ORIGINAL ARTICLE

Bird diversity and endemism along a land-use gradient in Madagascar: The conservation value of vanilla agroforests

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Funding information
Volkswagen Foundation, Grant/Award Number: 11-76251-99-35/13 (ZN3119).

Associate Editor: Eleanor Slade
Handling Editor: Eleanor Slade

Abstract

Land-use change is the most important driver of biodiversity loss worldwide and particularly so in the tropics, where natural habitats are transformed into large-scale monocultures or heterogeneous landscape mosaics of largely unknown conservation value. Using birds as an indicator taxon, we evaluated the conservation value of a landscape mosaic in northeastern Madagascar, a biodiversity hotspot and the center of global vanilla production. We assessed bird species richness and composition by conducting point counts across seven prevalent land-use types (forest- and fallow-derived vanilla agroforests, woody and herbaceous fallow that are part of a shifting cultivation system, rice paddy, forest fragment and contiguous old-growth forest). We find that old-growth forest had the highest species richness, driven by a high share of endemics. Species richness and community composition in forest-derived vanilla agroforest were similar to forest fragment, whereas fallow-derived vanilla agroforest was most comparable to woody fallow. The open land-use types herbaceous fallow and rice paddy had fewest species. Across forest fragments, vanilla agroforests, and woody fallows, endemic bird species richness was positively correlated to landscape-scale forest cover. We conclude that both fallow- and forest-derived vanilla agroforests play an important but contrasting role for bird conservation: Fallow-derived agroforests are less valuable but take fallow land out of the shifting cultivation cycle, possibly preventing further degradation. Conversely, forest-derived agroforests contribute to forest degradation but may avoid total loss of tree cover from forest fragments. Considering the land-use history of agroforests may thus be a promising avenue for future research beyond the case of vanilla.

Abstract in Malagasay is available with online material

KEYWORDS
agroecology, agroforestry, biodiversity, land-use history, land-use change, ornithology, shifting cultivation, SAVA region

1 | INTRODUCTION

While intact forests within protected areas are indispensable to protect biodiversity (Gibson et al., 2011; Gray et al., 2016), heterogeneous landscapes with a mosaic of small-scale agriculture, agroforestry, and forest remnants also have the potential to sustain high levels of biodiversity in the tropics (Bhagwat, Willis, Birks, & Whittaker, 2008; Melo, Arroyo-Rodríguez, Fahrig, Martínez-Ramos, & Tabarelli, 2013; Schroth et al., 2004). Similarly, such landscapes can provide ecosystem services that offer resilient livelihood options for rural people (Gordon, Manson, Sundberg, & Cruz-Angón, 2007). However, optimizing landscapes for the benefit of biodiversity and humans alike remains a major challenge, partly so due to a strong context dependency caused by dissimilar abiotic, biotic, and socioeconomic conditions in different parts of the world (Frishkoff, Ke, Martins, Olimpi, & Karp, 2019).

In Madagascar, high levels of endemism (Goodman & Benstead, 2005) coincide with high rates of habitat loss (Rakotomanana, Jenkins, & Ratsimbazafy, 2013), making the island one of the hottest biodiversity hotspots (Myers, Mittermeier, Mittermeier, da Fonseca, & Kent, 2000). Over the past 50 years, Madagascar lost approximately half of its forest cover (Vieilledent et al., 2018), illustrating the need for forest preservation while highlighting the potentially increasing role of the resulting human-dominated landscape for conservation. However, the distribution of species in agricultural landscapes of Madagascar has rarely been assessed (exceptions are Martin, Viano, Ratsimisetra, Laloë, & Carrière, 2012; Ndriantsoa, Riemann, Raminosoa, Rödel, & Glos, 2017 and Rocha, Virtanen, & Cabeza, 2015), as most research focuses on forested protected areas (Irwin et al., 2010). In our study region in northeastern Madagascar, ongoing land-use change has resulted in a small-scale landscape mosaic encompassing agroforests, shifting cultivation, forest fragments, and rice paddies, resembling landscapes found throughout eastern Madagascar (Zaehringer, Schwilch, Andriamihaja, Ramamonjisoa, & Messerli, 2017). At the national scale, northeastern Madagascar holds the highest percentage of forest cover (Vieilledent et al., 2018) and counts among the most biodiverse regions of the country (Brown et al., 2016), emphasizing the need for a sustainable land-use transformation.

Concurrently, northeastern Madagascar is the global center of vanilla production, where smallholders produce roughly 40% of the world's vanilla in agroforestry systems (FAO, 2020), making vanilla the country's top export commodity (Comtrade, 2017). The current expansion of vanilla agroforests, which is instigated by record-high prices (Hänke et al., 2018; Llopis et al., 2019), raises questions on the impacts of vanilla cultivation on biodiversity. Indeed, very little is known about the factors influencing biodiversity in vanilla agroforests and how they could be managed in a biodiversity-friendly way; contra to other agroforestry commodities like coffee or cacao (Schroth et al., 2004; Tscharntke et al., 2011). Furthermore, important linkages between vanilla cash-cropping and alternative forms of land use, such as the land-intensive and potentially unsustainable shifting cultivation (locally referred to as *tavy*, Styger, Rakotondramasy, Pfeffer, Fernandes, & Bates, 2007), remain largely unstudied (Llopis et al., 2019).

Malagasy vanilla agroforests are strikingly heterogeneous due to differences in land-use history. In northeastern Madagascar, around 30% of agroforests are directly derived from forest (Hänke et al., 2018) by thinning of trees, cleaning of the understory, and planting vanilla under remaining trees (Martin, Osen, et al., 2020). Roughly 70% of agroforests originate from fallow land (Hänke et al., 2018) that had once burned within the shifting cultivation cycle for hill rice cultivation (Styger et al., 2007). The transformation of these frequently burned plots into agroforestry systems and the cessation of fires allow the regeneration of trees. Interestingly, land-use history is largely neglected in the literature on biodiversity and ecosystem services in tropical agroforestry systems (Martin, Osen, et al., 2020). Given the rapid expansion of vanilla agroforests in northeastern Madagascar in recent years (Llopis et al., 2019), further insights are needed to elucidate the conservation potential of vanilla agroforests in this biodiversity hotspot.

Here, we use birds as a model group to study the conservation value of vanilla agroforests and other prevalent land-use types in northeastern Madagascar, as well as old-growth forests as a baseline. We compare bird species richness, composition, and endemism between land-use types and focus on vanilla agroforests of different land-use history. We also focus on endemism, because endemic species are emblematic of Malagasy biodiversity (Goodman & Benstead, 2005) and because endemic species have been shown to be more susceptible to land-use change (Fordham & Brook, 2010; de Lima, Dallimer, Atkinson, & Barlow, 2013) and may thus serve as a proxy for conservation value (Waltert et al., 2011). We firstly investigate how total and endemic bird species richness differs among land-use types. Secondly, we study how and why bird communities differ in species composition across land uses. Thirdly, we use this knowledge to derive management advice for vanilla agroforests that might optimize their value for bird conservation. Ultimately, we show that the differentiation of agroforests based on land-use history is a meaningful approach with applications beyond the case of vanilla.

2 | METHODS

2.1 | Study region and study design

We conducted our study in the SAVA region in northeastern Madagascar (Figure 1). The annual rainfall is 2,223 mm with a mean annual temperature of 24.0°C (mean across 80 plots; data extracted from the CHELSA climatology (Karger et al. 2017)). The potential natural vegetation is tropical rainforest, but only 35% of forest cover remains (Ferreira Arruda, 2018).

We collected data in 10 villages covering all prevalent land-use types as well as old-growth forest. In each village, we selected

one rice paddy, one herbaceous fallow, one woody fallow, and one forest fragment plus three vanilla agroforests summing up to 70 plots within 10 villages. Not in all villages were fallow- and forest-derived vanilla agroforests available, leading to an unbalanced design for vanilla agroforests (Figure 1d). Additionally, we studied 10 old-growth forest plots at two sites inside Marojejy National Park, the only place with contiguous low-altitude old-growth forest persisting in our study area. We chose the two old-growth forest sites within the same park as a compromise between low-altitude, maximum distance between the two sites and accessibility. See Supporting Information (SI) for choice of villages and old-growth forest sites.

2.2 | Sampled land-use types

One of the old-growth forest sites had experienced selective logging in the past but is now well protected while the other site is still subjected to selective logging (personal communication Jean-Chrysostome Bevao; see SI for details on old-growth forest).
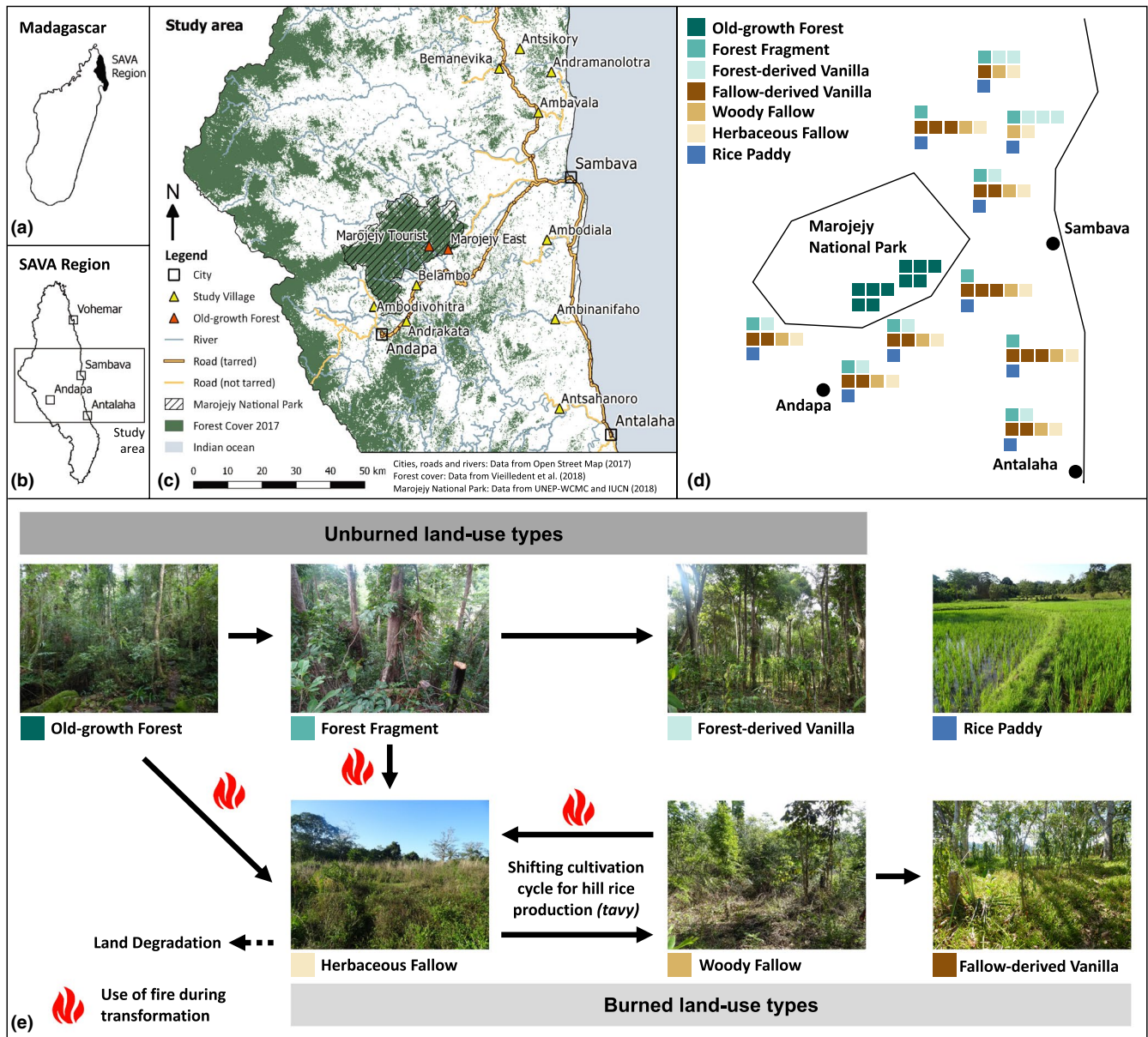

FIGURE 1 Study design overview. a) The island of Madagascar off East Africa with the SAVA region. b) SAVA region. c) Study area with forest cover 2017 (Vieilledent et al., 2018), roads, rivers, and the three major cities Sambava, Antalaha, and Andapa as well as the 10 study villages, Marojejy National Park, and the two sampling sites therein. d) A schematic overview of the study area, depicting which land-use types were sampled in each of the 10 villages and the two sampling sites inside Marojejy National Park. e) Possible transformation pathways from old-growth forest into different land-use types that we assessed in this study. Rice paddies are usually established on floodplains and are thus not part of the displayed transformation pathways

Forest fragments lie scattered throughout the study region. All 10 fragments were unburned but used for extraction of timber, firewood, and other natural products with few large trees remaining.

Herbaceous fallows *(Malagasy: matrangy)* are part of the shifting cultivation cycle for hill rice production *(tavy)*. All 10 herbaceous fallows have been burned repeatedly and last burned at the end of 2016, about one year before the first data collection in 2017, followed by hill rice cultivation. Thereafter, the land was left fallow until the end of data collection in December 2018. By late 2018, first woody plants had emerged on certain herbaceous fallows. Without further intervention, this succession on herbaceous fallows results in woody fallows *(savoka)*, which are characterized by a mix of herbaceous plants, shrubs, small trees, and occasionally bamboo. The 10 woody fallows chosen for our study had last burned 4–16 years prior to data collection. Lastly, we studied 10 irrigated rice paddies *(horoka)*, mostly situated on floodplains. See Figure 1 for a schematic overview.

Vanilla planifolia is a climbing orchid native to Central America, which is locally farmed in agroforestry systems using small trees as a support, while a variety of taller trees form the canopy above (Havkin-Frenkel & Belanger, 2018). We selected 20 vanilla agroforests that were established on fallow land, formerly part of the shifting cultivation cycle ("Fallow-derived vanilla"). Those agroforests are established on formerly forested open land and are thus "open-land-derived" following the concept of Martin, Osen, et al., (2020). We selected 10 additional vanilla agroforests which were directly established inside forest fragments and thus "forest-derived" (Martin, Osen, et al., 2020). See SI for details.

2.3 | Plot design

We collected all data within circular 25 m radius plots. Adjacent land is often used differently, which is reflected in the small mean sizes of each land unit in which we established the plots (Table S1). The mean minimum distance from one plot to the closest neighboring plot was 719 m (*SD* = 438 m) with a minimum of 260 m. Plot elevation spanned from 7 to 819 m.a.s.l. (mean = 192 m, *SD* = 207 m).

2.4 | Point counts

On all 80 plots, two observers jointly conducted two 40 min fixed-radius point counts (Bibby, Burgess, Hill, & Mustoe, 2000) before 8:15 a.m. during the breeding season (late August–December). We thus sampled all plots with the same effort of 80 min. We completed the first round of point counts on all plots, except in old-growth forest, in 2017, and the second round in 2018, reversing the order between years. We sampled in old-growth forest in 2018 only but waited 11 weeks between point counts on the same plot. Point-count times and observers are listed in Table S2. Lesser Vasa Parrot

(Coracopsis nigra) and Greater Vasa Parrot (*C. vasa*) were difficult to distinguish in the field (Hawkins, Safford, & Skerrett, 2015) and consequently counted as one species. We excluded all species only seen in flight or outside the plot and worked with presence/ absence data only for further analysis. See SI for details.

2.5 | Basal area, canopy closure, and landscape-scale forest cover data

Within each plot, we measured the diameter at breast height (dbh) of all living trees, palms, and herbs with a dbh ≥ 8 cm following Condit (2008). We then calculated the basal area per tree and summed up basal area of all trees per plot. From the tree dataset, we also derived the number of large trees, defined as the number of trees on each plot which had a basal area and height within the upper quartile basal area and height of all trees across the land-use types. Information for basal area and the number of large trees is missing for two plots due to denied plot access.

We obtained mean canopy closure values from five hemispherical images per plot, using a Nikon D5100 camera equipped with a Sigma Circular Fisheye 4.5 mm 1:2.8 lens mounted on a tripod at 2.4 m height. We determined exposure following the histogram-exposure protocol of Beckschäfer, Seidel, Kleinn, and Xu (2013), and extracted canopy closure values by applying a minimum thresholding algorithm.

We assessed proportion of forest cover in a 250-m-radius buffer around plot-centers using the *raster* R-package (Hijmans et al., 2019) and 2017 binary forest cover data with 30 m resolution (Vieilledent et al., 2018). We henceforth call this variable "landscape-scale forest cover".

2.6 | Endemism level, nativeness, and IUCN red-list status

We assigned all species to one of five different levels of endemism, that is, 1) non-endemic, 2) species-level endemic, 3) genus-level endemic, 4) subfamily-level endemic, and 5) family-level endemic. We based this categorization on the BirdLife species factsheet data (BirdLife International, 2018), where species only occurring in Madagascar are listed as country-endemics. We then checked for each endemic species whether there are other species of the same genus/ subfamily/ family occurring outside Madagascar and attributed each species to the according endemism level. We assigned three bird species breeding only in Madagascar but migrating outside the country to non-endemic. We treated the two very similar Vasa Parrot species as one species and categorized it as non-endemic as one of them (*C. vasa*) also occurs outside Madagascar. We supplemented the data with native/ non-native status (BirdLife International, 2018) and the threat category from the red list (IUCN, 2018). See Table S3.

2.7 | Statistical analysis

To assess the representativeness of our sample, we computed species accumulation curves and sample completeness per land-use type with raw incidence data in the R-package *iNext* (Hsieh, Ma, & Chao, 2016), using each plot as one incidence. We used an analysis of variance (ANOVA) and pairwise Tukey's honest significance tests to assess differences in plot-level species richness between land-use types. To test for differences in endemic species richness, we used weighted regression with Bonferroni correction because a Levene test showed heteroscedasticity in the variances between land-use types. For both tests, we applied a significance level of $p < .05$.

To derive the total number of species (gamma diversity) per endemism level for each land-use type, we subsampled the fallow-derived vanilla plots as we had 20 plots thereof (compared to 10 for all other land-use types). To do so, we randomly selected one fallow-derived vanilla plot within each village and a 10th randomly from the remaining fallow-derived vanilla plots (as one village did not have a fallow-derived vanilla, see Figure 1d). We tested whether the observed number of species per endemism level differed from random expectation by creating null models of species richness per endemism level for each land-use type. For each land-use type and each endemism level, we drew 1,000 times the realized number of species from the total species pool (57 species) without substitution to estimate expected means and standard deviation (*SD*). We calculated the means and *SD* for the sum of endemism levels equal or below each level for all endemic levels; for example, the estimate for endemic genera represents the sum of family-, subfamily-, and genus-level endemics which can be expected under random conditions based on the land-use-type-specific null model. The non-endemic estimate was the null estimate for non-endemic species only, plus the effectively realized number of endemic species for each land-use type. We then tested whether the number of species per endemism level found in each land-use type was within one or two *SD*.

To visualize the co-occurrence of species across land-use types, we used *UpsetR* (Conway, Lex, & Gehlenborg, 2017). To investigate differences in species composition between land-use types, we used the *metaMDS* function of the R-package *vegan* (Oksanen et al., 2019) with two dimensions and standard settings. We tested for differences between land-use types using the *adonis* function of *vegan* and the *pairwise.adonis* function with Bonferroni correction to test for pairwise differences between land-use types. We then displayed the correlation of three environmental variables (basal area, landscape-scale forest cover, and elevation; for two plots with missing basal area data, we used mean basal area data for the land-use type) with the site scores to the NMDS plot using the *envfit* function of *vegan*.

To analyze the drivers of non-endemic and endemic species richness across land-use types with tree presence outside old-growth forest (forest fragment, forest- and fallow-derived vanilla, woody fallow), we generated two generalized linear models (GLMs) with a Poisson error structure in the *lme4* package (Bates, 2014). We fitted basal area, altitude, landscape-scale forest cover, and land-use type

as predictor variables. Two additional predictor variables, canopy closure and number of large trees, were strongly correlated with basal area (Spearman rank correlation: 0.770 for canopy closure and 0.829 for large trees; Figure S3), which is why we a priori included only basal area in the models. For both models, we scaled numeric variables to facilitate interpretability of the model outputs. We excluded data from two fallow-derived vanilla plots for the GLMs due to missing basal area data. Lastly, we extracted Nagelkerke's R^2 for all GLMs (Nagelkerke, 1991). We analyzed data using R version 3.5.3 (R Core Team, 2019).

3 | RESULTS

We detected 2,506 birds belonging to 57 species, of which 31 were endemic and four red-listed by the IUCN. Species accumulation curves indicated still increasing species numbers after 10 plots per land-use type. However, sample coverage was > 80% for all land-use types except rice paddy, suggesting an adequate sampling of the bird communities (Figure S1). At plot level, old-growth forest had on average 12.3 species, which was twice the average of all other land-use types (6.1 species). Rice paddy, in contrast, had only 2.9 species on average, which was significantly less than other land-use types except herbaceous fallow which had 5.6 species. Considering endemic species only, rice paddy had fewer species than the unburned land-use types old-growth forest, forest fragment, and forest-derived vanilla, but not significantly fewer species than fallow-derived vanilla, woody fallow and herbaceous fallow (Figure 2, test results Table S4 and S5).

We encountered two non-native species: Common Myna (*Acridotheres tristis*) occurred on 12 burned plots and Helmeted Guineafowl (*Numida meleagris*) on one forest-derived vanilla plot. Four detected species are IUCN listed, all of which are endemic: We found Dusky Tetraka (*Crossleyia tenebrosa*) and Helmet Vanga (*Euryceros prevostii*), listed as "vulnerable", in old-growth forest, Madagascar Sparrowhawk (*Accipiter madagascariensis*), listed as "near threatened", in one forest fragment and Madagascar Rail (*Rallus madagascariensis*), listed as "vulnerable", in one rice paddy plot (Table S3). Gamma diversity across ten plots per land-use type was 34 species (25 endemic) in old-growth forest, 23 (11 endemic) in forest fragments, 25 (14 endemic) in forest-derived vanilla, 19 (8 endemic) in fallow-derived vanilla, 22 (8 endemic) in woody fallow, 16 (7 endemic) in herbaceous fallow, and 15 (2 endemic) in rice paddy (Figure 3). Endemic species were overrepresented in old-growth forest and underrepresented in the burned land-use types and rice paddy when compared to the land-use-type-specific null models. Conversely, the bird communities in forest fragments and forest-derived vanilla depicted a relatively representative subset of the overall community (Figure 3).

Species composition (Figure 4b) differed significantly between land-use types (Multivariate ANOVA based on dissimilarities: $R^2 = .35$, $p < .001$, $df = 6$). Pairwise comparisons revealed significant differences between old-growth forest and all other land-use
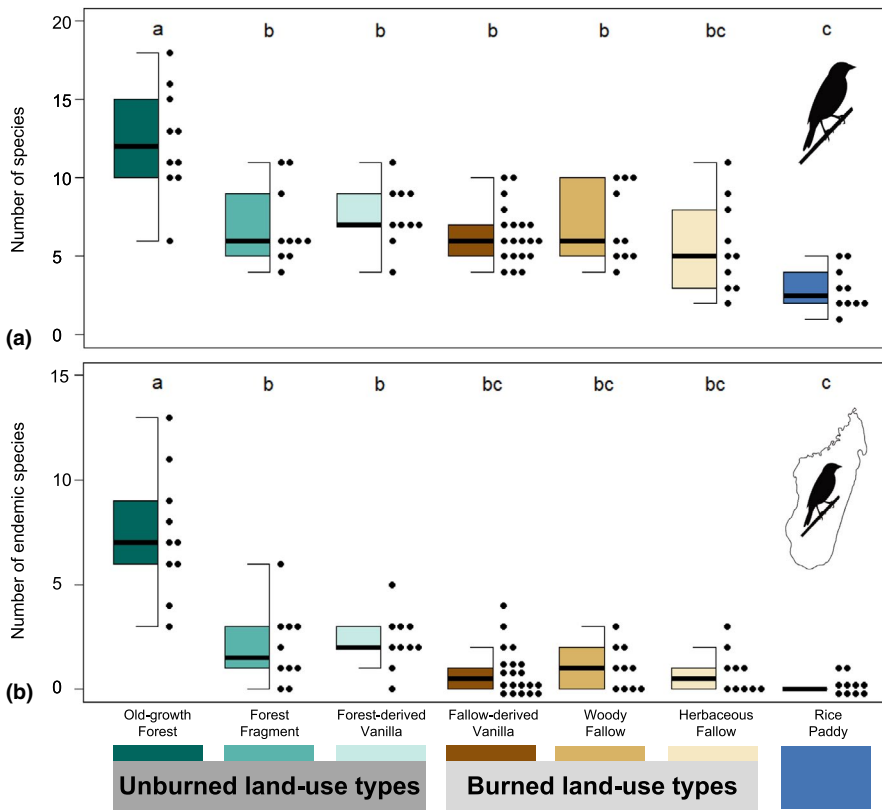
FIGURE 2 Plot-level bird species richness in seven prevalent land-use types in northeastern Madagascar (*n* = 10, except fallow-derived vanilla *n* = 20) for a) all species and b) endemic species only. The black horizontal line represents the median for each land-use type, and the lower and upper hinges of each box correspond to the first and third quartiles. The upper whiskers extend to the largest value whereas the lower whiskers extend to the smallest value, no further than 1.5× the inter-quartile range from the hinges of the box. Letters indicate significant differences between land-use types based on pairwise Tukey's honest significance tests for a) and a weighted regression for b) because a Levene test showed heteroscedasticity in the variances for species richness between land-use types for the latter (numeric test results in Table S4 and Table S5)

types as well as significant differences between pairs of burned and unburned land-use types (Table S6). Pairs within the burned respectively unburned land-use types were usually not significantly different (Table S6). These patterns were driven by 13 mainly endemic species occurring exclusively in old-growth forest and another twelve species being confined to unburned land-use types. Burned land-use types, on the other hand, only harbored four exclusive species while rice paddies had six thereof. 22 species occurred in both burned and unburned land-use types (Figure 4a). Basal area,

landscape-scale forest cover, and elevation structured bird community composition (Figure 4b).

In land-use types with tree presence outside old-growth forest (forest fragment, forest-derived vanilla, fallow-derived vanilla, and woody fallow), the plot-level parameters basal area and elevation had weak and non-significant associations with non-endemic and endemic species richness (Table 1). In contrast, landscape-scale forest cover was strongly and significantly associated with endemic species richness: Where landscape-scale forest cover was high, we found 43%
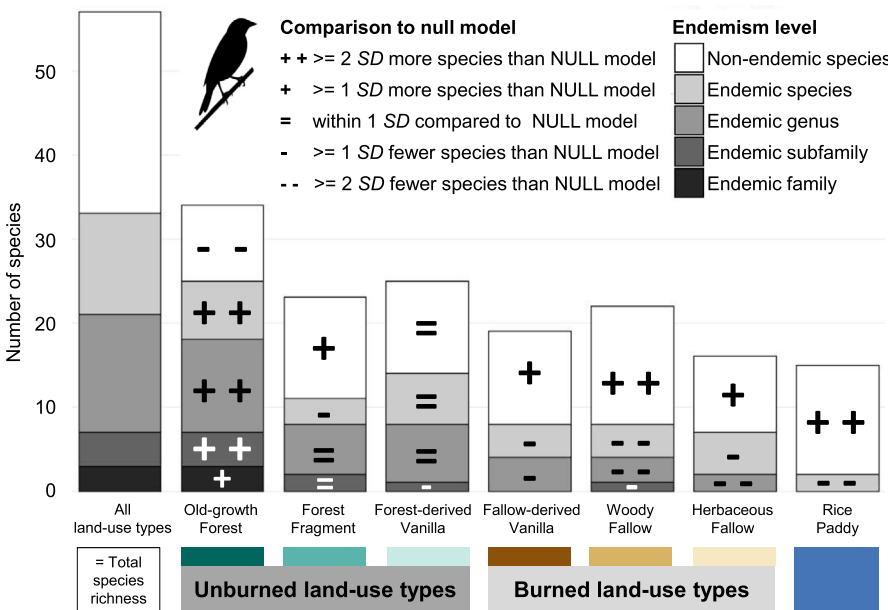

FIGURE 3 *Total number of bird species (gamma diversity) and number of species per endemism level across all plots (n = 80) and in each land-use type (n = 10 plots per land-use type; 10/20 subsampled for fallow-derived vanilla). Endemics made up a larger proportion than expected from a null model in old-growth forests. The unburned land-use types forest fragment and forest-derived vanilla came closest to the null model, while non-endemic species were heavily overrepresented in burned land-use types and rice paddies. Species endemic on family level did only occur in old-growth forest. Figure S2 shows all null model estimates and one respectively two standard deviations including those for endemism levels without observations*

FIGURE 4 Bird species composition across seven land-use types in northeastern Madagascar. a) Distribution of species by land-use type. Vertical bars show the number of species occurring in each of the unique combinations of land-use types depicted with the connected points. The color of the vertical bars corresponds to species occurring in any combination of unburned (dark gray), burned (light gray), or unburned and burned land-use types (black). The vertical bar representing species occurring exclusively in rice paddy is in blue. The horizontal bars depict the gamma diversity per land-use type. b) Species composition across land-use types from nonmetric-multidimensional scaling (stress value = 0.174). Colors depict the different land-use types, and ellipsoids indicate standard error of the weighted average of scores for each land-use type. Pairwise comparison between land-use types is displayed in Table S6. Basal area, landscape-scale forest cover, and elevation are plotted as environmental variables
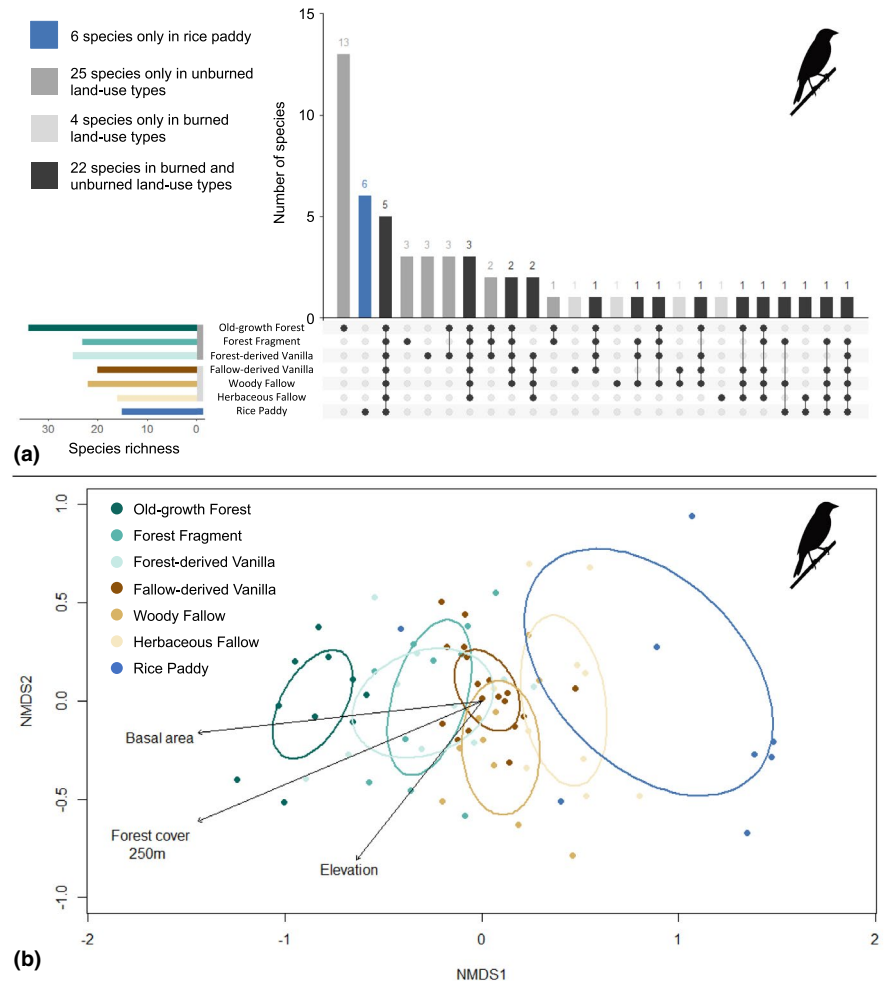
more endemic bird species than in plots with low landscape-scale forest cover (Table 1). Overall, the model explaining endemic species richness performed well (Nagelkerke's R^2 = .47) while the model explaining non-endemic species richness performed poorly (Nagelkerke's R^2 = .13).

4 | DISCUSSION

We assessed the value of a smallholder landscape mosaic in northeastern Madagascar for bird conservation by comparing six land-use types with old-growth forest. Alpha and gamma diversity were highest in old-growth forest and lowest in rice paddy. Conversely, alpha diversity did not differ significantly between other land-use types and between the two kind of vanilla agroforests. Here, the number of endemic species, species composition, and gamma diversity revealed differences. Furthermore, endemic species were overrepresented in old-growth forest, representatively occurring in forest fragment and forest-derived vanilla and underrepresented in fallow-derived vanilla, woody fallow, herbaceous fallow and rice paddy. Across plots outside old-growth forest with tree presence, landscape-scale forest cover was strongly positively associated with endemic species richness, but not with non-endemic species

richness. Overall, these results highlight the value of old-growth forest for birds and the important role of forest-derived vanilla agroforests for endemic birds.

4.1 | High value of old-growth forests for bird conservation

We present compelling evidence for the importance of old-growth forests for bird conservation, corroborating findings from Madagascar (Irwin et al., 2010; Rocha et al., 2015) and other tropical regions (Gibson et al., 2011). Firstly, old-growth forest had the highest alpha and gamma diversity of all land-use types studied. Secondly, bird communities in old-growth forest had many unique species and distinct community assemblages. Thirdly, endemic species were overrepresented in old-growth forest and species endemic on family level only occurred therein. These results are in line with other studies across tropical land-use gradients, which suggest that endemic species are often better suited for assessing the conservation value of a habitat than total species richness (de Lima et al., 2013; Waltert et al., 2011). Fourthly, we encountered threatened and near-threatened species most frequently in old-growth forest. Similarly, the only two other studies comparing

TABLE 1 General linear models (GLMs) explaining non-endemic species richness and endemic species richness in land-use types with tree presence outside old-growth forest (forest fragment, forest-derived vanilla, fallow-derived vanilla, and woody fallow, 48 plots, 2 plots excluded due to missing basal area data).

Response	Number of non-endemic species				Number of endemic species			
Predictors	Estimate	Standard Error	Z-value	P-value	Estimate	Standard Error	Z-value	p-value
Intercept	**1.56**	**0.17**	**9.37**	**<.001**	0.56	0.26	1.95	.052
Basal area	−0.02	0.10	−0.17	.868	−0.08	0.20	−0.38	.705
Elevation	−0.03	0.07	−0.49	.622	0.08	0.11	0.73	.465
Landscape-scale forest cover	0.06	0.07	0.88	.382	**0.35**	**0.12**	**2.85**	**<.001**
Forest-derived vanilla	0.03	0.20	0.14	.891	−0.04	0.31	−0.12	.90
Fallow-derived vanilla	0.16	0.21	0.75	.45	−0.55	0.42	−1.31	.190
Woody fallow	0.21	0.27	0.75	.45	−0.59	0.54	−1.08	.278
Observations	48				48			
Nagelkerke's R^2	0.125				0.466			

Note: Comparison of land-use types is against forest fragment. Bold font represents significant predictors.

bird diversity between forest sites and agricultural sites in eastern Madagascar found a strong turnover of species between forest and the agricultural mosaic (Martin et al., 2012; Rocha et al., 2015). The uniqueness of bird communities found in old-growth forests thus underlines the importance of well-governed protected areas and forest conservation policies in Madagascar to preserve its highly endemic biodiversity (Rakotomanana et al., 2013).

4.2 | Rice paddies harbor few but specialized birds

Although rice paddies had the lowest species richness, they might play an important role for certain specialized wetland species, as a total of six species were exclusively found in them; one of which was the endemic and red-listed Madagascar rail *(Rallus madagascariensis)*. However, many other species typically found in wetlands did not occur in rice paddy, emphasizing the conservation needs for wetlands in Madagascar (Kull, 2012).

4.3 | Vanilla agroforests as a conservation opportunity?

Vanilla agroforests are an important land use in the study area, but little is known about the value of vanilla agroforest for biodiversity. The lack of ecological research in vanilla agroforests is surprising given our knowledge on the contributions of other agroforests to biodiversity conservation (Bhagwat et al., 2008). The only studies available for vanilla are from a recent rapid biodiversity assessment (Hending, Andrianiaina, Rakotomalala, and Cotton, 2018; Hending, Andrianiaina, Maxfield, Rakotomalala, and Cotton, 2019): The authors reported fewer lemur sightings in vanilla agroforests than in forests and a diverse plant community in traditionally, less intensively managed vanilla agroforests in proximity to forests.

Similarly, we find vanilla agroforests to host fewer bird species than old-growth forest and show that landscape-scale forest cover is essential for endemic birds. The conservation value of vanilla agroforestry can, however, only be assessed relative to other land uses, and, most importantly, in comparison to the land use the agroforest was derived from. This important distinction lacks in previous studies (Hending et al., 2018, 2019).

The conversion of existing forest fragments into forest-derived vanilla agroforests causes, perhaps surprisingly, little change for birds. We explain this by the small size, the high level of wood extraction, and abundant disturbances in studied forest fragments, which has already caused losses in bird diversity compared to the contiguous old-growth forest. This pattern is typical for tropical rainforest fragments, which are sensitive to disturbance and fragmentation (Turner, 1996).

As an alternative to forest-derived vanilla agroforestry, a forest fragment could also be burned and used for hill rice production, which would convert the land into an herbaceous fallow in the short run and a woody fallow thereafter. According to our results, this conversion leads to a loss of higher-level-endemic species, making vanilla farming a more bird-friendly land-use option in comparison to burning for shifting hill rice cultivation. Another open question is how forest-derived agroforests are able to sustain tree cover in the long run: Agroforests often loose shade-trees over time, as shown for cacao (Tscharntke et al., 2011) and coffee (Geeraert et al., 2019). In contrast, a first study in Malagasy vanilla agroforest shows stable canopy cover along a chronosequence, suggesting that the loss of shade-trees may be less pronounced in vanilla agroforestry (Martin, Wurz, et al., 2020).

Fallow-derived vanilla had a lower conservation value than forest-derived vanilla and was most similar to woody fallow, which is the land-use type these agroforests were derived from. However, concluding a low conservation value of fallow-derived vanilla for biodiversity would be short-sighted. Instead of establishing a vanilla agroforest, a woody fallow owner may also continue the shifting

cultivation cycle. Ultimately, the land under shifting cultivation might enter a degradation cycle with disastrous effects for biodiversity, ecosystem services, and rice production (Styger et al., 2007), making vanilla farming, respectively the transformation from shifting cultivation to permanent agroforestry, a more biodiversity-friendly land-use option.

Conversely, planting vanilla inside old-growth forest would lead to a marked loss in bird species, with higher-level endemics being more likely to be lost. This underpins the limits of agroforests and heavily used forest fragments for bird conservation, while stressing the importance of old-growth forest conservation (see above). In spite of this, we have little evidence of large-scale encroachment of vanilla agroforests into old-growth forest at places we have visited. At least in Marojejy National Park, fast-paying activities like illegal logging of precious wood (Patel, 2007) seem to threaten biodiversity at a greater extent than vanilla cultivation.

Besides direct effects, vanilla cultivation could also indirectly influence biodiversity in our study region by generating income as a high-value cash crop. High vanilla prices could enable farmers to reduce the land-intensive shifting cultivation for staple crop production and purchase imported rice instead, thus reducing the pressures on remaining forests. Yet this option is impeded by fluctuating vanilla prices and the great risk of vanilla theft in the region (Laney & Turner, 2015), which both make an exclusive focus on vanilla cultivation a risky option for farmers. Vanilla cultivation could also negatively affect biodiversity, because farmers often invest their return from vanilla sales into house construction (Hänke et al., 2018), which might lead to an increase in demand for local timber. This, in turn, might drive selective logging in forests (Zaehringer et al., 2017), with potentially negative effects for biodiversity (Irwin et al., 2010).

We conclude that while fallow-derived agroforests are less valuable for birds than forest-derived agroforests, they may take fallow land out of the shifting cultivation cycle, possibly preventing further ecological degradation. Conversely, forest-derived agroforests may degrade forest, but the change compared to already-disturbed forest fragments is limited. Additionally, forest-derived agroforests may avoid the loss of tree cover from forest fragments by offering an income from vanilla farming.

4.4 | Bird-friendly vanilla agroforest management

Landscape-scale forest cover benefits endemic bird species richness and is maintained by old-growth forest, forest fragments, and forest-derived vanilla agroforest. Keeping trees in forest-derived agroforests may, however, be directly and indirectly disadvantageous for farmers, leading to possible conservation trade-offs. Directly, since trees cannot be used for timber and fuelwood (Zaehringer et al., 2017), and indirectly, because trade-offs could exist between yields and canopy closure. However, a recent study has shown no trade-offs between yields and canopy cover under current farming practices (Martin, Wurz, et al., 2020). Nonetheless, given these

potential economic losses for farmers, sustainability standards could provide incentives to keep trees producing "high-shade vanilla", following examples from coffee and cacao (Perfecto, Vandermeer, Mas, & Pinto, 2005; Tscharntke et al., 2015). Importantly, sustainability standards should encourage tree recovery in fallow-derived agroforests and tree maintenance in forest-derived agroforests, but avoid incentivizing the establishment of new forest-derived agroforests (Martin, Osen, et al., 2020). Sustainability standards should thus be sensible to land-use history, leading to an agricultural landscape with optimized benefits for people and nature.

4.5 | Landscape forest cover as a predictor of bird diversity outside old-growth forest

Landscape-scale forest cover had a positive effect on endemic species richness in vanilla agroforests, forest fragments and woody fallows and also affected community composition. Non-endemic bird species richness was, however, not affected (Table 1). Consistent with findings from Afrotropical agroforestry (Waltert et al., 2011), this suggests that endemic bird species need a minimum amount of forest cover on a landscape-scale to survive. This threshold is likely species-specific (Ocampo-Ariza et al., 2019) and currently unknown for our study area. Forest cover in the agricultural landscape is maintained by forest fragments and forest-derived vanilla agroforests. This highlights the importance of landscape-scale action in conserving old-growth forest as well as tree cover within agroforests and forest fragments (Perfecto et al., 2005; Tscharntke et al., 2015). Given the recent loss of forest cover, some bird species in the region might show an extinction debt, since present-day forest cover might not provide enough habitat for their current populations to persist in the long run (Kuussaari et al., 2009). This might confound our results, but our study design is not aimed at investigating extinction debts. However, evidence suggests that extinction debts are highest for long-lived species (Kuussaari et al., 2009), and since most species in our study are relatively small and short-lived, we suggest a minor role of extinction debts on the results of our study.

4.6 | Conclusion

Old-growth forests are indispensable for many endemic bird species. However, vanilla agroforestry may provide an important habitat for birds within the agricultural landscape mosaic, but their conservation value fundamentally depends on land-use history: Forest-derived agroforests are most similar to small and selectively logged forest fragments, whereas fallow-derived agroforests are most similar to fallow land. Importantly, forest-derived vanilla agroforest may avoid the loss of forest fragments, while fallow-derived vanilla agroforest may reduce land degradation through shifting cultivation, by providing a more attractive alternative land use. The stark contrasts between fallow-derived and

forest-derived vanilla agroforests further suggest that a differentiation based on land-use history represents a promising avenue for future research and applications in tropical agroforestry systems—beyond vanilla.

CONFLICT OF INTEREST

The corresponding author confirms on behalf of all authors that there have been no involvements that might raise the question of bias in the work reported or in the conclusions, implications, or opinions stated.

AUTHORS' CONTRIBUTIONS

DAM, KO, AW, AA, and HK conceived the ideas and designed methodology; DAM, RA, SD, and ER collected bird data; KO collected and processed tree and canopy closure data; DAM analyzed the data and led the writing of the manuscript. All authors contributed to the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository: https://doi. org/10.5061/dryad.83bk3j9nm (Martin, Andriafanomezantsoa, et al. 2020).

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REFERENCES

Bates, D. M. (2014). lme4: Mixed-effects modeling with R (Version 1.1-21). Retrieved from https://CRAN.R-project.org/package=lme4

Beckschäfer, P., Seidel, D., Kleinn, C., & Xu, J. (2013). On the exposure of hemispherical photographs in forests. *Iforest - Biogeosciences and Forestry*, 6(4), 228–237. https://doi.org/10.3832/ifor0957-006

Bhagwat, S. A., Willis, K. J., Birks, H. J. B., & Whittaker, R. J. (2008). Agroforestry: A refuge for tropical biodiversity? *Trends in Ecology & Evolution*, 23(5), 261–267. https://doi.org/10.1016/j. tree.2008.01.005

Bibby, C. J., Burgess, N. D., Hill, D. A., & Mustoe, S. (2000). *Bird census techniques*. Amsterdam, The Netherlands: Elsevier.

BirdLife International (2018). BirdLife International: Data Zone. Retrieved from http://datazone.birdlife.org/home. Accessed 26.11.2018.

Brown, J. L., Sillero, N., Glaw, F., Bora, P., Vieites, D. R., & Vences, M. (2016). Spatial biodiversity patterns of madagascar's amphibians and reptiles. *PLoS One*, 11(1), e0144076. https://doi.org/10.1371/journ al.pone.0144076

Comtrade, U. N. (2017). United Nations. Retrieved from https://comtr ade.un.org. Accessed 30.10.2019.

Condit, R. (2008). Methods for estimating aboveground biomass of forest and replacement vegetation in the tropics. *Center for Tropical Forest Science Research Manual*, 73, 1–73.

Conway, J. R., Lex, A., & Gehlenborg, N. (2017). UpSetR: An R package for the visualization of intersecting sets and their properties. *Bioinformatics*, 33(18), 2938–2940. https://doi.org/10.1093/bioin formatics/btx364

de Lima, R. F., Dallimer, M., Atkinson, P. W., & Barlow, J. (2013). Biodiversity and land-use change: Understanding the complex responses of an endemic-rich bird assemblage. *Diversity and Distributions*, 19(4), 411–422. https://doi.org/10.1111/ddi.12015

FAO (2020). FAOSTAT. Food and Agriculture Organisation of the United Nations. Retrieved from http://www.fao.org/faostat/en/#home; accessed 16.7.2020.

Ferreira Arruda, T. (2018). Spatial-temporal patterns of deforestation in Northeast Madagascar [MSc Thesis]. University of Goettingen.

Fordham, D. A., & Brook, B. W. (2010). Why tropical island endemics are acutely susceptible to global change. *Biodiversity and Conservation*, 19(2), 329–342. https://doi.org/10.1007/s10531-008-9529-7

Frishkoff, L. O., Ke, A., Martins, I. S., Olimpi, E. M., & Karp, D. S. (2019). Countryside biogeography: the controls of species distributions in human-dominated landscapes. *Current Landscape Ecology Reports*, 4(2), 15–30. https://doi.org/10.1007/s40823-019-00037-5

Geeraert, L., Hulsmans, E., Helsen, K., Berecha, G., Aerts, R., & Honnay, O. (2019). Rapid diversity and structure degradation over time through continued coffee cultivation in remnant Ethiopian Afromontane forests. *Biological Conservation*, 236, 8–16. https://doi.org/10.1016/j. biocon.2019.05.014

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., … Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, 478(7369), 378–381. https://doi. org/10.1038/nature10425

Goodman, S. M., & Benstead, J. P. (2005). Updated estimates of biotic diversity and endemism for Madagascar. *Oryx*, 39(1), 73–77. https:// doi.org/10.1017/S0030605305000128

Gordon, C., Manson, R., Sundberg, J., & Cruz-Angón, A. (2007). Biodiversity, profitability, and vegetation structure in a Mexican coffee agroecosystem. *Agriculture, Ecosystems & Environment*, 118(1), 256–266. https://doi.org/10.1016/j.agee.2006.05.023

Gray, C. L., Hill, S. L. L., Newbold, T., Hudson, L. N., Börger, L., Contu, S., … Scharlemann, J. P. W. (2016). Local biodiversity is higher inside than outside terrestrial protected areas worldwide. *Nature Communications*, 7, 12306. https://doi.org/10.1038/ncomms12306

Hänke, H., Barkmann, J., Blum, L., Franke, Y., Martin, D. A., Niens, J., …Wurz, A. (2018). Socio-economic, land use and value chain perspectives on vanilla farming in the SAVA Region (north-eastern Madagascar): The Diversity Turn Baseline Study (DTBS). July 2019 Edition. https://doi.org/10.13140/RG.2.2.22059.80163.

Havkin-Frenkel, D., & Belanger, F. C. (Eds.) (2018). *Handbook of vanilla science and technology*, 2nd ed. Hoboken, NJ: Wiley.

Hawkins, A. F. A., Safford, R., & Skerrett, A. (2015). *Birds of Madagascar and the Indian Ocean Islands*. London, UK: Christopher Helm.

Hending, D., Andrianiaina, A., Maxfield, P., Rakotomalala, Z., & Cotton, S. (2019). Floral species richness, structural diversity and conservation value of vanilla agroecosystems in Madagascar. *African Journal of Ecology*, 58(1), 100–111. https://doi.org/10.1111/aje.12682

Hending, D., Andrianiaina, A., Rakotomalala, Z., & Cotton, S. (2018). The Use of Vanilla Plantations by Lemurs: encouraging findings for both lemur conservation and sustainable agroforestry in the sava region, Northeast Madagascar. *International Journal of Primatology*, 39(1), 141–153. https://doi.org/10.1007/s10764-018-0022-1

Hijmans, R. J., van Etten, J., Cheng, J., Mattiuzzi, M., Sumner, M., Greenberg, J. A., ...Shortridge, A. (2019). Package 'raster' (Version 3.0-7). Retrieved from https://CRAN.R-project.org/package=raster

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7(12), 1451–1456. https://doi.org/10.1111/2041-210X.12613

Irwin, M. T., Wright, P. C., Birkinshaw, C., Fisher, B. L., Gardner, C. J., Glos, J., ... Ganzhorn, J. U. (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation*, 143(10), 2351–2362. https://doi.org/10.1016/j.biocon.2010.01.023

IUCN (2018). The IUCN Red List of Threatened Species (Version 2018-2). Retrieved from http://www.iucnredlist.org. Accessed 26.11.2018.

Karger, D. N., O. Conrad, J. Böhner, T. Kawohl, H. Kreft, R. W. Soria-Auza, N. E. Zimmermann, H. P. Linder, and M. Kessler.2017. Climatologies at high resolution for the earth's land surface areas. *Scientific Data* 4(1): 1–20. https://doi.org/10.1038/sdata.2017.122

Kull, C. A. (2012). Air photo evidence of historical land cover change in the highlands: Wetlands and grasslands give way to crops and woodlots. *Madagascar Conservation & Development*, 7(3), 144–152. https://doi.org/10.4314/mcd.v7i3.7

Kuussaari, M., Bommarco, R., Heikkinen, R. K., Helm, A., Krauss, J., Lindborg, R., ... Steffan-Dewenter, I. (2009). Extinction debt: A challenge for biodiversity conservation. *Trends in Ecology & Evolution*, 24(10), 564–571. https://doi.org/10.1016/j.tree.2009.04.011

Laney, R., & Turner, B. L. (2015). The Persistence of Self-Provisioning Among Smallholder Farmers in Northeast Madagascar. *Human Ecology*, 43(6), 811–826. https://doi.org/10.1007/s10745-015-9791-8

Llopis, J. C., Harimalala, P. C., Bär, R., Heinimann, A., Rabemananjara, Z. H., & Zaehringer, J. G. (2019). Effects of protected area establishment and cash crop price dynamics on land use transitions 1990–2017 in north-eastern Madagascar. *Journal of Land Use Science*, 14(1), 52–80. https://doi.org/10.1080/1747423X.2019.1625979

Martin, D. A., Andriafanomezantsoa, R., Dröge, S., Osen, K., Rakotomalala, E., Wurz, A., ...Kreft, H. (2020). Data from: Bird diversity and endemism along a land-use gradient in Madagascar: The conservation value of vanilla agroforests. Dryad Digital Repository,https://doi.org/10.5061/dryad.83bk3j9nm

Martin, D. A., Osen, K., Grass, I., Hölscher, D., Tscharntke, T., Wurz, A., & Kreft, H. (2020). Land-use history determines ecosystem services and conservation value in tropical agroforestry. *Conservation Letters*, e12740. https://doi.org/10.1111/conl.12740

Martin, D. A., Wurz, A., Osen, K., Grass, I., Hölscher, D., Rabemanantsoa, T., ... Kreft, H. (2020). Shade-tree rehabilitation in vanilla agroforests is yield neutral and may translate into landscape-scale canopy cover gains. *EcoEvoRxiv Preprints*. https://doi.org/10.32942/osf.io/63fc2

Martin, E. A., Viano, M., Ratsimisetra, L., Laloë, F., & Carrière, S. M. (2012). Maintenance of bird functional diversity in a traditional agroecosystem of Madagascar. *Agriculture, Ecosystems & Environment*, 149, 1–9. https://doi.org/10.1016/j.agee.2011.12.005

Melo, F. P. L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., & Tabarelli, M. (2013). On the hope for biodiversity-friendly tropical landscapes. *Trends in Ecology & Evolution*, 28(8), 462–468. https://doi.org/10.1016/j.tree.2013.01.001

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853–858. https://doi.org/10.1038/35002501

Nagelkerke, N. J. D. (1991). A note on a general definition of the coefficient of determination. *Biometrika*, 78(3), 691–692. https://doi.org/10.1093/biomet/78.3.691

Ndriantsoa, S. H., Riemann, J. C., Raminosoa, N., Rödel, M.-O., & Glos, J. S. (2017). Amphibian diversity in the matrix of a fragmented landscape around ranomafana in Madagascar Depends on matrix quality. *Tropical Conservation Science*, 10, 1–16. https://doi.org/10.1177/1940082916686065

Ocampo-Ariza, C., Denis, K., Njie Motombi, F., Bobo, K. S., Kreft, H., & Waltert, M. (2019). Extinction thresholds and negative responses of Afrotropical ant-following birds to forest cover loss in oil palm and agroforestry landscapes. *Basic and Applied Ecology*, 39, 26–37. https://doi.org/10.1016/j.baae.2019.06.008

Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ...Wagner, H. (2019). vegan: Community Ecology Package (Version 2.5-4). Retrieved from https://CRAN.R-project.org/package=vegan

Patel, E. R. (2007). Logging of Rare Rosewood and Palisandre (Dalbergia spp.) within Marojejy National Park, Madagascar. *Madagascar Conservation & Development*, 2(1), 11–16. https://doi.org/10.4314/mcd.v2i1.44124

Perfecto, I., Vandermeer, J., Mas, A., & Pinto, L. S. (2005). Biodiversity, yield, and shade coffee certification. *Ecological Economics*, 54(4), 435–446. https://doi.org/10.1016/j.ecolecon.2004.10.009

R Core Team (2019). *R: A language and environment for statistical computing*.Vienna: R Core Team.

Rakotomanana, H., Jenkins, R. K. B., & Ratsimbazafy, J. (2013). Conservation Challenges for Madagascar in the Next Decade. In P. H. Raven, N. S. Sodhi & L. Gibson (Eds.), *Conservation Biology: Voices from the Tropics* (pp. 33–39). Oxford, UK: John Wiley & Sons. https://doi.org/10.1002/9781118679838.ch5

Rocha, R., Virtanen, T., & Cabeza, M. (2015). Bird assemblages in a malagasy forest-agricultural frontier: effects of habitat structure and forest cover. *Tropical Conservation Science*, 8(3), 681–710. https://doi.org/10.1177/194008291500800307

Schroth, G., Harvey, C. A., da Fonseca, G. A. B., Gascon, C., Vasconcelos, H. L., & Izac, A.-M.-N. (2004). *Agroforestry and biodiversity conservation in tropical landscapes*. Washington, USA: Island Press.

Styger, E., Rakotondramasy, H. M., Pfeffer, M. J., Fernandes, E. C. M., & 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(3–4), 257–269. https://doi.org/10.1016/j.agee.2006.07.012

Tscharntke, T., Clough, Y., Bhagwat, S. A., Buchori, D., Faust, H., Hertel, D., ... Wanger, T. C. (2011). Multifunctional shade-tree management in tropical agroforestry landscapes—A review. *Journal of Applied Ecology*, 48(3), 619–629. https://doi.org/10.1111/j.1365-2664.2010.01939.x

Tscharntke, T., Milder, J. C., Schroth, G., Clough, Y., DeClerck, F., Waldron, A., ... Ghazoul, J. (2015). Conserving biodiversity through certification of tropical agroforestry crops at local and landscape scales. *Conservation Letters*, 8(1), 14–23. https://doi.org/10.1111/conl.12110

Turner, I. M. (1996). Species loss in fragments of tropical rain forest: a review of the evidence. *Journal of Applied Ecology*, 33(2), 200–209. https://doi.org/10.2307/2404743

Vieilledent, G., Grinand, C., Rakotomalala, F. A., Ranaivosoa, R., Rakotoarijaona, J.-R., Allnutt, T. F., & Achard, F. (2018). Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biological Conservation*, 222, 189–197. https://doi.org/10.1016/j.biocon.2018.04.008

Waltert, M., Bobo, K. S., Kaupa, S., Montoya, M. L., Nsanyi, M. S., & Fermon, H. (2011). Assessing conservation values: biodiversity and

endemicity in tropical land use systems. *PLoS One*, *6*(1), e16238. https://doi.org/10.1371/journal.pone.0016238

Zaehringer, J. G., Schwilch, G., Andriamihaja, O. R., Ramamonjisoa, B., & Messerli, P. (2017). Remote sensing combined with social-ecological data: The importance of diverse land uses for ecosystem service provision in north-eastern Madagascar. *Ecosystem Services*, *25*, 140–152. https://doi.org/10.1016/j.ecoser.2017.04.004

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.