Habitat Separation of Sympatric *Microcebus* spp. in the Dry Spiny Forest of South-Eastern Madagascar

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Key Words

Competition · Habitat selection · Coexistence · Community ecology · Speciation · Primates · Lemurs · *Microcebus*

Abstract

We investigated whether or not habitat structure contributes to the separation of two sister species of lemurs and their hybrids. For this, we studied *Microcebus murinus* and *M. griseorufus* along a continuous vegetation gradient where populations of the two species occur in sympatry or in allopatry. In allopatry, the two species are generalists without any sign of microhabitat selectivity. In sympatry, both species differed significantly and discriminated against certain habitat structures: *M. murinus* was found in microhabitats with larger trees than average while *M. griseorufus* utilized microhabitats with smaller trees. Hybrids between the two species did not show any significant discrimination for or against microhabitat structure and did not differ in their habitat utilization from either parent species. Both species can go into torpor and hibernation. *M. griseorufus* is seen more frequently during the cool dry season than *M. murinus*. We assume that *M. murinus* goes into extended torpor or hibernation more frequently than *M. griseorufus*. We interpret the different occurrence of large-sized trees in microhabitats of *M. murinus* as a prerequisite for *M. murinus* to be able to spend extended periods of time in tree holes that are isolated and allow hibernation at reduced temperature levels.

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Introduction

Understanding the mechanisms that lead to distinct species distributions and allow ecologically similar species to coexist are fundamental issues in community ecology. According to classical ideas, competition over limited resources is avoided by interspecific differences in habitat utilization, diet or activity patterns [Schoener,

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1974]. In addition, species can use the same type of resource if they differ in body mass by a factor of 2 or in linear morphological measurements by a factor of 1.4 [Hutchinson, 1959]. These mechanisms seem to operate in and to structure most primate communities [Schreier et al., 2009]. However, some sympatric species of mouse lemurs (*Microcebus* spp.) from Madagascar are of special interest as they seem to violate these assumptions at least in some communities where similarly sized species coexist without obvious niche separation. In western Madagascar, *Microcebus murinus* is a very widespread species, ranging from littoral humid forest in the south-east to the north-west [Mittermeier et al., 2008]. Its range overlaps with *Microcebus ravelobensis* in the dry deciduous forest of north-western Madagascar, followed by *M. myoxinus* further south, then with *M. berthae* in a small area of the Menabe (western, central Madagascar), and finally with *M. griseorufus* in the south [Mittermeier et al., 2010].

These congeneric mouse lemur species differ in habitat utilization [Rendigs et al., 2003; Schwab and Ganzhorn, 2004; Dammhahn and Kappeler, 2008a, b; Génin, 2008; Rakotondravony and Radespiel, 2009; Rakotondranary et al., 2011a], food composition [Radespiel et al., 2006; Dammhahn and Kappeler, 2008a, b, 2010; Rakotondranary et al., 2011b; Thorén et al., 2011b] and activity patterns [Thorén et al., 2011b]. Different habitat utilization might be due to different competitive potential of two sympatric species, such as in Ampijoroa where *M. murinus* outcompetes *M. ravelobensis* [Thorén et al., 2011a].

While these phenomena are consistent with the predictions of classical community ecology, the causal relationships between the distribution of the species and these environmental conditions remain enigmatic. For example, *M. murinus* is found in habitats ranging from highly disturbed habitats, evergreen humid forest to dry spiny forest with significant changes in life history traits [Ramanamanjato and Ganzhorn, 2001; Lahann et al., 2006], and with populations being structured and patchily distributed within a seemingly uniform type of forest [Radespiel et al., 2001; Fredsted et al., 2004].

These phenomena indicate that observed differences in habitat utilization of different species or the same species at different sites could be the consequence of competitive exclusion on a very small scale [Schwab and Ganzhorn, 2004; Dammhahn and Kappeler, 2008a; Thorén et al., 2011a], or adaptations to limiting factors, such as tree holes used for sleeping sites or well-insulated places for hibernation [Ganzhorn and Schmid, 1998; Schmid, 1998; Radespiel et al., 2003].

We used *M. murinus*, *M. griseorufus* and their hybrids in the dry spiny forest at Andohahela National Park to investigate the role of habitat structure in the separation of sympatric congeneric mouse lemurs. Along the vegetation gradient of Andohahela National Park, *M. murinus* and *M. griseorufus* show clear associations with specific habitat types: *M. griseorufus* occurs in the dryer parts of the habitats while *M. murinus* is found in the more mesic sites [Rakotondranary et al., 2011a]. This matches the situation found elsewhere [Yoder et al., 2002; Génin, 2008]. However, in Andohahela the two species also occur sympatrically and hybridize at the ecotone between dry spiny and gallery forests [Gligor et al., 2009; Hapke et al., 2011; Rakotondranary et al., 2011a]. These seemingly clear habitat associations of the two species indicate that habitat structure could be a niche dimension for species separation. If habitat structure contributes to species separation, we predict that the association of the two species with specific habitat structures differs between communities where the two species are sympatric versus communities where they are allopatric.

Fig. 1. Study sites in and between parcels 1 and 2 of Andohahela National Park (modified from Rakotondrany et al. [2011a]).

In the paper, we address the following questions:

- (1) What are the characteristics of available habitats at sites where the species live in allopatry and at sites where they live sympatrically?
- (2) Are there differences in microhabitat structures used by the species and their hybrids in sympatry?
- (3) Are there indications for changes in habitat selectivity by *M. murinus* and *M. griseorufus* in sympatry versus allopatry, indicating character displacement?
- (4) How do hybrids between *M. murinus* and *M. griseorufus* use and select microhabitats?

Methods

Study Sites

The study was conducted from September 2006 to June 2009 in parcel No. 2 and between parcels No. 1 and 2 of Andohahela National Park (fig. 1, table 1) [Rakotondrany et al., 2011a]. The vegetation of the study region is classified as dry spiny forest [Moat and Smith, 2007] and characterized by a steep rainfall gradient from 400 mm in the west to 2,400 mm/year in the east with pronounced vegetation differences on the scale of a few kilometres [Goodman, 1999; Rakotondrany et al., 2011a].

Table 1. Geographical coordinates of transects in and around Andohahela National Park (from Rakoton-dranary et al. [2011a])

Site	Transect name	Starting point			End point		
		southern latitude	eastern longitude	altitude m	southern latitude	eastern longitude	altitude m
Hazofotsy	T01	24°50'18.99"	046°31'37.74"	88	24°50'32.17"	046°31'46.06"	96
Ambatoabo	T04	24°49'14.20"	046°40'05.38"	154	24°49'07.45"	046°39'49.33"	142
Ankoba	T07	24°47'59.33"	046°41'22.76"	209	24°48'13.24"	046°41'21.52"	240
Ankoba	T09	24°47'42.67"	046°41'17.72"	191	24°47'35.70"	046°41'31.60"	193
Mangatsiaka	T15	24°58'00.79"	046°33'15.44"	82	24°57'50.49"	046°33'28.08"	104
Mangatsiaka	T17	24°58'06.25"	046°33'45.50"	74	24°58'06.46"	046°34'01.71"	76
Mangatsiaka	T18	24°58'00.09"	046°33'12.47"	71	24°57'44.86"	046°33'12.34"	88

We selected 1 site where *M. griseorufus* is the only *Microcebus* species (Hazofotsy, 1 transect: T01), 2 sites where *M. murinus* live in allopatry (Ambatoabo, 1 transect: T04; Ankoba, 2 transects: T07, T09) and 1 site where *M. griseorufus* and *M. murinus* occur in sympatry (Mangatsiaka, 3 transects: T15, T17, T18 [Rakoton-dranary et al., 2011a]). Thus, 7 transects were established, each composed of 20 trapping points, spaced at 25-metre intervals. At each trapping point, we installed 2 Sherman traps ($7.7 \times 7.7 \times 23$ cm) in a tree. Traps were baited with bananas for 4 successive nights per transect. At each transect, we performed one capture session at the end of the wet season after the birth season (April, May, June) and one in the dry season (September, October, November), thus accumulating 7 transects $\times$ 40 traps $\times$ 2 trapping sessions $\times$ 4 nights = 2,240 trap nights on the transects. The transects and the vegetation are described in detail by Rakoton-dranary et al. [2011a] and Andriaharimalala et al. [2011]. Since low capture rates in Ambatoabo and Ankoba prohibited statistical analyses, and since the vegetation of these sites was rather similar [Andriaharimalala et al., 2011], these two sites were combined for the present analysis. Transects were established a few metres off the trail to avoid edge effects and a situation in which the trail would have intersected the vegetation description described below. The placement of traps was not always possible at the exact site of the 25-metre interval. In that case, the trap was placed in the nearest structure that supported a trap in a functional state. At Mangatsiaka where mouse lemur species live in sympatry, we added a rectangular trapping grid with 200 trapping stations (10×20 stations spaced at 25-metre intervals) to increase sample size for possible hybrids and improve the spatial resolution of the distribution of hybrids and the parent species. In the grid we performed two trapping sessions during the dry and one in the wet season. The coordinates of the south-western corner of the trapping grid were 24°57'52.27" S, 46°33'17.25" E.

Species Identification

M. murinus and *M. griseorufus* are sister species [Yoder and Yang, 2004] that hybridize [Gligor et al., 2009]. In the field, animals were classified based on morphological criteria [Rakoton-dranary et al., 2011a]. Identifications were verified on the bases of mitochondrial DNA and microsatellites [Hapke et al., 2011]. Capture and genetic verification of species identification were necessary to develop morphological criteria that will guarantee correct assignment of morphotypes to species and to identify hybrids.

Vegetation Descriptions

The point-centred quarter method was used for microhabitat descriptions at each trapping point. For this, each sample point represents the centre of four compass directions that divide the sampling plot into four quarters. In each quarter, the distance from the centre of the nearest

Table 2. Characteristics of microhabitats at the different study sites and *Microcebus* spp. occurring at the site

	Hazofotsy (Mg)	Mangatsiaka (Mg, Mm, Mg × Mm)	Ambatoabo and Ankoba (Mm)	χ^2
Number	20	260	60	
Distance of large trees ≥10 cm DBH	5.5 ^a 2.7/4.0	3.3 ^b 2.6/4.2	3.1 ^b 2.4/3.9	23.14***
DBH of large trees ≥10 cm DBH	16.8 ^a 15.1/20.6	14.5 ^b 13.0/16.4	16.7 ^a 14.3/21.2	26.15***
Distance of small trees 5–9.9 cm DBH	5.7 ^a 4.4/7.0	2.6 ^b 2.2/3.3	2.5 ^b 2.0/2.9	45.73***
DBH of small trees 5–9.9 cm DBH	8.2 ^a 7.7/8.7	6.8 ^b 6.5/7.5	7.1 ^b 6.5/7.7	42.22***

Mg = *M. griseorufus*; Mm = *M. murinus*; Mg × Mm = hybrids between the two species. Values are medians and quartiles. Number = Number of microhabitat descriptions; χ^2 values indicate overall differences between sites according to Kruskal-Wallis analysis of variance; *** $p < 0.001$. Different superscript letters indicate significant differences between sites with $p < 0.05$ according to pairwise Mann-Whitney U tests after Bonferroni correction.

plant to the sampling point is measured ($d_1 - d_4$) [Ganzhorn et al., 2011]. We measured two size classes of trees: trees ≥10 cm DBH (diameter at breast height) and trees of 5–9.9 cm DBH. Thus, 4 trees of each size class were recorded per sample point. Density of trees per hectare can be calculated as: density (individuals/ha) = $10,000/(d + 0.5 \times \text{DBH})^2$ where d equals the mean distance of the trees to the centre of the sampling point and DBH is the mean DBH. However, ratios of this kind are not isometric due to the quadratic denominator. Therefore we do not consider these density calculations any further.

Microhabitat Utilization

None of the measures used to characterize the vegetation structure of microhabitats where animals were caught differed between the seasons. Therefore we did not consider the seasons separately in subsequent analyses. The vegetation characteristics of microhabitats where animals were caught were compared between sites within the two mouse lemur species and between species and their hybrids at Mangatsiaka where the two parent species and their hybrids occur in sympatry.

Selectivity for specific habitat structures was calculated as the value of microhabitats used by *Microcebus* spp. divided by the median of the variable in the representative sample of microhabitat descriptions for each site. The medians used are listed in table 2. A value of 1 indicates no selectivity, e.g. if large trees in a microhabitat used by *Microcebus* in Hazofotsy had an average DBH of 16.8 cm, we divided this value by the median of the DBH of the representative sample of microhabitats for Hazofotsy (=16.8 cm). The resulting selectivity index would be '1', indicating no selectivity. If the large trees of the microhabitat used by *Microcebus* had an average DBH of 25.0 cm, the selectivity index would be $25.0/16.8 = 1.49$. This would indicate that the animal had been caught in a microhabitat with larger DBH than generally available. The method follows that used by Andrianasolo et al. [2006] except that we used the median instead of the mean because our measurements of the representative samples deviated from normality.

Table 3. Occurrence of *Microcebus* spp. and vegetation characteristics of microhabitats used by *Microcebus* spp. where the taxa occurred in sympatry or in allopatry

	Hazofotsy (allopatric) <i>M. griseorufus</i>	Mangatsiaka (sympatric)			Ambatoabo and Ankoba (allopatric) <i>M. murinus</i>
		<i>M. griseorufus</i>	<i>M. murinus</i>	hybrids	
Number	9	21	65	28	6
Distance of large trees ≥ 10 cm DBH	5.7 ± 1.9	3.4 ± 1.2	3.8 ± 1.7	3.5 ± 1.3	3.3 ± 0.7
DBH of large trees ≥ 10 cm DBH	16.3 ± 2.8	13.5 ± 1.8^a	16.5 ± 4.8^b	$16.0 \pm 4.2^{a,b}$	18.7 ± 9.2
Distance of small trees 5–9.9 cm DBH	5.7 ± 2.1	2.4 ± 0.8	2.9 ± 1.3	3.0 ± 1.2	2.8 ± 0.4
DBH of small trees 5–9.9 cm DBH	8.5 ± 0.6	6.8 ± 0.5	6.9 ± 0.6	6.9 ± 0.8	7.5 ± 0.5

Values are means and standard deviations. Number = Number of microhabitats where *Microcebus* were caught. Figures with superscript letters indicate statistically significant differences between taxa in sympatry according to analysis of variance; different superscripts indicate differences between taxa with $p < 0.05$ according to Scheffé's post-hoc test. Statistical tests were only performed for the differences between taxa in sympatry.

Statistical Analyses

Most vegetation measurements deviated significantly from normality in the representative samples. Therefore we used non-parametric Kruskal-Wallis analysis of variance and Mann-Whitney U tests for statistical comparisons of the representative samples. Significance levels for multiple comparisons were Bonferroni corrected. All but one variable of the microhabitats used by *Microcebus* did not deviate from normality. We applied parametric analysis of variance (ANOVA) and Scheffé's post-hoc test to compare microhabitats used by *Microcebus* spp. Statistical significance of selectivity was tested with the 1-sample t test for deviations from a value of '1' (a value of 1 would indicate no selectivity). Each trapping station entered the analysis only once even when more than 1 animal had been caught at this station. We carried out the statistical tests using SPSS [1999]. Results were considered relevant at significance levels of $p \leq 0.05$.

Results

Vegetation Structure of Representative Samples

All measures of vegetation structures differed significantly between sites (all $p < 0.001$; table 2). The forest of Hazofotsy differs in all vegetation characteristics from the forests of Mangatsiaka. The distances of trees to the central point of the microhabitat of the forest of Ambatoabo-Ankoba were similar to those of the forest of Mangatsiaka but lower than in Hazofotsy, indicating higher tree densities. Large trees of Ambatoabo-Ankoba had similar DBH than in Hazofotsy. Trees at these two sites had larger DBH than trees in Mangatsiaka.

Vegetation Characteristics and Selectivity of Microhabitats by *Microcebus* spp.

Large trees had lower DBH in microhabitats utilized by *M. griseorufus* (13.5 ± 1.8 cm) than in microhabitats used by *M. murinus* (16.5 ± 4.8 cm; ANOVA: $F = 3.91$, $p = 0.02$; table 3). Hybrids between the two species used microhabitats with large trees of 16.0 ± 4.2 cm. They were similar in size as in microhabitats used by *M. murinus* and larger than in microhabitats frequented by *M. griseorufus*, but the micro-

Table 4. Selectivity of *Microcebus* spp. for microhabitat structures

	Hazofotsy <i>M. griseorufus</i>	Mangatsiaka			Ambatoabo and Ankoba <i>M. murinus</i>
		<i>M. griseorufus</i>	<i>M. murinus</i>	hybrids	
N	9	21	65	28	6
Distance of large trees ≥ 10 cm DBH	1.04 ± 0.35	1.02 ± 0.37	<i>1.16 ± 0.51</i>	1.05 ± 0.40	1.06 ± 0.23
DBH of large trees ≥ 10 cm DBH	0.97 ± 0.17	<i>0.93 ± 0.12</i>	<i>1.14 ± 0.33</i>	1.10 ± 0.29	1.12 ± 0.55
Distance of small trees 5–9.9 cm DBH	1.00 ± 0.36	0.94 ± 0.30	<i>1.13 ± 0.50</i>	1.15 ± 0.47	1.13 ± 0.17
DBH of small trees 5–9.9 cm DBH	1.03 ± 0.07	1.00 ± 0.07	1.01 ± 0.09	1.02 ± 0.12	1.06 ± 0.07

Significant deviations from 1 (= no selectivity) with $p < 0.05$ (based on 1-sample t test) are in italics.

habitats of the hybrids did not differ from those utilized by either one of the parent species.

Transformation of the raw data into selectivity indices revealed that in allopatry neither *M. griseorufus* nor *M. murinus* used microhabitats that differed in their structures from the microhabitats that were available at Hazofotsy and Ambatoabo-Ankoba, respectively. However, both species showed significant deviations from the representative samples where they occurred in sympatry at Mangatsiaka. At Mangatsiaka, *M. griseorufus* were caught in microhabitats where large trees had lower diameters than the trees from the representative sample (1-sample t test for deviations from 1: $t = 2.58$, $p = 0.018$; table 4). *M. murinus* was found in microhabitats where trees had larger DBH than in the representative samples ($t = 3.33$, $p = 0.001$). The distances of large and small trees to the central point in microhabitats of *M. murinus* were larger than in the representative samples (large trees: $t = 2.56$, $p = 0.013$; small trees: $t = 2.17$, $p = 0.034$). Hybrids did not show any selectivity in relation to habitat structures.

If the microhabitats were weighted by the number of captures at the given microhabitat, significance levels were reinforced and the results were confirmed. Most notably, the hybrids did not show any sign of selectivity despite increased sample size. This documents their intermediate position between the two parent species.

Discussion

If resources are limited and communities approach equilibrium, species with similar ecological requirements can coexist only if they differ in at least 1 niche dimension [Gause, 1934]. Species that use the same resource in a similar way while they are in allopatry have to modify their modes of resource exploitation when they come into contact to be able to coexist. This results in behavioural, physiological or morphological divergence, termed character displacement. This has been nicely described for Darwin finches on very short time scales [Grant and Grant, 2006]. Possible competition seems to be aggravated between congeneric species and should be most pronounced in sister species because they share more genes with each other than they do with any other species [Simberloff and Dayan, 1991; Houlé, 1997].

The lemurs of Madagascar may be of special interest in this respect as they have undergone a remarkable radiation resulting in many species with much smaller distributions than other primate radiations [Martin, 1995; Mittermeier et al., 2010]. This raises two questions: first, what the environmental conditions were that might have favoured the evolution of distinct species on a very small scale; second, which mechanisms allow species to maintain their identity and how they share limited resources where they are in contact. The first question has been addressed in a number of studies [Richard and Dewar, 1991; Wilmé et al., 2006; Pearson and Raxworthy, 2009; Vences et al., 2009]. Recently, the second question has been reviewed for primates in general by Schreier et al. [2009]. In their analysis, apart from dietary differences, interspecific differences in habitat utilization are major components for the separation of possible competitors in sympatry. This has been described for congeneric and sympatric species especially in Madagascar (*Eulemur* [Freed, 1996; Overdorff, 1996], *Haplemur* [Tan, 1999], *Cheirogaleus* [Lahann, 2008], *Microcebus* [Rakotondravony and Radespiel, 2009]), but also in South America, Asia and Africa [reviewed by Fleagle et al., 1999; Schreier et al., 2009]. Different ways of habitat utilization have been linked to specific modes of locomotion, such as different adaptations for a terrestrial versus arboreal lifestyle [Rodman, 1979], or the utilization of vertical versus horizontal structures [Ganzhorn, 1989; Demes et al., 1995; Warren and Crompton, 1998]. Other benefits of utilizing different or specific habitat structures have been linked to sleeping sites [Heymann, 1995; Radespiel et al., 2003].

In the case of mouse lemurs, species separation and coexistence of similar species has been linked to different habitat components [Radespiel et al., 2003; Rendigs et al., 2003; Rakotondravony and Radespiel, 2009; Thorén et al., 2011b]. The evolutionary benefit of one type of habitat utilization over the other remains enigmatic. In case of sister species, such as *M. murinus* and *M. griseorufus*, competition is expected to be even stronger due to their phylogenetic similarity [Houlé, 1997]. This is supported by the information available so far that suggests a strict separation of the two species based on habitat types, with *M. griseorufus* occurring in dry spiny forest and *M. murinus* restricted to gallery and more mesic forests [Yoder et al., 2002; Rasozanabary, 2004; Génin, 2008; Gligor et al., 2009; Rakotondranary et al., 2011a]. Yet, the reason for the clear separation is unclear. *M. murinus* occurs in a wide range of habitats with considerable phenotypic plasticity [Lahann et al., 2006]. Similarly, *M. griseorufus* occupies a wide variety of habitat types in regions where it is the only *Microcebus* species present [Rakotondranary et al., 2010]. In allopatry, neither species shows any selectivity for specific habitat structures [Andrianasolo et al., 2006; Rakotondranary et al., 2010]. In the present study, this flexibility is reflected by the lack of habitat selection where the two species occur allopatrically. However, at sites where the two species meet, they both deviate in their utilization of habitat structures from what is available in the habitat. In sympatry, microhabitats used by *M. murinus*, *M. griseorufus* and hybrids differ in the diameter of large trees. *M. griseorufus* occur in forest patches with smaller diameters of large trees. In sympatry, the diameters of trees used by *M. murinus* and hybrids are larger compared to those used by *M. griseorufus*. Large trees might provide more holes for shelter than smaller trees and may be important for nest sites that, in the case of *Microcebus*, allow the species to enter prolonged phases of reduced energy metabolism [Radespiel et al., 2003; Andrianasolo et al., 2006; Kobbe and Dausmann, 2009; Schmid and Ganzhorn, 2009; Kobbe et al., 2011]. Visual night surveys at the beginning of the dry season in the Mikea for-

est at a site where both species occur sympatrically left the impression that *M. murinus* had accumulated body fat and was not encountered during transect walks while fat accumulation was not obvious in *M. griseorufus* and the latter was still seen on the walks [Ganzhorn and Randriamanalina, 2004]. After some intensive rains, rather fat *M. murinus* were seen on the transects again but had disappeared again a few days later. We interpret this as *M. murinus* entering torpid states more frequently than *M. griseorufus*. This would match the findings from Ampijoroa and Kirindy/CFPF where *M. murinus* enters torpid states while the sympatric *M. ravelobensis* and *M. berthae* do not or do so less frequently [Schmid et al., 2000; Radespiel et al., 2003; Dammhahn and Kappeler, 2008a, b, 2010]. Access to tree holes in large trees would facilitate torpid states or reduced activity and could explain why *M. murinus* is not encountered frequently during transect walks at that time of the year.

In contrast to the parent species, hybrids between *M. murinus* and *M. griseorufus* have broad habitat tolerances and do not show any deviation from the structures of the representative samples in the dry spiny forest where they are sympatric with both parent species. These differences between the parent species, where they occur in sympatry, and the lack of habitat selectivity in hybrids from the same site indicate that there are species-specific advantages associated with the utilization of specific habitat structures, though the evolutionary benefits are not understood. These subtle advantages could either have led to speciation at ecotones [Richard and Dewar, 1991; Wilmé et al., 2006; Pearson and Raxworthy, 2008; Vences et al., 2009] or they maintain species identities at secondary contact zones where species meet again after they have evolved distinct adaptations in allopatry.

These differences in habitat utilization supplement the separation of *Microcebus* species along the classical niche dimensions of food and activity [Schoener, 1974; Dammhahn and Kappeler, 2008a, b, 2010; Rakotondravony and Radespiel, 2009; Rakotondranary et al., 2011b]. As a next step, we ought to search for the evolutionary advantage of those specific habitat components for species that are very similar otherwise.

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