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# QUANTIFYING THE CONSERVATION VALUE OF PLANTATION FORESTS FOR A MADAGASCAN HERPETOFAUNA

*BETH EVANS*

*Madagascar Research and Conservation Institute, Nosy Komba, Madagascar  
current address: 121 Heathway, Erith, Kent DA8 3LZ, UK, email: bethkevans94@gmail.com*

**Abstract.**—Plantations are becoming a dominant component of the forest landscape of Madagascar, yet there is very little information available regarding the implications of different forms of plantation agriculture for Madagascan reptiles and amphibians. I determined the conservation value of bamboo, secondary, open-canopy plantation, and closed-canopy plantation forests for reptiles and amphibians on the island of Nosy Komba, in the Sambirano region of north-west Madagascar. Assistants and I conducted 220 Visual Encounter Surveys between 29 January 2016 and 5 July 2017 and recorded 3,113 reptiles (32 species) and 751 amphibians (nine species). Closed-canopy plantation supported levels of alpha diversity and community compositions reflective of natural forest, including several threatened and forest-specialist species. Open-canopy plantation exhibited diminished herpetofaunal diversity and a distinct community composition dominated by disturbance-resistant generalist species. Woody tree density and bamboo density were positively correlated with herpetofaunal species richness, and plantation species richness, plantation species density, sapling density, and the proportion of wood ground cover were negatively associated with herpetofaunal diversity. I recommend the integration of closed-canopy plantations on Nosy Komba, and across wider Madagascar, to help mitigate the negative effects of secondary forest conversion for agriculture on Madagascan herpetofauna; however, it will be necessary to retain areas of natural forest to act as sources of biodiversity for agroforestry plantations. It will also be necessary to employ plantation management techniques that maintain environmental variables known to enhance alpha diversity.

**Key Words.**—agroforestry; amphibians; Madagascar; reptiles; Sambirano; secondary forest; smallholder agriculture

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## INTRODUCTION

Madagascar is an important hotspot of global biodiversity (Mittermeier et al. 1998; Myers et al. 2000; Ramanamanjato and Ganzhorn 2001; Andreone 2004). The isolated evolutionary history of the island combined with topographic and climatic variation has led to the development of a unique array of flora and fauna with high levels of diversity and endemism (Andreone et al. 2003; Irwin et al. 2010). In particular, the north-west of Madagascar is known for its faunistic and floristic uniqueness (Vences and Glaw 2005), high levels of biodiversity (Jenkins et al. 2014; Brown et al. 2016), and support of several range-restricted species and the distinct Sambirano eco-region (Blumgart et al. 2017).

The unique biodiversity of Madagascar is at risk due to rapid rates of deforestation (Ingram and Dawson 2005; Jenkins et al. 2014). Indeed, pervasive human disturbance and degradation of forests is the primary cause of population extinctions and species-range declines in the tropics, particularly for agriculture (Gardner et al. 2007c; Gibbs et al. 2010; Canale et al. 2012). In Madagascar, natural forest cover declined at a rate of 0.55% yr<sup>-1</sup> between 2005–2010, an increase in deforestation of 0.1% from 2000–2005 (Food and Agricultural Organization [FAO] 2010).

Forest degradation in Madagascar is driven by a combination of social, economic, and political factors. Extreme rates of poverty and rapid population growth are placing ever increasing pressure on ecosystem services and natural resources. Simultaneously, globalism and increasing international demand for agricultural and forestry products are creating economic incentives for deforestation to produce marketable commodities and support tourism industries (Clark 2012; Carrasco et al. 2017). Consequently, deforestation in Madagascar is primarily driven by smallholder agriculture (Malhi et al. 2014). Indeed, between 1998 and 2011, the area of agricultural land in Madagascar increased 2.3–13.4% (FAO 2010), and as of 2012, 82% of the population worked within the agricultural sector (Clark 2012).

Conversion of natural forest to smallholder plantation systems (defined here as a farm supporting a single family with a combination of subsistence and cash crops) is accompanied by changes in canopy structure and leaf litter environments, which ultimately result in the loss of microhabitats and biodiversity (Gardner et al. 2007b). As herpetofauna are highly sensitive to environmental perturbations (both natural and anthropogenic; Wanger et al. 2009; Catenazzi et al. 2016), conversion of primary and secondary forest to plantation results in a loss of herpetofaunal richness and diversity (Vallan 2002;

D’Cruze and Kumar 2011; Blumgart et al. 2017), and a distinctive shift in community composition in terms of breeding guilds, relative representation of families and sub-families, and the balance of specialist and generalist species (Vallan 2002; D’Cruze and Kumar 2011).

Madagascan herpetofauna are particularly at risk of local extinction caused by novel disturbance due to their isolated evolutionary history (Gardner et al. 2007b; Wanger et al. 2009; D’Cruze and Kumar 2011). Consequently, an incredible 40% of Madagascan herpetofauna have been classified as threatened (CE, EN, or VU) by the International Union of Conservation of Nature (IUCN): 36% of Madagascan reptiles and 46% of amphibians (IUCN 2018). Of these species, 91% live in forest habitats and 84% are threatened by agriculture (IUCN 2018). Considering Madagascan forest herpetofauna alone, 93% are threatened by agriculture (IUCN 2018).

The current land sparing, land saving approach to conservation in Madagascar has been ineffective at controlling rates of deforestation and land-use change that threaten herpetofaunal diversity and ecosystem services (Erdmann 2010; Toillier et al. 2011; Andreone et al. 2012; Neugarten et al. 2016; Waeber et al. 2016). The combination of a government with little power to enforce laws regarding natural resource use (Freudenberger. 2010. *Paradise Lost? 25 years of USAID Environment Programs in Madagascar*. Available from [www.usaid.gov](http://www.usaid.gov). [Accessed 21 June 2018]; Andreone et al. 2012) and limited progress in national poverty alleviation efforts have further hampered traditional conservation strategies (Waeber et al. 2016). Without a dramatic shift in the political and socio-economic climate of Madagascar, as well as significant advances in the agricultural sector and technical capacity of the country, Madagascan tropical landscapes are expected to consist of fragmented mosaics of natural forest and agricultural areas (Hartley 2002; Gardner et al. 2007a; Bhagwat et al. 2008; Folt and Reider 2013). There is a desperate need for a new conservation paradigm that incorporates the goals of environmental conservation and human development without sacrificing ecosystem services and climate stability (Scherr and McNeely 2008). Greater emphasis needs to be placed on understanding the role of rural systems in fulfilling this objective (Chazdon et al. 2009a).

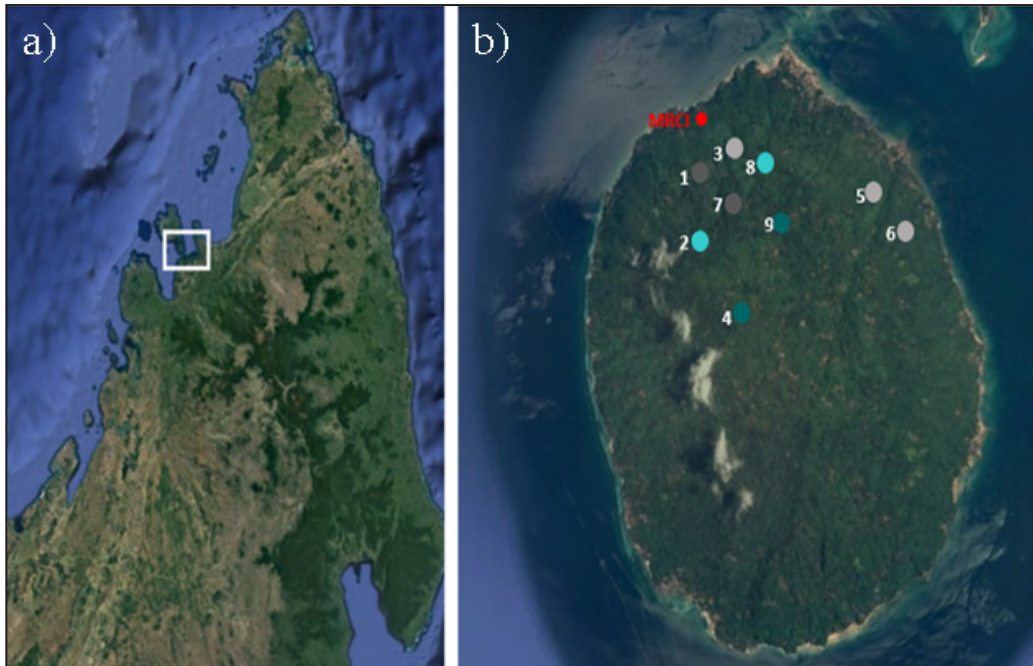
The role of functionally complex smallholder production systems in acting as a refugia for biodiversity and maintaining vital ecosystem services has been discussed extensively (Scherr and McNeely 2008; Perfecto and Vandermeer 2010; Folt and Reider 2013; Roberts and Daly 2014; Alamgir et al. 2016). Agroforestry production systems such as low-intensity coffee and cocoa plantations have been found to support high levels of biological diversity (Schroth and Harvey

2007; Tschardt et al. 2011; Blumgart et al. 2017), which exceed that of intensively managed mono-crop production systems (McNeely and Schroth 2006; Palacios et al. 2013). Furthermore, in the wider tropics, the integration of forest and trees into agricultural matrices has been shown to maintain or enhance crop yields compared to monoculture plantations (Reed et al. 2017). In the case of Madagascar, complex, multi-storied, traditional production systems have the potential to support valuable, if biologically diminished, herpetofaunal assemblages while supporting smallholder food production (Padoch and Pinedo-Vasquez 2010; Roberts and Daly 2014; Blumgart et al. 2017).

Quantitative studies on the conservation and productive value of smallholder agriculture in Madagascar are limited (Irwin et al. 2010). There is also limited biodiversity data available from Madagascan secondary forest despite the growing importance of secondary habitats in conserving forest biodiversity, and the fact it comprises 73% of the forest cover of the nation (Chazdon et al. 2009b; FAO 2010; Herrera-Montes and Brokaw 2010; Melo et al. 2013). Furthermore, at present, there is only one study assessing the impacts of land-use change on biodiversity within the Sambirano eco-region (Blumgart et al. 2017), with none assessing shifts in community composition. Worryingly, despite herpetofauna sensitivity to habitat change and the fact they constitute 50% of terrestrial vertebrates, they account for a mere 15% of research focusing on the impacts of plantation establishment (Palacios et al. 2013). The ambiguous conclusions drawn from a synthesis of these results would be inadequate to inform effective policies in Madagascar. Deficiency in available research limits the effectiveness of conservation efforts to preserve herpetofauna communities (Palacios et al. 2013; Jenkins et al. 2014). Indeed, research effort into Sambirano forest is not representative of the wealth of herpetofaunal diversity and abundance of range-restricted species that reside within this eco-region.

A better understanding of the unique ecosystems of Madagascar is essential to support desperately needed multi-disciplinary conservation strategies in this highly diverse and threatened nation. I aim to provide a comprehensive assessment of the biodiversity conservation value of forest mosaics containing areas of smallholder plantation for Madagascan herpetofauna, in areas dominated by secondary forest. I attempt to provide a starting point for future Madagascan conservation projects and a foundation for future scientific studies and conservation efforts within the Sambirano eco-region.

The island of Nosy Komba, located within the northwestern Sambirano eco-region of Madagascar, provided a landscape of small, open and closed-canopy plantations embedded in a matrix of secondary and



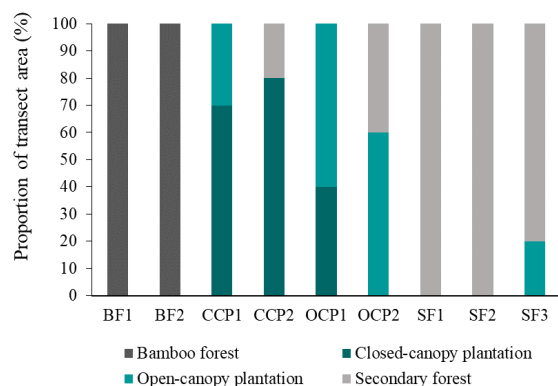
**FIGURE 1.** (a) Location of Nosy Komba in relation to mainland Madagascar and (b) the position of the Madagascar Research and Conservation Institute (MRCI) camp and study sites on Nosy Komba. Nosy Komba is highlighted by a white box (a), MRCI base camp is indicated by a red filled circle, and study sites are shown by colored filled circles (b; dark green = closed-canopy plantation, light green = open-canopy plantation, dark gray = bamboo forest, and light gray = secondary forest). Study site label numbers refer to the corresponding transect number, e.g., 1 shows the position of site BF1. (Map from Google Earth™. 2018 Google; Image: Landsat/Copernicus (a); Image: 2018 TerraMetrics/ Image: 2018 National Centre for Space Studies/Airbus/ Image: 2018 Digital Globe (b); data: Scripps Institute of Oceanography, National Oceanic and Atmospheric Administration, U.S Navy, National Geospatial-Intelligence Agency, General Bathymetric Chart of the Oceans).

bamboo forest. I selected nine study sites containing varying proportions of secondary forest, bamboo forest, closed-canopy plantation, and open-canopy plantation. I assessed responses of two taxa considered highly vulnerable to habitat modification (reptiles and amphibians; Wanger et al. 2009) to forest conversion for plantation agriculture using five response metrics (observed richness, estimated total richness, species diversity, community structure, and threatened species abundance). I attempted to determine the capacity of forest mosaics containing different plantation forest types to support diverse assemblages of herpetofauna within a matrix of secondary forest. Consequently, the results of this study will inform on the potential of smallholder agricultural systems within Madagascar to preserve biodiversity in congruence with protected areas of natural forest. I expected that: (1) compared to natural forest (secondary and bamboo forest), plantation forest will support an altered composition of reptiles and amphibians with diminished species richness and diversity; (2) closed-canopy plantation will support a higher richness and diversity of reptiles and amphibians than open-canopy plantation, with a community composition that more resembles a natural forest; and (3) natural forest will contain more threatened species and individuals than plantation forest.

## MATERIALS AND METHODS

**Study site.**—Nosy Komba (alternatively known as Nosy Ambariovato;  $-13^{\circ}19'60''S$ ,  $48^{\circ}14'60''E$ ) is an offshore volcanic island situated within the Sambirano eco-region of north-west Madagascar (Blumgart et al. 2017; Fig. 1). Located approximately 2.7 km from Nosy Be (Roberts and Daly 2014), Nosy Komba is 25 km<sup>2</sup> in area (Roberts and Daly 2014) and reaches an altitude of 622 m at its peak (Roberts and Daly 2014). Historical felling of Nosy Komba during the French colonization of Madagascar (1894–1959) has resulted in the loss of all primary forest (Roehrer-MacGregor, C. 2013. French in Madagascar: A Colonial Language After Independence. Syracuse University SURFACE. Available from [https://surface.syr.edu/honors\\_capstone/51/](https://surface.syr.edu/honors_capstone/51/) [Accessed 18 January 2018]; Roberts and Daly 2014). This large-scale felling event made Nosy Komba the ideal location to study the effect of land-use change within secondary forest habitats on herpetofauna community assemblages. A landscape dominated by secondary forest with an island-wide insular fauna removed the uncertainty of previous land-use influence on measured biodiversity values.

The north side of Nosy Komba is characterized by a mosaic of regenerated secondary forest interspersed



**FIGURE 2.** The proportions of transect area (%) of Bamboo Forest (BF), Closed-canopy Plantation (CCP), Open-canopy Plantation (OCP), and Secondary Forest (SF) found within nine forest transects of the Madagascar Research and Conservation Institute. The nine sites are named based on the predominant vegetation type found within. For example, sites comprised primarily of BF are named BF1 and BF2; sites comprised primarily of CCP are named CCP1 and CCP2, etc. Color designations are dark green = CCP, light green = OCP, dark gray = BF, and light gray = SF.

with plantation, bamboo forest, open grassland, and swamps. The local community informed researchers that rice cultivation on the island is illegal, so agriculture predominantly consists of plantation forest. The higher altitudes support a variety of mono-crop and mixed-species plantations, including coffee, pepper, cocoa, chili, banana, sugarcane, vanilla, pineapple, lime, mango, and jackfruit. The upper area of the northern part of the island is covered by a large swathe of bamboo forest. Bamboo forest is a degraded form of secondary forest invaded by a species of bamboo introduced from the mainland (Roberts and Daly 2014); however, in this study bamboo forest is considered an independent habitat type due to its unique environmental characteristics and herpetofaunal species composition (Madagascar Research and Conservation Institute, unpubl. data).

I focused survey efforts entirely on the north side of the island within a 2 km radius of Madagascar Research and Conservation Institute (MRCI) base camp (-13°44'69.09"S, 48°33'60.63" E; Fig. 1). I established nine study sites within this landscape, encompassing four major forest types: (1) secondary Sambirano forest (SF, SF1–3, > 30 y since abandonment), (2) bamboo forest (BF, BF1, and 2), (3) monoculture open-canopy plantation (OCP, OCP1, and 2), and (4) polyculture closed-canopy plantation (CCP, CCP1, and 2). I categorized forest type based on environmental characteristics at ground, understory, and canopy level (Table 1). I established one 250 m line transect at each site. Study sites were spatially independent from one another (a minimum of 200 m between them) and of sufficient size (> 15,000 m<sup>2</sup>) to minimize pseudo-replication and edge effects. Care was taken to avoid placing lines along habitat edges, and to ensure that at

**TABLE 1.** Environmental characteristics of sites categorized into secondary forest (SF), bamboo forest (BF), open-canopy plantation (OCP), and closed-canopy plantation (CCP) by Madagascar Research and Conservation Institute, Nosy Komba, Madagascar. All values represent the average per one 50 × 60 m subplot. Heading abbreviations are TD = density of woody and palm trees > 15 cm in circumference at breast height (CBH); SD = density of woody and palm trees < 15 cm CBH; CC = the coverage (%) and continuity (homogenous [Ho] or heterogeneous [Het]) of the forest canopy; HPA = the abundance of individual plants belonging to species harvested for human agriculture; and BD = bamboo density. Abbreviations inside the table are Homo = homogenous, Hetero = heterogeneous.

Forest Type	TD	SD	CC	HPA	BD
Secondary forest	19.17	95.07	66.71/Ho	2.65	14.88
Bamboo forest	17.88	45.38	78.3/Ho	0.86	60.71
Open-canopy plantation	8.83	34.50	60.64/Het	28.71	0.43
Closed-canopy plantation	11.00	3.45	74.85/Het	28	0

least 10 m of continuous habitat was available on either side of the line, with no permanent water bodies or major paths (visually appraised).

Because of the smallholder nature of agriculture on the island and subsequent patchiness of the landscape, five transects spanned multiple habitat types. These study sites are representative of the forests of Nosy Komba as a whole, thus providing a realistic indication of the biodiversity conservation value of secondary forest-plantation forest mosaics. For a study site to be classified as a specific forest type, that forest needed to be the dominant habitat type across the transect (Fig. 2). The approximate percentages of habitat by site were: (1) 100% bamboo forest (BF1 and BF2); (2) 70% closed canopy plantation and 30% open canopy plantation (CCP1); (3) 80% closed canopy plantation and 20% secondary forest (CCP2); (4) 40% closed canopy plantation and 60% open canopy plantation (OCP1); (5) 60% open canopy plantation and 40% secondary forest (OCP2); (6) 100% secondary forest (SF1 and SF2); and (7) 20% open canopy plantation and 80% secondary forest (SF3).

**Data collection.**—Staff and volunteers of the MRCI Terrestrial Science Project and I collected data 29 January 2016 and 5 July 2017. Surveys were made using Visual Encounter Survey (VES) methodology based on techniques described by Dodd (2010, 2016). One member of the MRCI staff, accompanied by three to five volunteers, conducted the surveys after participants were trained in species identification and passing a computer identification test. We conducted 220 VESs (strip width = 30 m, mean duration = 51 min): 44 in BF, 56 in CCP, 51 in OCP, and 67 in SF. The survey frequency varied between sites and forest types due to the young nature

**TABLE 2.** Environmental characteristics measured during habitat surveys for reptiles and amphibians at the Madagascar Research and Conservation Institute, Nosy Komba, Madagascar, and abbreviations and descriptions of these characteristics. In Description, weeds refer to any ground-level leafy plant.

Environmental characteristic	Abbreviation	Description
Leaf litter depth (cm)	LLD	Depth of leaf litter at the center of the survey plot.
Bare ground (%)	Bare	Proportion of ground cover in 2 × 2 m plot comprised of bare ground.
Rock (%)	Rock	Proportion of ground cover in 2 × 2 m plot comprised of rock.
Weed (%)	Weed	Proportion of ground cover in 2 × 2 m plot comprised of weeds.
Wood volume (%)	Wood	Proportion of ground cover in 2 × 2 m plot comprised of wood.
Grass (%)	Grass	Proportion of ground cover in 2 × 2 m plot comprised of grass.
Leaf litter (%)	Leaf	Proportion of ground cover in 2 × 2 m plot comprised of leaf litter.
Understory level 1	US1	Number of leaves in contact with touch-pole at center of plot 0–0.5 m from the ground.
Understory level 2	US2	Number of leaves in contact with touch-pole at center of plot 0.5–1 m from the ground.
Understory level 3	US3	Number of leaves in contact with touch-pole at center of plot 1–1.5 m from the ground.
Understory level 4	US4	Number of leaves in contact with touch-pole at center of plot 1.5–2 m from the ground.
Understory level 5	US5	Number of leaves in contact with touch-pole at center of plot 2–2.5 m from the ground.
Understory level 6	US6	Number of leaves in contact with touch-pole at center of plot 2.5–3 m from the ground.
Woody tree density	Woody	The number of trees (> 15 cm in circumference) recorded in a 50 × 5 m subplot.
Palm tree density	Palm	The number of palm trees recorded in a 50m×5m subplot.
Sapling density	Saplings	The number of saplings (< 15 cm in circumference) recorded in a 50 × 5 m subplot.
Plantation species richness	Plantrich	Number of plantation species (e.g., pineapple, coffee, cocoa) recorded in a 50 × 5 m subplot.
Plantation species density	Plantdensity	Number of plantation species individuals recorded in a 50 × 5 m subplot.
Bamboo density	Bamboo	Number of bamboo plants recorded in a 50 × 5 m subplot.
Canopy cover (%)	CC	Proportion of sky obscured by canopy when standing in the center of the survey plot.

of MRCI and its status as a volunteer-based organization and we surveyed transects established later or located further from base camp less regularly. We conducted 179 surveys that began between 0830 and 1030 and 41 that began between 1900 and 2000. The search time duration varied between 39 and 58 min. Additionally, I provided volunteers with extensive training on survey methods and required them to take part in practice surveys prior to active participation (Appendix).

I randomized the sampling order of sites to avoid systematic biases in seasonal effects, project management, and surveyor efforts. Therefore, sampling at each survey site encompassed a wide range of environmental conditions and herpetofaunal patterns of activity. We collected data across all four recognized climatic periods on Nosy Komba: (1) wet season (January-February), (2) long transition period (March-August), (3) dry season (September-October), (4) short transition period (November-December).

**Habitat surveys.**—Staff and volunteers of the MRCI Terrestrial Science Project and I collected habitat survey data 29 January 2016 and 5 July 2017. I split transects into five 50 × 60 m subplots for data collection and recorded all trees, saplings, and plantation species within them. We also measured environmental characteristics in ten 2 × 2 m plots within each subplot. These environmental characteristics included leaf litter

depth in cm, % of different ground coverings (% bare ground, % rock, % weed, % wood volume, % grass, % leaf litter), number of leaves in contact with a touch-pole at the center of the plot at different heights above the ground; densities of different tree types, species richness, plantation species density, plantation species richness, bamboo density, and % canopy cover (Table 2).

**Data analysis.**—Amphibians and reptiles are often studied as a single assemblage, referred to as herpetofauna (Gardner et al. 2007c). This approach fails to consider the contrasting life histories and survival strategies (Gibbon et al. 2000) or the differing responses to land-use change reported for these taxa (Gardner et al. 2007b; Palacios et al. 2013). Consequently, I measured the responses of amphibians and reptiles to land-use change separately.

Each of the five 50 × 60 m subplots contained only one forest type. Several transects spanned more than one forest type and forming subplots allowed for consideration of this environmental stochasticity when making inferences. I calculated site level species richness and diversity values as an average of subplot totals and ordinated subplots as separate points during non-metric multi-dimensional scaling (NMDS). I made comparisons between study sites rather than forest types to account for the uniqueness of each transect within

a smallholder-dominated landscape (Fig. 2). This approach consistently explained the highest proportion of variation in the data when compared to models that treated each site as a singular point and compared response metrics between forest types (e.g.,  $r^2 = 0.49$  vs. 0.17). I standardized the raw data to account for unequal survey effort between sites by dividing abundance data by total surveyor hours.

I conducted data analysis using R version 3.3.2. (R Core Team 2016), and R software packages rcompanion version 1.10.1. (Mangiafico 2017), vegan version 2.4–3. (Oksanen et al. 2017), car (Fox and Weisberg 2011), dunn.test version 1.3.4. (Dinno 2017), lmtest (Zeileis and Hothorn 2002), mgcv (Wood 2011), mblm (Komsta 2013), and vegan3d version 1.1–0. (Oksanen, Kindt and Simpson 2017). I considered all test results significant at  $\alpha = 0.05$ . I estimated species richness using EstimateS (Colwell, R.K. 2013. EstimateS: Statistical estimation of species richness and shared species from samples. Version 9. User's Guide and Application. Available from <http://purl.oclc.org/estimates> [Accessed 21 November 2018]). I calculated the number of species recorded within each subplot as a measure of species richness, and the Simpson's reciprocal index value (SDI) as a measure of species diversity. Ecological species diversity accounts for both presence and abundance, thus considering species richness and evenness. I calculated species richness and diversity for each site as an average of their five subplots, which enabled me to account for site-level heterogeneity in forest cover and management, and minimize the contribution of individuals recorded only once, and possibly present due to spillover from surrounding habitats.

I applied Shapiro Wilk and Levene tests to assess the assumptions of normally distributed data and equal variances of groups. Where the assumption of normal distribution of data was met, I tested for differences in species richness and SDI values between transects using one-way ANOVA applied to a simple linear regression model. I identified significant pairwise differences using Tukey post-hoc tests. Where parametric assumptions were not met, I used Kruskal-Wallis to compare median richness and SDI values between study sites, and identified significant pairwise differences using Dunn's post-hoc tests.

As species counts alone often underestimate the true richness of a given sample, I applied the Chao1 method to determine the lower-bound of species richness at each survey site (Chao and Chiu 2016). I calculated the completeness of samples from each site by dividing observed total richness values with estimated richness values to form a percentage (Barlow et al. 2007). Completeness values provided an insight into the number of unrecorded species present on Nosy Komba,

allowing for consideration of the magnitude of negative bias they potentially contribute (Chao and Chiu 2016).

I produced a Bray-Curtis dissimilarity matrix to determine beta diversity for pair-wise site comparisons (Bray and Curtis 1957; Anderson et al. 2011). I applied the vegdist function to our community matrices, with community matrix referring to data containing the abundance of all reptile and amphibian species recorded on Nosy Komba at each study site. I tested for homogeneity of multivariate dispersions between sites, an assumption for PERMANOVA, using the betadisper function. I applied a PERMANOVA to the Bray-Curtis matrix using the adonis function to determine if differences in beta diversity between sites were significant (Anderson 2017). I applied SIMPER analysis to the reptile and amphibian community matrices using the simper function to determine species with the highest contribution to each dissimilarity. I  $\log(x+1)$  transformed the community matrices prior to analysis to downplay the contribution of the most dominant species.

I visually compared community compositions through the application of NMDS (Beals 1984). NMDS places each site into multidimensional space created by the abundance axes of the total landscape species array. I applied the metaMDS function to the reptile and amphibian community matrices to create an ordination graph. Ellipses demonstrate the community composition of entire sites (based on data from all five subplots). They were produced using the ordiellipse function based on output of the NMDS.

I compared the average abundance of endangered and vulnerable individuals within a  $50 \times 60$  m subplot using one-way ANOVA. I determined significance in pairwise comparisons using the Tukey post-hoc test. The endangered species data was square root transformed to achieve a normal distribution. Abundances of individual threatened species were also compared using one-way ANOVA and Kruskal-Wallis.

I detected correlations between environmental variables (Table 2) and reptile and amphibian species richness and diversity using Spearman's rank sum test. I selected this test due to the abnormal distribution of the environmental data. Correlation of species richness and diversity to combinations of environmental characteristics required addition of variable ranks. I incorporated variables with significant correlations into generalized additive models (GAMs) using the gam function of the mgcv package. I conducted likelihood ratio tests on the GAMs using the lrtest function to ascertain the significance of the relationships. I used Sen-Siegel non-parametric linear regression to assess the relationship between plantrich and herpetofaunal diversity, as the GAM fit was deemed inadequate. This

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**TABLE 3.** Average herpetofaunal abundance per survey, total species richness, and proportion of unique species recorded over the survey period at nine forest sites of the Madagascar Research and Conservation Institute, Nosy Komba, Madagascar. Also given are the number of species observed as a proportion of estimated total richness and landscape total. Abbreviations are n = Average number of individuals recorded per survey effort; S = total number of species observed; C = number of species observed as a percentage of the average estimated richness; ES = number of species not found elsewhere as a percentage of landscape total; and NS = number of species observed as a percentage of landscape total (completeness).

Site	Amphibians					Reptiles				
	n	S	C	ES	NS	N	S	C	ES	NS
BF1	3.20	5	71.60	0	56	17.20	21	66.08	0	64
OCP1	1.22	3	66.12	0	33	21.73	19	74.70	0	58
SF1	0.12	2	42.86	0	22	6.36	16	64.41	0	48
CCP1	8.76	6	75.61	0	67	14.09	26	77.70	6	79
SF2	1.44	4	59.00	0	44	14.04	21	73.99	0	64
SF3	1.76	3	67.67	0	33	8.16	19	76.30	0	58
BF2	4.03	8	67.52	11	89	13.86	23	70.39	3	70
OCP2	0.50	4	45.80	0	44	12.14	16	78.00	0	48
CCP2	4.80	6	62.11	0	67	11.7	21	57.42	3	64
All		9					33			

required the `mb1m` function of the `mb1m` package. I accepted test results as significant if they were smaller than the Bonferroni-corrected  $\alpha$  value.

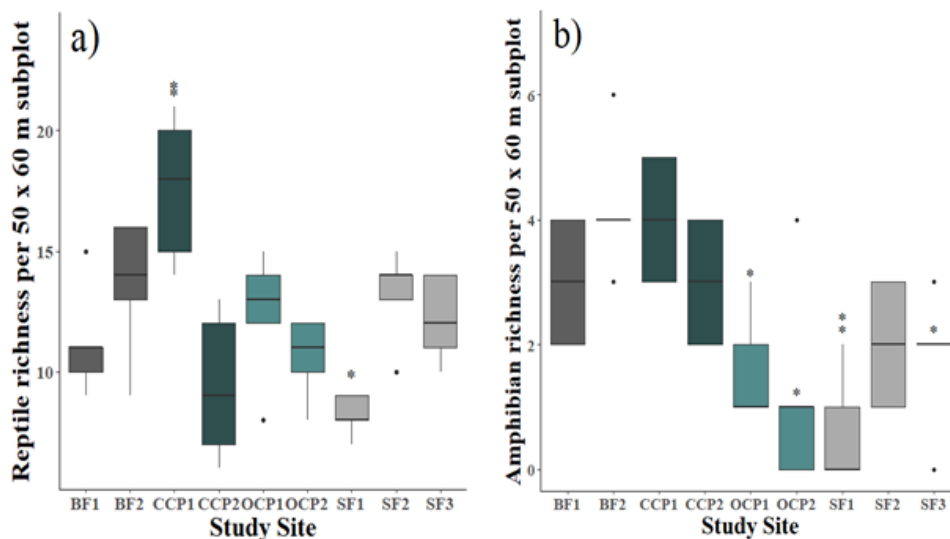
### RESULTS

Across all study sites, 3,113 reptiles and 751 amphibians were recorded (32 reptile and nine amphibian species). During the survey period, 84% of species historically recorded on Nosy Komba were identified (Andreone et al. 2003; Glaw and Vences 2007; Roberts and Daly 2014; Blumgart et al. 2017). The snake *Alluaudina bellyi* (no English common name) was recorded at study site CCP1; this is the first time *A. bellyi* has been officially documented on Nosy Komba (see Supplementary Information Table 1 for a full description of species recorded during the survey period). Two reptile species, *Phelsuma laticauda* (Broad-tailed Day Gecko or Gold-dust Day Gecko) and *P. grandis* (Giant Madagascar Day Gecko), comprised over 1/3 of the total herpetofaunal abundance with 1,449 individuals found. The frog species *Cophyla phyllodactyla* (Whistling Treefrog) contributed 510 individuals to overall herpetofauna abundance. The remaining abundance consisted of a combination of reptile and amphibian species. I define rare species as having fewer than five recorded individuals (which may not mean ecological rarity), and these were *A. bellyi*, *Brookesia minima* (Minute Leaf Chameleon), *Calumma nasutum* (Nose-horned Chameleon), *Ebenavia inunguis* (Madagascar Clawless Gecko), *Ithycyphus miniatus* (Tiny Night Snake), *Liophidium torquatum* (no English common name), *Madascincus polleni* (Madagascar Coastal Skink), *Paroedura oviceps* (Nosy Be Ground Gecko), *Phelsuma dubia* (Zanzibar Day Gecko), *Thamnosophis stumpffi* (Yellow-striped Water Snake), *Gephyromantis granulatus* (Grainy Madagascar Frog),

*Gephyromantis pseudoasper* (Massif Madagascar Frog), *Mantidactylus ulcerosus* (Warty Madagascar Frog), and *Rhombophryne testudo* (Nosy Be Burrowing Frog) made up less than 1% of total abundance.

The reptile community of Nosy Komba is heavily dominated by very few species. *Phelsuma grandis* and *P. laticauda* contributed 24.25% and 21.72% of total reptile abundance, respectively. Another 15.27% was contributed by *Trachylepis gravenhorstii* (Gravenhorst's Mabuya) and *Zonosaurus madagascariensis* (Madagascar Plated Lizard). The remaining reptile species individually constituted < 6% of total reptile abundance. Considering amphibians, one species, *C. phyllodactyla*, comprised 55% of total amphibian abundance. *Stumpffia psologlossa* (Madagascar Stump-toed Frog) and *Stumpffia pygmaea* (Andoany Stump-toed Frog) also contributed 12.02% and 19.78%, respectively. Most of the aforementioned species are considered generalist or highly adaptable to human modified landscapes. Species within the genera *Calumma*, *Mantella*, *Uroplatus*, *Leioheterodon*, *Lygodactylus*, and *Madagascarophis* were present on the island in much lower abundances. However, the least represented species in terms of abundance were within the genera *Alluaudina*, *Dromicodryas*, *Ebenavia*, *Ithycyphus*, *Liophidium*, *Lycodryas*, *Madascincus*, *Sanzinia*, *Boophis*, *Gephyromantis*, *Mantidactylus*, *Rhombophryne*, and *Thamnosophis*. Coverage of the nine study sites varied from 42.86–75.61% for amphibians and from 57.42–77.70% for reptiles, suggesting the true richness of all sites is higher than recorded by MRCI (Table 3). The large variation in coverage between sites should be taken into consideration when making inferences from results presented here.

The highest number of amphibian species ( $n = 8$ ) was recorded in BF2 (100% bamboo forest), representing 89% of the landscape total. Plantation study sites CCP1



**FIGURE 3.** Median (a) reptile and (b) amphibian species richness recorded within a 50 × 60 m subplot during time constrained Visual Encounter Surveys at nine study sites across Nosy Komba, Madagascar. The black line indicates the median species richness, the box represents the upper and lower quartiles, and the dotted lines display standard error. Empty points represent outliers. An asterisk (\*) indicates a significant difference in average diversity value for the respective site, with a dot (·) =  $P < 0.100$ , \* =  $P < 0.050$ , \*\* =  $P < 0.010$ , \*\*\* =  $P < 0.001$ . Color designations are dark green = closed-canopy plantation, light green = open-canopy plantation, dark gray = bamboo forest, and light gray = secondary forest.

and CCP2 (70% and 80% closed-canopy plantation, respectively) each contained six, covering 67% of the landscape total. Site BF1 supported five species, constituting 56% of the landscape total and exceeding the average. Site SF1 (100% secondary forest) contained the lowest number of amphibians, with only two of nine recorded at this site (22% of the landscape total). Only three amphibian species were recorded at sites OCP1 (60% open-canopy plantation) and SF3 (80% secondary forest). Twenty-six of 33 reptile species recorded on Nosy Komba were observed at CCP1, followed by 23 species at BF2. Sites SF1 and OCP2 (60% open-canopy plantation) supported the lowest diversity of reptile species, with only 16 species (48% of landscape total) recorded at each. SF3 and OCP1 supported a reptile diversity lower than the average.

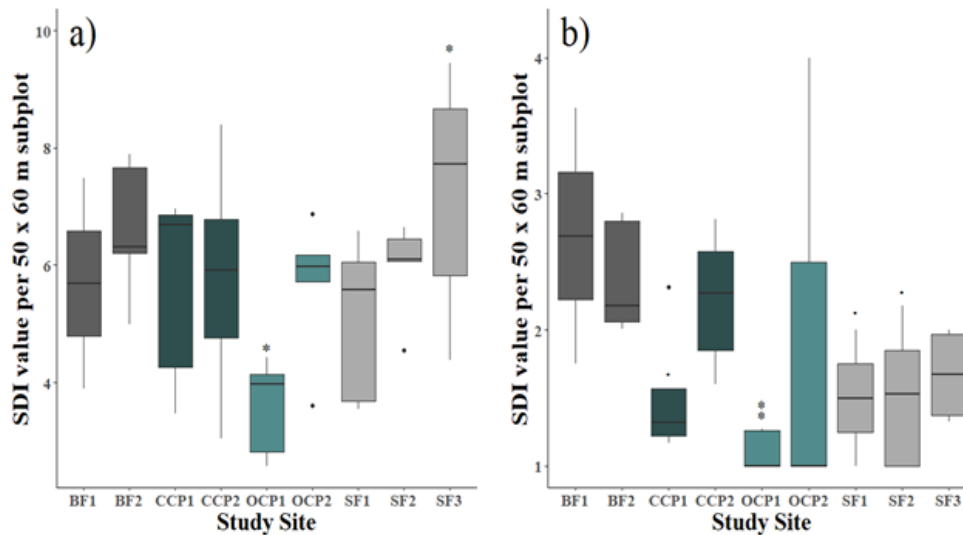
Reptile species richness data were normally distributed ( $W = 0.97$ ,  $df = 8$ ,  $P = 0.201$ ) whereas amphibian richness data was not ( $W = 0.94$ ,  $df = 8$ ,  $P = 0.026$ ). Species richness was significantly different between survey sites for reptiles ( $F_{8,36} = 6.70$ ,  $P < 0.001$ ,  $r^2 = 0.60$ ) and amphibians ( $\chi^2 = 26.01$ ,  $P < 0.001$ ; Fig. 3). CCP1 had a significantly higher richness of reptiles than all other sites (Tukey HSD,  $P < 0.001$ ). SF1 demonstrated an average reptile richness which was low enough to warrant further exploration using post-hoc tests (Tukey HSD,  $P = 0.051$ ). A Tukey post-hoc test revealed SF1 had a significantly lower richness of reptiles than CCP1 (Tukey HSD,  $P < 0.001$ ) and BF2 (Tukey HSD,  $P = 0.021$ ). CCP1 displayed the highest average amphibian richness followed by BF2 and CCP2,

whereas amphibian richness was significantly lower in OCP1 (Dunn's test,  $P = 0.049$ ), OCP2 (Dunn's test,  $P = 0.013$ ), and SF1 (Dunn's test,  $P = 0.001$ ). The lowest average amphibian species richness was recorded in SF1.

Reptile SDI data were normally distributed ( $W = 0.97$ ,  $P = 0.472$ ); amphibian SDI data were not normally distributed despite being square-root transformed ( $W = 0.92$ ,  $P = 0.016$ ). I identified no significant differences in SDI values between study sites for reptiles ( $F_{8,36} = 2.17$ ,  $P = 0.056$ ; Fig. 4a) or amphibians ( $\chi^2 = 15.01$ ,  $P = 0.060$ ; Fig. 4b). When assessing both species incidence and evenness, site SF3 demonstrated the highest reptile diversity and OCP1 the lowest. Site OCP1 was found to support significantly lower average reptile SDI values than all other study sites (Tukey HSD,  $P = 0.020$ ). Considering amphibian diversity, the highest average SDI value was recorded in BF2. The lowest amphibian diversity was recorded in OCP1 and was statistically significant (Dunn's test,  $P = 0.009$ ). Sites CCP1, SF1, and SF2 also supported lower amphibian diversity values which, although non-significant, required further consideration due to their sufficiently low  $P$  values (Dunn's tests,  $P = 0.091$ ,  $P = 0.090$ , and  $P = 0.094$ , respectively).

Community compositions varied significantly between survey sites for reptiles ( $F_{8,36} = 3.76$ ,  $P = 0.001$ ,  $r^2 = 0.46$ ) and amphibians ( $F_{8,36} = 3.73$ ,  $P = 0.001$ ,  $r^2 = 0.50$ ). The NMDS ordinations (Fig. 5) present visual representations of the reptile and amphibian community matrices for each survey site



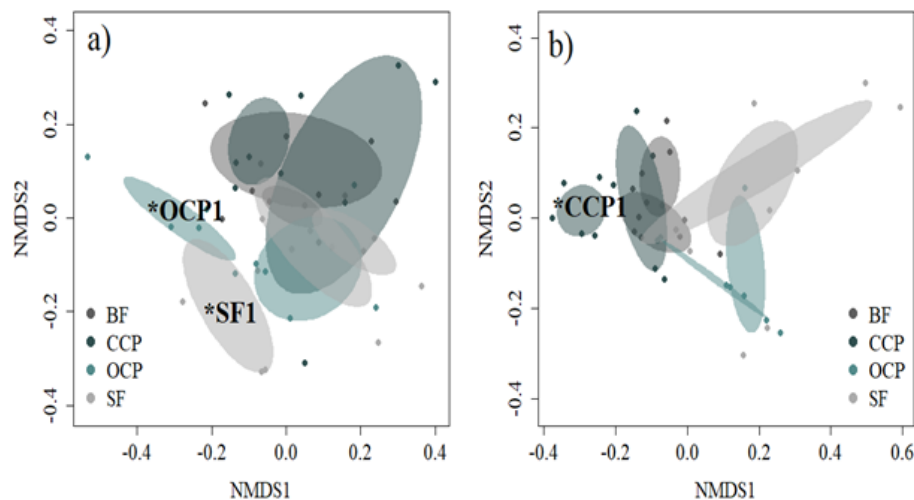


**FIGURE 4.** Average reptile (a) and amphibian (b) Simpson's reciprocal index (diversity) value recorded within a 50 × 60 m subplot during time constrained Visual Encounter Surveys at nine Nosy Komba, Madagascar, study sites. The black line indicates the median species diversity, the box represents the upper and lower quartiles, and the dotted lines display standard error. Empty points represent outliers. An asterisk (\*) indicates a significant difference in average diversity value for the respective site, with a dot (·) =  $P < 0.100$ , \* =  $P < 0.050$ , \*\* =  $P < 0.010$ , \*\*\* =  $P < 0.001$ . Color designations are dark green = closed-canopy plantation, light green = open-canopy plantation, dark gray = bamboo forest, and light gray = secondary forest.

(ellipses) and subplot (points). Site OCP1 had the highest cumulative dissimilarity value when comparing reptile communities, suggesting a comparatively unique community assemblage (Table 4). Site SF1 demonstrated the highest cumulative dissimilarity value when comparing amphibian communities (Table 4).

Dissimilarities between survey sites were heavily determined by generalist species such as *P. grandis*, *P. laticauda*, *Z. madagascariensis*, *S. psologlossa*, *S.*

*pygmaea*, *T. gravenhorstii*, *Furcifer pardalis* (Panther Chameleon), *Geckolepis maculate* (Fish-scale Gecko), and *C. phyllodactyla* (see Simper analysis results in the online Supplementary Information). All sites supported a unique assemblage of herpetofauna in terms of incidence and abundance of species. When considering reptiles only, OCP1 and SF1 displayed the most independent community compositions, overlapping only with each other (Fig. 5a). These



**FIGURE 5.** Non-metric multi-dimensional scaling (NMDS) ordination of (a) reptile ( $K = 3$ , stress = 0.15) and (b) amphibian ( $K = 2$ , stress = 0.09) community assemblages of nine study sites at Nosy Komba, Madagascar. Individual points represent 50 × 60 m subplots (five at each site). Ellipses demonstrate the standard deviation from the centroid for the community assemblages of each study site in multidimensional space. Sites OCP1, SF1 (a), and CCP1 (b) are indicated by an asterisk (\*). Color designations are dark green = closed-canopy plantation, light green = open-canopy plantation, dark gray = bamboo forest, and light gray = secondary forest.

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TABLE 4. Bray-Curtis dissimilarity values obtained for pairwise comparisons of amphibian and reptile community assemblages of study sites BF1-CCP2 at the Madagascar Research and Conservation Institute, Nosy Komba, Madagascar. Explanation of trail sites is given in Figure 2. Abbreviations are C = comparison, R = reptiles, A = amphibians.

C	R	A	C	R	A
BF1 v. OCP1	0.5	0.45	SF1 v. BF2	0.44	0.91
BF1 v. SF1	0.39	0.88	SF1 v. OCP2	0.45	0.62
BF1 v. CCP1	0.35	0.5	SF1 v. CCP2	0.48	0.92
BF1 v. SF2	0.37	0.43	CCP1 v. SF2	0.40	0.74
BF1 v. SF3	0.49	0.74	CCP1 v. SF3	0.49	0.88
BF1 v. BF2	0.38	0.27	CCP1 v. BF2	0.38	0.52
BF1 v. OCP2	0.45	0.77	CCP1 v. OCP2	0.52	0.91
BF1 v. CCP2	0.37	0.25	CCP1 v. CCP2	0.40	0.47
OCP1 v. SF1	0.51	0.81	SF2 v. SF3	0.37	0.53
OCP1 v. CCP1	0.5	0.76	SF2 v. BF2	0.18	0.47
OCP1 v. SF2	0.55	0.26	SF2 v. OCP2	0.35	0.48
OCP1 v. SF3	0.67	0.57	SF2 v. CCP2	0.42	0.54
OCP1 v. BF2	0.55	0.54	SF3 v. BF2	0.46	0.71
OCP1 v. OCP2	0.56	0.55	SF3 v. OCP2	0.39	0.62
OCP1 v. CCP2	0.67	0.6	SF3 v. CCP2	0.39	0.77
SF1 v. CCP1	0.4	0.96	BF2 v. OCP2	0.40	0.78
SF1 v. SF2	0.43	0.84	BF2 v. CCP2	0.40	0.13
SF1 v. SF3	0.47	0.86	OCP2 v. CCP2	0.38	0.81

transects had higher abundances of generalist species *P. abbotti* (Abbott's Day Gecko), *P. grandis*, *P. laticauda*, and *T. gravenhorstii* and lower abundances of forest specialist species than the other study sites. The remaining sites showed considerable overlap in their community compositions. Amphibian community compositions proved to be much more variable than for reptiles (Fig. 5b), with dissimilarity values determined by five of the nine recorded species: *C. phyllodactyla*, *Mantella ebenau* (Ebenau's Golden Frog), *S. pygmaea*, *S. psologlossa*, and *Boophis tephraeomystax* (Dumeril's Bright-eyed Frog). CCP1 demonstrated the most independent amphibian assemblage due to its high abundance of *C. phyllodactyla*.

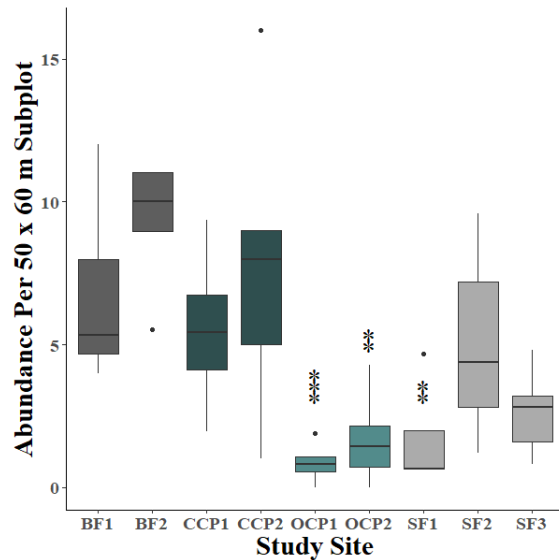
Staff and volunteers recorded 12 species of threatened herpetofauna (three amphibian and nine reptile) on Nosy Komba during the survey period. Of these species, *B. minima* (Madagascar Dwarf Chameleon), *P. seippi*, *Z. subunicolour* (Nosy Be Plated Lizard), *R. testudo*, *S. pygmaea*, and *S. psologlossa* were classified as endangered; *B. ebenau* (Northern Leaf Chameleon), *Lygodactylus madagascariensis* (Madagascar Dwarf Gecko), *T. stumpffi*, *Uroplatus ebenau* (Nosy Be Flat-tailed Gecko), and *U. henkeli* (Henkel's Leaf-tailed Gecko) as vulnerable; and *P. oviceps* as near threatened. Site CCP1 hosted the highest richness of threatened herpetofauna species (11), followed by CCP2 (n = 8). Site SF1 supported the fewest threatened species (n = 2), including no species of threatened amphibian, followed

by OCP1 (n = 5) and OCP2 (n = 5). BF2 hosted the highest proportion (27.8%) of threatened reptiles when considering abundance, followed by CCP1 (21.2%). OCP1, OCP2, and SF1 supported the lowest proportions of threatened reptiles, comprising 2.9%, 3.3%, and 4.8%, respectively. For threatened amphibians, CCP1 hosted 37.5% of the total abundance and BF2 hosted 32.1%. SF3 and OCP2 each supported only 1.1% of threatened amphibians, and OCP1 hosted 2.2%. No threatened amphibians were recorded on SF1.

Data for threatened species were normally distributed after square-root transformation ( $W = 0.97$ ,  $P = 0.423$ ). Study sites supported significantly different abundances of threatened herpetofauna ( $F_{8,36} = 6.43$ ,  $P < 0.001$ ,  $r^2 = 0.50$ ; Fig. 6). The average abundance of threatened herpetofauna recorded in a 50 × 60 m subplot was found to be significantly lower in OCP1 (Tukey HSD,  $P < 0.001$ ), OCP2 (Tukey HSD,  $P = 0.002$ ), SF1 (Tukey HSD,  $P = 0.004$ ), and SF3 (Tukey HSD,  $P = 0.028$ ) than the remaining study sites.

When considering individual threatened species, *P. seippi* ( $F_{8,36} = 4.28$ ,  $P = 0.001$ ,  $r^2 = 0.37$ ), *S. pygmaea* ( $\chi^2_{8,36} = 25.42$ ,  $P = 0.001$ ), and *U. henkeli* ( $F_{8,36} = 32.67$ ,  $P < 0.001$ ,  $r^2 = 0.85$ ) abundances varied significantly between study sites. Workers recorded significantly lower abundances of *P. seippi* in OCP1 and CCP1 and significantly higher abundances of *U. henkeli* in CCP1 than remaining sites (Tukey HSD,  $P = 0.003$ ). *Stumpffia psologlossa* in CCP2 had a significantly higher

## DISCUSSION



**FIGURE 6.** The average abundance of threatened (endangered or vulnerable) herpetofauna recorded within a 50 × 60 m subplot of nine Nosy Komba, Madagascar, study sites across the survey period 29 January 2016 and 5 July 2017. Species were classified as vulnerable or endangered according to the International Union for Conservation of Nature Red List (IUCN 2018). Asterisks (\*) indicate a significant difference in abundance to BF1, as determined by one-way ANOVA: \* =  $P < 0.05$ , \*\* =  $P < 0.01$ , \*\*\* =  $P < 0.001$ . Dark green = closed-canopy plantation, light green = open-canopy plantation, dark gray = bamboo forest, and light gray = secondary forest.

abundance than all other sites (Tukey HSD,  $P = 0.035$ ) and lower abundances of *S. pygmaea* in SF1 and SF3 which neared significance (Tukey HSD,  $P = 0.064$  and  $0.071$ , respectively). Subplots of CCP1 also supported significantly higher abundances of *U. henkeli* than all other study sites (Tukey HSD,  $P = 0.005$ ).

Amphibian species richness and diversity were not significantly correlated with any environmental variables, despite finding a moderate correlation between amphibian species richness and canopy cover ( $r = 0.45$ ,  $df = 8$ ,  $P = 0.162$ ). Reptile species richness was significantly positively correlated with a combination of bamboo density, woody tree density, and understory density from 1.5–2 m height ( $r = 0.50$ ,  $df = 8$ ,  $P < 0.001$ ). Reptile diversity was significantly and negatively correlated with wood volume ( $r = -0.57$ ,  $df = 8$ ,  $P < 0.050$ ). Negative correlations between plantation species richness and reptile diversity ( $r = -0.36$ ,  $df = 8$ ,  $P < 0.098$ ) and plantation species diversity and reptile diversity ( $r = -0.45$ ,  $df = 8$ ,  $P = 0.086$ ) neared significance, prompting further exploration of these relationships using regression analysis. Incorporation of these independent variables into GAMs revealed significant predictive relationships for all discussed environmental variables with either reptile or amphibian diversity ( $P < 0.050$ ; Table 5).

Based on studies that found diminished herpetofaunal diversity levels within agroforestry systems, I expected reptile and amphibian richness and diversity to be lower at sites comprised primarily of plantation compared to natural forest (secondary or bamboo forest; Wanger et al. 2009; Louzada et al. 2010; Gillespie et al. 2012). I did not find this to be the case for either reptiles or amphibians. Closed-canopy plantation sites consistently demonstrated higher richness and ecological diversity values than SF: more reptile and amphibian species were recorded in CCP than natural forest, excluding BF2; average reptile species richness was significantly higher in CCP1 than all other sites; amphibian species richness was higher in sites CCP1 and CCP2 than all natural forest sites (again excluding BF2); and site CCP2 demonstrated the highest average amphibian SDI value per subplot. These results are in accordance with studies claiming agroforestry systems resemble natural forest (Perfecto et al. 2007; Schroth and Harvey 2007; Bhagwat et al. 2008). They are also supported by Schroth et al. (2013), who hypothesized that agroforestry systems such as CCP could act as secondary habitats for disturbance-tolerant species.

Based on studies that found agroforestry systems unable to support the full suite of species present in natural forest, and in particular forest specialist species, I also assumed plantation habitats would contain a highly altered herpetofaunal assemblage dominated by adaptable, generalist species (Faria et al. 2007; Harvey and Gonzalez 2007; Scales and Marsden 2008; Gillespie et al. 2012; Cortés-Gómez et al. 2013). Again, I did not find this. When considering reptile assemblages, all sites excluding OCP1 and SF1 displayed considerable overlap in community composition irrespective of habitat type. Furthermore, forest specialist species *B. minima*, *Z. subunicolor*, *B. ebenai*, *T. stumpffi*, and *U. henkeli* were recorded in CCP, demonstrating the potential for plantation sites to support community assemblages reflective of natural forest. The amphibian community composition of CCP sites also demonstrated considerable overlap with BF, a natural forest habitat.

In contrast to my prediction, the two sites containing the highest number of threatened species were both CCP, and SF contained significantly lower abundances of threatened herpetofauna per subplot than both BF and CCP. This result was unexpected, as previous studies have reported diminished threatened species abundances in plantation habitats (Palacios et al. 2013). The finding suggests that, at least in terms of preserving threatened species of herpetofauna, CCP sites could play a vital role in future conservation efforts on Nosy Komba and should be favored over OCP. Some species, however, are simply more tolerant of disturbance than is currently

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**TABLE 5.** Spearman Rank Correlation co-efficient and likelihood ratio test chi-square values for measured environmental characteristics and herpetofaunal species richness and Simpson's reciprocal index values. Values in bold were determined using Sen Siegel non-parametric linear regression and report the slope of the fit line. Only characteristics found to have a strong or moderate correlation with herpetofaunal, amphibian, or reptile species richness or diversity are presented. Significance levels of correlative and regressive relationships are \* =  $P < 0.10$  and \*\* =  $P < 0.05$ .

Environmental Factor	Spearman Rank Correlation		Likelihood Ratio Test	
	Reptiles	Amphibians	Reptiles	Amphibians
Bamboo density	0.43	0.22	8.42	2.83
Woody tree density	0.30	0.25	21.5	8.60
Canopy cover	-0.07	0.45	0.68	11.07
Bamboo density+ woody tree density	0.43	0.39	9.27	8.44
Bamboo density+ woody tree density+ US4	0.50**	0.37	13.1**	7.98
Bamboo density+ woody tree density+ US4+ grass	0.45	0.37	12.7**	8.35
Canopy cover	0.28	0.36	4.55	4.44
Plantation sp. density	-0.45*	-0.43	32.6**	6.68
Plantation sp. richness	-0.36*	-0.29	-0.15**	-0.12
US2	-0.34*	-0.12	9.00	4.09
Wood volume	-0.57**	-0.11	22.4**	5.18
Woody tree density+ sapling density+ bamboo density	0.38	0.11	6.53	0.14

understood; there is a notable lack of information on Madagascan herpetofauna and much of the existing literature is fairly dated.

As predicted, OCP sites demonstrated significantly lower amphibian richness and lower amphibian and reptile SDI values than both BF and CCP. These findings are consistent with the wider scientific literature, in which monoculture plantations have been reported to support a less diverse and specialized assemblage of species compared to agroforestry systems for a variety of taxa (Harvey et al. 2006; Faria et al. 2007; Harvey and Gonzalez 2007; McNeely and Schroth 2006). Unexpectedly, this result does not extend to reptile richness, which increased within OCP. As suggested in other studies within similar results, this could be the result of accumulation of disturbance-resistant generalist species through the creation of new microhabitats (Palacios et al. 2013; Russildi et al. 2016), and is unlikely be preserved into the future if sensitive, specialist species are lost after an initial delayed response to land-use change (Barlow et al. 2007). Indeed, the distinct amphibian community composition of OCP (both from natural forest and CCP), suggests that a lack of structural complexity and floral diversity; hot, dry climatic conditions caused by a sparse canopy cover; and intensive human management are already causing shifts to a simpler community assemblage (Deheuvels et al. 2014). This is further supported by results from the SIMPER analysis, which revealed that OCP1 was dominated by generalist *Phelsuma* geckos and the highly abundant leaf-litter skink *T. gravenhorstii*, but was lacking forest specialist species.

My results suggest that on Nosy Komba, CCP is better able to preserve ecologically diverse herpetofaunal

communities that resemble those of natural forests. This may be because CCP maintains a structurally complex habitat with a diverse and permanent layer of multi-purpose shade trees, thus more closely resembling natural forest. Therefore, a diversity of niche space is preserved and a cool, moist micro-climate is created for amphibian species. This assumption was supported by significant correlative and predictive relationships between herpetofaunal diversity and the combined environmental characteristics of woody tree density, bamboo density, and U4, suggesting that amphibian species richness is higher in CCP than OCP due to its structural complexity and greater extent of homogeneous canopy cover. Numerous studies have reported similar results (Cortés-Gómez et al. 2013; D'Cruze and Kumar 2011; Faria et al. 2007; Jenkins et al. 2014; Wanger et al. 2009).

**Study limitations.**—The use of a limited set of methods may have resulted in a biased understanding of herpetofaunal responses to land-use change on Nosy Komba due to underestimation of herpetofaunal richness and diversity in natural forest sites (Ribeiro-Júnior et al. 2008; Whitworth et al. 2017). Many study sites were not surveyed enough to achieve full species saturation (Veith et al., 2004); visual encounter surveys were biased toward identification of diurnal and extroverted species and against more reclusive species, e.g., leaf litter amphibians; and the higher structural complexity of natural forest habitats created more surveyor disturbance and allowed herpetofauna to conceal themselves. Additionally, I conducted more diurnal surveys, favoring species more active or visible during the day.

A lack of information on relevant biotic and abiotic variables within Nosy Komba forest habitats prevents a clear understanding of the influence of forest type on herpetofaunal assemblages. For example, site SF1 demonstrated an altered ratio of generalist to forest specialist species and lower reptile and amphibian diversity compared to other natural forest sites. Contrary to being representative of the biodiversity of natural forest on Nosy Komba, these values are likely a result of intensive human disturbance prior to full clearance of the site in 2016. In addition, the amphibian community assemblage of CCP1 was distinctly different to all other study sites, with a much higher proportion of *C. phyllodactyla*. Rather than being representative of the community assemblage of CCP sites, this could be explained by the stand of bamboo forest within CCP1, a preferred habitat for *C. phyllodactyla* (Glaw and Vences 2007).

Finally, many factors known to influence the abundance of individual herpetofauna species and the composition of herpetofaunal assemblages have not been incorporated into this analysis. These factors include, but are not limited to, altitude (Malonza 2015), plantation management (Faria et al. 2007; Harvey and Gonzalez 2007), composition of the surrounding forest matrix (Bennett et al. 2006; Anand et al. 2010; Gardner et al. 2010; Prevedello and Vieira 2010; Ndirantsoa et al. 2017), plantation proximity to natural vegetation (Anand et al. 2010; Clough et al. 2010; Ferraz et al. 2014), and the extent of forest habitat at the landscape scale (Bennett et al. 2006; Tschardt et al. 2008; Gardner et al. 2010; Ndirantsoa et al. 2017). Given that replication in this study was inadequate to mediate variability in these factors between sites, it cannot be stated with absolute certainty that the reported herpetofaunal assemblages are a response to forest type rather than site specific characteristics. For example, it can be assumed that stands of secondary forest on Nosy Komba act as sources of herpetofaunal diversity for surrounding plantations, creating potentially misleading results for sites such as CCP2 and OCP1 (McNeely and Schroth 2006; Faria et al. 2007; Tschardt et al. 2008).

**Future implications.**—The results of this study demonstrate that CCP, when set within a matrix of secondary forest, is capable of preserving diverse herpetofaunal communities resembling those of bamboo forest when key environmental characteristics are thoughtfully managed. Consequently, the wide-spread integration of low-intensity, multi-crop, closed-canopy plantations on Nosy Komba could be viewed as a sustainable solution to human development on the island by providing a refugia for herpetofauna, which also acts

as a source of income for rural households (Dewi et al. 2013). This form of diversified food production system will no doubt become more relevant on the island, both for subsistence agriculture and economic stability, in light of changing temperature and precipitation patterns predicted by the IPCC as a result of climate change (Pachauri et al. 2014). The limitations of this study necessitate further research on Nosy Komba to support our findings; however, this research should not be conducted at the expense of expanding sustainable agriculture on the island, as continued land-use change is inevitable given the demographic and economic factors already placing pressure on Nosy Komba's natural resources.

**Conclusions.**—The results of this study contribute to a growing source of scientific literature focused on the implications of land-use change for Madagascan herpetofauna in secondary Sambirano forest. On Nosy Komba, OCP exhibited simple community assemblages dominated by generalist species and low levels of herpetofaunal diversity. In contrast, CCP supported diverse assemblages of reptiles and amphibians reflective of natural forest composition. This is due to the retention of high woody tree and bamboo densities and a dense understory, which maintain structural complexity and favorable micro-climates. It is also in part due to the low-intensity management style of mixed-type plantations and resultant low levels of human disturbance; however, natural forest stands appear to be playing a role in acting as biodiversity sources for CCP sites. Therefore, from my results, it can be said that CCP is capable of sustaining specialist, threatened, and range-restricted species when in proximity to natural forest. Although further research will be essential to confirm the preliminary findings presented here, my results suggest that at the very least CCP presents a viable alternative to devastating OCP systems, and could play an important role in preserving herpetofaunal populations until legal protection of natural forests and effective community development projects can be put in place.

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**BETH K. EVANS** completed her B.Sc. in Environmental Biology at Lancaster University, Lancashire, UK, in 2018. She has worked as a Research Ecologist for Madagascar Research and Conservation Institute on Nosy Komba, Madagascar, and for Fuze-Ecoteer in Merapoh, Malaysia. Her research interests include eco-agriculture and conservation ecology. She is currently working for Child.org as Spectacular Events Project Manager. (Photographed by Una Freysdottir).

## APPENDIX

### Madagascar Research and Conservation Institute

Madagascar Research and Conservation Institute (MRCI) is a volunteer-based research center located on the north coast of Nosy Komba. The center is involved in both marine and terrestrial ecological research, with an emphasis on vertebrate species. The work of MRCI contributes to national conservation efforts in the wake of extensive habitat degradation and destruction in Madagascar. Madagascar Research and Conservation Institute also runs a community development and education program which operates in four villages on Nosy Komba. Staff and volunteers of the Terrestrial Science Project collected the wealth of data presented here and provided invaluable support and resources to produce this report. The author of this study took part in a total of 61 visual encounter surveys in the capacity of MRCI volunteer and staff member, accounting for 28% of the total data.

#### Visual Encounter Survey Methods

1. Weather and environmental conditions (temperature, relative humidity, and cloud cover, wind, and rainfall on a scale of 1–5) were recorded before the start of the transect.
2. The survey began at the signal of the lead researcher, and the start time recorded.
3. Surveyors traversed the transect line at a rate of 10 min per 50 m, looking for reptiles and amphibians within various microhabitats (leaf litter, understory vegetation, observable parts of the canopy and tree trunks, rock and bark crevices, river beds and water pools). Active searching and conversation were not permitted to ensure continuity between survey groups and individuals.
4. When an observation was made, the group was signaled to stop and the survey information recorded by the lead researcher. Information recorded with each observation included: time of observation, distance along the transect, substrate on which the specimen was found, distance from the transect line, vertical height, and snout to vent length (SVL) of the specimen. The search time was paused to allow for this recording of information.
5. Once the relevant information had been recorded, the survey continued and the search time resumed.
6. When the last surveyor passed the end of the transect, the end time was recorded and total search time calculated.

#### Habitat Survey Methods

The number of woody trees, palm trees, saplings, bamboo plants, and plantation species and individuals were recorded up to 5 m from the transect line on both sides within each subplot. Two surveyors were positioned on each side of the transect line, and slowly walked parallel to it with one individual counting and one recording information. Ground cover composition was assessed by establishing a 2 x 2 m plot 1m from the transect line, and visually determining the proportions of leaf litter, rock, weeds, wood, grass, and bare ground (as a %). The first plot was established at the start of each 50 m subplot; following plots were set up 5 m from the end of the previous one. Leaf litter was measured by placing a ruler at the center of the plot. Canopy cover was visually assessed by a researcher standing at the center of the plot. Understory density was measured using a touch-pole placed at the center of the plot. The number of leaves touching the pole within six 50 cm intervals was recorded. The side of the transect line chosen for plot establishment was selected randomly by flipping a coin.