Conservation value of vanilla agroecosystems for vertebrate diversity in north-east Madagascar

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Abstract As a result of increasing global demand for food, large areas of natural habitat are being converted to agroecosystems to accommodate crop cultivation. This agricultural expansion is most prominent in the tropics, where many rural communities are dependent solely on farming income for their livelihoods. Such agricultural land conversion can have severe implications for local fauna. In this study, we compared vertebrate species diversity between natural forest habitat and three types of vanilla plantations maintained under varying management regimes in north-east Madagascar. We used diurnal and nocturnal transects to survey vertebrate diversity. Natural forest habitat contained the greatest vertebrate species diversity, and had proportionally more threatened and endemic species than all vanilla plantation types. However, we observed a greater number of species and a higher inverse Simpson index in minimally managed vanilla plantations located within or near natural forest compared to intensively managed vanilla plantations. These findings are important and encouraging for animal conservation and sustainable crop cultivation in Madagascar, and suggest that newly created vanilla plantations, and already existing plantations, should endeavour to follow the more traditional, minimalistic management approach to improve sustainability and promote higher faunal diversity.

Keywords Agroforestry, animal conservation, biodiversity, habitat management, Madagascar, species richness, vanilla plantation, vertebrate surveys

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Introduction

As a result of global human population expansion, almost half of the Earth's land cover has been modified to accommodate agricultural areas (Vitousek et al., 1997; Foley et al., 2005; Pongratz et al., 2008; Flohre et al., 2011; Hanke et al., 2014). This global demand for arable land is predicted to increase further as human populations continue to rise and encroach on remaining areas of natural habitat (Dunn, 2004; Godfray et al., 2010; Phalan et al., 2011; Tscharntke et al., 2012). Land conversion can have a profoundly detrimental effect on the diversity of native fauna and flora (Tilman et al., 2002; Pongratz et al., 2008; Medan et al., 2011), and data on the effects of specific agricultural practices on biodiversity are urgently needed to curb loss of species, especially in the tropics (Dunn, 2004; Harvey et al., 2006; Newbold et al., 2020).

Cash-crop plantations are one example of anthropogenic, agricultural environments that have replaced areas once dominated by natural forest (Vallan et al., 2004; Razakamanarivo et al., 2012). These plantations are agroecosystems, functional areas of agricultural activity that harbour an ecosystem of living organisms, and they are often associated with reduced biodiversity (Perfecto & Vandermeer, 2008). For instance, amphibian diversity was lower in exotic tree plantations converted from intact forest (Vallan, 2002; Vallan et al., 2004). However, some species are known to make use of these agricultural environments. Crop species such as coffee, tea, cacao and rubber are sometimes cultivated in diversified agroforestry systems in which native trees are integrated with the crop plants (Leakey, 1996), and these systems are beneficial to native vertebrates as they provide potential travel routes, refuges and feeding opportunities (Donald, 2004; Faria et al., 2007; Ranganathan et al., 2008; Clough et al., 2009; Anand et al., 2010; Venugopal, 2010; Eppley et al., 2015; Webber et al., 2020). The method of cultivation in such diversified systems appears to have consequences for biodiversity, with systems managed under less intensive regimes suffering the lowest biodiversity loss (Faria et al., 2007; Perfecto & Vandermeer, 2008).

Madagascar is known for its exceptional biodiversity and endemism (Myers et al., 2000; Goodman & Benstead, 2005; Wilme et al., 2006). Driven by a rapid increase in human population, prices of and international demand for cash crops, and a consequent increase in demand for crop cultivation areas (Irwin et al., 2010; Rogers et al., 2010; Schwitzer et al., 2011; Llopis et al., 2019), Malagasy habitats are suffering large-scale fragmentation and loss of primary vegetation (Ganzhorn et al., 2001; Harper et al., 2007; Vieilledent et al., 2018). It remains unclear how animal species respond to these agricultural environments, whether they are a suitable habitat for Madagascar's already fragile biota and if agroforestry brings oppurtunities for biodiversity conservation (Ganzhorn, 1987; Ramanamanjato & Ganzhorn, 2001).

Cash-crop plantations such as vanilla, cacao, coffee, sugarcane and timber (e.g. *Eucalyptus* sp.) are common in north-east Madagascar (Ramanamanjato & Ganzhorn, 2001; Razakamanarivo et al., 2012; Bomgardner, 2016) and have replaced pre-existing natural forests (Irwin et al., 2010; Schwitzer et al., 2011). These highly modified, agricultural environments may retain some species but others may be lost during the land conversion process (Gibbs et al., 2009). Furthermore, the availability of suitable habitat in agricultural environments (such as agroforests) depends on many factors, including management techniques, landscape composition and distance to forest (Ocampo-Ariza et al., 2019; Warren-Thomas et al., 2020). Although these modified environments are degraded compared to natural forest habitat, they may be crucial for species conservation (Perfecto & Vandermeer, 2008). For instance, Madagascar's eucalyptus plantations harbour a variety of animals, including seven species of threatened lemurs (Ganzhorn, 1987; Ramanamanjato & Ganzhorn, 2001). Despite this conservation potential, the biodiversity value of Madagascar's cash-crop plantations remains poorly known.

In this study, we used rapid visual surveys to assess species richness and calculate the inverse Simpson index for vertebrates in vanilla plantations of the Sava region of north-east Madagascar, the country's principal vanilla-growing region, with c. 24,500 ha of vanilla plantations (ILO, 2011). As recent studies have demonstrated the value of Madagascar's vanilla plantations for biodiversity (Hending et al., 2018, 2020a; Martin et al., 2021; Osen et al., 2021; Raveloaritiana et al., 2021), we compared species diversity and richness in vanilla plantations with that in natural forests. We hypothesized that vanilla plantations would contain lower vertebrate diversity than natural forests, as was also observed in studies on other groups of organisms (e.g. Hending et al., 2018, 2020a), and we also predicted that vertebrate diversity would vary significantly between vanilla plantations maintained under different management regimes.

Study area

The Sava region of north-east Madagascar covers an area of > 25,000 km² (Bomgardner, 2016). We conducted our investigation within the Vohemar District, in the 2,500 km² Loky-Manambato Protected Area, and the Bemarivo area of the Sambava District. The remaining forest habitat in the Sava region is under threat from slash-and-burn agriculture as a result of rapid human population growth, wood exploitation and, in the case of the Loky-Manambato Protected Area, gold mining (Meyler et al., 2012; Quemere et al., 2012; Schwitzer et al., 2013).

Methods

Habitat definition and survey area selection

Following Hending et al. (2018), we defined four habitat types for rapid biodiversity assessment, using geographical and observational data to facilitate consistent and meaningful comparisons.

Natural forest Primary, secondary or degraded forest, comprising ≥ 75% native tree species, which has generated at the site, within or outside a protected area.

Forest vanilla eco-plantation Plantations that are directly derived from the forest. Vanilla vines are grown upon pre-existing, naturally growing tutor trees that are not managed. Sites are connected to or in close proximity of (< 100 m) the nearest natural forest.

Non-forest vanilla eco-plantation Plantations that are directly derived from a natural habitat that is not forest (e.g. grassland, savannah). Vanilla vines are grown upon pre-existing, naturally growing tutor trees that are not managed. Other crop species are often grown alongside the vanilla. Sites are > 0.5 km from the nearest natural forest.

Intensive vanilla plantation Plantations derived from the clearing of pre-exiting habitat outside the forest. Vanilla is grown upon tutor tree species that are planted (i.e. not naturally growing), heavily managed and densely planted to make maximum use of available space. Other crop species are often grown alongside the vanilla and natural fertilizers may be used at these sites to enhance soil quality.

The eco-plantation classification reflects the pre-existing ecosystem within which the vanilla is grown, rather than a judgement of the plantation's ecological merits or shortcomings.

We surveyed sites in each habitat during 10 January–25 April 2017, the wet season in the Sava region, with nine sites in natural forest, six in forest eco-plantation, six in non-forest eco-plantation and five in intensive plantation (Fig. 1, Table 1). This was the total number of sites available to us within the surveyed area. We recorded waypoints for the perimeter of each survey site using a GPS, and from these we calculated areas and measured the distance from the perimeter of each site to the nearest natural forest, with *ArcGIS 10.6* (Esri, Redlands, USA).

Vertebrate surveys

We assessed vertebrate biodiversity (mammals, birds, reptiles and amphibians) at each site using 1–3 parallel

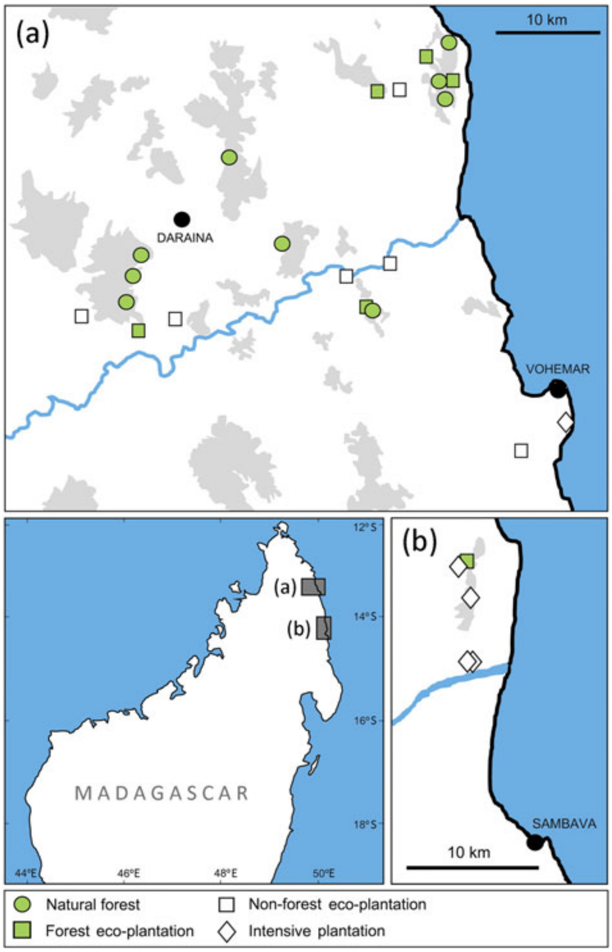

FIG. 1 Localities of natural forest, forest eco-plantation, non-forest eco-plantation and intensive plantation sites surveyed in the Sava region of northern Madagascar near Vohemar-Daraina (a) and Sambava (b). Forested areas are shaded.

transects, depending on the shape and size of each site. All transects were based on trails, established by either villagers (in forests) or farmers (in plantations), which passed through the middle of the forest or plantation. Visibility was limited to c. 10 m either side of the transects because of the density of surrounding vegetation. Two investigators (DH and AA) walked along each transect, recording all vertebrate species observed. We surveyed each transect on one day only, at 05.00, 12.00 and 21.00, to maximize the chances of observing both diurnal and nocturnal fauna, walking at a pace of 1 km/h to ensure a consistent survey rate across transects. We used binoculars and hand-held high-lumen torches to assist with animal identification during diurnal and nocturnal transects, respectively. We only recorded birds that were perched or terrestrially active (bird flyovers were not counted). We searched under stones and under vegetation to survey for amphibians and small reptiles. We captured and handled reptiles and frogs, the only amphibians in Madagascar, so that we could accurately identify them. All species were identified using field keys (Garbutt,

TABLE 1 Centroid location, distance to the nearest forest fragment, and area of each vanilla plantation surveyed in the Sava region, north east Madagascar (Fig. 1), during 10 January–25 April 2017, by habitat type (see text for definitions).

Site (by habitat type)	Latitude	Longitude	Distance to nearest forest (km)	Area (ha)
Natural forest				
Analamazava	S13°15′ 23.70″	E49°36′ 58.31″		216
Analamanara	S13°17′ 18.92″	E49°50′ 21.52″		104
Bemosy	S13°14′ 16.12″	E49°37′ 24.22″		584
Bekaroaka	S13°08′ 56.75″	E49°42′ 21.40″		5,424
Antsahabe	S13°16′ 51.47″	E49°36′ 36.30″		265
Bobankora	S13°13′ 39.59″	E49°45′ 19.24″		1,416
Misorolava	S13°05′ 43.59″	E49°54′ 30.74″		194
Ampasira	S13°04′ 45.36″	E49°54′ 11.50″		278
Angengo	S13°02′ 36.25″	E49°54′ 43.72″		263
Forest eco-plantations				
Berondra	S13°18′ 23.23″	E49°37′ 16.98″	0.06	0.47
Analamanara	S13°17′ 06.65″	E49°50′ 09.99″	0.00	1.10
Andranga	S13°04′ 39.75″	E49°54′ 55.12″	0.05	1.90
Ankalotany	S13°03′ 31.04″	E49°53′ 32.70″	0.01	0.61
Antingana	S13°05′ 15.63″	E49°50′ 41.33″	0.01	1.60
Manasibe	S14°03′ 59.54″	E50°07′ 30.78″	0.02	1.60
Non-forest eco-plantations				
Ankaramy	S13°17′ 43.59″	E49°39′ 23.02″	1.66	0.92
Ampondra 1[1]	S13°24′ 52′98″	E49°58′ 35.91″	3.48	4.50
Ampondra 2[1]	S13°24′ 50.73″	E49°58′ 42.90″	3.99	0.39
Ampondra 3[1]	S13°24′ 49.43″	E49°58′ 45.70″	4.03	0.34
Mahasoa	S13°14′ 43.70″	E49°51′ 21.94″	3.48	1.70
Mafokovo	S13°15′ 25.12″	E49°48′ 52.64″	0.89	0.60
Antsoha	S13°17′ 33.74″	E49°34′ 05.56″	1.19	0.53
Angalanerana	S13°05′ 13.78″	E49°51′ 55.38″	2.13	1.80
Intensive plantations				
Floribis	S13°23′ 14.39″	E50°01′ 04.02″	17.03	27.00

Table 1 (*cont.*)

Site (by habitat type)	Latitude	Longitude	Distance to nearest forest (km)	Area (ha)
Angalandrava	S14°08′ 14.58″	E50°07′ 28.50″	5.02	0.45
Bemanevika	S14°08′ 23.26″	E50°07′ 41.51″	4.06	0.49
Tsaratanana	S14°05′ 30.27″	E50°07′ 41.44″	0.20	0.42
Biarafa	S14°04′ 12.32″	E50°07′ 10.57″	0.26	2.90

[1]The three Ampondra sites were adjacent or close to each other, and therefore survey data were combined to avoid potential pseudo-replication.

2007; Glaw & Vences, 2007; Mittermeier et al., 2010; Sinclair & Langrand, 2013).

Data Analysis

We performed all statistical analyses in *R 4.02* (R Core Team, 2017). Varitions between surveyed sites in area (forests 104–5,424 ha; plantations 0.42–27 ha) and transect length (forests 700–1,050 m; plantations 200–1,000 m), may have led to differences in survey effort and thus detection bias acros sites, and therefore we tested for differences in survey effort (transect length) using a t test (between forests and plantations) and a one-way ANOVA (between plantation types). We also examined whether plantation areas varied between plantation types using a Kruskal–Wallis test (residual distribution was non-normal and could not be appropriately transformed).

We noted the IUCN Red List status of all species recorded, and whether each species was endemic to Madagascar, regionally native, migratory or invasive to Madagascar using the field keys and the IUCN Red List (IUCN, 2020). We compared mean total observed number of species between habitat types using a generalized linear mixed model (GLMM), as a proxy of total biodiversity. We then repeated this analysis separately for major taxonomic groups. We controlled for survey effort, vegetation type (as a proxy of visibility, obtained from Hending et al., 2020b), transect length, elevation, mean temperature, annual precipitation and site location as random factors in the GLMMs. Mean temperature and precipitation were obtained for each site from Worldclim (Hijmans et al., 2005, 1 km² resolution) and mean elevation from the Shuttle Radar Topography Mission raster layers (Jarvis et al., 2008; 90 × 90 m resolution) using the *R* packages *raster* (Hijmans, 2017) and *sp* (Bivand et al., 2013). Similarly, GLMMs were used to compare the per cent of species that were native, endemic or invasive to the study sites, or categorized as threatened, between habitat types. Habitat type was coded as a fixed factor in all GLMMs. We performed post-hoc sequential Holm–Bonferroni multiple comparisons between habitat types for all GLMMs.

To control for differences between sites, we used *EstimateS 9* (Colwell, 2013) to calculate the expected number of species (*S*) per *N* individuals in each habitat type using rarefaction (Colwell & Coddington, 1994; Lande et al., 2000; Colwell et al., 2004). Transect data from all sites of each habitat type were pooled to form one dataset for each habitat, and the number of knots was the total number of individual animals (*N*) observed in each habitat type (Colwell & Coddington, 1994; Colwell et al., 2004). As the number of individuals observed was different between habitats, we extrapolated the observed number of individuals from the three vanilla plantations up to the maximum number of individual animals (knots) observed in the natural forest habitat (the habitat with the greatest number of individuals; $N = 834$). We used rarefied and extrapolated *S* values (and associated 95% confidence intervals, derived from 100 randomization runs) to construct comparable species diversity–individual accumulation curves for each habitat type.

In addition, we also used *EstimateS* to calculate the inverse Simpson index ($\lambda = 1/D$; Simpson, 1949), which accounts for the number of individuals of each species observed and therefore controls for differences in species abundance between sites. We used the index values to construct diversity index–individual accumulation curves, with associated 95% confidence intervals (derived from 100 randomizations), for each of the four habitat types. We created diversity index–individual accumulation curves for three taxonomic groups (birds, reptiles and frogs) to investigate the distributions of these groups among the habitat types. We did not repeat this process for mammals as sample sizes were too small for rarefaction, but we present these data as box plots.

Results

Mean transect lengths in forests were significantly longer than those in plantations (forest 916 ± SE 40.8 m, plantation 521 ± SE 58.8 m; $t = 4.57$, df = 24, $P < 0.001$). In vanilla plantations, transect lengths were longer in larger plantations ($r_s = 0.556$, $N = 17$, $P = 0.021$). However, neither transect length nor plantation area differed significantly between the three plantation types (transect length, one-way ANOVA: $F_{2,14} = 0.193$, $P = 0.827$; plantation area, Kruskal–Wallis: $\chi^2 = 0.518$, df = 2, $P = 0.772$), suggesting that any differences between plantations were not the result of biased survey effort.

We recorded a total of 190 vertebrate species: 74 birds, 62 reptiles, 38 frogs and 16 mammals, including nine lemur species (see Supplementary Table 1 for a list of all species). Of these species 136 are endemic to Madagascar, and

TABLE 2 Summary of the observed total number and mean number of species, mean number of species of birds, reptiles, frogs and mammals, per cent of species that are native, migratory or invasive, and per cent of species in each of four groups of IUCN Red List categories in each of the four habitat types (see text for definitions) in the Sava region, north-east Madagascar. Values with the same superscript letter within a row are not significantly different from each other in a GLMM of habitat type (corrected for multiple comparisons, following sequential Holm–Bonferroni correction).

	Habitat type (N sites)					
	Natural forest (N = 9)	Forest eco-plantation (N = 6)	Non-forest eco-plantation (N = 6)	Intensive plantation (N = 5)	*t* (df)	P
Total number of species (all sites)	171	89	69	59		
Mean ± SE number of species (per site)	33.89 ± 1.47^{a}	20.00 ± 0.86^{b}	15.83 ± 1.14^{bc}	14.20 ± 3.40^{c}	−7.81 (20.757)	≤ 0.001
Group (mean number ± SE)						
Birds	29.67 ± 1.43^{a}	13.67 ± 2.03^{b}	14.83 ± 2.07^{b}	9.40 ± 3.14^{b}	−4.40 (6.395)	0.004
Reptiles	15.11 ± 1.39^{a}	9.50 ± 1.20^{b}	7.67 ± 1.02^{b}	6.40 ± 0.68^{b}	−5.00 (19.555)	≤ 0.001
Frogs	5.33 ± 1.34^{a}	2.67 ± 0.68^{b}	3.00 ± 0.45^{b}	1.80 ± 0.80^{b}	≤ 0.01 (1.947)	≤ 0.001
Mammals	6.00 ± 0.59^{a}	2.50 ± 0.37^{b}	1.50 ± 0.32^{b}	1.40 ± 0.27^{b}	−5.59 (21.525)	≤ 0.001
Native status (mean % ± SE)						
Native (endemic)	67.44 ± 2.22^{a}	49.00 ± 2.79^{b}	49.17 ± 4.84^{b}	40.20 ± 3.21^{b}	5.35 (23.215)	≤ 0.001
Native (non-endemic)	24.78 ± 1.68^{a}	39.76 ± 2.14^{bc}	31.83 ± 3.96^{ab}	51.00 ± 4.73^{c}	5.12 (23.679)	≤ 0.001
Migratory	5.96 ± 1.32^{a}	7.38 ± 1.21^{ab}	12.77 ± 2.23^{b}	4.88 ± 2.16^{a}	2.23 (18.913)	0.038
Invasive	1.89 ± 0.54^{a}	4.02 ± 1.33^{ab}	6.30 ± 0.62^{b}	3.98 ± 1.65^{ab}	2.14 (24.000)	0.043
Red List category (mean % ± SE)						
Least Concern	82.97 ± 1.09^{a}	89.83 ± 0.86^{b}	96.50 ± 2.05^{c}	98.20 ± 1.23^{c}	8.84 (6.962)	≤ 0.001
Near Threatened	1.81 ± 0.56					
Threatened (CR, EN, VU)[1]	12.51 ± 1.00^{a}	6.43 ± 1.95^{b}	2.33 ± 1.73^{b}	0.58 ± 0.56^{b}	−5.29 (19.931)	≤ 0.001
Other (DD, NE)[1]	3.46 ± 0.46^{a}	3.97 ± 1.53^{ab}	2.63 ± 0.92^{b}	1.25 ± 1.25^{b}	−20,982 (1.400)	≤ 0.001

[1]CR, Critically Endangered; DD, Data Deficient; EN, Endangered; NE, Not Evaluated; VU, Vulnerable.

27 are categorized as threatened on IUCN Red List (as of 2018: 17 Vulnerable, eight Endangered and two Critically Endangered). Observed species counts and analysis of species diversity between habitat types are summarized in Table 2.

When data were pooled for all sites of each habitat, the number of animal species observed differed significantly between habitat types, with forests having the highest observed mean species diversity (Table 2). When controlling for differences between habitats in the number of individuals, natural forests also had significantly higher mean species diversity than all three types of vanilla plantation (Fig. 2a). This conclusion held whether the comparisons of species diversity were performed at the extrapolated values of the habitat with the highest number of observed individuals ($N = 834$ for natural forest) or the rarefied values of the habitat with the lowest number of individuals ($N = 251$ for intensive plantation). Within vanilla plantations, we observed significantly fewer species in intensive plantations compared to forest eco-plantations (Table 2; see Supplementary Table 2 for full GLMM results).

Comparisons of the inverse Simpson's diversity index at the largest common number of individuals across all four habitats ($N = 251$; Fig. 2b) suggest that natural forest had a significantly higher diversity index than forest eco-plantations. Furthermore, forest eco-plantations had a significantly higher index than non-forest eco-plantations and intensive plantations; non-forest eco-plantations and intensive plantations had similar values of the index (Fig. 2b).

The observed species diversity of all taxon-specific groups was highest in natural forest, and there were no observed differences in species diversity between the three types of vanilla plantation (Table 2). After accounting for species abundance, we observed some consistent taxon-specific differences between vanilla plantations in the inverse Simpson index, with forest eco-plantations having higher values than other plantation types (Figs 3 & 4). There were few differences between non-forest eco-plantations and intensive plantations for any taxon, except for frogs, where diversity was significantly lower in intensive plantations (Fig. 3c).

When all taxa were pooled for each habitat type, the highest number of native species (both endemic and non-endemic) was observed in natural forest, and the lowest in intensive plantations (Table 2). There were slight differences of only marginal significance in the number of migratory species (Table 2). A significantly lower per cent of

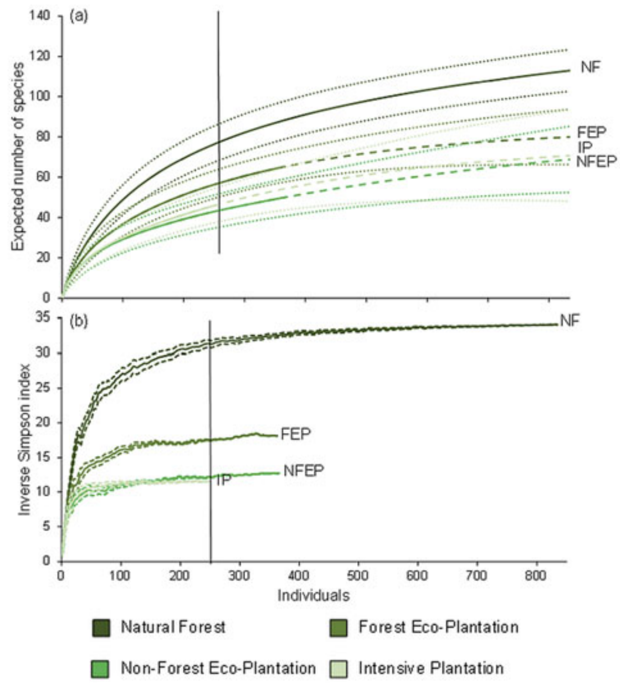

FIG. 2 (a) Expected number of animal species computed by rarefaction (S, solid lines), and (b) the inverse Simpson diversity index, with upper and lower 95% confidence intervals (dotted lines), among individuals in the four habitat types in the Sava region, north-east Madagascar (Fig. 1); extrapolations up to 834 knots (individuals) are depicted by the dashed extensions in (a). The vertical line indicates the point of comparison (the point of the maximum runs for the habitat with the fewest observed species). Rarefaction, extrapolation, diversity indices and associated confidence intervals were computed in *EstimateS* (Colwell, 2013).

species categorized as Least Concern were observed in natural forest compared to vanilla plantations, and conversely there was a higher per cent of threatened or Near Threatened species in natural forest (Table 2). There were few significant differences between the different vanilla plantation habitats based on threat status, although forest eco-plantations had a significantly lower per cent of Least Concern species and a higher per cent of threatened species compared to non-forest eco-plantations and intensive plantations (Table 2).

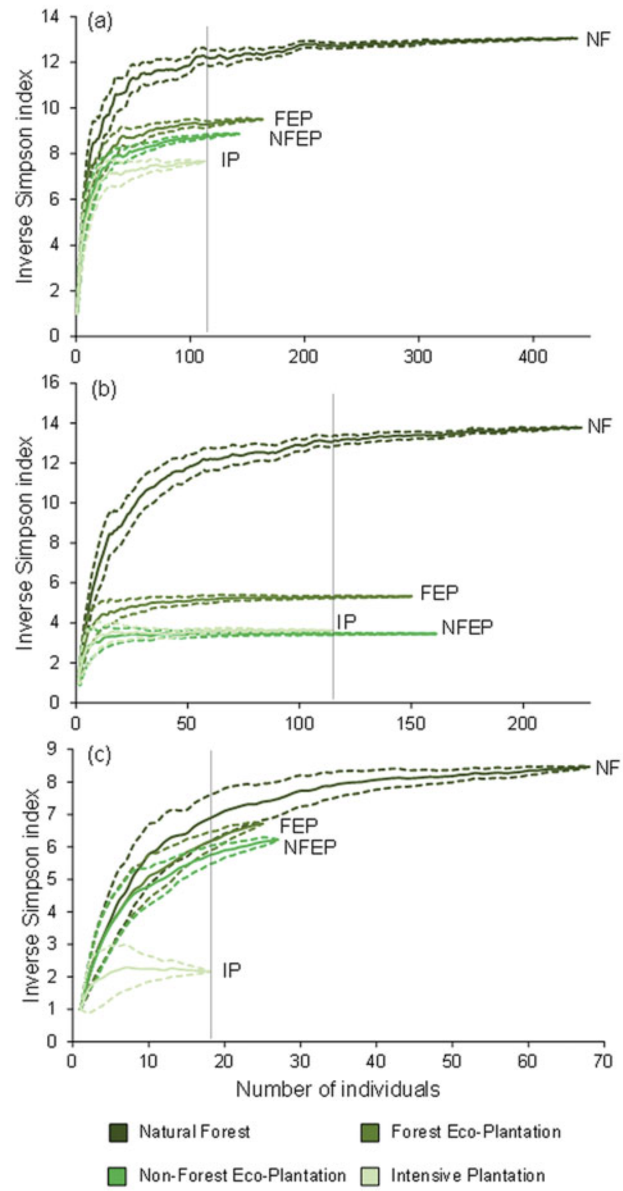

FIG. 3 Inverse Simpson index–individual curves (with associated 95% confidence intervals) of (a) birds, (b) reptiles and (c) frogs observed in the four habitat types in the Sava region, north-east Madagascar. The vertical line indicates the point of comparison (the point of the maximum runs for the habitat with the fewest observed species). Diversity indices and associated confidence intervals were computed in *EstimateS* (Colwell, 2013). Note the differing x- and y-axis scales.

Discussion

Forests vs plantations

Vertebrate diversity was the greatest in natural forest habitat. Although vanilla plantations are capable of supporting biodiversity, our results indicate that increased management and modification of these plantations result in degradation of this species diversity. This is unsurprising, considering that biodiversity has been previously observed to be lower in plantations than natural forests (Vallan, 2002; Perfecto & Vandermeer, 2008). When focusing on specific taxa, we found that bird and reptile diversity were significantly higher in natural forest than in all vanilla plantation types. For reptiles this finding was surprising; although some reptile species prefer habitats with prominent leaf-litter, and are known to show negative responses to habitat degradation (Perfecto et al., 1996; Faria et al., 2007), other reptile species prefer open habitats (e.g. Vallan et al., 2004). Avian diversity can be high in plantation ecosystems (Greenberg et al., 1997; Clough et al., 2009), but some terrestrial and forest-

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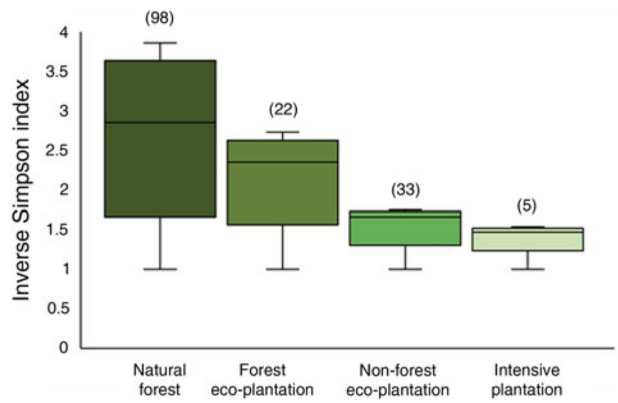

FIG. 4 Box plots (median, upper and lower quartiles, and maximum and minimum values) of the inverse Simpson diversity index for mammals observed in the four habitat types in the Sava region, north-east Madagascar (numbers in parentheses indicate sample size from which diversity indices were computed).

specialized species are disturbed by agricultural activity, making our finding unsurprising. Frog diversity also varied significantly, and was highest in natural forest, an expected finding considering that many Malagasy frog species prefer undisturbed habitats, as they require food resources from forest tree species and dead wood or tree holes for breeding (Vallan, 2002; Vallan et al., 2004). However, many of Madagascar's frog species are highly cryptic (e.g. Lehtinen et al., 2007), and the total amphibian diversity would have been difficult to detect in our rapid survey. There was a significantly higher mammal diversity in natural forest than in vanilla plantations, perhaps because forests contain the high canopies required by some mammal species, such as lemurs (Vargas et al., 2002), and the prey required by carnivores (Karpanty & Wright, 2007). Natural forests also had more endemic species, fewer invasive species and a higher per cent of threatened species compared to vanilla plantations. This reinforces the view that natural forests are refuges for Madagascar's most threatened fauna, over 85% of which is endemic (Goodman & Benstead, 2005).

Although we found significant differences in vertebrate diversity and abundance between forest and plantation habitats, we expect that other factors may also contribute to animal diversity at each site, in addition to anthropogenic influences. For example, floral diversity also varies greatly between natural and agricultural habitats (Hending et al., 2020a) and, in many cases, animal diversity correlates directly with plant diversity (Huston, 1979; Faria et al., 2007); this correlation may occur within Madagascar's vanilla agroecosystems. The area of each site is also likely to have an influence, as some of the vanilla plantation sites surveyed were very small (e.g. < 1 ha) and fragmented. These small sites may be unable to support animals that require large ranges, such as some lemurs (Mittermeier et al., 2010), carnivores (Gerber et al., 2012) and insectivorous mammals (Levesque et al., 2012). Additionally, the presence and abundance of some animals may be related to particular abiotic conditions (unrelated to habitat types) that are not uniform among our study sites; e.g. frogs require nearby water sources to survive (Glaw & Vences, 2007), the presence of which was variable between study sites (D. Hending & A. Andrianiaina, pers. obs., 2018).

Effect of plantation management regime

The diversity indices suggest that forest eco-plantations support significantly higher vertebrate diversity than non-forest vanilla plantations. These findings mostly also hold true when individual groups of taxa are compared (Figs 3 & 4). In most cases, intensively managed vanilla plantations had the lowest vertebrate species diversity, which suggests that vertebrate diversity correlates negatively with habitat degradation and anthropogenic disturbance in Madagascar's vanilla cultivation areas, and possibly in agroecosystems more generally. Thus we accept our hypothesis that animal diversity is affected by vanilla plantation management regime.

The variation in animal diversities among vanilla plantation types is most likely because of species-specific habitat requirements and tolerance levels to human disturbance and habitat alteration (Tews et al., 2003). Although some species may tolerate or even prefer disturbed, open habitat, (e.g. reptiles: Pike et al., 2011; mouse lemurs: Hending, 2021), many species in Madagascar's vanilla cultivation region may only be able to survive in intact, natural forest (e.g. the Critically Endangered golden-crowned sifaka *Propithecus tattersalli*; Quemere et al., 2012). Furthermore, intensively managed habitat types are unlikely to have the opportunities for feeding and movement that eco-plantations provide for native fauna (e.g. lemurs; Hending et al., 2018).

Limitations

The results of this study provide evidence that natural forest habitat, and forested vanilla plantations, contain higher vertebrate richness and diversity than agricultural habitats, particularly in agroecosystems located outside forest matrices. However, as this investigation was a rapid biodiversity assessment, we had limited survey time at each study site and therefore not all species would have been detected. Our surveys of reptiles, birds and small mammals was based solely on visual observations, and we therefore only recorded species close to ground level; some small, arboreal species such as some snakes (e.g. *Stenophis* spp.; Glaw & Vences, 2007), and mammals (e.g. *Eliurus* spp.; Goodman & Carleton, 1998), may therefore have been overlooked. Additional species such as the fanaloka *Fossa fossana* and the fossa *Cryptoprocta ferox* may have also been missed (we only saw one fossa individual, at one study site) as they tend to avoid areas of human activity (i.e. transect lines; Albignac, 1984).

Implications for animal conservation and sustainable agroforestry

Little natural forest remains in the Sava region, and in Madagascar generally, and that which remains is highly degraded and fragmented (Schwitzer et al., 2013). The continued conversion of existing forest to vanilla plantations will severely threaten Madagascar's faunal diversity, particularly species only capable of surviving within natural forest. However, vanilla plantations that have already been derived from forest may serve as a suitable alternative to more slash-and-burn agriculture, which would avoid further forest conversion. The results of our study suggest that minimally managed and modified plantations, especially those located in or near natural forest habitat, can support relatively high vertebrate diversity, although this may only persist within a multifunctional landscape. Although it remains to be seen whether animals can use them long-term, forest eco-plantations may be a suitable habitat and a valuable haven for a subset of forest specialist animals, and vanilla cultivation in Madagascar should be encouraged to replicate these habitat types (whilst not compromising the little forest that remains). These viable habitats lie between isolated fragments of natural forest, and open areas and gallery forest or other degraded patches of vegetation could therefore be repurposed as vanilla plantations to improve habitat availability and increase their economic value. Threatened mammals, birds, reptiles and frogs, which we observed in vanilla plantations, would be able to use these matrices to travel between natural forests, and important seed dispersing species would contribute to the further regeneration of the forest (Bollen et al., 2004; Hending et al., 2017; Hending et al., 2018). Our findings are both encouraging and important for agroforestry in Madagascar, and locally for the coordination of responsible and sustainable cultivation of the vanilla crop within the Sava region. Any further conversion of forest for vanilla cultivation should, however, be discouraged.

Madagascar's vanilla industry is worth an estimated USD 200 million per annum (AFB, 2016). Over 200,000 of Madagascar's farmers, most of whom reside in the Sava region, depend on this industry for their livelihoods (AFB, 2016), and the financial value of the vanilla industry, along with sustainability certification schemes, should provide sufficient incentives for farming communities to establish and maintain sustainable plantations. The high level of animal diversity in forest eco-plantations suggests a potentially high conservation value for the vanilla industry. Overall, forest eco-plantations appear to be the most sustainable method of vanilla cultivation in terms of both animal conservation and agriculture.

In summary, eco-plantations in or within close proximity to natural forests should be promoted for the responsible and sustainable cultivation of vanilla, as they have high value for both species conservation and sustainable agroforestry. In addition to vanilla, Madagascar's farmers depend on a variety of crops for food and export income (e.g. coconut, cacao; Dorosh & Haggblade, 1993). To further our knowledge of faunal diversity in these agroecosystems, rapid biodiversity assessments should be conducted, to facilitate a better understanding of the effects of agricultural land conversion on animal diversity and to provide insight into the relationship between animal diversity and agricultural intensity in the tropics.

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Conflict of interest None.

Ethical standards This research abided by the *Oryx* guidelines on ethical standards, and was conducted according to the laws of both the UK and Madagascar.

Data availability The datasets generated and/or analysed are available from the authors on request.

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