009, Naeem *et al.* 2012, De Beenhouwer *et al.* 2013, Whelan *et al.* 2015), mainly where groups contained species integral to specific functions (e.g., keystone species; Luck *et al.* 2003, Sekercioglu *et al.* 2004, Flynn *et al.* 2009). Ecosystem functioning is inextricably linked to the provision of ecosystem services essential to human well-being (e.g., clean water and crop pollination), preserving which depends on the protection of ecosystems and their biological underpinnings. This is especially true of avifauna, which plays a crucial role in maintaining myriad ecosystem functions, including pollination, predation, seed dispersal, and nutrient cycling (Sekercioglu 2012, Whelan *et al.* 2015, Ayodeji and Kilishi 2019).

In the tropics, there is a desperate need to embrace a new development paradigm which recognizes the interconnectedness of diverse wildlife communities and vital ecosystem services and seeks to preserve both (Scherr and McNeely 2008, Chazdon *et al.* 2009a, Perfecto and Vandermeer 2010, Tscharntke *et al.* 2012, Melo *et al.* 2013, Cottee-Jones *et al.* 2015). This is particularly true in Madagascar, where over 80% of the population rely heavily upon ecosystem services (Neugarten *et al.* 2016) and shifting agriculture poses a significant threat to avifaunal communities (13% listed as threatened and 44% in decline; Ingram and Dawson 2005, Gardner *et al.* 2010, Irwin *et al.* 2010, Clark 2012, IUCN 2019)

The continued destruction of Madagascar's natural systems will benefit neither the country's wildlife nor the majority of its local population, yet history shows there is limited political drive and available resources in Madagascar to enforce effective conservation measures (Clark 2012, Toillier *et al.* 2011). Consequently, it appears that preserving species within human-modified landscapes, although unideal, will be necessary (Clough *et al.* 2016).

A growing body of literature is dedicated to assessing the value of multi-tiered, structurally complex, and low-intensity agriculture in maintaining biodiversity across the tropics (Schroth and Harvey 2007, Steffan-Dewenter *et al.* 2007, Bhagwat *et al.* 2008) and in Madagascar specifically (Gardner *et al.* 2010, Dewi *et al.* 2013). This is because the structural complexity of agroforestry systems allows them to retain some functional complexity and maintain vital function and services such as carbon sequestration, soil fertility, drought resistance, biological pest control, and biodiversity conservation (Sileshi *et al*. 2007, Clough *et al*. 2009, Jose 2009, Tscharntke *et al.* 2011, Martin *et al.* 2012, De Beenhouwer *et al.* 2013, Perfecto *et al.* 2014). Indeed, their resemblance to natural forest and provision of niche and resource diversity supports a variety of avian functional guilds and even some forest specialist species (Philpott *et al.* 2008, Martin *et al.* 2012). It is therefore unsurprising to find that previous studies have claimed agroforestry systems can support high levels of avian ecological and functional diversity (Waltert *et al.* 2005, Harvey and Gonzalez-Villalobos 2007, Bhagwat *et al.* 2008, Rocha *et al.* 2015).

Much of sub-Saharan Africa provides an ideal environment for agroforestry for myriad reasons: (1) small-holder farming is the dominant land-use type; (2) local communities are dependent on ecosystem services; (3) there is a limited legal designation and enforcement of protected areas (Erdmann *et al.* 2010); (4) most new cropland created by 2030 is expected to occur within sub-Saharan Africa and South America (Phalan *et al.* 2013); and (5) the Afro-tropics has been identified as a conservation priority for forest-dependent birds (Buchanan *et al.* 2011). However, there is currently a disproportionate focus on Neotropical agroforestry systems within scientific literature (Sileshi *et al.* 2007, De Beenhouwer *et al.* 2013, Maas *et al.* 2016), and a lack of consideration of changes to avian functional groups within Afro-tropical studies (Sekercioglu 2012).

In light of the lack of data available for the Afro-tropics, this study aimed to determine the avian conservation value of plantation forests on the small Madagascan Island of Nosy Komba. However, rather than merely assessing ecological diversity within Madagascan plantation systems, this study aimed to explore these systems' stability utilizing insights provided by functional diversity metrics (Cadotte *et al.* 2011, Calba *et al.* 2014, Monnet *et al.* 2014).

Located in the Sambirano eco-region of the north-west, Nosy Komba provided various landscapes embedded in a mosaic of secondary and bamboo forests. Fifteen study sites were selected within low-intensity agroforestry systems (closed-canopy plantation; CCP), open-canopy monoculture plantations (OCP), and secondary forest (SF). Avian diversity, chosen for its vulnerability to habitat-change and value as a bioindicator, was assessed using four response metrics (observed richness, estimated total richness, species diversity, and community composition). Changes in ecosystem service provision potential for each habitat type was assessed using avian functional diversity metrics (functional richness, evenness, and divergence) as a proxy.

Based on existing literature, predictions were as follows: (1) avian richness in plantation systems will be equal to that of the secondary forest, (2) plantation forests will demonstrate lower avian diversity and an altered community composition relative to the secondary forest, (3) closed-canopy plantation will support a more diverse assemblage of birds more closely resembling secondary forest composition than open-canopy plantation, and (4) open-canopy plantation will exhibit lower avian functional diversity than both secondary forest and closed-canopy plantation.

Material and methods

Nosy Komba (alternatively known as Nosy Ambariovato) (13° 28'16.62" S, 48° 20'56.17" E) is a volcanic island situated within the Sambirano eco-region of north-west Madagascar, approximately 2.7 km from Nosy Be. The island is about 25 km² in the area and reaches a peak altitude of 622 m (Roberts and Daly 2014).

The island has lost all of its primary forests due to historical felling during the French colonization of Madagascar (1894–1959; Rohrer-MacGregor, C. 2013. French in Madagascar: A Colonial Language After Independence. Syracuse University SURFACE. Available from https://surface.syr.edu/honors_capstone/51/ [Accessed 18 January 2018], Roberts and Daly 2014). Nosy Komba's north side is dominated by a mosaic of the plantation, bamboo forest, open grassland, and swamps situated within a regenerated secondary forest matrix. The higher altitudes support mono-crop and mixed-species plantations, including coffee, pepper, cocoa, chili, sugarcane, vanilla, and fruit plantations. The northern part of the island is dominated by invasive bamboo from the mainland (Roberts and Daly 2014).

Site selection

Surveys were focused within a 2km radius of the Madagascar Research and Conservation Institute (MRCI) base camp (13° 44' S, 48° 33' E, Fig. 1). Fifteen study sites were established, encompassing three habitat types: (1) secondary Sambirano forest (> 30 years since abandonment) (SF, n = 8), (2) mono-crop open canopy plantation (OCP, n = 3), and (4) mixed-crop closed-canopy plantation (CCP, n = 4). We categorized forest types according to the characteristics described in table 1. Distance point-counts had a 25 m fixed radius. All sites were spatially independent of one another (a minimum of 200 m between them) to minimize the risk of duplicate recordings.

Bird and habitat measurements

Bird abundance within the three habitat types was quantified using point-count surveys. Surveys were conducted by one member of MRCI staff and three to five volunteers. All surveyors were trained in species identification and passed a computer identification test before participation. Surveyors waited five minutes upon arrival at a study site before beginning a survey. In this time, the weather conditions (cloud cover, precipitation, and wind speed) were assessed. After this rest period, birds occurring within the 25 m fixed radius were recorded. The information recorded with each observation included: species, number of individuals, distance from the observer, substrate, and time.

Point-count surveys were conducted between 30 May 2016 and 5 July 2017. All inquiries were 10 minutes in duration and commenced between 06:00 and 10:00. The number of studies conducted at each site varied from 7 to 65; the number of surveys within each habitat type is as follows: CCP (n = 159), SF (n = 147), and OCP (n = 176).

Study sites were incorporated into five-set routes. Routes were selected for the survey via random selection, and the direction of sampling was regularly alternated to avoid systematic bias. Therefore, sampling encompassed a wide range of environmental conditions and avifaunal activity patterns. Data was not collected during Nosy Komba's wet season (January-February), as avifaunal activity was deemed too low.

Habitat surveys were conducted between 29 January 2016 and 5 July 2017. Two transects were established in a cross formation, with the center point of the study is located at the intersection. The direction of the transect lines was determined using compass points. Five 1 x 1 m plots were formed 1 m from the transect line along all four arms. The side of the transect line to establish the plot was determined by flipping a coin. The environmental characteristics measured within subplots are detailed in table 1.

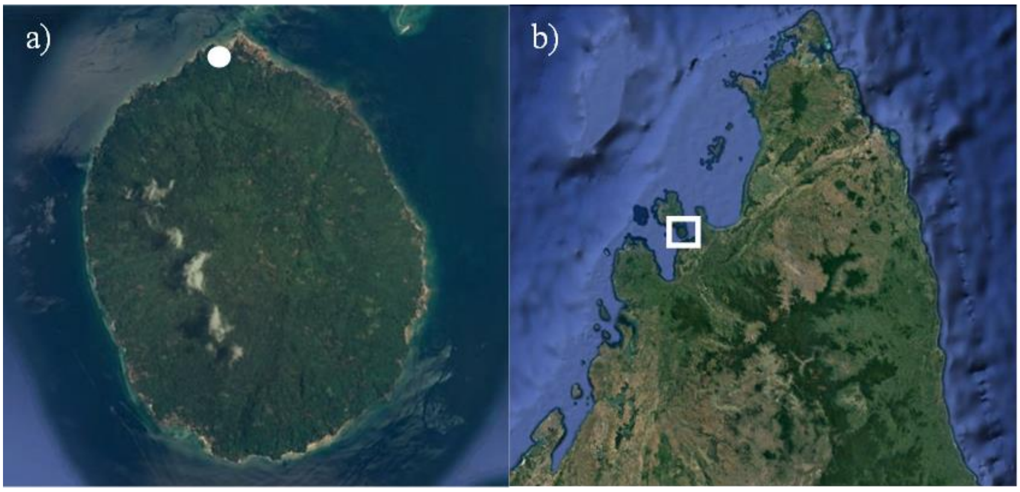

Figure 1. Location of Nosy Komba in relation to mainland Madagascar (b) and the position of the Madagascar Research and Conservation Institute (MRCI) camp on Nosy Komba (a). Nosy Komba is highlighted by a white box (b), MRCI base camp is indicated by a white circle (a). (Map sourced from Google EarthTM. 2018 Google; Image: Landsat/Copernicus (a); Image: 2018 TerraMetrics/ Image: 2018 National Centre for Space Studies/Airbus/ Image: 2018 Digital Globe (b); data: Scripps Institute of Oceanography, National Oceanic and Atmospheric Administration, U.S Navy, National Geospatial-Intelligence Agency, General Bathymetric Chart of the Oceans)

Data analysis

Data analysis was completed using R statistical software v. 3.2.2 (R Core Team 2016), and packages car (Fox and Weisberg

2011), cluster (Maechler *et al.* 2016), Dunn Test (Dinno 2017), *FD* (Laliberte *et al.* 2010), companion (Mangiafico 2017), and vegan (Oksanen *et al.* 2017). The analysis was conducted exclusively on observational data, as inexperienced surveyors were unable to determine whether calling birds were within the survey threshold.

Real species richness was estimated for each site using the Chao1 function within EstimateS (Colwell 2013). This method accounts for uneven sampling effort between sites and heterogeneity in species detection probabilities in different habitats (Chao and Chiu 2016). Bird detection probability was calculated for each habitat type as the ratio between observed species richness and estimated species richness. Observed species richness and diversity were compared between habitats using one-way ANOVA (lm) or Kruskal-Wallis (Kruskal test) tests from the packages rcompanion and car, respectively. Species richness refers to the total number of species recorded. Species diversity refers to values produced utilizing Simpson's Diversity Index and accounts for presence and abundance. Post-hoc Tukey Honest Significant Difference and Dunn tests were used to assess the significance of pairwise comparisons using packages Vegan and Dunn.test. Data was standardized for research effort using the equation (x/n), where n = surveyor hours and x = species abundance.

Table 1. Environmental characteristics of sites categorized into the secondary forest (SF), open-canopy plantation (OCP), and closed-canopy plantation (CCP) by Madagascar Research and Conservation Institute, Nosy Komba, Madagascar. Values represent the sum of seventeen 1 × 1 m subplots within each study site, averaged across the entire forest type. Heading abbreviations are tree density = density of woody and palm trees > 15 cm in circumference at breast height (CBH); sapling density = density of woody and palm trees < 15 cm CBH; canopy cover = coverage (%) of the forest canopy; and human-plant abundance = the abundance of individual plants belonging to species harvested for human agriculture

Forest type	Tree density	Sapling density	Canopy cover (%)	Human plant abundance
Secondary forest	22	206.67	78.75	10
Open-canopy plantation	8.34	27.67	38.69	141.25
Closed-canopy plantation	21.67	85.67	67.11	73.67

Community composition was compared between habitats using Bray-Curtis dissimilarity on abundance data with the PERMANOVA (vegan) test statistic. Community composition was visually represented by non-metric multidimensional scaling (NMDS; vegan) with 100 iterations. SIMPER analysis was applied to the Bray-Curtis matrix to determine which species contributed significantly to the dis-similarities. Data were log(x + 1) transformed before SIMPER analysis to minimize the contribution of highly abundant species such as Souimanga Sunbird (*Cinnyris sovimanga*) and Madagascar Bulbul (*Hypsipetes madagascariensis*). The nestedness of communities across forest types was calculated using the nestednodf function (vegan) by comparing nestedness values for study sites within each forest type and then across the entire landscape.

Functional richness, evenness, and divergence were calculated using the dfFD function of the FD package applied to bird useful trait and abundance matrices (Laliberte *et al.* 2014). Functional richness refers to the number of species with unique trait combinations, whereas functional evenness represents the distribution of abundances across niche space (i.e., the number of individuals with each trait combination; Mason *et al.* 2005). Functional divergence represents the degree of niche differentiation within a habitat (Mason *et al.* 2005).

Traits included in the analysis of functional diversity were selected based on the methodology of Philpott *et al.* (2009) and included: staple diet, foraging strata, minimum weight, maximum weight, and migration behavior. A detailed breakdown of these traits can be found in table 3 of the supplemental information. Significant differences between forest types for all four variables were tested for using ANOVA or Kruskal-Wallis tests. A disproportionate contribution of just one trait was ruled out by removing individual characteristics, repeating the analysis, and comparing the results for significance. The correlation between functional diversity metrics and species richness and ecological diversity was assessed using Pearson's correlation coefficient, where the assumptions of the test were met, and Spearman rank-order correlation where they were not (cor.test). Significant correlations were further explored using a simple linear regression model (lm) or generalized linear model (glm) where the assumptions for the former were not met.

Results

A total of 482 point-count surveys were conducted between 30 May 2016 and 5 July 2017. Across this period, 2201 records (single detections of bird individuals) were obtained representing 20 species, all classified as Least Concern except for Madagascar Sparrowhawk (*Accipiter madagascariensis*) which is classified as near threatened (IUCN 2019). However, the populations of several recorded species are in decline, and seven of the 20 species are endemic to Madagascar (Table 1, supplemental information; IUCN 2019).

Recorded species represent 67% of the known landscape composition (Table 2). The true gamma diversity of Nosy Komba is likely to be higher than observed, as only the northern side of the island has been surveyed, and birds that inhabit coastal areas exclusively were not included. Species detection probability (Sobs/Sest) across all study sites averaged 75.45 % ± 0.086 (Table 2). Open-canopy plantation demonstrated the highest average detection probability (90.97 % ± 0.056), followed by CCP (79.21 % ± 0.21). The average detection probability within SF sites was 69.07 % ± 0.13, a value significantly lower than other forest types ($F_{2,12} = 16.28$, $P < 0.001$, $r^2 = 0.69$).

Table 2. Average avian abundance per survey[a], observed species richness[b], estimated total species richness (Chao 1), the proportion of estimated total species richness observed[d], and the number of unique species[d] recorded within closed-canopy plantation (CCP), open-canopy plantation (OCP), and secondary forest (SF) over the survey period. The number of species observed as a proportion of total richness[e] (all species recorded on surveys) and total landscape richness[f] (species recorded opportunistically and on surveys) are also presented

Birds							
Forest Type	n[a]	sobs[b]	Chao 1	Coverage[c]	Excl. species[d]	Completeness[e]	Landscape completeness[f]
CCP	1.22	16	18	89	0	69	53
OCP	0.12	19	23	83	2	83	63
SF	8.76	12	22	55	1	52	40
All		20	27	74			67

Avian richness was estimated to be highest in OCP, followed by SF then CCP (Table 2). Open-canopy plantation supported the greatest proportion of the recorded and known landscape total (Table 2). When considering the forest type as a whole, observed species richness was highest in OCP and lowest in SF (Table 2). This pattern was not supported by average species richness levels when standardized for surveyor effort or as a multi-site average, with both plantation sites demonstrating average species richness levels lower than that of SF (Fig. 2). However, these differences in average species richness were not statistically significant ($F_{2,12}$ = 2.43, P = 0.130, r^2 = 0.17). Conversely, average avian ecological diversity was found to be highest in OCP, followed by CCP and then SF, but again, these differences were non-significant ($\chi^2_{2,12}$ = 3.47, P = 0.177).

Community composition varied significantly between habitat types (K = 2, $F_{2,12}$ = 2.83, P = 0.004, r^2 = 0.38). Closed-canopy plantation and OCP had the lowest dissimilarity value of 0.15, followed by a dissimilarity value of 0.20 for CCP and SF. Open-canopy plantation and SF demonstrated the greatest dissimilarity in community composition with a value of 0.29. Figure 3 shows a limited overlap between the community compositions of the three habitat types. Indeed, figure 3 shows no overlap between the community compositions of OCP and SF habitats when plotted in multidimensional space, whereas CCP overlaps only sparingly with both OCP and SF. Table 4 of the supplemental information presents the species with the greatest contributions to each pairwise dis-similarity. Plantation habitats supported more Crested Drongo (*Dicrurus forficatus*), Madagascar Bee-eater (*Merops superciliosus*), Madagascar Bulbul, Madagascar Buzzard (*Buteo brachypterus*), Madagascar Red Fody (*Foudia madagascariensis*), Souimanga Sunbird, Madagascar Coucal (*Centropus toulou*), and Madagascar White-eye (*Zosterops maderaspatanus*) than SF sites. Open-canopy plantation supported more African Palm Swift (*Cypsiurus parvus*) and Madagascar Green Pigeon (*Treron australis*) than SF and CCP sites. Secondary forest supported one unique species (Madagascar Sparrowhawk), and OCP supported two (Madagascar Green/ Long-billed Sunbird [*Cinnyris notatus*] and Madagascar Brush Warbler [*Nesillas typica*]).

Avifauna communities across the fifteen study sites on Nosy Komba displayed a high degree of nestedness (NODF = 82.65). This level of nestedness exceeded that of communities within CCP, SF, and OCP when calculated individually (NODF = 47.31, NODF = 30.42, and NODF = 37.24, respectively). Open-canopy plantation communities also demonstrated a high degree of nestedness with both CCP (NODF = 72.40) and SF (NODF = 80.40) communities. In contrast, the level of nestedness between SF and CCP communities was lower (NODF = 61.84).

The abundances of insectivores, invertivores, nectivores, graminivores, ground feeders, understory feeders, and canopy feeders varied significantly between forest types (df = 2 and 12, $P < 0.050$). Significantly more individuals in each category were recorded within OCP sites than SF sites (df = 2 and 12, $P < 0.050$), and OCP sites also contained significantly higher abundances of graminivores, ground feeders, and canopy feeders than CCP (df = 2 and 12, $P < 0.050$). Closed-canopy plantation hosted significantly more nectivores than SF ($F_{2,12}$ = 18.63, $P < 0.001$, R^2 = 0.72).

All functional traits included in the analysis had a significant effect on calculated FRic values (df = 14, $P < 0.010$). Feeding behavior and diet had a significant effect on FEve values (df = 14, $P < 0.010$), and feeding behavior, minimum and maximum body size significantly impacted upon FDiv values. These results suggest that all selected functional traits impact considerably on at least one functional diversity metric, validating their inclusion in the analysis.

Functional richness and functional evenness were significantly different between forest types (Fig. 4a, $\chi^2_{2,12}$ = 6.82, P = 0.033; Fig. 4b, $F_{2,12}$ = 6.14, P = 0.015, r^2 = 0.42). Open-canopy plantation had the highest functional richness of 0.32 ± 0. Closed-canopy plantation and secondary forest demonstrated functional richness values of 0.24 ± 0.055, and 0.16 ± 0.027, respectively (Fig. 4a). In contrast, SF had the highest functional evenness, with a value of 0.72 ± 0.040. Closed-canopy plantation and OCP had functional evenness values of 0.53 ± 0.048, and 0.51 ± 0.023, respectively (Fig. 4b). Differences in functional divergence and dispersion between forest types were non-significant.

Standardised species richness had a significant positive correlation with FRic (*r* = 0.79, df = 14, *P* = 0.00048) and a moderate negative correlation with FEve which neared significance (*r* = -0.50, df = 14, *P* = 0.060). Species ecological diversity had a significant positive correlation with FEve (*r* = 0.88, df = 14, P = 1.74e-05) and a significant negative correlation with FRic (*r* = -0.81, df = 14, *P* = 0.0023). When incorporated into simple linear or generalised linear models, all of the aforementioned correlations were found to have a statistically significant regressive relationship (*P* < 0.050).

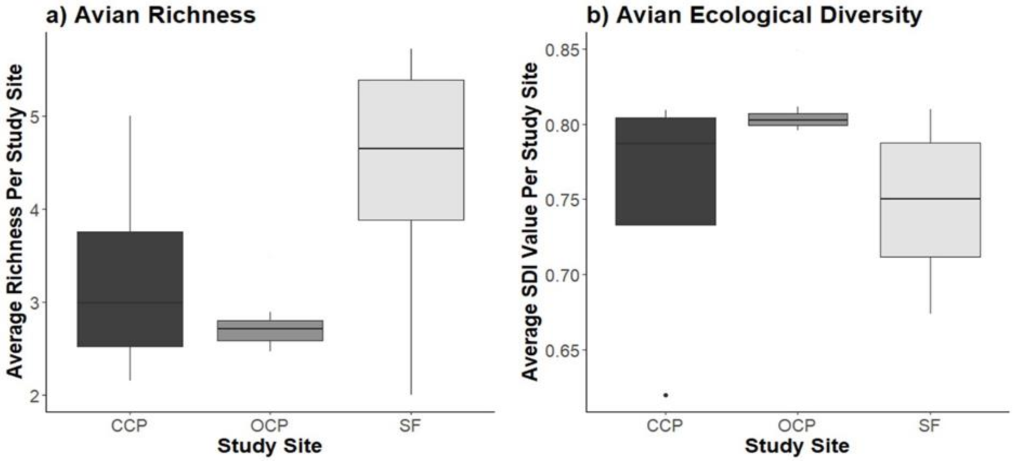

Figure 2. Box plots demonstrating the average avian richness (a) and ecological diversity (b) of bird communities recorded during 10-minute point-count surveys within closed-canopy plantation (CCP), open-canopy plantation (OCP), and secondary forest (SF) sites on Nosy Komba, Madagascar. The black lines indicate mean avian richness and ecological diversity, the boxes show 95% confidence intervals, and the dotted lines display standard error. Filled points represent outliers

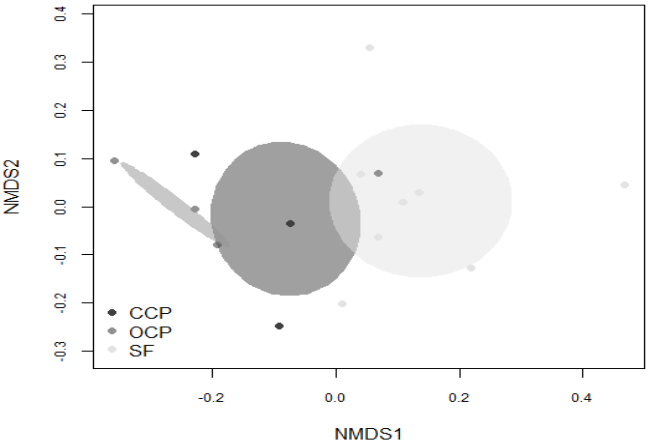

Figure 3. Non-metric multi-dimensional scaling ordination of avian community assemblages within 15 study sites on Nosy Komba, Madagascar (K = 2, stress = 0.08, *P* = 0.004, R^2 = 0.38). Points represent individual study sites and ellipses demonstrate the standard deviation from the centroid for the community

assemblages of each study site in multidimensional space. Colour designations are: light green = closed-canopy plantation (CCP), blue = open-canopy plantation (OCP), and dark green = secondary forest (SF).

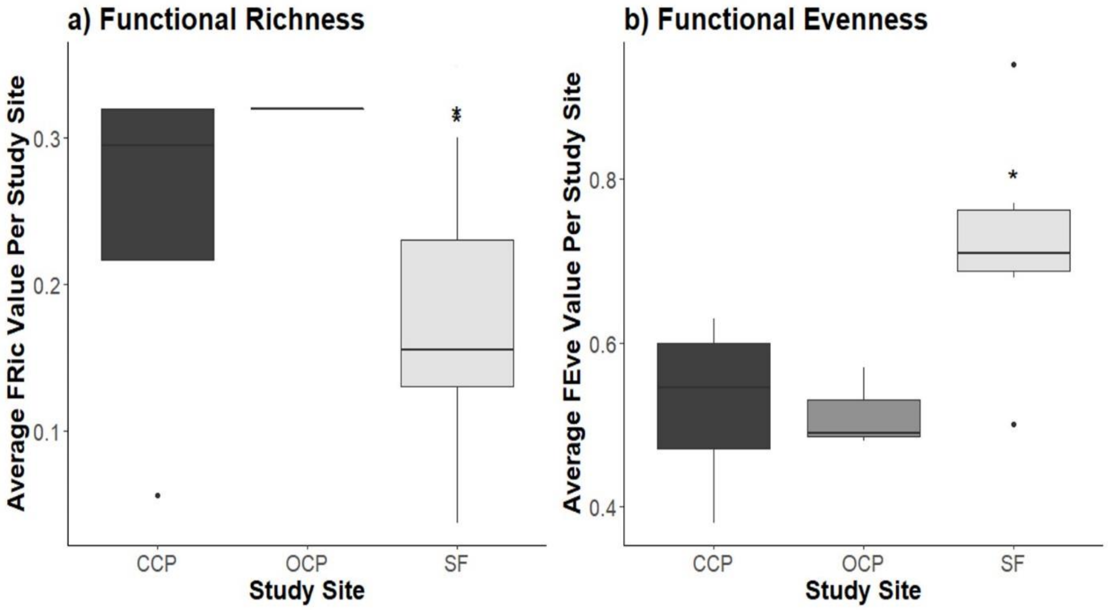

Figure 4. Box plots demonstrating the functional richness (FRic; a) and functional evenness (FEve; b) of bird communities recorded during 10-minute point-count surveys within closed-canopy plantation (CCP), open-canopy plantation (OCP), and secondary forest (SF) on Nosy Komba, Madagascar. The black lines indicate mean FRic or FEve, the boxes show 95% confidence intervals, and the dotted lines display standard error. Empty points represent outliers. A * indicates a significant difference with at least one other study site, revealed by Dunn (a) or Tukey (b) post-hoc tests. *= P<0.05, **= P<0.01, ***= P<0.001.

Discussion

On Nosy Komba, plantation habitats are an essential source of food and household income. Consequently, there has been a steady conversion of Nosy Komba's forest to plantation agriculture and simplification of existing plantation systems, development activities facilitated by a complete lack of legal protection of Nosy Komba's forest and limited political will to support the development of Nosy Komba's communities (Freudenberger. 2010. Paradise Lost? 25 years of USAID Environment Programs in Madagascar. Available from www.usaid.gov. [Accessed 21 June 2018], Andreone *et al.* 2012, Waeber *et al*. 2016). Given the potential impacts of the widespread simplification of forest habitats, this study contributes to a growing body of scientific literature assessing the implications of land-use change for Madagascan birds in the context of smallholder-driven plantation agriculture. It is one of few studies to assess the impact of plantation establishment on avian community composition *and* functional diversity within Madagascar's secondary forest, the conservation value of which is expected to increase over time (Chazdon *et al*. 2009b). It is also the first to assess the impact of land-use change on avian communities within the Sambirano eco-region.

Estimated avian richness was found to be similar between habitat types (Table 2). Though average richness per study site was higher in open-canopy plantations (OCP) than secondary forest (SF) and closed-canopy plantation (CCP; Fig. 2a), no significant difference was found between them. Similarly, no significant difference in avian ecological diversity was identified between the two plantation habitats and SF.

Though previous studies witnessed a decline in avian richness and ecological diversity within plantations compared to the natural forest (Sodhi *et al.* 2005, Philpott *et al.* 2008, Beenhouwer *et al.* 2013, Edwards *et al.* 2017), some have reported similar or even higher levels of avian richness in agricultural settings (Maas *et al.* 2009, Van Der Wal *et al.* 2012, Luck *et al.* 2013). This increase in richness is the result of niche creation or increased availability of existing niche space, which facilitates an influx of individuals/species with traits capable of utilizing the new resources (Martin *et al*. 2012, Sekercioglu 2012, Greenler and Ebersole 2015).

In many circumstances, a change in habitat structure and resource availability triggers the loss of specialist, endemic, and disturbance-sensitive species, impacting detrimentally on ecological diversity even when richness values are unaffected (Waltert *et al.* 2005, Komar 2006, Maas *et al.* 2009, Sekercioglu 2012). However, in the case of Nosy Komba, its secondary forest has already been rendered ecologically impoverished by historical felling activities (Barlow *et al.* 2007, Sayer *et al.* 2017). Consequently, sensitive species only contribute minimally to observable ecological diversity values. Instead, the loss of remaining specialist and sensitive individuals from OCP habitats and the domination of this habitat type by a few abundant species can be inferred from the high degree of nestedness between OCP communities and the two remaining forest types, which suggests OCP is an ecologically impoverished subset of natural forest rather than a diverse habitat type in its own right. It is further supported by the observed shift in avian community assemblage along a gradient with habitat disturbance.

Indeed, despite no significant differences in avian richness and ecological diversity, the community compositions of OCP, CCP, and SF were significantly different (Fig. 3).

Closed-canopy plantation supported a community assemblage more closely resembling SF than OCP, and, unlike CCP, OCP demonstrated no overlap with SF in the NMDS ordination. However, both plantation habitats were comprised primarily of generalist and forest generalist species such as crested drongo and souimanga sunbirds, lacking forest specialist species. This replacement of specialist individuals with generalist species could lead to altered proportions of functional groups within plantations, as reported for other tropical regions (e.g., Waltert *et al.* 2005, Komar 2006, Harvey and Gonzalez-Villalobos 2007, Clough *et al.* 2009, Sekercioglu 2012, Van Der Wal *et al.* 2012, Perfecto *et al.* 2014, Maas *et al.* 2016). Given the value of ecosystem services to Madagascar's human population (Neugarten *et al.* 2016), it is necessary to consider how a shift in avifaunal composition and representation of guilds impacts on ecosystem functioning.

Both open and closed-canopy plantation exhibited higher average functional richness (FRic) than SF, and the average FRic of OCP exceeded that of CCP. These results mirror previous studies observing similar or higher levels of avian functional diversity in agricultural habitats than corresponding intact forest sites (Martin *et al.* 2012, Luck *et al.* 2013, Cottee-Jones *et al.* 2015). As with species richness, it is likely a result of the recruitment of species to plantation habitats with novel functional traits, an extrapolation supported by the significant predictive relationship between avian richness and FRic in this study.

Higher functional richness is associated with improved ecosystem functioning and potentially better and more stable provision of essential ecosystem services (Cardinale *et al.* 2006, Flynn *et al.* 2009, Philpott *et al.* 2009). Therefore, considering only FRic it could be inferred that plantation habitats support ecosystem functioning and ecosystem service provision to an equal or greater extent than natural forest. However, it is uncertain whether higher FRic values alone demonstrate the ability of plantation habitats to support ecologically and functionally diverse avian assemblages in the long-term because there is a risk that niche spaces are experiencing low avian abundance will become uninhabited as a result of increasing human disturbance. Functional evenness (FEve) could be a better indicator of ecosystem functioning longevity, particularly in the context of small and highly variable plantation forest fragments (Mason *et al.* 2005).

Unlike with FRic, the three surveyed habitat types on Nosy Komba demonstrated significantly different FEve values, with SF maintaining considerably higher levels of functional evenness than both plantation habitats. This result has been reported previously by Barbaro *et al*. (2014). In the context of Nosy Komba, it could be inferred that human-modification has already altered the abundance and distribution of bird species within available niche space, suggesting vulnerability to further loss of bird species and functional traits which may inhibit ecosystem functioning and service provision (Philpott *et al.* 2009, Garcia and Martinez 2012, Sekercioglu *et al.* 2004, Whelan *et al*. 2015). Inhibition of ecosystem functioning within Nosy Komba's plantation habitats would have profound effects on communities reliant on ecosystem services, especially when combined with the impact of climate change (Neugarten *et al.* 2016). However, it should be noted that CCP demonstrated higher FEve than OCP.

Higher levels of functional evenness recorded within CCP compared to OCP are no doubt related to the habitat's ability to maintain a community composition more closely resembling natural forest (Fig. 3). The higher structural complexity of CCP (including large trees, denser understory, and more diverse floral assemblage) creates viable niche space for a higher proportion of SF's avian species (Philpott *et al.* 2008, Farwig *et al.* 2008, Van Der Wal *et al.* 2012), and the low-intensity management style renders this habitat type more suitable for species sensitive to human disturbance. However, unlike OCP, which is expected to decline in functional richness after an initially delayed loss of bird species vulnerable to human disturbance (Barlow *et al.* 2007), CCP is better positioned to maintain levels of avian ecological and functional diversity into the future. This insight is consistent with other studies conducted within both the neo and Afro-tropics (e.g. McNeely and Schroth 2006, Harvey and Gonzalez-Villalobos 2007).

Instead of legally protecting vast areas of Nosy Komba's secondary forest, an action which is no doubt preferable for the long-term preservation of diverse avifauna communities but is questionable in terms of ethicalness and feasibility, CCP could become a key focus for conservation activities on the island (De Groot *et al.* 2010), playing a vital role in preserving ecological diversity and maintaining ecosystem functioning and ecosystem service provision. (Fischer *et al*. 2007, Tscharntke *et al*. 2012, Maas *et al.* 2016). However, further research in Madagascar will be necessary to determine whether these results hold for other secondary forest systems, particularly within the more diverse rainforest systems of the east.

Conclusion

On Nosy Komba, both open and closed-canopy plantation are able to support numbers of avifauna species similar to that of secondary forest, suggesting some conservation value when small in area and located within a matrix of natural forest. However, the establishment of plantation on Nosy Komba disproportionately impacts sensitive forest-specialist species, resulting in profoundly altered community assemblages, which could threaten ecosystem functioning in the long-term. The results of this study suggest that the impacts of plantation establishment are mitigated to an extent when complex, shaded, low-intensity systems are adopted by small-holders, which appear to act as intermediaries between natural forest and open-canopy plantation both in terms of community structure and functional evenness. Given the inevitability of further forest loss and plantation establishment on Nosy Komba, closed-canopy systems at present appear to provide the best compromise between human development, species conservation, and ecosystem service preservation on the island.

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