

Research Article

Bird assemblages in a Malagasy forest-agricultural frontier: effects of habitat structure and forest cover

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Abstract

Increasing global human population and per-capita food consumption are expected to exacerbate the already massive agricultural footprint in tropical ecosystems. Madagascar is home to exceptional levels of biodiversity and is in the midst of severe land-use change, mostly driven by slash-and-burn, smallholder agriculture. Understanding the consequences of these agricultural practices for Malagasy native species is therefore of the foremost importance for the conservation of the nation's biodiversity. We surveyed bird assemblages inside and surrounding Ranomafana National Park, southeastern Madagascar, obtaining nearly 1,000 records of more than 60 species. At each study point, habitat structure was characterized by its vegetation complexity, and forest cover was quantified within circles of radii of 100, 500 and 750 m. We found that species richness was higher in forest than in agricultural areas, and responses to land-use change were found to be guild-specific, with frugivores being especially depleted outside forest areas, whereas granivores had higher species richness in the agricultural matrix. The number of recorded species with forest affinities was highly associated with landscape-scale forest cover, while open area and generalist species responded mainly to site-scale habitat structure. Our results demonstrate a turnover from forest-associated species to open area and habitat generalist species in Madagascar's smallholder agricultural areas. Our study underscores the conservation value of landscape-scale forest cover and of site-scale vegetation complexity. A double-stranded conservation approach, in which both landscape-scale forest cover and vegetation complexity are preserved would benefit conservation of the island's forest avifauna.

Keywords Biodiversity, agriculture, slash-and-burn, Ranomafana, Madagascar

Received: 19 April 2015; Accepted: 23 June 2015; Published: 28 September 2015

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Cite this paper as: Ricardo Rocha, Tarmo Virtanen and Mar Cabeza. 2015. Bird assemblages in a Malagasy forest-agricultural frontier: effects of habitat structure and forest cover. *Tropical Conservation Science* Vol. 8 (3): 681-710. Available online: www.tropicalconservationscience.org

Disclosure: Neither Tropical Conservation Science (TCS) or the reviewers participating in the peer review process have an editorial influence or control over the content that is produced by the authors that publish in TCS.

Introduction

Since its development, agriculture has been one of the chief drivers of land-use change, creating new landscapes with different capacities for retaining the communities of their original habitats [1-2]. Despite intensive landscape transformation, some agricultural areas do however retain a remarkable amount of biodiversity. In Europe, numerous species of conservation concern rely on habitats maintained or created by low-intensity farming [3] associated with more than 50% of the continent's important conservation areas [4]. In the tropics, an increasing body of literature shows that agricultural landscapes are not featureless areas of unsuitable habitat for biodiversity, but can indeed be remarkably rich in species richness and abundance [5-7]. However, the capacity of tropical agricultural landscapes to retain biodiversity is far from uniform, and assemblage composition in modified landscapes is often very different from that of the native habitats, after being depleted of old growth ecological specialists and local endemics [8-11].

Smallholder agriculture has been repeatedly identified as a main agent of tropical deforestation [12-14]. Much smallholder agriculture uses slash-and-burn cultivation, an ancient type of agriculture widespread in the tropics that has received little research attention or understanding of its impact upon native wildlife [15]. The few available studies suggest that compared to alternative agricultural land-use types with greater vegetation complexity such as multistrata agroforestry systems, bird assemblage composition in small-scale agricultural areas is very different from the old growth assemblages of the analysed areas [10, 16-20].

Madagascar is home to a unique combination of fauna and flora that is almost unmatched in its levels of endemism and species diversity [21-22]. The uniqueness of the island's biota and the magnitude of anthropogenic threat have led to its classification as one of the highest priorities for international conservation [23-24]. However, a combination of poverty, rapid population growth, insecure land-tenure, mining, hunting, agricultural expansion, and great demand for timber and charcoal production, poses a serious risk for much of the nation's remaining biodiversity [25-29].

Despite its proximity to the African continent, humans only reached the island some 2,000 years ago [30]. Human arrival was followed by the extinction of most of the islands' megafauna [31] and by a major change in forest cover [32]. In recent decades deforestation has continued apace, and in just half a century (c. 1953 to c. 2000), the island's total forested area decreased by nearly 40% [33] causing several recent faunal extinctions [34].

Although slash-and-burn (*Tavy* in Malagasy) is a chief driver of deforestation [35-36], studies analyzing its impact on the island's unique biota are notoriously scarce [37]. Two studies, however, have investigated how Malagasy bird assemblages react to agriculturally driven land-use change, both in the context of habitat loss and fragmentation [38-39] and focusing on species persistence in humanized matrix agroecosystems [40-41]. The studies show that Malagasy birds react to fragment area [38], matrix habitat type [41], and habitat structure [39], and are more likely to persist in matrix habitats containing isolated trees [40]. Elsewhere in the tropics the persistence of avifauna in humanized landscapes has been linked to local vegetation characteristics and the amount of forest cover at the landscape-level (e.g. [42-44]). However, in Madagascar this has not yet been explored, and as more than 50% of the breeding avifauna are endemic and many species are currently threatened by habitat loss, it is important to investigate this interaction [45].

Here, we investigate how Malagasy bird assemblages in a forest-agriculture frontier react to differences in habitat structure and forest cover, at a range of spatial-scales. Specifically, we ask: a) how do species richness and assemblage composition differ between continuous forest and smallholder agricultural sites? b) are differences guild-specific (*sensu* [46]), or associated with habitat preference or threat status? c) how is species richness affected by vegetation structure and the amount of forest cover at different spatial-scales? and d) does this relationship differ between forest-associated species and open habitat and generalist species?

Methods

Study area

We conducted the study in and around Ranomafana National Park, southeastern Madagascar. The park was established in 1991 and embraces ~43,500 ha of continuous humid forest within its core areas, and regenerating secondary forest especially near park edges. The park is surrounded by a very heterogeneous, rather open, smallholder agricultural matrix (Fig. 1 and 2). The area has annual rainfall varying from 1,700 to 4,300 mm, with a drier period from September to October and a rainfall peak from December to March [47]. Rice (dry and irrigated) is the main crop, and other crops include cassava, beans, peanuts, sugarcane, maize, taro, banana, peanuts, leafy vegetables, and sweet potatoes [48].

Survey design and bird census

A total of five transects (three in forest and two in agricultural areas), each consisting of 10 count stations, were spread across the landscape, and bird data were collected during November and December, 2010. Transects were as straight as possible and count stations were placed at intervals of 100 m along existing trails and footpaths.

Bird diversity data were recorded by a pair of observers acting as one (RR and local guide), using a fixed-radius point count method [49] in which all birds seen or heard within an approximate 50 m radius were recorded during five minutes at each station. Each of the 50 sampling points was visited three times, twice in the morning (05.30-09.30 a.m.) and once in the afternoon (16.00-17.30 p.m.) on days without strong rain or wind. A waiting period of two minutes prior

to the actual survey time was used to locate cryptic individuals and to allow birds to recover from disturbance by the arrival of the observers.

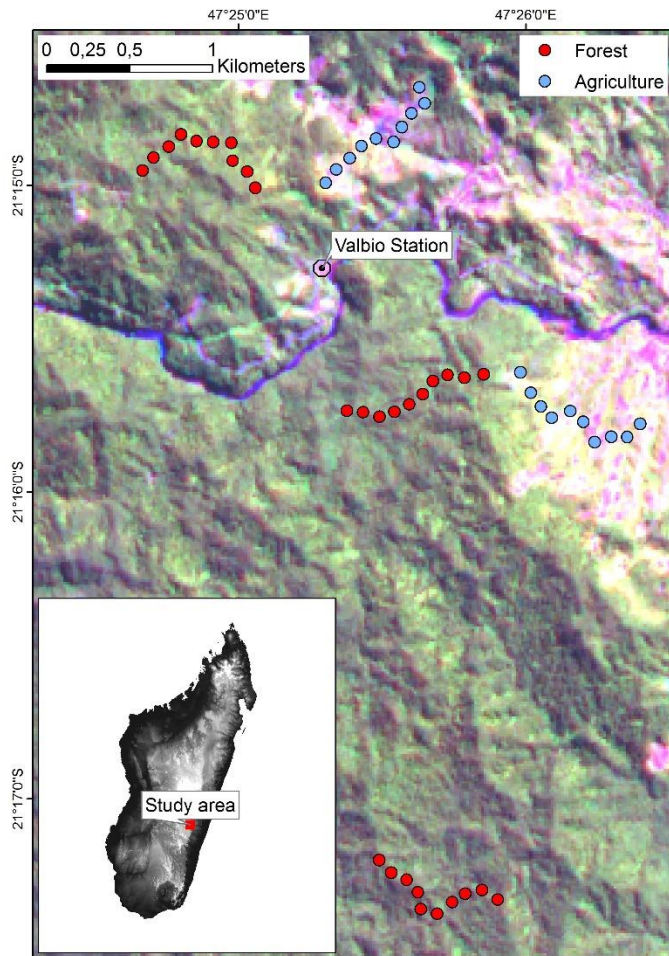


Fig.1. Location of the study area within Madagascar and detail of the study landscape where the location of the performed transects can be seen. Background image is from an Aster satellite image (acquired on 11.8.2004, channels 4,3,2=RGB).



Fig.2. Images from the study landscape. A: Mature forest inside Ranomafana National Park; B: Smallholder agricultural areas in the periphery of the park. Ranomafana National Park forest edge can be seen in the background. Photos by Tarmo Virtanen.

Habitat structure data

At each count station, local vegetation structure was characterized using protocols adapted from several sources [39, 50]. Tree basal area (m²/ha) was obtained using a relascope, and within a radius of 10 m, the diameter at breast height (DBH) of the nearest 10 trees from the count station was measured using a tape measure. Canopy cover was estimated from a canopy photo, and the height of the understory-, mid- and upper-canopy (m) was measured using a Hagl f Vertex IV measurement device. Abundance of bryophytes and lichens was visually classified into four categories (0 = none, 1 = very sparse, 2 = sparse, 3 = dense), and the percentage of leaf litter and bare ground cover was also visually estimated using six classes (0 = no cover, 1 = very sparse 0-20%, 2 = sparse 20-40%, 3 = medium 40-60%, 4 = dense 60-80%, 5 = very dense 80-100%). We used binoculars to locate, fruiting and flowering trees.

Landscape data

We used a handheld GPS (Garmin, Etrex Vista HCx) to record the geographical coordinates of each count station. A landcover map of the study landscape based on a classified Landsat 2007-08 image mosaic (30 m pixel size), verified by extensive ground-truthing [51], was used to determine the proportion of each land-use type within buffers of 100, 500 and 750 m radius. Additional GIS data layers were used to calculate the distance of each sampling site to the nearest human settlements and roads. Count site altitude and slope were extracted from a Digital Elevation Model of 15 m pixel size based upon Aster satellite image data (Appendix 1). These analyses were performed using ArcMap 9.0 (Environmental Systems Research Institute).

Statistical analysis

The difference in visual detectability between open habitats and dense tropical forest is great. This disparity affects the comparison of the number of conspecific individuals between habitat classes. To avoid this bias, we restricted our analysis to presence/absence data at each count station. A species was therefore counted as present at a given sampling station if it was recorded during at least one of the three survey visits. Additionally, since our focus was on habitat use, we excluded raptors and aerial feeders (swifts, swallows and bee-eaters) from the data analysis. We compared total species richness among different land-use types using randomized (1000x) sample-based rarefaction curves [52] calculated using EstimateS v.9 [53], and we assessed statistical significance against the 95% confidence intervals generated by the program. Bird species were assigned to different groups, based upon: feeding guilds; level of habitat preference in forest-, open area-, or both (generalist-species); and IUCN Red List Category [54] (Appendix 2). Guild and habitat preference classification was based on information collated from the available literature [38, 41, 55], in some cases supplemented by our personal observations. The same approach used to compare total species richness was used to explore habitat differences in the species richness of the different guilds, of forest vs open area and generalist species, and of non-threatened vs threatened (VU, EN or CR Red List Categories) and near threatened (NT) species.

Differences in assemblage composition among different sites were explored using a non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarity. This technique was selected because it makes no assumption about the distribution of the data and therefore is widely used for analysis of community data. Differences between forest and agricultural habitats were tested using a permutational multivariate analysis of variance (PERMANOVA) [56]. Both analyses were conducted using the "vegan" package in R v3.0.2 [57].

Vegetation structure values were $\log(x + 1)$ transformed, the mean and standard deviation were standardized to 0 and 1, respectively, and then submitted to a Principal Component Analysis (PCA). The scores of the first vegetation PCA axis were used as the predictor variable for habitat structure. To better interpret the generalized linear mixed model (GLMMs) habitat structure coefficients (see below), we used the inverse of the first PCA axis (PCA 1) as a model variable. This means that higher values correspond to more structurally complex habitats for vegetation structure.

The influence of habitat structure and landscape-scale attributes on total species richness and on the species richness of forest-associated species and open habitat and generalist species was investigated using GLMMs, specifying a Poisson distribution. Statistical inference in GLMMs can be undermined by severe collinearity between predictor variables [58]. In order to reduce collinearity between forest cover measurements at different scales, we recast each forest cover variable, so that the forest cover measurement at the largest radius (750 m) remained the same, while the variables measured at buffers of smaller radii have been recalculated by the difference between the original variable and the one that is nested within. Using this approach, the regression coefficients of new variables have different interpretations from the forest cover variable measured at the 750 m extent. Whereas the interpretation of the coefficients for forest cover measured at the 750 m extent remains the same, the coefficients of the new variables represent effects relative to the broader scale landscape context [59]. Subsequently, collinearity was assessed by calculating each predictor's variance inflation factors (VIFs) within a set of predictors that always included habitat structure and forest cover at the four analysed scales. Since VIFs >10 have been suggested to indicate "severe" collinearity [60], we used ecological rationale to reduce our set of predicting variables so that each predictor contained within the final set presented a VIF <5 . Our analyses were therefore restricted to a subset of *a priori* selected models, including reasonable combinations of habitat structure and forest cover at different scales. Transect was included in each model as a random term, and the most parsimonious models were selected using Akaike's information criterion corrected for small samples sizes (AIC_c) following Burnham and Anderson [61]. To quantify the goodness-of-fit for each model, we calculated marginal R^2 and conditional R^2 as they can be respectively interpreted as variance explained by only fixed effects and by both fixed and random effects [62]. The relative importance of each variable retained within the most parsimonious model sets was determined by performing hierarchical partitioning analysis [63] using the "hier.part" package, and spatial autocorrelation of the GLMMs residuals was inspected by means of Moran's I Test. GLMMs were fitted using Laplace approximation through the "lme4" package, and except otherwise specified, analyses were conducted in R v3.0.2 [57].

Results

We obtained 959 records from a total of 63 species, excluding all birds detected >50 m from the observer. Of these, six were records of raptors and aerial feeders and were therefore excluded from the analyses. Of the species considered in the analyses, 24 were detected only in forest stations and an additional six were detected only in agricultural count stations. Overall, the souimanga sunbird *Cinnyris souimanga* and the Madagascar bulbul *Hypsipetes madagascariensis* were the most recorded species, representing 9.8% and 9.1% of total observations, respectively. We obtained 45 records of seven threatened or near threatened species. Of these, 42 records, of six species, were from forest count stations, whereas the remaining three records were from agricultural areas and were all the Red-tailed Newtonia *Newtonia fanovanae* (Appendix 2).

Of the 57 species included in the analysis, 49 were classified as forest-associated species, whereas the remaining eight were open habitat or generalist species. All frugivorous and omnivorous species were classified as forest species, and the open habitat and generalist group was composed only of insectivorous and granivorous species. All species classified as forest-associated species were either regional endemics (Madagascar, Comores, Seychelles and Mascarene Islands) or restricted to Madagascar. Conversely, one open area specialist was a non-endemic native (the broad-billed roller *Eurystomus glaucurus*), and a second was an introduced species (the helmeted guineafowl *Numida meleagris*) (Appendix 2).

Species and guild richness

More species were recorded in forest ($S_{obs} = 52$) than in agriculture ($S_{obs} = 34$) count stations, and rarefied total species richness (\pm SD) differed significantly (as indicated by the 95% confidence intervals) between forest (47 ± 3.37) and agriculture assemblages (34 ± 3.28) (Fig. 3A). Rarefied species richness of forest-associated species was significantly higher in forest (43 ± 2.84) than in agriculture count stations (26 ± 4.09) (Fig. 3B), and the pattern was reversed for open area and generalist species, in which the rarefied species richness in agriculture (8 ± 0) more than double that for forest habitats (3.33 ± 0.8) (Fig. 3C). All but one of the species classified as threatened or near threatened were restricted to forest, which was reflected in the higher rarefied species richness of this group in forest habitats (6.12 ± 0.88 , forest; 1 ± 0 , agriculture) (Fig. 3D). The species-rich insectivorous group had higher species richness in forest (32.99 ± 2.57) than in agriculture areas (23 ± 3.71), but the difference was not significant (Fig. 3E). Higher rarefied species richness in forest than in agricultural sites was also observed for frugivores (3.66 ± 0.28 , forest; 2 ± 0 , agriculture) (Fig. 3F) and omnivores (3.99 ± 1.14 , forest; 3 ± 0.64 , agriculture) (Fig. 3D). Rarefied species richness of granivores was slightly higher in agricultural count stations (5 ± 0) than in forest habitats (3.89 ± 0.08) (Fig. 3H).

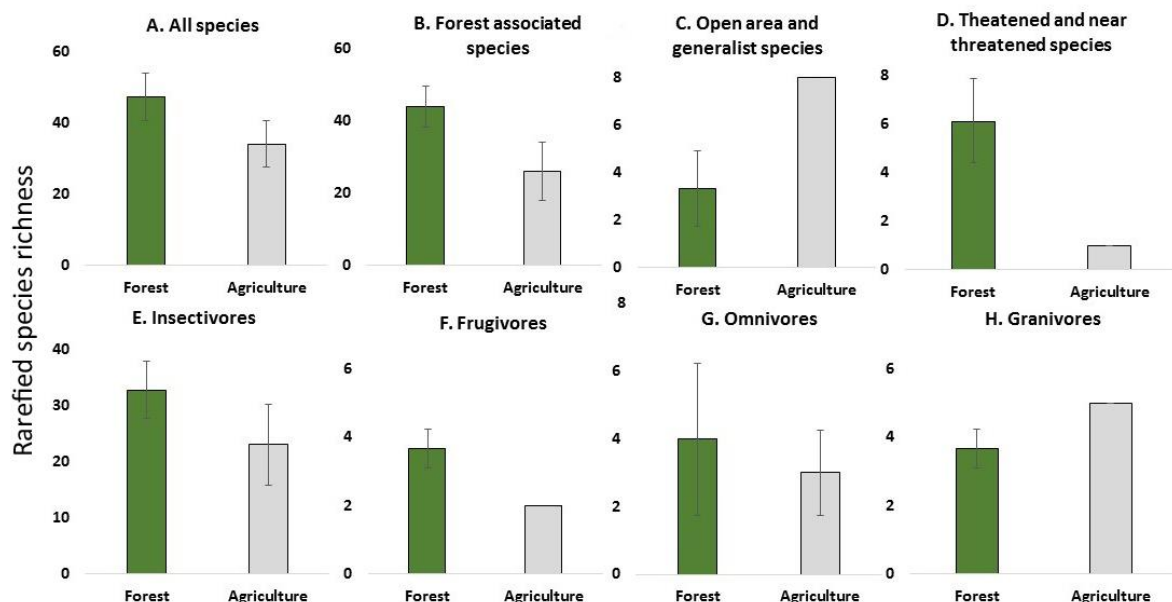


Fig.3. Sample based rarefaction for species richness in the two land-use types. Comparisons between forest and agriculture sites were based on the number of samples of the latter ($n = 20$ sampling sites). Error bars represent 95% confidence intervals and absence of error bars reflects confidence interval convergence to zero in the last data points (assessment of statistical significance between habitats is consequently not meaningful for panels C, D, F and H).

Assemblage structure

The NMDS ordination yielded a final solution with a stress value of 0.19, conveying a good representation of the data along the represented dimensions. Forest count stations were clearly separated from agricultural count stations, and grouping of same land-use count stations was significant ($F_1 = 24.615$, $R^2 = 0.339$, $P < 0.05$) showing that bird assemblages differ significantly between the two analysed habitats (Fig. 4).

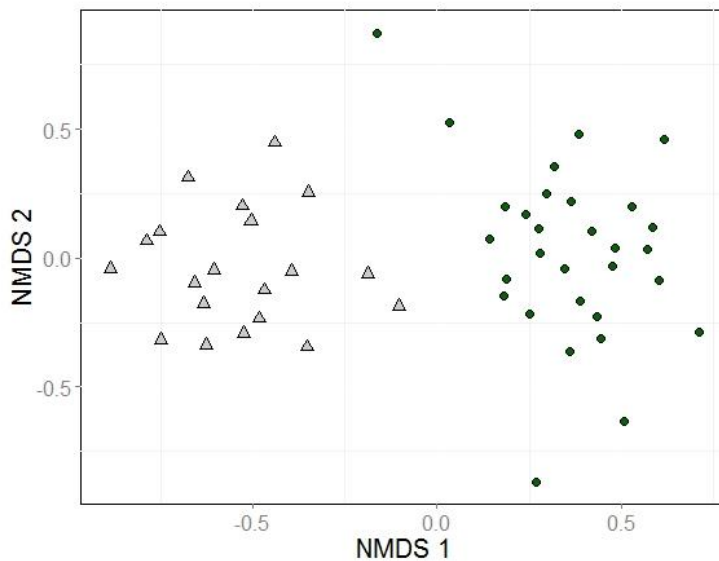


Fig.4. Ordination of study sites along non-metric multidimensional scaling (NMDS) axes showing independent clustering of forest (●) and agriculture sites (▲).

Bird-habitat relationships

The first axis of the vegetation composition PCA (PCA 1) accounted for 64.4% of the variance of the original vegetation data. This primary gradient was almost equally dictated by all vegetation variables, other than leaf litter and bare ground cover, which were better represented by the second PCA axis (PCA 2) (Appendix 3). PCA 1 represented a gradient from simpler habitat structural complexity, typical of open areas (positive values), to higher structural complexity, typical of forest sites (negative values), whereas PCA 2 represented a gradient from sites with higher bare ground percentage to sites with more leaf litter cover (Appendix 4).

For total species richness, forest cover at the landscape extent of 500 m was selected as the most parsimonious model (Akaike weight, $w_i = 0.52$), followed by forest cover at the landscape extent of 750 m ($w_i = 0.21$) (Appendix 5). Forest cover at the 500 m and 750 m landscape extents were again identified as the best predictors for the species richness of forest-associated species ($w_i = 0.35$ and $w_i = 0.26$, respectively). However, another plausible model ($\Delta_i < 2$) was recognized, including both habitat structure and forest cover at the 500 m extent ($w_i = 0.26$). Species richness of open habitat and generalist species was mainly associated with site-scale characteristics. For this group, one single-process model containing only habitat structure received the strongest support ($w_i = 0.43$) and, another plausible model ($\Delta_i < 2$), including habitat structure and forest cover at an extent of 100 m, was identified ($w_i = 0.35$). For all species or only forest-associated species, the relationships between species richness and habitat structure and forest cover were found to be positive. However, for only open habitat and generalist species, this relationship

was found to be negative (Fig. 5 plus Appendix 5 and Appendix 6 for additional modelling results).

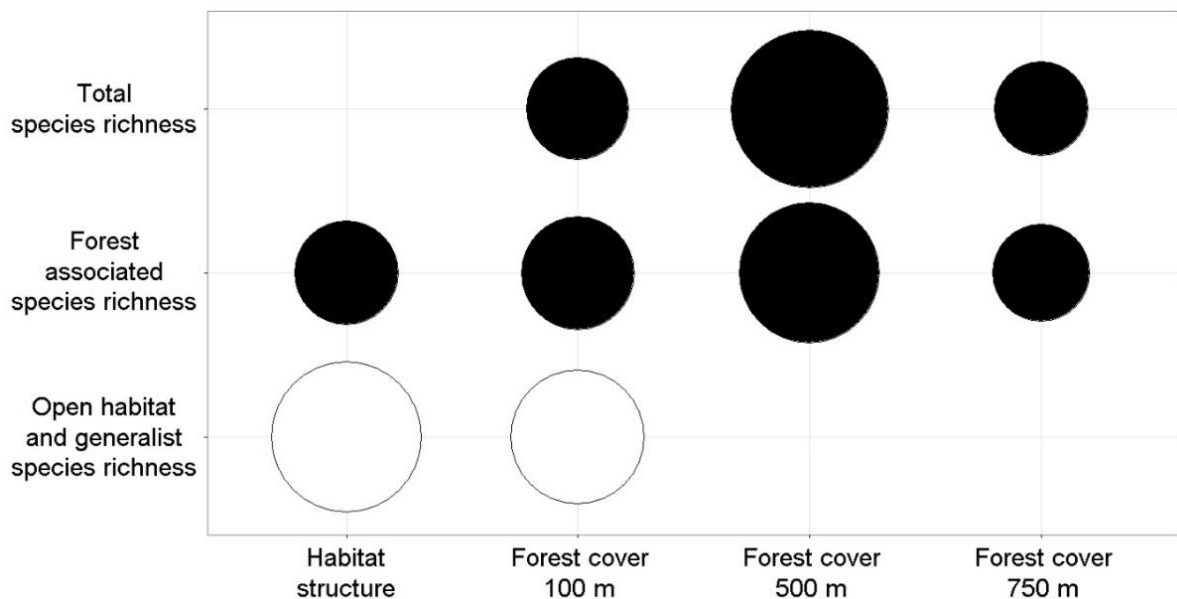


Fig.5. Model averaging results of the most parsimonious generalized linear mixed models (Akaike differences <2 from the best model) investigating the relationship between habitat structure [as given by the inverse of the 1st axis of the vegetation PCA, representing a gradient from higher structural complexity, typical of forest sites (positive values) to simpler habitat structural complexity, typical of open areas (negative values)] and landscape-scale forest cover on total species richness, forest-associated species richness, and open habitat and generalist species, Ranomafana, Madagascar. Symbol size is proportional to the variable relative importance as estimated by hierarchical partition analysis, and colour reflects the direction of the relationship: black – positive, white - negative. See Appendix 5 and Appendix 6 for additional modelling results.

Discussion

Consistent with previous studies [8-10, 18, 64], we found that compared to native forests, agricultural areas experience a considerable decrease in the overall number of species, a shift from more forest-associated birds towards open or habitat generalist species, and reduced resilience to habitat conversion in specific life history attributes such as insectivory. Our results therefore align with findings from elsewhere in the humid tropics, indicating that tropical forest bird assemblages are adversely affected by agriculture-driven habitat modification.

Species richness and assemblage structure

Of the 51 species detected during forest point counts, 24 (47%) were not detected in the sampled agricultural areas. This reveals an assemblage overlap of 53%, corresponding to 27 shared species between forest and agriculture count stations. A similar figure of assemblage overlap (48%) was found by a previous study analysing bird assemblages in forest areas and in the agricultural mosaic linking the national parks of Andringitra and Ranomafana [41], and a slightly lower overlap (35%), occurred between littoral forest remnants and the adjacent *Erica* spp.-dominated matrix in southeastern Madagascar [39]. The degree of structural contrast between the humanized matrix and the original forest habitats is a key determinant for species'

persistence [65]. More structurally complex agricultural habitats, like agroforestry plantations, accommodate bird assemblages more similar to undisturbed habitats than simpler ones (e.g. [10, 66]). The lower assemblage overlap found by Watson et al. [39], compared to the figures in our study and in Martin et al. [41], might be due to differences in contrast magnitude between the two sampled agricultural areas and the habitats they replaced.

Despite the geographic proximity of the Martin et al. [41] study landscape to ours, we found contrasting results in between-habitat (forest vs modified habitats) species richness patterns. Whereas we found higher species richness in forest count stations than in agricultural ones, Martin et al. [41] found richness to be higher in stations in the agricultural matrix, likely due to the greater diversity of agricultural habitats covered by Martin et al. [41]. Whereas our study was restricted to smallholder agricultural plots, Martin et al. [41] included forest patches, old fallows, eucalyptus plantations, isolated clumps, herbaceous fallows, dry crops and rice paddies. The much greater variety of humanized habitats sampled by Martin et al. [41] allowed the detection of a higher number of species exclusive to the agricultural mosaic. Whereas we only recorded six species in agricultural areas that failed to be detected in forest count stations, Martin et al. [41] found 14 (excluding the Madagascar kestrel *Falco newtoni*, not considered in this study). Six of these species were, however, aquatic, and therefore, given that we did not sample aquatic habitats, it is not surprising that we did not record them. A much more ubiquitous species in agricultural areas is the introduced common myna *Acridotheres tristis*, repeatedly recorded by Martin et al. [41], but although observed on several occasions during a non-survey period it was not captured by our study.

Bird guilds, species' habitat preferences and threat status

Different groups of bird species were found to respond differently to the conversion of forest into agricultural habitats. Not surprisingly, forest assemblages were characterised by a high proportion of forest-associated species, whereas agricultural areas were dominated by generalists and open habitat specialists. This high turn-over, from forest-associated species to bushland species, suggests that smallholder agriculture contributes little to the conservation of the forest bird assemblages native to our study landscape. Indeed, despite the proximity of our agricultural transects to the Ranomafana National Park border, only one of the six threatened or near threatened species sampled during this study was found to use the agricultural matrix. Insectivores present marked responses to land-use change [9, 67]. In our study, species richness of insectivores was found to be higher in forest areas, but the difference from agricultural stations was not significant. Our classification of "insectivores" grouped species with differences in foraging strategy and foraging strata. Martin et al. [41] subdivided this category into canopy insectivores, sallying insectivores, and terrestrial insectivores, enabling them to capture contrasting patterns within the "insectivore guild", so the species richness of canopy insectivores was greater in the forest corridor, while the species richness of sallying and terrestrial insectivores was higher in the agricultural matrix.

Despite some evidence of frugivore depletion in agricultural landscapes [10, 17, 20, 68], most literature presents the frugivore and omnivore guilds as less impacted by land-use change and often even more common in agricultural areas [8-9]. In our sampled landscape this trend held true for omnivores, for which no significant difference in species richness among forest and agriculture count stations was found, but not for frugivores, for which a pronounced decrease in the number of species was observed in the agricultural matrix. This reduction in frugivore species richness was found despite the fact that several fruit trees known to be used by some frugivores, such as *Ficus* spp., are planted by the farmers in their agricultural plots and are ubiquitous features in the landscape. Hunting pressure is one driver of lower abundance of

frugivorous birds in the agricultural landscapes of the endemic-rich island of São Tomé, West Africa [69]. In Madagascar several bird species, including the frugivorous Vasa parrots *Coracopsis* spp. and the Madagascar green pigeon *Treron australis*, are eaten in rural households [70-71]. Bird distribution in Madagascar's humanized landscapes likely reflects the synergistic effects of habitat modification and hunting. The interaction between these two drivers of biodiversity loss requires further study.

Habitat structure and landscape-scale forest cover

We found two notable patterns in our models of species richness in relation to habitat structure and landscape-scale forest cover. First, forest cover, especially at an extent of 500 m, was the best descriptor of total species richness in the landscape. Habitat amount has repeatedly been identified as the primary determinant of species richness and abundance [43, 72]. Our results are consistent with this, showing that forest cover has a stronger influence than local habitat structure on species richness. Secondly, forest-associated species and open area and generalist species present clear differences in species richness-environment relationships. Although higher habitat structural complexity was associated with higher species richness of forest-associated species, landscape-scale forest cover at the 500 m extent was still the predominant driver of forest-associated species numbers. Open habitat and generalist species richness, on the other hand, was chiefly dictated by habitat structural complexity and forest cover, at the smallest extent analysed (100 m). For this group, the relationship between forest cover and species richness was inverse to that found for forest-associated species. Open area and generalist species benefited from reduced forest cover and simpler habitat structure, suggesting that simple vegetation complexity, driven by the reduction of tree cover in agricultural landscapes, contributes to shifting bird assemblages from forest species to open/bushland species. This agrees with previous research indicating that trees are beneficial for the persistence of forest-associated bird species in Malagasy agricultural habitats [40] and indicates that the structurally simpler habitats typical of slash-and-burn farming areas favour a turnover from forest species to open area and generalist species.

Study limitations and directions to future research

Our study was conducted in a relatively small geographic area, during a short-time period (two months) at the beginning of the rainy season, and the point counts were limited to five minutes in duration, which may have been insufficient for bird species to reach an asymptote per point, especially in forest sites. Increased sampling could probably reveal extra species that might now be restricted to either forest or agricultural areas, and since resource abundance (e.g. fruit and insect) is likely to differ seasonally in response to changes in precipitation, additional sampling during both seasons could capture seasonal variations in bird assemblages in both forest and humanized habitats. Additional information about the use of pesticides and other chemicals by farmers would also greatly benefit the discussion of the observed patterns, especially for insectivorous species.

Determining which species' functional traits are vulnerable to human-caused environmental changes is an important challenge for the effective management and conservation of species-rich tropical landscapes [73]. We suggest that future studies identify which life history traits (e.g. body mass, clutch size and diet specialization) are affected by agriculture activities and how these interact with specific environmental characteristics (local vegetation structure and landscape attributes), resulting in local loss of functional traits.



Fig.6. Six Malagasy endemic birds. A: Velvet Asity *Philepitta castanea*; B: Madagascar Paradise Flycatcher *Terpsiphone mutata*; C: Pitta-like Ground-Roller *Atelornis pittoides*; D: Madagascar Red Fody *Foudia madagascariensis*; E: Lesser Vasa Parrot *Coracopsis nigra*; F: Chabert's Vanga *Leptopterus chabert*. Photos by Ricardo Rocha.

Implications for conservation

In addition to their intrinsic value, birds play pivotal roles as seed dispersers, pollinators, and suppressors of rodent and arthropod populations [74] (Fig. 6). Their biocontrol services greatly increase crop yields [75], and maintaining functionally diverse bird assemblages in agricultural landscapes is therefore an important management goal. Our study adds to the evidence that landscape-scale forest cover and site-scale vegetation complexity are important determinants of the persistence of bird diversity in tropical agricultural mosaics, and suggests that bird conservation in Malagasy agricultural landscapes will benefit from practices that preserve substantial amounts of tree cover.

The contribution of the rainforests of Madagascar to global biodiversity is well known. However, rapidly growing human population, coupled with high reliance on crops needing frequent agricultural expansion to compensate for soil poverty, creates an urgent need for management of human-modified landscapes to conserve the biodiversity of this endemic-rich nation. Some novel and agricultural habitats can harbour high abundances of insular rainforest endemics [76] while meeting the needs of an increasing human population and also sustaining high levels of biodiversity. The conservation literature calls agricultural land management practices that jointly provide wildlife habitat “land sharing”, whereas more intensive farming that protects some “spared” land is called “land sparing” [77]. Our results, highlighting the importance of landscape-scale forest cover, especially for IUCN-listed species, support the latter conservation

strategy. However, the relevance of vegetation structural complexity suggests that retaining substantial tree cover within agricultural areas increases assemblage similarly between forest and agricultural habitats.

As suggested by Dallimer et al. [76] for the island of Príncipe, a double-stranded conservation approach, in which landscape-scale forest cover is preserved while simultaneously retaining vegetation complexity within farmland, should be encouraged in Madagascar. Protected areas play a pivotal role in the maintenance of landscape-scale forest cover, but as elsewhere in the humid-tropics, Malagasy protected areas are too underfinanced to effectively impose restrictions on deforestation. Assessment of protected area effectiveness, the establishment of within-country research and management capacity, and engagement of local communities in conservation practices are crucial to the long-term persistence of the island's biodiversity and must also be a goal of research in Madagascar.

Acknowledgments

We thank Sarah Stow and Dina Herilala for their precious help during fieldwork, Eveliina Puhakka for undertaking the classification of the Landsat images used in the calculation of forest cover, the Centre ValBio staff for their hospitality and logistical support, James Kemp for revising the English, Elodie Roger for translating the abstract into French and three anonymous reviewers for helpful comments. We also thank the Department of Biosciences - University of Helsinki for supporting the RESPECT field course and the course participants and professors for their thrilling enthusiasm. R. Rocha benefited from a Finnish Government CIMO scholarship and M. Cabeza was funded by the Academy of Finland (grant # 257686).

References

- [1] Norris, K. 2008. Agriculture and biodiversity conservation: opportunity knocks. *Conservation Letters* 1:2-11.
- [2] Laurance, W. F., Sayer, J. and Cassman, K. G. 2014. Agricultural expansion and its impacts on tropical nature. *Trends in Ecology & Evolution* 29:107-116.
- [3] Doxa, A., Paracchini, M. L., Pointereau, P., Devictor, V. and Jiguet, F. 2012. Preventing biotic homogenization of farmland bird communities: The role of High Nature Value farmland. *Agriculture, Ecosystems & Environment* 148:83-88.
- [4] Bignal, E. M. and McCracken, D. I. 1996. Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology* 33:413-424.
- [5] Faria, D., Laps, R., Baumgarten, J. and Cetra, M. 2006. Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic Forest of Southern Bahia, Brazil. *Biodiversity & Conservation* 15:587-612.
- [6] Perfecto, I. and Vandermeer, J. 2008. Biodiversity conservation in tropical agroecosystems. *Annals of the New York Academy of Sciences* 1134:173-200.
- [7] Mendenhall, C. D., Karp, D. S., Meyer, C. F., Hadly, E. A. and Daily, G. C. 2014. Predicting biodiversity change and averting collapse in agricultural landscapes. *Nature* 509:213-217.
- [8] Naidoo, R. 2004. Species richness and community composition of songbirds in a tropical forest-agricultural landscape. *Animal Conservation* 7:93-105.
- [9] Waltert, M., Bobo, K. S., Sainge, N. M., Fermon, H. and Mühlenberg, M. 2005. From forest to farmland: habitat effects on afro-tropical forest bird diversity. *Ecological Applications* 15:1351-1366.
- [10] de Lima, R. F., Dallimer, M., Atkinson, P. W. and Barlow, J. 2013. Biodiversity and land-use change: understanding the complex responses of an endemic-rich bird assemblage. *Diversity and Distributions* 19:411-422.

- [11] Melo, F. P. L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M. and Tabarelli, M. 2013. On the hope for biodiversity-friendly tropical landscapes. *Trends in Ecology & Evolution* 28:462-468.
- [12] Rudel, T. K., Defries, R., Asner, G. P. and Laurance, W. F. 2009. Changing drivers of deforestation and new opportunities for conservation. *Conservation Biology* 23:1396-1405.
- [13] Wright, S. J. 2010. The future of tropical forests. *Annals of the New York Academy of Sciences* 1195:1-27.
- [14] Malhi, Y., Gardner, T. A., Goldsmith, G. R., Silman, M. R. and Zelazowski, P. 2014. Tropical Forests in the Anthropocene. *Annual Review of Environmental Resources* 39:125-159.
- [15] Gardner, T. A., Barlow, J., Parry, L. W. and Peres, C.A. 2007. Predicting the Uncertain Future of Tropical Forest Species in a Data Vacuum. *Biotropica* 39:25-30.
- [16] Luck, G. W. and Daily, G. C. 2003. Tropical countryside bird assemblages: richness, composition and foraging differ by landscape context. *Ecological Applications* 13:235-247.
- [17] Tejada-Cruz, C. and Sutherland, W. J. 2004. Bird responses to shade coffee production. *Animal Conservation* 7:169-179.
- [18] Marsden, S. J., Symes, C. T. and Mack, A. L. 2006. The response of a New Guinean avifauna to conversion of forest to small-scale agriculture. *Ibis* 148:629-640.
- [19] Borges, S. H. 2007. Bird assemblages in secondary forests developing after slash-and-burn agriculture in the Brazilian Amazon. *Journal of Tropical Ecology* 23:469-477.
- [20] Dawson, J., Turner, C., Pileng, O., Farmer, A., McGary, C., Walsh, C., Tamblyn, A. and Yosi, C. 2011. Bird communities of the lower Waria Valley, Morobe Province, Papua New Guinea: a comparison between habitat types. *Tropical Conservation Science* 4:317-348
- [21] Goodman, S. M. and Benstead, J. P. 2005. Updated estimates of biotic diversity and endemism for Madagascar. *Oryx* 39:73-77.
- [22] Vieites, D. R., Wollenberg, K. C., Andreone, F., Köhler, J., Glaw, F. and Vences, M. 2009. Vast underestimation of Madagascar's biodiversity evidenced by an integrative amphibian inventory. *Proceedings of the National Academy of Sciences* 106:8267-8272.
- [23] Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A. and Kent, J. 2000. Biodiversity hotspots for conservation priorities. *Nature* 403:853-858.
- [24] Funk, S. M. and Fa, J. E. 2010. Ecoregion prioritization suggests an armoury not a silver bullet for conservation planning. *PLoS ONE* 5:e8923.
- [25] Brown, K. A. and Gurevitch, J. 2004. Long-term impacts of logging on forest diversity in Madagascar. *Proceedings of the National Academy of Sciences of the United States of America* 101:6045-6049.
- [26] Randrianandrianina, F., Andriafidison, D., Kofoky, A. F., Ramilijaona, O., Ratrimomanarivo, F., Racey, P. A. and Jenkins, R. K. 2006. Habitat use and conservation of bats in rainforest and adjacent human-modified habitats in eastern Madagascar. *Acta Chiropterologica* 8:429-437.
- [27] Cardiff, S. G. and Andriamanalina, A. 2007. Contested spatial coincidence of conservation and mining efforts in Madagascar. *Madagascar Conservation & Development* 2:28-34.
- [28] Styger, E., Rakotondramasy, H. M., Pfeffer, M. J., Fernandes, E. C. M. and Bates, D.M. 2007. Influence of slash-and-burn farming practices on fallow succession and land degradation in the rainforest region of Madagascar. *Agriculture, Ecosystems & Environment* 119:257-269.
- [29] Cardiff, S. G., Ratrimomanarivo, F. H., Rembert, G. and Goodman, S. M. 2009. Hunting, disturbance and roost persistence of bats in caves at Ankarana, northern Madagascar. *African Journal of Ecology* 47:640-649.
- [30] MacPhee, R. D. E. and Burney, D.A. 1991. Dating of modified femora of extinct dwarf hippopotamus from Southern Madagascar: Implications for constraining human colonization and vertebrate extinction events. *Journal of Archaeological Science* 18:695-706.

- [31] Crowley, B. E. 2010. A refined chronology of prehistoric Madagascar and the demise of the megafauna. *Quaternary Science Reviews* 29:2591-2603.
- [32] Gade, D. W. 1996. Deforestation and its effects in highland Madagascar. *Mountain Research and Development* 16:101-116.
- [33] Harper, G.J., Steininger, M. K., Tucker, C. J., Juhn, D. and Hawkins, F. 2007. Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation* 34:325-333.
- [34] Hanski, I., Koivulehto, H., Cameron, A. and Rahagalala, P. 2007. Deforestation and apparent extinctions of endemic forest beetles in Madagascar. *Biology Letters* 3:344-347.
- [35] Agarwal, D. K., Silander Jr, J. A., Gelfand, A. E., Dewar, R. E. and Mickelson Jr, J. G. 2005. Tropical deforestation in Madagascar: analysis using hierarchical, spatially explicit, Bayesian regression models. *Ecological Modelling* 185:105-131.
- [36] Allnutt, T. F., Asner, G. P., Golden, C.D. and Powell, G. V. 2013. Mapping recent deforestation and forest disturbance in northeastern Madagascar. *Tropical Conservation Science* 6:1-15.
- [37] Irwin, M. T., Wright, P. C., Birkinshaw, C., Fisher, B. L., Gardner, C. J., Glos, J., Goodman, S. M., Loiselle, P., Rabeson, P., Raharison, J.-L., Raherilalao, M. J., Rakotondravony, D., Raselimanana, A., Ratsimbazafy, J., Sparks, J. S., Wilmé, L. and Ganzhorn, J. U. 2010. Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation* 143:2351-2362.
- [38] Watson, J. E. M., Whittaker, R. J. and Dawson, T. P. 2004. Habitat structure and proximity to forest edge affect the abundance and distribution of forest-dependent birds in tropical coastal forests of southeastern Madagascar. *Biological Conservation* 120: 311-327.
- [39] Watson, J. E. M., Whittaker, R. J. and Dawson, T. P. 2004. Avifaunal responses to habitat fragmentation in the threatened littoral forests of south-eastern Madagascar. *Journal of Biogeography* 31: 1791-1807.
- [40] Martin, E., Ratsimisetra, L., Laloë, F. and Carrière, S. 2009. Conservation value for birds of traditionally managed isolated trees in an agricultural landscape of Madagascar. *Biodiversity and Conservation* 18:2719-2742.
- [41] Martin, E. A., Viano, M., Ratsimisetra, L., Laloë, F. and Carrière, S. M. 2012. Maintenance of bird functional diversity in a traditional agroecosystem of Madagascar. *Agriculture, Ecosystems & Environment* 149: 1-9.
- [42] Stratford, J. A. and Stouffer, P. C. 2013. Microhabitat associations of terrestrial insectivorous birds in Amazonian rainforest and second-growth forests. *Journal of Field Ornithology* 84: 1-12.
- [43] Moran, C. and Catterall, C. P. 2014. Responses of seed-dispersing birds to amount of rainforest in the landscape around fragments. *Conservation Biology* 28: 551–560.
- [44] Zuluaga, G. J. C. and Rodewald, A. D. 2015. Response of mixed-species flocks to habitat alteration and deforestation in the Andes. *Biological Conservation* 188: 72–81.
- [45] Hawkins, A. F. A. and Goodman, S. M. 2003. Introduction to the birds. In: *The Natural History of Madagascar*. S. M. Goodman and J. P. Benstead (Eds.), pp.1019–1044. University of Chicago, Chicago.
- [46] Fauth, J. E., Bernardo, J., Camara, M., Resetarits, W. J., VanBuskirk, J. and McCollum, S. A. 1996. Simplifying the jargon of community ecology: A conceptual approach. *American Naturalist* 147: 282-286.
- [47] Wright, P. C. and B. Andriamihaja. 2003. The conservation value of long-term research: a case study from the Parc National de Ranomafana. In: *The Natural History of Madagascar*. S. M. Goodman and J. P. Benstead (Eds.), pp.1485–1488. University of Chicago, Chicago.

- [48] Kari, S. and Korhonen-Kurki, K. 2013. Framing local outcomes of biodiversity conservation through ecosystem services: a case study from Ranomafana, Madagascar. *Ecosystem Services* 3: e32-e39.
- [49] Gregory, R. D., Gibbons, D. W. and Donald, P. F. 2004. Bird census and survey techniques. In: *Bird Ecology and Conservation. A handbook of techniques*. W. J. Sutherland, Newton, I. and Green, R. E. (Eds.), pp.17–55 in Oxford University Press, Oxford, UK.
- [50] Dallimer, M. and King, T. 2008. Habitat preferences of the forest birds on the island of Príncipe, Gulf of Guinea. *African Journal of Ecology* 46: 258-266.
- [51] Puhakka, E. 2012. Tropical rainforest corridor in Madagascar: satellite image -based land cover classification, landscape analysis and forest quality measurements. M.Sc. Thesis, Department of Environmental Sciences, University of Helsinki, 102 p.
- [52] Gotelli, N. J. and R. K. Colwell. 2001. Quantifying biodiversity: procedures and pitfalls in the measurement and comparison of species richness. *Ecology Letters* 4: 379-391.
- [53] Colwell, R. K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. Persistent URL <purl.oclc.org/estimates>.
- [54] IUCN 2014. *2014 IUCN Red List of Threatened Species*. <http://www.iucnredlist.org> Databased consulted on July 2014.
- [55] Wilmé, L. and Goodman. S. M. 2003. Biogeography, guild structure and elevation variation of Madagascar forest birds. In: *The Natural History of Madagascar*. S. M. Goodman and J. P. Benstead (Eds.), pp.1045–1058. University of Chicago, Chicago.
- [56] Anderson, M. 2005. PERMANOVA: a fortran Computer Program for Permutational Multivariate Analysis of Variance. Auckland, Department of Statistics, University of Auckland. 24p.
- [57] R Development Core Team (2013) R: A language and environment for statistical computing. <http://www.r-project.org> assessed on June 2013.
- [58] Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B., Leitão, P. J., Münkemüller, T., McClean, C., Osborne, P. E., Reineking, B., Schröder, B., Skidmore, A. K., Zurell, D. and Lautenbach, S. 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography* 36: 027-046.
- [59] Rhodes, J. R., McAlpine, C. A., Zuur, A. F., Smith, G. M. and Ieno, E. N. 2009. GLMM applied on the spatial distribution of koalas in a fragmented landscape. In: *Mixed effects models and extensions in ecology with R*. Zuur, A., Ieno, E. N., Walker, N., Saveliev, A. A., Smith, G. M. (Eds), pp. 469-492. Springer, New York.
- [60] Burnham, K. P. and Anderson, D. R. 2002. *Model Selection and Inference: a Practical Information-Theoretic Approach*. Springer, New York.
- [61] Neter, J., Wasserman, W. and Kutner, M. H. 1990. *Applied linear statistical models. Regression, analysis of variance, and experimental design*. Irwin, Homewood, USA
- [62] Nakagawa, S. and Schielzeth. 2013. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4: 133-142.
- [63] Chevan A., Sutherland, M. 1991. Hierarchical partitioning. *The American Statistician* 45: 90–96.
- [64] Goodale, E., Kotagama, S. W., Raman, T. S., Sidhu, S., Goodale, U., Parker, S. and Chen, J. 2014. The response of birds and mixed-species bird flocks to human-modified landscapes in Sri Lanka and southern India. *Forest Ecology and Management* 329: 384-392.
- [65] Driscoll, D. A., Banks, S. C., Barton, P. S., Lindenmayer, D. B. and Smith, A. L. 2013. Conceptual domain of the matrix in fragmented landscapes. *Trends in Ecology & Evolution* 28: 605-613.

- [66] McDermott, M. E. and Rodewald, A. D. 2014. Conservation value of silvopastures to Neotropical migrants in Andean forest flocks. *Biological Conservation* 175: 140-147.
- [67] Schulze, C. H., Waltert, M., Kessler, P. J. A., Pitopang, R., Veddeler, D., Mühlenberg, M., Gradstein, S. R., Leuschner, C., Steffan-Dewenter, I. and Tscharntke, T. 2004. Biodiversity indicator groups for tropical land-use systems: comparing plants, birds and insects. *Ecological Applications* 14: 1321-1333.
- [68] Matlock Jr, R. B., Rogers, D., Edwards, P. J. and Martin, S. G. 2002. Avian communities in forest fragments and reforestation areas associated with banana plantations in Costa Rica. *Agriculture, Ecosystems & Environment* 91: 199-215.
- [69] Carvalho, M., Fa, J. E., Rego, F. C., de Lima, R. F., Santos, G. and Palmeirim, J. M. 2015. Factors influencing the distribution and abundance of endemic pigeons on São Tomé Island (Gulf of Guinea). *Bird Conservation International* 25: 71-86.
- [70] Jenkins, R. K., Keane, A., Rakotoarivelo, A. R., Rakotomboavonjy, V., Randrianandrianina, F. H., Razafimanahaka, H. J., Ralaiarimalala, S. R. and Jones, J. P. G. 2011. Analysis of patterns of bushmeat consumption reveals extensive exploitation of protected species in eastern Madagascar. *PLoS ONE* 6: e27570.
- [71] Gardner, C. J. and Davies, Z. G. 2014. Rural bushmeat consumption within multiple-use protected areas: qualitative evidence from southwest Madagascar. *Human Ecology* 42: 21-34.
- [72] Rueda, M., Hawkins, B. A., Morales-Castilla, I., Vidanes, R. M., Ferrero, M. and Rodríguez, M. A. 2013. Does fragmentation increase extinction thresholds? A European-wide test with seven forest birds. *Global Ecology and Biogeography* 22: 1282-1292.
- [73] Farneda, F. Z., Rocha, R., López-Baucells, A., Groenenberg, M., Silva, I., Palmeirim, J. M., Bobrowiec, P. E. D. and Meyer, C. F. J. 2015. Trait-related responses to habitat fragmentation in Amazonian bats. *Journal of Applied Ecology in press* DOI: 10.1111/1365-2664.12490
- [74] Whelan, C. J., Wenny, D. G. and Marquis, R. J. 2008. Ecosystem services provided by birds. *Annals of the New York Academy of Sciences* 1134: 25-60.
- [75] Maas, B., Clough, Y. and Tscharntke, T. 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. *Ecology Letters* 16: 1480–1487.
- [76] Dallimer, M., Parnell, M., Bicknell, J. E. and Melo, M. 2012. The importance of novel and agricultural habitats for the avifauna of an oceanic island. *Journal for Nature Conservation* 20: 191-199.
- [77] Phalan, B., Onial, M., Balmford, A. and Green, R. E. 2011. Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science* 333: 1289-1291.

Appendix 1 Description and summary statistics (mean + SD) of habitat structure and landscape-scale descriptors used to characterize forest and agriculture point stations in Ranomafana, Madagascar.

Values	Description	Forest (n = 30)	Agriculture (n = 20)
<i>Habitat structure</i>			
Tree basal area (m ² /ha)	Cross-sectional area at breast height	16.86 (± 9.77)	1.9 (± 4.6)
Perimeter (cm)	Diameter at breast height of the nearest 10 trees northwards	36.83 (± 14.88)	5.775 (± 11.85)
Understory height (m)	Height of the understory vegetation	2.98 (± 2.68)	0.16 (± 0.14)
Mid-canopy height (m)	Height of the mid-canopy vegetation	10.52 (± 5.6)	1.39 (± 1.52)
Upper-canopy height (m)	Height of the upper-canopy vegetation	20.05 (± 5.15)	4.75 (± 6.01)
Tree cover (%)	Visually estimated using 6 categorical classes (0 = no cover to 5 = very dense)	4.8 (± 0.41)	0.55 (± 0.76)
Leaf litter cover (%)	Visually estimated using 6 categorical classes (0 = no cover to 5 = very dense)	3.43 (± 0.94)	3.5 (± 1.47)
Bare ground cover (%)	Visually estimated using 6 categorical classes (0 = no cover to 5 = very dense)	2.86 (± 1.2)	2.7 (± 1.42)
Abundance of bryophytes	Visually estimated using 4 categorical classes (0 = no cover to 3 = very dense)	2.53 (± 0.51)	0.45 (± 0.60)
Abundance of lichens	Visually estimated using 4 categorical classes (0 = no cover to 3 = very dense)	2.03 (± 0.67)	0.45 (± 0.60)

<i>Landscape-scale attributes</i>			
Forest cover 100 m (%)	Percentage of forest cover within 100 m radius (measured from a Landsat image)	94.86 (\pm 6.97)	9.43 (\pm 17.47)
Forest cover 500 m (%)	Percentage of forest cover within 500 m radius (measured from a Landsat image)	89.81 (\pm 7.22)	35.29 (\pm 17.96)
Forest cover 750 m (%)	Percentage of forest cover within 750 m radius (measured from a Landsat image)	85.31 (\pm 10.35)	44.66 (\pm 13.86)
Altitude (m)	Count station altitude (extracted from a Digital Elevation Model)	1013.3 (\pm 70.44)	839.65 (\pm 70.54)
Slope (m)	Count station slope (extracted from a Digital Elevation Model)	16.63 (\pm 9.53)	16.97 (\pm 9.18)
Distance to roads (m)	Euclidean distance from count station to nearest road	1604.86 (\pm 1255.09)	548.49 (\pm 142.94)
Distance to human settlements (m)	Euclidean distance from count station to nearest human settlement	2187.1 (\pm 935.1)	682.98 (\pm 169.88)

Appendix 2) List of within survey time recorded species.

Species ¹	English name ¹	Level of endemism ²	Dominant habitat type ³	Feeding guild ⁴	IUCN threat level ⁵	Habitat-level response ⁶	
						Forest (n = 30)	Agriculture (n = 20)
Accipitridae							
<i>Accipiter henstii</i> ⁷	Henst's Goshawk	M	F	Ca	NT	6.27	0
<i>Buteo brachypterus</i> ⁷	Madagascar Buzzard	R	F	Ca	LC	3.33	5
Apodidae							
<i>Apus balstoni</i> ⁷	Madagascar Black Swift	R e	G	In	LC	0	5
Brachypteraciidae							
<i>Atelornis pittoides</i>	Pitta-like Ground-Roller	M	F	In	LC	43.33	0
<i>Brachypteracias leptosomus</i>	Short-legged Ground-Roller	M	F	In	VU	6.67	0
Campephagidae							
<i>Coracina cinerea</i>	Madagascar Cuckooshrike	R e	F	In	LC	66.67	15
Columbidae							
<i>Alectroenas madagascariensis</i>	Madagascar Blue Pigeon	M	F	Fr	LC	10	0
<i>Nesoenas picturata</i>	Madagascar Turtle Dove	R e	F	Gr	LC	30	0
Coraciidae							
<i>Eurystomus glaucurus</i>	Broad-billed Roller	n e mig	OA	In	LC	3.33	0
Cuculidae							
<i>Centropus toulou</i>	Madagascar Coucal	R e	G	Ca	LC	16.67	80
<i>Coua caerulea</i>	Blue Coua	M	F	In	LC	13.33	20
<i>Coua cristata</i>	Crested Coua	M	F	In	LC	3.33	5
<i>Coua reynaudii</i>	Red-fronted Coua	M	F	In	LC	23.33	10
<i>Cuculus rochii</i>	Madagascar Cuckoo	M mig	F	In	LC	90	25
Dicruridae							
<i>Dicrurus forficatus</i>	Madagascar Crested Drongo	R e	F	In	LC	43.33	35

Estrildidae								
<i>Lepidopygia nana</i>	Madagascar Mannikin	M	G	Gr	LC	0	60	
Falconidae								
<i>Falco newtoni</i> ⁷	Madagascar Kestrel	R e	G	Ca	LC	0	40	
Hirundinidae								
<i>Phedina borbonica</i> ⁷	Mascarene Martin	R e	G	In	LC	3.33	30	
Leptosomidae								
<i>Leptosomus discolor</i>	Madagascar Cuckoo Roller	R	F	In	LC	16.67	5	
Megaluridae								
<i>Dromaeocercus brunneus</i>	Brown Emutail	M	F	In	LC	3.33	0	
Meropidae								
<i>Merops superciliosus</i> ⁷	Madagascar Bee-eater	n	G	In	LC	0	30	
Mesitornithidae								
<i>Mesitornis unicolor</i>	Brown Mesite	M	F	Om	VU	3.33	0	
Monarchidae								
<i>Terpsiphone mutata</i>	Madagascar Paradise Flycatcher	R e	G	In	LC	86.67	20	
Motacillidae								
<i>Motacilla flaviventris</i>	Madagascar Wagtail	M	OA	In	LC	0	40	
Muscicapidae								
<i>Copsychus albospecularis</i>	Madagascar Magpie Robin	M	F	In	LC	40	50	
<i>Monticola sharpei</i>	Forest Rock-Thrush	M	F	In	LC	10	5	
<i>Saxicola sibilla</i>	Malagasy Stonechat	M	OA	In	LC	0	55	
Nectariniidae								
<i>Cinnyris notatus</i>	Madagascar Green Sunbird	R	F	In	LC	20	15	
<i>Cinnyris souimanga</i>	Souimanga Sunbird	R e	F	In	LC	96.67	95	
Numididae								
<i>Numida meleagris</i>	Helmeted Guineafowl	int	OA	Gr	LC	0	10	
Philepittidae								

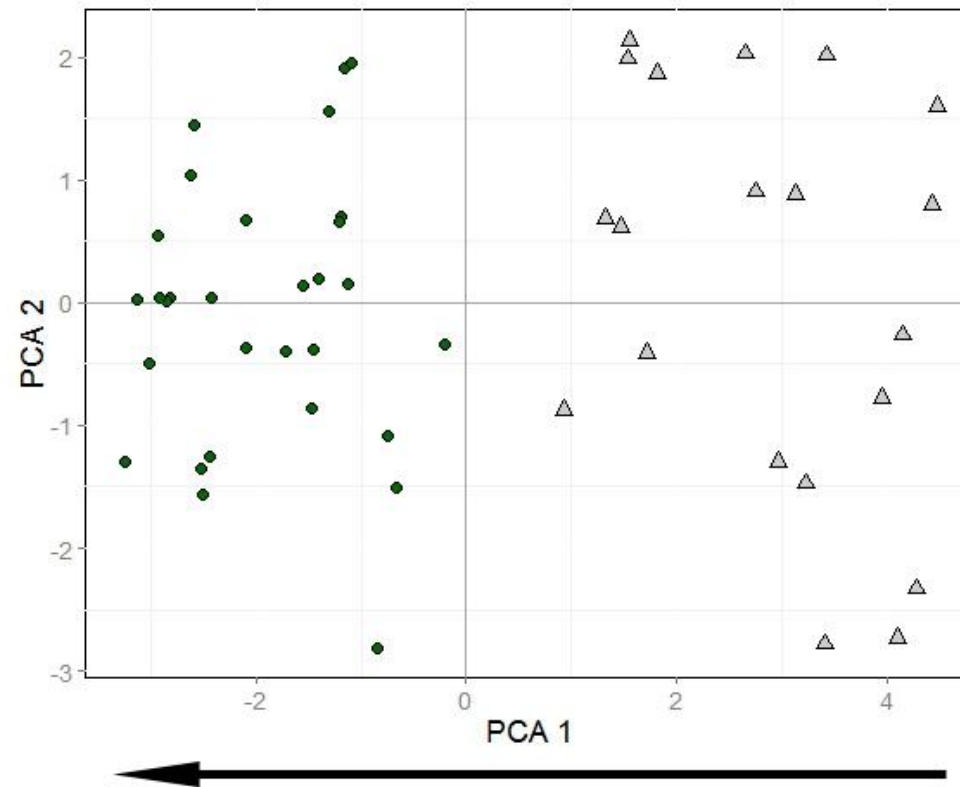
<i>Neodrepanis coruscans</i>	Yellow-bellied Sunbird-Asity	M	F	In	LC	13.33	0
<i>Philepitta castanea</i>	Velvet Asity	M	F	Fr	LC	33.33	0
Ploceidae							
<i>Foudia madagascariensis</i>	Madagascar Red Fody	M	OA	Gr	LC	3.33	90
<i>Foudia omissa</i>	Forest Fody	M	F	Gr	LC	43.33	0
<i>Ploceus nelicourvi</i>	Nelicourvi Weaver	M	F	In	LC	70	15
Psittacidae							
<i>Coracopsis nigra</i>	Lesser Vasa Parrot	M	F	Fr	LC	86.67	20
<i>Coracopsis vasa</i>	Greater Vasa Parrot	M	F	Fr	LC	6.67	0
Pycnonotidae							
<i>Hypsipetes madagascariensis</i>	Madagascar Bulbul	R e	F	Fr	LC	86.67	95
Rallidae							
<i>Mentocrex kioloides</i>	Madagascar Wood Rail	M	F	Om	LC	3.33	0
<i>Sarothrura insularis</i>	Madagascar Flufftail	M	F	In	LC	0	30
Sylviidae							
<i>Acrocephalus newtoni</i>	Madagascar Swamp Warbler	M	F	In	LC	16.67	5
<i>Bernieria madagascariensis</i>	Long-billed Tetraka	M	F	In	LC	33.33	5
<i>Crossleyia xanthophrys</i>	Yellow-browed Oxylabes	M	F	In	NT	3.33	0
<i>Nesillas typica</i>	Madagascar Bush Warbler	R e	F	In	LC	56.67	45
<i>Oxylabes madagascariensis</i>	White-troated Oxylabes	M	F	In	LC	16.67	0
<i>Xanthomixis cinereiceps</i>	Grey-crowned Tetraka	M	F	In	NT	20	0
<i>Xanthomixis zosterops</i>	Spectacled Tetraka	M	F	In	LC	40	0
Threskiornithidae							
<i>Lophotibis cristata</i>	Madagascar Crested Ibis	M	F	Ca	NT	6.67	0
Timaliidae							
<i>Neomixis tenella</i>	Common Jery	M	F	In	LC	40	5
<i>Neomixis viridis</i>	Green Jery	M	F	In	LC	26.67	0
Turnicidae							

<i>Turnix nigricollis</i>	Madagascar Buttonquail	M	G	Gr	LC	0	10
Vangidae							
<i>Artamella viridis</i>	White-headed Vanga	M	F	In	LC	3.33	0
<i>Calicalicus madagascariensis</i>	Red-tailed Vanga	M	F	In	LC	50	0
<i>Cyanolanius madagascarinus</i>	Madagascar Blue Vanga	R e	F	In	LC	40	60
<i>Leptopterus chabert</i>	Chabert's Vanga	M	F	In	LC	3.33	5
<i>Mystacornis crossleyi</i>	Crossley's Vanga	M	F	In	LC	13.33	5
<i>Newtonia amphichroa</i>	Dark Newtonia	M	F	In	LC	20	5
<i>Newtonia brunneicauda</i>	Common Newtonia	M	F	In	LC	6.67	5
<i>Newtonia fanovanae</i>	Red-tailed Newtonia	M	F	In	VU	46.67	15
<i>Schetba rufa</i>	Rufous Vanga	M	F	In	LC	3.33	0
<i>Tylas eduardi</i>	Tylas	M	F	In	LC	13.33	0
<i>Vanga curvirostris</i>	Hook-billed Vanga	M	F	Ca	LC	10	0
<i>Xenopirostris polleni</i>	Pollen's Vanga	M	F	In	NT	33.33	0
Zosteropidae							
<i>Zosterops maderaspatanus</i>	Madagascar White-eye	M	F	In	LC	66.67	65

¹ Nomenclature based in Sinclair, I., Langrand, O. (2013). Birds of the Indian Ocean islands. New Holland Publishers, Cape Town, South Africa; ² Level of endemism: M = Madagascar, R = regional endemic (Madagascar, Comores, Seychelles and Mascarene Islands), e = Subspecies endemic to Madagascar, n = non endemic, mig = migratory species, int = introduced; ³ Dominant habitat type: F = Forest, G = Generalist, OA = Open area species; ⁴ Feeding guild: Ca = Carnivore, Fr = Frugivore, Gr = Granivore, In = Insectivore, Om = Omnivore; ⁵ IUCN threat level: LC = Least concern, NT = Near threatened, VU = Vulnerable; ⁶ Percentage of within habitat count stations in which the species was recorded; ⁷ Species not included in the analyses.

Appendix 3) Variable loadings, eigenvalues and proportion of variance explained by the first two axes of a Principal Component Analysis (PCA) on the habitat structure descriptors.

Habitat structure variabes	PCA 1	PCA 2
height of the upper-canopy	-0.36	-0.01
height of the mid-canopy	-0.35	0.07
height of the understory	-0.34	0.03
tree perimeter	-0.34	-0.08
tree basal area	-0.34	0.08
% of canopy cover	-0.34	0.04
% of leaf litter cover	-0.07	0.07
% of bare ground cover	-0.03	-0.07
abundance of lichen	-0.34	-0.04
abudance of bryophyte	-0.37	0.04
Eigenvalue	6.4	1.7
% explained	64.4	17.4
Comulative proportion	64.4	81.8



Appendix 4) Results of the first two Principal Component Analysis (PCA) axes describing habitat structure in count stations located in forest and agricultural areas, Ranomafana, Madagascar. Forest sites are represented by (●) and agriculture sites by (▲). Arrow direction denotes an increase in structural habitat complexity.

Appendix 5) The 95% confidence set of models for the relationship between habitat structure and landscape-scale forest cover on total species richness, forest-associated species richness, and open habitat and generalist species, Ranomafana, Madagascar. For each model, the model rank, the number of estimated parameters (K), sample-size adjusted Akaike's information criteria (AICc), Akaike differences (Δ_i), Akaike weights (w_i), cumulative Akaike weight (Cum_w), log-likelihood ($\log(L)$), marginal R^2 (mR^2) and conditional R^2 (cR^2) are presented. Variable abbreviations: PCA 1 = 1st axis of the habitat structure Principal Component Analysis; FC_100 = forest cover at the 100 m scale; FC_500 = forest cover at the 500 m scale; FC_750 = forest cover at the 750 m scale.

Model structure	Model rank	K	AICc	Δ_i	w_i	Cum_w	$\log(L)$	mR^2	cR^2
<i>Total species richness</i>									
FC_100 + FC_500	1	4	263.06	0	0.52	0.52	-127.09	0.37	0.37
FC_100 + FC_500 + FC_750	2	5	264.88	1.82	0.21	0.73	-126.76	0.39	0.39
-(PCA1) + FC_100 + FC_500	3	5	265.34	2.28	0.17	0.90	-126.99	0.38	0.38
-(PCA1) + FC_100 + FC_500 + FC_750	4	6	267.42	4.36	0.06	0.96	-126.73	0.39	0.39
<i>Forest-associated species richness</i>									
FC_100 + FC_500 + FC_750	1	5	255.01	0	0.35	0.35	-121.82	0.57	0.57
-(PCA1) + FC_100 + FC_500	2	5	255.67	0.66	0.26	0.60	-122.15	0.56	0.56

FC_100 + FC_500	3	4	255.67	0.66	0.26	0.86	-123.39	0.54	0.54
-(PCA1) + FC_100 + FC_500 + FC_750	4	6	257.46	2.45	0.1	0.97	-121.75	0.57	0.57
<i>Open habitat and generalist species richness</i>									
-(PCA1)	1	3	135.65	0	0.43	0.43	-64.56	0.36	0.36
-(PCA1) + FC_100	2	4	136.06	0.41	0.35	0.78	-63.58	0.38	0.38
-(PCA1) + FC_100 + FC_500	3	5	138.53	2.88	0.1	0.88	-63.58	0.37	0.37
-(PCA1) + FC_100 + FC_500 + FC_750	4	6	140.91	5.26	0.03	0.91	-63.48	0.38	0.38
FC_100 + FC_500 + FC_750	5	5	141.02	5.37	0.03	0.94	-64.83	0.35	0.35
FC_100	6	3	141.13	5.48	0.03	0.97	-67.3	0.28	0.28

Appendix 6) Summary results of model averaging of the most parsimonious generalized linear mixed models (Akaike differences <2 from the best model) investigating the relationship between habitat structure and landscape-scale forest cover on total species richness, forest-associated species richness and open habitat and generalist species, Ranomafana, Madagascar.

	Intercept	Habitat structure	Forest cover 100 m	Forest cover 500 m	Forest cover 750 m
<i>Total species richness</i>					
Estimate	2.57		0.03	0.18	0.04
Unconditional SE	0.04		0.06	0.06	0.05
Confidence interval	2.49, 2.65		-0.08, 0.14	0.06, 0.3	-0.06, 0.15
Hierarchical partitioning (%)			20	47.3	16.8
<i>Forest-associated species richness</i>					
Estimate	2.4	0.1	0.09	0.21	0.1
Unconditional SE	0.04	0.07	0.07	0.07	0.06
Confidence interval	2.32, 2.49	-0.03, 0.23	-0.04, 0.22	0.07, 0.35	-0.01, 0.21
Hierarchical partitioning (%)		20.4	24.3	37.2	18
<i>Open area and generalist species</i>					

Estimate	0.38	-0.47	-0.19		
Unconditional SE	0.12	0.14	0.14		
Confidence interval	0.14, 0.62	-0.75, -0.19	-0.46, 0.08		
Hierarchical partitioning (%)		42.8	33.8		

Appendix 7) Moran's I values of the model residuals of the most parsimonious generalized linear mixed models (Akaike differences <2 from the best model) investigating the relationship between habitat structure and landscape-scale forest cover on total species richness, forest-associated species richness and open habitat and generalist species, Ranomafana, Madagascar.

Model structure	I	$E(I)$	$sd(I)$	p-value
<i>Total species richness</i>				
FC_100 + FC_500	0.03	-0.02	0.04	0.239
FC_100 + FC_500 + FC_750	0.02	-0.02	0.04	0.374
<i>Forest-associated species richness</i>				
FC_100 + FC_500 + FC_750	0.02	-0.02	0.04	0.395
-(PCA1) + FC_100 + FC_500	0.06	-0.02	0.04	0.085
FC_100 + FC_500	0.06	-0.02	0.04	0.081
<i>Open habitat and generalist species richness</i>				
-(PCA1)	-0.01	-0.02	0.04	0.735
-(PCA1) + FC_100	-0.05	-0.02	0.04	0.516