Int J Primatol (2018) 39:141–153
https://doi.org/10.1007/s10764-018-0022-1

The Use of Vanilla Plantations by Lemurs: Encouraging Findings for both Lemur Conservation and Sustainable Agroforestry in the Sava Region, Northeast Madagascar

Dan Hending[1] · Angelo Andrianiaina[2] · Zafimahery Rakotomalala[2] · Sam Cotton[1]

Received: 5 October 2017 / Accepted: 16 January 2018 / Published online: 22 February 2018

Abstract Extensive areas of forest are cleared every year to establish new agricultural land in the tropics, resulting in a catastrophic loss in habitat for the world's primates. A prominent example of this process is Madagascar, where an increasing demand for arable land has led to the once-forested landscape to be now dominated by agricultural areas used for the cultivation of food and cash crops. Despite the prominence of these plantations throughout Madagascar, their suitability as a habitat to support endemic lemur populations remains unclear. Here, we assessed lemur presence in vanilla plantations, Madagascar's principal export crop, within the northeastern Sava region with the use of line transects. We confirmed the presence of five lemur species, four of which were nocturnal cheirogaleids, in these vanilla plantations. Intensively farmed vanilla plantations and those in existing stands of vegetation supported at least one species of lemur. Furthermore, lemurs were significantly more likely to be present in plantations grown close or adjacent to natural forest fragments, compared to more intensively farmed, anthropogenic sites. In comparison, we observed eight lemur species in natural forest fragment sites in close proximity to the vanilla plantation sites, four of which we did not observe in any of the plantation sites. Our results provide evidence of lemurs using vanilla plantations and show that vanilla plantations may act as extensions of suitable habitat for lemurs, suggesting that they may also function as matrices between isolated forest fragments through which gene flow can occur. These

Handling Editor: Joanna M. Setchell

✉ Sam Cotton
scotton@bristolzoo.org.uk

[1] Department of Field Conservation & Science, Bristol Zoological Society, Bristol Zoo Gardens, Clifton, Bristol BS8 3HA, UK

[2] The University of Antananarivo, 566 Analamanga, 101 Antananarivo, BP, Madagascar

are important and encouraging findings for both lemur conservation and for sustainable agroforestry undertaken by local farming communities.

Keywords Habitat extension · Lemurs · Madagascar · Sava region · Vanilla plantation

Introduction

Nearly 80% of all new agricultural land in the tropics, including plantations, croplands, and grazing pastures, is currently established through the clearing of preexisting natural forest habitat (Foley *et al.* 2005; Gibbs *et al.* 2010; Lambin and Meyfroidt 2011). This extensive forest loss is predicted to increase as human populations, and therefore the demand for arable land, continues to rise rapidly on a global scale (Flohre *et al.* 2011; Foley *et al.* 2005; Godfray *et al.* 2010). This magnitude of habitat loss is a serious concern for many primate species, more than half of which are now threatened with extinction as a direct result of habitat loss (Cowlishaw 1999; Estrada and Coates-Estrada 1988; Johns and Skorupa 1987; Mittermeier *et al.* 2010). Although 90% of primate taxa worldwide are thought to be completely dependent on forest habitat (Chapman *et al.* 2006; Mittermeier and Cheney 1987), studies of Neotropical (Clarke *et al.* 2002; Estrada 2006), African (Cowlishaw 1999; Isabiryse-Basuta and Lwanga 2008), and Asian primates (Johns 1986; Srivastava 2006) suggest a degree of tolerance and adaptability to anthropogenic, agricultural landscapes. However, it is often unclear whether these agricultural landscapes and the introduced plant species in them can support permanent, stable populations of primates (Gérard *et al.* 2015; Irwin *et al.* 2010; Perfecto and Vandermeer 2008).

The lemurs of Madagascar inhabit a landscape under ever-increasing agricultural expansion and intensification (Keck *et al.* 1994). As a result of rapid and widespread decline of their forest habitat, lemurs have become the most imperilled group of mammals on Earth, with 94% of species now threatened with extinction (Schwitzer *et al.* 2014). Much of this habitat destruction has been caused by human population growth and an increased demand for arable land for the cultivation of food and cash crops (Irwin *et al.* 2010; Schwitzer *et al.* 2011). Tolerance of these degraded, anthropogenic habitats varies greatly among even the most closely related lemur species (Lehman *et al.* 2016; Setash *et al.* 2017). For example, in the nocturnal Cheirogaleidae, some species have more generalist adaptations to degraded habitat types, such as broad ecological feeding niches, varied diets, and the ability to use matrix habitats as migration corridors, in comparison to other more specialized species (Kappeler and Rasoloarison 2003; Rakotoniaina *et al.* 2016; Schäffler and Kappeler 2014). Large agricultural areas are now increasingly common throughout Madagascar's landscape, much of which is dominated by highly anthropogenic grasslands (Vorontsova *et al.* 2016). Yet there have been surprisingly few studies of the use of these agricultural habitats by lemurs, and we do not know whether they are suitable/sink habitats for lemurs or merely potential travel corridors between natural forest fragments (Irwin *et al.* 2010). There are reports of lemurs in eucalyptus and exotic tree plantations and anecdotal reports of the black lemur (*Eulemur macaco*) and blue-eyed black lemur (*E. flavifrons*) in cash-crop plantations of mango, cashew, coconut, and pepper (Ganzhorn 1987; Petter *et al.* 1977; Ramanamanjato and Ganzhorn 2001; Schwitzer *et al.* 2007; Scobie *et al.* 2017; Simmen *et al.* 2007). Moreover, researchers have recently observed five species of lemur in cacao plantations in northwest Madagascar (A. Webber *pers. comm.*). Given the large and increasing expanse of agricultural habitats in Madagascar, there is a pressing need for additional and more in-depth studies to better understand the use of plantations by lemurs.

Bourbon vanilla (*Vanilla planifolia*) is Madagascar's most well-known, trademark cash crop (AFB 2016). Approximately 80% of the world's vanilla is cultivated and processed in northern Malagasy plantations, contributing nearly $200 million in export income (in 2015), making it the country's second-most valuable export after raw nickel (AFB 2016). Vanilla plantations are now widespread in many areas of northern Madagascar, particularly in the Sava region of the northeast, and are the main source of income for many farmers in the region (Bomgardner 2016; Perfecto and Vandermeer 2008). Vanilla is an orchid that originates from Mexico, where it is pollinated by a few hymenopteran species (Lubinsky *et al.* 2006). In Madagascar, where these species are absent, pollination has to be done manually, making it a labor-intensive crop. Vanilla plants are grown on the trunks/stems of other types of vegetation for support (known as "tutor" plants), and the seed pods are harvested, dried, and used to flavor many products and foods. The crop is grown using a variety of cultivation methods, ranging from traditional small-scale plantations in and around existing forests (where the vanilla plants grow on preexisting vegetation that act as natural tutors), to large intensively farmed plantations grown on an industrial scale (where vanilla is grown among rows of a few specifically planted and highly modified, introduced tutor species). However, despite their wide-scale distribution, the biodiversity contained in these vanilla plantations remains understudied, and we do not know whether they harbor lemur populations, nor whether they have a role to play in the conservation of lemur populations (Ganzhorn 1987; Hending *et al.* 2017). In this study, we assessed lemur diversity in natural forest fragments and vanilla plantations of the Sava region, northeastern Madagascar. We compared lemur diversity among plantation types of varying management intensity, with the aim of determining whether lemurs were present within these different agricultural habitats. We hypothesized that some of the species of lemurs, particularly the nocturnal species, that are present within the natural forest fragments would be present in plantations in close proximity to natural habitat, but not in highly anthropogenic, intensively managed plantations. This is because some lemurs, such as the nocturnal species, are known to tolerate and inhabit degraded habitats (Kappeler and Rasoloarison 2003).

Methods

Site Selection

We made all observations between January 10 and April 25, 2017 in the Loky–Manambato Protected Area, the Vohemar district, and the Sambava district of the Sava region, north eastern Madagascar. We surveyed 17 cash-crop vanilla plantations, classified as either 1) *ecoplantations*, where the preexisting vegetation has not been removed, modified, or managed and vanilla is grown on preexisting vegetation tutors ($N = 12$) (Fig. 1), or 2) *intensive/nontraditional plantations*, where the preexisting vegetation has been heavily modified, managed, removed, or planted to make maximal use of space; vanilla is grown on modified or introduced tutors; and natural fertilizers are used to modify soil quality (N = 5) (Fig. 1) (Goldthorpe 1988). The term *ecoplantation* reflects growing the vanilla crop in a preexisting ecosystem (such as forest or other vegetation), rather than a judgment of its ecological merits or shortcomings. We subclassified ecoplantations based on their proximity to forest fragments as either 1) *forest plantations*: located ≤100 m of a forest fragment (N = 6), or 2) *nonforest plantations*: located >100 m from a forest fragment (N = 6); the 100-m threshold for determining whether an ecoplantation was "forest" or "nonforest" was an arbitrary distinction, but the vegetation of forest plantations was always closely connected with the vegetation of a natural forest fragment, whereas nonforest plantations were much further from the nearest forest fragment. We measured the area of each plantation site using GPS waypoints of the site perimeter and ArcGIS (ArcGIS, Esri, Redlands, CA, USA). We deemed all plantations studied to be stable in their position and agricultural intensity; ecoplantations are regarded as the traditional method of vanilla cultivation by members of the vanilla farming community, are family owned, and have frequently been cultivated over several generations; in contrast, intensive plantations tend to be managed by corporate or nongovernmental organizations under long-term programs. We also surveyed nine natural forest fragments in close proximity to the vanilla plantations (Fig. 2). Forest fragments comprised predominantly native floral species in mostly primary growth, with some secondary growth evident in places (Kirby *et al.* 1984).

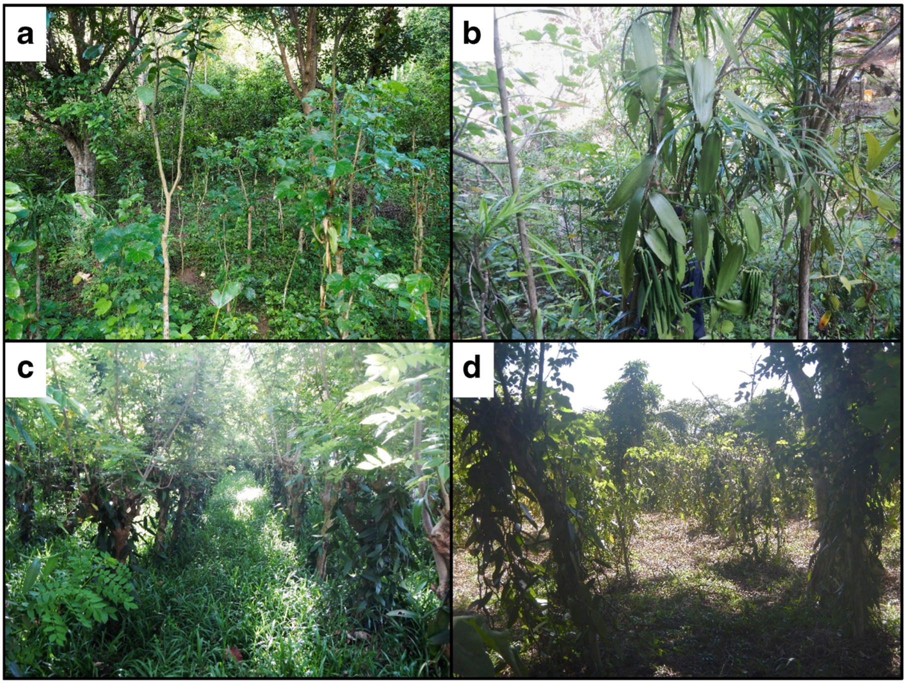

Fig. 1 Photographs showing the structure of ecoplantations and intensive plantations of the Sava region, studied January 10–April 25, 2017. (**a**) Structure of preexisting vegetation in an ecoplantation at Brondra. (**b**) Vanilla growing on preexisting vegetation at Brondra. (**c**) Rows of planted tutor trees supporting vanilla at the intensive plantation Floribis. (**d**) Rows of planted tutor trees supporting vanilla at an intensive plantation in Angalandrava.

Transect Sampling

To assess the presence of lemurs, we used one or two parallel line transects (total range of transect lengths in vanilla plantations = 0.2–1.1 km, in forests = 0.7–1.05 km) established on preexisting trails within the study sites. Two researchers walked at a slow and constant pace (1 km/h) along each transect three times: at dawn (05:00 h), midday (12:00 h), and at

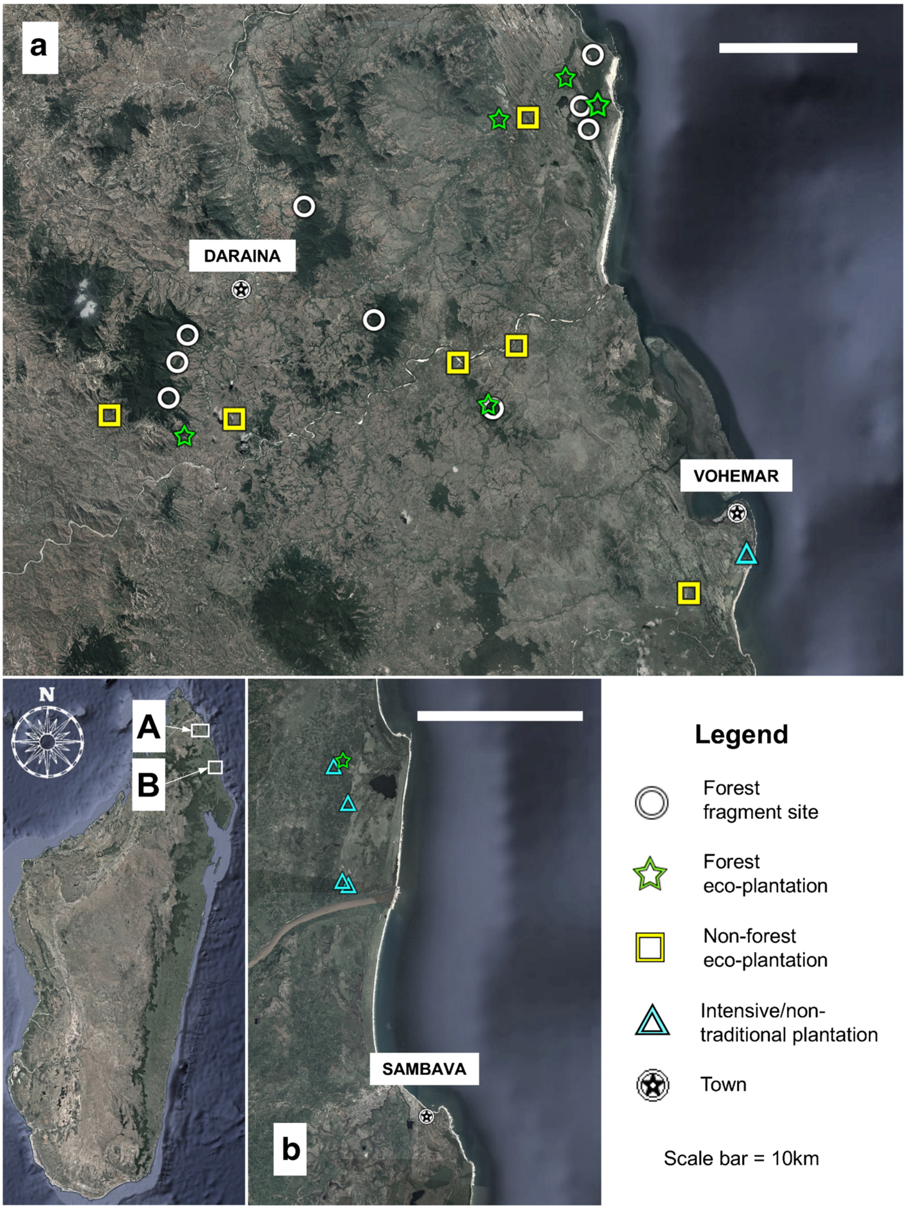

Fig. 2 Locations of forest fragment sites and vanilla plantations sampled in the Sava region of northern Madagascar near Vohemar–Daraina (**a**) and Sambava (**b**), January 10–April 25, 2017.

night (21:00 h), noting any lemur species observed along the transect line. We used head torches (Tikka, Petzl, Crolles, France) and high-lumen flashlights (EC20, Nitecore, Guangzhou, China) to aid nocturnal lemur sightings and identification. We identified lemur species using field keys and published data on geographic ranges (Louis *et al.* 2008; Mittermeier *et al.* 2010). We distinguished between the sympatric, morphologically similar dwarf lemurs by their size, pelage color, and geographic range (Blanco and Godfrey 2013; Frasier *et al.* 2016; Mittermeier *et al.* 2010).

Data Analysis

We conducted all statistical analysis in IBM SPSS 23.0 (SPSS Inc., Chicago, IL, USA) and set an α level of 0.05 to test for statistical significance. We examined if plantation type (i.e., forest ecoplantation, nonforest ecoplantation, intensive/nontraditional) influenced whether any lemurs were observed (response = lemurs present or absent) using a Fisher's exact test, and made explicit contrasts between plantation type pairs after adopting post hoc Holm–Bonferroni corrections. This approach is conservative, as it asks only whether lemurs (of any species) were present or absent in a plantation, and does not consider the number of species or individuals observed. Both plantation area and transect length varied between sites, and in some instances, transect lengths were constrained by plantation area. This may have led to differences in survey effort across different plantation types, introducing bias in the likelihood of observing lemurs. We therefore examined whether plantation areas and transect lengths varied systematically between plantation types using a Kruskal–Wallis test and a one-way ANOVA, respectively (in the former, the distribution of residuals was nonparametric and could not be appropriately transformed). Similarly, differences in sightings of lemurs between forest and vanilla plantations may have arisen because of a systematic bias in survey effort between the two contrasting habitat types. We tested for differences in survey effort (transect length) using a *t*-test.

Data Availability The datasets generated and analyzed during the current study are available from the corresponding author on reasonable request.

Ethical Note

All research complied with UK Home Office policies when working with animals and all research adhered to the legal requirements of Madagascar. Research in the Loky–Manambato Protected Area was permitted by Madagascar's Ministry of Environment (permit number 295/16/MEEF/SG/DGF/DSAP/SCB.Re).

Results

We observed five lemur species in vanilla plantations (Table I); the diurnal crowned lemur, *Eulemur coronatus* ($N = 2$ plantations); and four nocturnal species: the northern rufous mouse lemur, *Microcebus tavaratra* ($N = 2$ plantations), Sheth's dwarf lemur, *Cheirogaleus shethi* ($N = 2$ plantations), Crossley's dwarf lemur, *C. crossleyi* ($N = 2$

Table I Location, areas, and total transect lengths walked in vanilla plantations of different types and natural forest fragments in the Sava region of northeast Madagascar, January 10–April 25, 2017

Site Type		Site	Central Location	Area (Ha)	Transect Length (km)	Distance from nearest forest fragment (km)	Lemur Species (Individuals): Diurnal/Cathemeral: *Propithecus tattersalli*	Diurnal/Cathemeral: *Eulemur coronatus*	Diurnal/Cathemeral: *Eulemur sanfordi*	Nocturnal: *Microcebus tavaratra*	Nocturnal: *Lepilemur milanoii*	Nocturnal: *Cheirogaleus shethi*	Nocturnal: *Cheirogaleus crossleyi*	Nocturnal: *Cheirogaleus major*	Nocturnal: *Phaner electromontis*	Number of Species
Vanilla Plantations	Eco (forest)	Brondra	(S13°18'23.23, E49°37'16.98)	0.47	0.55	0.06							2			1
		Analamanara	(S13°17'06.65, E49°50'09.99)	1.10	0.70	0						1	1			2
		Andranga	(S13°04'39.75, E49°54'55.12)	1.90	0.35	0.05						1				1
		Ankalotany	(S13°03'31.04, E49°53'32.70)	0.61	0.35	0.01		4*		1						2
		Antingana	(S13°05'15.63, E49°50'41.33)	1.60	0.40	0.01		11								1
		Manasibe	(S14°03'59.54, E50°07'30.78)	1.60	0.65	0.02								1		1
	Eco (non forest)	Ankaramy	(S13°17'43.59, E49°39'23.02)	0.92	0.35	1.66										0
		Ampondra	(S13°24'50.73, E49°58'42.90)	5.23	1.00	3.48										0
		Mahasoa	(S13°14'43.70, E49°51'21.94)	1.70	0.50	3.48										0
		Mafokovo	(S13°15'25.12, E49°48'52.64)	0.60	0.30	0.89										0
		Antsoha	(S13°17'33.74, E49°34'05.56)	0.53	0.20	1.19										0
		Angalanerana	(S13°05'13.78, E49°51'55.38)	1.80	0.50	2.13				1						1
	Intensive	Floribis	(S13°23'14.39, E50°01'04.02)	27	1.00	17.03										0
		Angalandrava	(S14°08'14.58, E50°07'28.50)	0.45	0.50	5.02										0
		Bemanevika	(S14°08'23.26, E50°07'41.51)	0.49	0.45	4.06										0
		Tsaratanana	(S14°05'30.27, E50°07'41.44)	0.42	0.30	0.20										0
		Biarafa	(S14°04'12.32, E50°07'10.57)	2.90	0.65	0.26								1		1
Natural Forest		Analamazava	(S13°15'23.70, E49°36'58.31)	216	1.05	-	10		4	1	1		1		1	6
		Analamanara	(S13°17'18.92, E49°50'21.52)	104	0.80	-		5		1		2			3	4
		Bemosy	(S13°14'16.12, E49°37'24.22)	584	0.80	-	5	2	2	1						4
		Bekaraoka	(S13°08.56.75, E49°42'21.40)	5424	1.00	-	4	9		3	1	3			2	6
		Antsahabe	(S13°16'51.47, E49°36'36.30)	265	1.00	-			3							1
		Bobankora	(S13°13'39.59, E49°45'19.24)	1416	0.70	-	5	3		2	2	1			2	6
		Misorolava	(S13°05'43.59, E49°54'30.74)	194	1.00	-		5		7	2	5				4
		Ampasira	(S13°04'45.36, E49°54'11.50)	278	1.00	-		5		3	3	3				4
		Angengo	(S13°02'36.25, E49°54'43.72)	263	0.90	-		5		2	4	3				4

We also provide the number of lemurs of each species observed during transect walks

[a] We did not observe *E. coronatus* in the Ankalotany plantation during formal transect walks; we observed them while we performed other fieldwork at the study sites but include them here for completeness

plantations), and the greater dwarf lemur, *C. major* ($N = 2$ plantations). We observed at least one species of lemur in 8 of the 17 sampled sites (47%; Table I). There was a significant difference in the presence of lemurs between plantation types (Fisher's exact test: $P = 0.006$), with lemurs (of any species) significantly more likely to be found in forest ecoplantations compared to other plantation types (Fisher's exact test post hoc comparisons following Holm–Bonferroni corrections; lemurs present in 6/6, 1/6, and 1/5 forest ecoplantations, nonforest ecoplantations, and intensive/nontraditional plantations, respectively; Table I). Transect length covaried with plantation area ($r_s = 0.556$, $N = 17$, $P = 0.021$). However, neither transect length nor plantation area differed significantly between 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 the greater incidence of lemurs in forest ecoplantations was not the result of biased survey effort in that plantation type.

We typically observed only one individual of each of the four nocturnal species at each site where present (except for Brondra; Table I). However, we observed 11 *Eulemur coronatus* individuals in one tree in Antingana, an ecoplantation located at the edge of a forest fragment. We also observed *E. coronatus* in the Ankalotany plantation, but not during formal transect walks. All individuals of all five species were foraging or resting when first sighted. We did not observe any lemurs using the vanilla plants themselves as a food source, or as a travel route.

We observed four lemur species that were present in vanilla plantations in the natural forest sites: *Cheirogaleus shethi*, *C. crossleyi*, *Eulemur coronatus*, *Microcebus tavaratra*. We also observed an additional four lemur species that were not present in any vanilla plantations: golden-crowned sifaka (*Propithecus tattersalli*), Sanford's lemur (*E. sanfordi*), Daraina sportive lemur (*Lepilemur milanoi*), and the amber mountain fork-marked lemur (*Phaner electromontis*). We observed *C. major* only in plantations. Mean transect lengths in forests were significantly longer than those in plantations (forest transect length mean ± SE = 916 ± 40.8 m, plantation mean ± SE = 521 ± 58.8 m; two-tailed *t*-test: $t = 4.57$, df = 24, $P < 0.001$), so it is possible that our observations of additional lemur species in forests arose from greater sampling effort.

Discussion

Our observations provide evidence of the presence of lemurs in vanilla plantations. Cheirogaleid lemurs have previously been observed in exotic tree and eucalyptus plantations (Ganzhorn 1987; Ramanamanjato and Ganzhorn 2001; Scobie *et al.* 2017). Given this adaptability to anthropogenically disturbed habitats, and their tolerance for shrub layer and understory habitat (Kappeler and Rasoloarison 2003), it is perhaps unsurprising that we found the four nocturnal cheirogaleid species (*Microcebus tavaratra*, *Cheirogaleus shethi*, *C. crossleyi*, and *C. major*) in vanilla plantations. Most of our lemur observations were in vanilla plantations close to or within forest fragments (forest ecoplantations), suggesting that lemurs use these plantations for dispersal or as travel corridors between forest fragments, or as extensions of forest habitat. However, we also observed one *C. major* individual in a heavily degraded and disturbed intensive/nontraditional vanilla plantation (Biarafa; Table I), suggesting that cheirogaleid lemurs can use even the most anthropogenic plantations.

To sustain permanent populations of these four lemur species, plantations need to contain food sources such as fruiting trees, flowers, nectar, and insects (or large quantities of gum) to meet their dietary requirements (Atsalis 1999; Génin *et al.* 2010; Lahann 2007). In addition, suitable sleeping trees with adequate insulation properties would be needed to shelter these species during bouts of daily and seasonal torpor (Schmid 2000; Schülke and Ostner 2007). Although we observed many trees in our study sites that can provide both feeding and sleeping opportunities for these species, further research is needed to determine whether permanent populations of cheirogaleid lemurs can be sustained in vanilla plantations.

It is perhaps surprising that we witnessed numerous *Eulemur coronatus* individuals at two vanilla plantation sites. These individuals were feeding on fruit trees that are known to constitute part of their diet (Wilson *et al.* 1989), suggesting that flora found in vanilla plantations provide feeding opportunities for native lemur populations. These fruits occurred within the plantation sites and were not part of the vanilla farmer's crop; thus the lemurs were not regarded as crop pests by the plantation owners. Further research is needed to fully determine vanilla plantation use by lemurs, and investigate how it varies between plantations with different management practices (Irwin *et al.* 2010; Schwitzer *et al.* 2011).

We observed an additional four lemur species in natural forest fragments that were not present in any vanilla plantation sites (*Propithecus tattersalli*, *Eulemur sanfordi*, *Lepilemur milanoi*, and *Phaner electromontis*). These additional species sightings may have arisen as a result of the greater sampling effort in forests compared to plantations. However, we feel that this explanation is unlikely, based on the biology of the different species observed. The apparent absence of *P. tattersalli*, *E. sanfordi*, and *L. milanoi* from vanilla plantations is likely because these species are much less tolerant of human-altered habitats, in comparison to the adaptable, more generalist cheirogaleids that we witnessed in vanilla plantations (Schwitzer *et al.* 2011; Vargas *et al.* 2002). Furthermore, *Phaner* are thought to require large trees with a high canopy for nocturnal travel and a diet preference of tree gum (Charles-Dominique and Petter 1980; Génin *et al.* 2010), suggesting they would avoid the understory habitats characteristic of the Sava region vanilla plantations where there are fewer potential feeding opportunities.

The remaining natural forest in the Sava region is diminished and highly fragmented. The reduced population sizes and geographical isolation that result from fragmentation may lead to higher genetic differentiation between lemur populations and lower levels of intrapopulation genetic variance for some species (Frankham *et al.* 2010; Holmes *et al.* 2013; Keller and Waller 2002). Although genetic diversity has been found to be high in some lemur species within our study area, such as *Propithecus tattersalli* (Quéméré *et al.* 2010), migration routes are needed for gene flow to continue (Quéméré *et al.* 2009). Small, isolated populations have a poor prognosis given the rate of deforestation in Madagascar (Schwitzer *et al.* 2014), especially given their susceptibility to deleterious stochastic events. Yet they could potentially be rescued if more means of gene flow (migration routes) between them were established. Our findings suggest that appropriately managed vanilla plantations, particularly those in close proximity to natural forest fragments, are suitable extensions of habitat for some lemur species, providing feeding opportunities and marginal travel corridors. Vanilla plantations therefore represent potentially valuable habitat extensions for some lemur species, through which gene flow can occur between forest fragments to improve population connectivity (Baden *et al.* 2014; Quéméré *et al.* 2009). This information is important for future assessments of lemur habitat use and population densities and distributions in areas of widespread vanilla cultivation, such as in the Sava region (AFB 2016).

Vanilla is a valuable crop, generating income for more than 200,000 people in Madagascar (AFB, 2016), most of whom live in the Sava region. Given its financial worth, vanilla has provided, and is likely to continue to provide, sufficient incentives for local people to establish, protect, and maintain plantations. Although natural forests are the best ecosystem for maintaining species biodiversity, our results suggest that forest ecoplantations have the highest conservation value of the three studied plantation types (in addition to their high financial worth), and are the most encouraging method of vanilla cultivation from both sustainable agricultural livelihood and lemur conservation perspectives. If vanilla plantations are established at the local (e.g., village or homestead) level then the payoff for exploiting forest via, for example, *tavy* (slash and burn agriculture), will likely be shifted such that the forest, and the vanilla it contains, is more valuable than converted land, thereby reducing the threat of habitat loss. Many of the vanilla farmers also employ guards to deter theft of vanilla plants and pods (S. Cotton *et al. unpubl. report*); this may inadvertently reduce the likelihood of hunting in plantations by people from elsewhere, protecting lemurs and other fauna. The existing network of vanilla plantations could therefore be further expanded to provide additional habitat for some species of lemurs, a winning combination in terms of both species conservation and sustainable agroforestry for local farming communities.

Acknowledgements We express our thanks to all the plantation owners and farmers who allowed us to survey their plantations. In addition, we thank the many individuals who helped us in countless ways, offered hospitality, and acted as guides and/or cooks during our time in the Sava region. We especially thank everyone at Fanamby's offices in Daraina and Vohemar for their support, assistance, and advice. We also thank MICET for assistance with permits, and colleagues for helpful discussion. Funding was provided by Conservation International through its Verde Ventures Investment program. Finally, we thank the editor and two anonymous reviewers whose constructive comments enabled us to improve the overall quality of this article.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

AFB. (2016). VANILLA – Madagascar: Speculative traders are blamed for the price hike – which fails to benefit producers. *Africa Research Bulletin*, 21295.

Atsalis, S. (1999). Diet of the brown mouse lemur (*Microcebus rufus*) in Ranomafana National Park, Madagascar. *International Journal of Primatology, 20*(2), 193–229. https://doi.org/10.1023/A:1020518419038.

Baden, A., Holmes, S. M., Johnson, S. E., Engberg, S. E., Louis, E. E., & Bradley, B. J. (2014). Species-level view of population structure an gene flow for a critically endangered primate (*Varecia variegate*). *Ecology and Evolution, 4*(13), 2675–2692. https://doi.org/10.1002/ece3.1119.

Blanco, M. B., & Godfrey, L. R. (2013). Does hibernation slow the "pace of life" in dwarf lemurs (*Cheirogaleus* spp.)? *International Journal of Primatology, 34*(1), 130–147. https://doi.org/10.1007/s10764-012-9653-9.

Bomgardner, M. M. (2016). The problem with vanilla. *Chemical and Engineering News, 94*, 38–42.

Chapman, C. A., Lawes, M. J., & Eeley, H. A. (2006). What hope for African primate diversity? *African Journal of Ecology, 44*(2), 116–133. https://doi.org/10.1111/j.1365-2028.2006.00636.x.

Charles-Dominique, P., & Petter, J. J. (1980). Ecology and social life of *Phaner furcifer*. In P. Charles-Dominique, H. M. Cooper, A. Hladik, C. M. Hladik, E. Pages, et al (Eds.), *Nocturnal Malagasy primates* (pp. 75–96). New York: Academic Press.

Clarke, M. R., Collins, D. A., & Zucker, E. L. (2002). Responses to deforestation in a group of mantled howlers (*Alouatta palliate*) in Costa Rica. *International Journal of Primatology, 23*(2), 365–381. https://doi.org/10.1023/A:1013839713223.

Cowlishaw, G. (1999). Predicting the pattern of decline of African primate diversity: An extinction debt from historical deforestation. *Conservation Biology, 13*(5), 1183–1193. https://doi.org/10.1046/j.1523-1739.1999.98433.x.

Estrada, A. (2006). Human and non-human primate co-existence in the Neotropics: A preliminary view of some agricultural practices as a compliment for primate conservation. *Ecological and Environmental Anthropology, 2*, 17–29.

Estrada, A., & Coates-Estrada, R. (1988). Tropical rain forest conversion and perspectives in the conservation of wild primates (*Alouatta* and *Ateles*) in Mexico. *American Journal of Primatology, 14*(4), 315–327. https://doi.org/10.1002/ajp.1350140402.

Flohre, A., Fischer, C., Aavik, T., Bengtsson, J., Berendse, F., Bommarco, R., Ceryngier, P., Clement, L. W., Dennis, C., Eggers, S., Emmerson, M., Geiger, F., Guerrero, I., Hawro, V., Inchausti, P., Liira, J., Morales, M. B., Oñate, J. J., Pärt, T., Weisser, W. W., Winqvist, C., Thies, C., & Tscharntke, T. (2011). Agricultural intensification and biodiversity partitioning in European landscapes comparing plants, carabids and birds. *Ecological Applications, 21*(5), 1772–1781. https://doi.org/10.1890/10-0645.1.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., et al (2005). Global consequences of land use. *Science, 309*(5734), 570–574. https://doi.org/10.1126/science.1111772.

Frankham, R., Ballou, J. D., & Briscoe, D. A. (2010). *Introduction to conservation genetics*. Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9780511809002.

Frasier, C. L., Lei, R., McLain, A. T., Taylor, J. M., Bailey, C. A., et al (2016). A new species of dwarf lemur (Cheirogaleidae: *Cheirogaleus medius* group) from the Ankarana and Andrafiamena-Andavakoera massifs, Madagascar. *Primate Conservation, 30*, 59–72.

Ganzhorn, J. U. (1987). A possible role of plantations for primate conservation in Madagascar. *American Journal of Primatology, 12*(2), 205–215. https://doi.org/10.1002/ajp.1350120208.

Génin, F., Masters, J. C., & Ganzhorn, J. U. (2010). Gummivory in cheirogaleids: Primitive retention or adaptability to hypervarible environments? In A. M. Burrows & L. T. Nash (Eds.), *The evolution of exudotivory in primates* (pp. 123–140). New York: Springer Science+Business Media. https://doi.org/10.1007/978-1-4419-6661-2_6.

Gérard, A., Ganzhorn, J. U., Kull, C. A., & Carriére, S. M. (2015). Possible roles of introduced plants for native vertebrate conservation: The case of Madagascar. *Restoration Ecology, 23*(6), 768–775. https://doi.org/10.1111/rec.12246.

Gibbs, H. K., Ruesch, A. S., Achard, F., Clayton, M. K., Holmgren, P., *et al.* (2010). Tropical forests were the primary sources of agricultural land in the 1980s and 1990s. *Proceedings of the National Academy of Sciences of the USA*, *107*, 16732–16737.

Godfray, H. C. J., Beddington, J. R., Crute, I. R., Haddad, L., Lawrence, D., Muir, J. F., Pretty, J., Robinson, S., Thomas, S. M., & Toulmin, C. (2010). Food security: The challenge of feeding 9 billion people. *Science, 327*(5967), 812–818. https://doi.org/10.1126/science.1185383.

Goldthorpe, C. C. (1988). A definition and typology of plantation agriculture. *Singapore Journal of Tropical Geography, 8*, 26–43.

Hending, D., Andrianiaina, A., Rakotomalala, Z., & Cotton, S. (2017). Range extension and behavioural observations of the recently described Sheth's dwarf lemur (*Cheirogaleus shethi*). *Folia Primatologica, 88*(5), 401–408. https://doi.org/10.1159/000481531.

Holmes, S. M., Baden, A. L., Brenneman, R. A., Engberg, S. E., Louis, E. E., & Johnson, S. E. (2013). Patch size and isolation influence genetic patterns in black-and-white ruffed lemur (*Varecia variegata*) populations. *Conservation Genetics, 14*(3), 615–624. https://doi.org/10.1007/s10592-013-0455-1.

Irwin, M. T., Wright, P. C., Birkinshaw, C., Fisher, B. L., Gardner, C. J., Glos, J., Goodman, S. M., Loiselle, P., Rabeson, P., Raharison, J. L., Raherilalao, M. J., Rakotondravony, D., Raselimanana, A., Ratsimbazafy, J., Sparks, J. S., Wilmé, L., & Ganzhorn, J. U. (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation, 143*(10), 2351–2362. https://doi.org/10.1016/j.biocon.2010.01.023.

Isabiryse-Basuta, G. M., & Lwanga, J. S. (2008). Primate populations and their interaction with changing habitats. *International Journal of Primatology, 29*(1), 35–48. https://doi.org/10.1007/s10764-008-9239-8.

Johns, A. D. (1986). Effects of selective logging on the behavioural ecology of west Malaysian primates. *Ecology, 67*(3), 684–694. https://doi.org/10.2307/1937692.

Johns, A. D., & Skorupa, J. P. (1987). Responses of rain-forest primates to habitat disturbance: A review. *International Journal of Primatology, 8*(2), 157–191. https://doi.org/10.1007/BF02735162.

Kappeler, P. M., & Rasoloarison, R. M. (2003). *Microcebus*, mouse lemurs, Tsidy. In S. M. Goodman & J. P. Benstead (Eds.), *The natural history of Madagascar* (pp. 1310–1315). Chicago: University of Chicago Press.

Keck, A., Sharma, N. P., & Feder, G. (1994). *Population growth, shifting cultivation, and unsustainable agricultural development: A case study in Madagascar*. Washington, DC: The World Bank.

Keller, L. F., & Waller, D. M. (2002). Inbreeding effects in wild populations. *Trends in Ecology and Evolution, 17*(5), 230–241. https://doi.org/10.1016/S0169-5347(02)02489-8.

Kirby, K. J., Petersen, G. F., Spencer, J. W., & Walker, G. J. (1984). *Inventories of ancient semi-natural woodland*. Nature Conservancy Council: Focus on Nature Conservation.

Lahann, P. (2007). Feeding ecology and seed dispersal of sympatric cheirogaleid lemurs (*Microcebus murinus*, *Cheirogaleus medius*, *Cheirogaleus major*) in the littoral rainforest of south-east Madagascar. *Journal of Zoology, 271*(1), 88–98. https://doi.org/10.1111/j.1469-7998.2006.00222.x.

Lambin, E. F., & Meyfroidt, P. (2011). Global land use change, economic globalization, and the looming land scarcity. *Proceedings of the National Academy of Sciences of the USA*, *108*, 3465–3472.

Lehman, S. M., Radespiel, U., & Zimmermann, E. (2016). Conservation biology of the cheirogaleidae: Future research direction. In S. M. Lehman, U. Radepsiel, & E. Zimmermann (Eds.), *The dwarf and mouse lemurs of Madagascar: Biology, behaviour and conservation biogeography of the Cheirogaleidae* (pp. 520–540). Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9781139871822.028.

Louis, E. E., Engberg, S. E., McGuire, S. M., McCormick, M. J., Randriamampionona, R., et al (2008). Revision of the mouse lemurs, *Microcebus* (primates, Lemuriformes), of northern and northwestern Madagascar with descriptions of two new species at Montagne d'Ambre National Park and Antafondro classified Forest. *Primate Conservation, 23*(1), 19–38. https://doi.org/10.1896/052.023.0103.

Lubinsky, P., Van Dam, M., & Van Dam, A. (2006). Pollination of vanilla and evolution in Orchidaceae. *Lindleyana, 75*, 926–929.

Mittermeier, R. A., & Cheney, D. L. (1987). Conservation of primates and their habitats. In B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, & T. T. Struhsaker (Eds.), *Primate societies* (pp. 477–490). Chicago: University of Chicago Press.

Mittermeier, R. A., Louis, E. E., Richardson, M., Schwitzer, C., Lingrand, O., et al (2010). *Lemurs of Madagascar* (3rd ed.). Arlington, VA: Conservation International.

Perfecto, I., & Vandermeer, J. (2008). Biodiversity conservation in tropical agroecosystems: A new conservation paradigm. *Annals of the New York Academy of Sciences, 1134*(1), 173–200. https://doi.org/10.1196/annals.1439.011.

Petter, J. J., Albignac, R., & Rumpler, Y. (1977). Mammiferes lemuriens (Primates prosimiens). Faune de Madagascar No. 44. Paris: ORSTOM-CNRS.

Quéméré, E., Crouau-Roy, B., Rabarivola, C., Louis, E. E., & Chikhi, L. (2010). Landscape genetics of an endangered lemur (*Propithecus tattersalli*) within its entire fragmented range. *Molecular Ecology, 19*(8), 1606–1621. https://doi.org/10.1111/j.1365-294X.2010.04581.x.

Rakotoniaina, J. H., Kappeler, P. M., Ravoniarimbinina, P., Pechouskova, E., Hämäläinen, A. M., *et al.* (2016). Does habitat disturbance effect stress, body condition and and parasitism in two sympatric lemurs? *Conservation Physiology*, doi: cow034.

Ramanamanjato, J. B., & Ganzhorn, J. U. (2001). Effects of forest fragmentation, introduced *Rattus rattus* and the role of exotic tree plantations and secondary vegetation for the conservation of an endemic rodent and a small lemur in littoral forests of southeastern Madagascar. *Animal Conservation, 4*(2), 175–183. https://doi.org/10.1017/S1367943001001202.

Schäffler, L., & Kappeler, P. M. (2014). Distribution and abundance of three cheirogaleid species in Menabe central, western Madagascar. *Lemur News, 18*, 38–43.

Schmid, J. (2000). Daily torpor in the gray mouse lemur (*Microcebus murinus*) in Madagascar: Energetic consequences and biological significance. *Oecologia, 123*(2), 175–183. https://doi.org/10.1007/s004420051003.

Schülke, O., & Ostner, J. (2007). Physiological ecology of cheirogaleid primates: Variation in hibernation and torpor. *ActaEthologica, 10*, 13–21.

Schwitzer, N., Randriatahina, G. H., Kaumanns, W., Hoffmeister, D., & Schwitzer, C. (2007). Habitat utilization of blue-eyed black lemurs, *Eulemur flavifrons* (gray, 1867) in primary and altered forest fragments. *Primate Conservation, 22*(1), 79–87. https://doi.org/10.1896/052.022.0106.

Schwitzer, C., Glatt, L., Nekaris, K. A. I., & Ganzhorn, J. U. (2011). Responses of animals to habitat alteration: An overview focussing on primates. *Endangered Species Research, 14*(1), 31–38. https://doi.org/10.3354/esr00334.

Schwitzer, C., Mittermeier, R. A., Johnson, S. E., Donati, G., Irwin, M., Peacock, H., Ratsimbazafy, J., Razafindramanana, J., Louis, E. E., Chikhi, L., Colquhoun, I. C., Tinsman, J., Dolch, R., LaFleur, M., Nash, S., Patel, E., Randrianambinina, B., Rasolofoharivelo, T., & Wright, P. C. (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science, 343*(6173), 842–843. https://doi.org/10.1126/science.1245783.

Scobie, K., Schwitzer, C., & Holderied, M. (2017). Observations of *Avahi meridionalis* in *Eucalyptus* plantations. *Lemur News, 20*, 9.

Setash, C. M., Zohdy, S., Gerber, B. D., & Karanewsky, C. J. (2017). A biogeographical perspective on the variation in mouse lemur density throughout Madagascar. *Mammal Review, 47*(3), 212–229. https://doi.org/10.1111/mam.12093.

Simmen, B., Bayart, F., Marez, A., & Hladik, A. (2007). Diet, nutritional ecology, and birth season of *Eulemur macaco* in an anthropogenic forest in Madagascar. *International Journal of Primatology, 28*(6), 1253–1266. https://doi.org/10.1007/s10764-007-9217-6.

Srivastava, A. (2006). Conservation of threatened primates of northeast India. *Primate Conservation, 20*, 107–113. https://doi.org/10.1896/0898-6207.20.1.107.

Vargas, A., Jiminez, I., Palomares, F., & Palacios, M. J. (2002). Distribution, status, and conservation needs of the golden-crowned sifaka (*Propithecus tattersalli*). *Biological Conservation, 108*(3), 325–334. https://doi.org/10.1016/S0006-3207(02)00117-9.

Vorontsova, M. S., Besnard, G., Forest, F., Malakasi, P., Moat, J., Clayton, W. D., Ficinski, P., Savva, G. M., Nanjarisoa, O. P., Razanatsoa, J., Randriatsara, F. O., Kimeu, J. M., Luke, W. R. Q., Kayombo, C., & Linder, H. P. (2016). Madagascar's grasses and grasslands: Anthropogenic or natural? *Proceedings of the Royal Society B: Biological Sciences, 283*(1823), 20152262. https://doi.org/10.1098/rspb.2015.2262.

Wilson, J. M., Stewart, P. D., Ramangason, G. S., Denning, A. M., & Hutchings, M. S. (1989). Ecology and conservation of the crowned lemur, *Lemur coronatus*, at Ankarana, N. Madagascar. *Folia Primatologica, 52*(1-2), 1–26. https://doi.org/10.1159/000156379.