

Extinction and ecological retreat in a community of primates

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The lemurs of Madagascar represent a prodigious adaptive radiation. At least 17 species ranging from 11 to 160 kg have become extinct during the past 2000 years. The effect of this loss on contemporary lemurs is unknown. The concept of competitive release favours the expansion of living species into vacant niches. Alternatively, factors that triggered the extinction of some species could have also reduced community-wide niche breadth. Here, we use radiocarbon and stable isotope data to examine temporal shifts in the niches of extant lemur species following the extinction of eight large-bodied species. We focus on southwestern Madagascar and report profound isotopic shifts, both from the time when now-extinct lemurs abounded and from the time immediately following their decline to the present. Unexpectedly, the past environments exploited by lemurs were drier than the protected (albeit often degraded) riparian habitats assumed to be ideal for lemurs today. Neither competitive release nor niche contraction can explain these observed trends. We develop an alternative hypothesis: ecological retreat, which suggests that factors surrounding extinction may force surviving species into marginal or previously unfilled niches.

Keywords: Madagascar; lemur; $\delta^{13}\text{C}$; $\delta^{15}\text{N}$; competitive release; niche contraction

1. INTRODUCTION

Lemurs represent a prodigious radiation of primates in Madagascar [1,2]. Yet many are at risk of extinction [2], and at least 17 species have vanished during the past 2000 years [3]. The cause (or combination of causes) that resulted in these extinctions is debated, but humans were probably a central factor [3–5]. Much of this debate has stemmed from unresolved temporal sequences. There is evidence of habitat change in the southwest shortly after the arrival of humans on Madagascar [6], but major anthropogenic changes occurred relatively recently [7]. Connecting these factors to the extinctions of particular species has been challenging [3,5], and thus the effects of such extinctions on the behavioural ecology of living lemurs is uncertain [8,9].

The principle of competitive release predicts that surviving lemurs have expanded or shifted into the dietary niches vacated by potential competitors [10–12]. However, if the disappearance of competitors resulted from factors that also affected available resources, or if survivors lacked the capacity to expand their resource use to exploit vacated niche space, then competitive release could be dampened. Collectively, the survivors might

instead occupy a constricted niche space relative to the entire pre-extinction community, exploiting a subset of the resources formerly used by the intact community [11]. Such a scenario represents classic niche contraction. A third possibility has received little attention. If ecosystem collapse forces survivors to exploit new habitats or resources (e.g. introduced plant species), then niche contraction may be accompanied by a community-wide shift into marginal or previously unfilled ‘novel’ niche space [13,14]. We call this latter scenario ecological retreat.

Here, we test the predictions of competitive release, classic niche contraction and ecological retreat using stable carbon and nitrogen isotope values ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$)¹ from extant and recently extinct sympatric lemur species. Isotopic niches reflect aspects of habitat and diet, but in condensed form (e.g. herbivorous species can have overlapping isotopic niches but exploit different plants). They are most useful when isotopic gradients across habitats or dietary resources are strong. Such is the case in Madagascar, where (i) different plant types (C_3 , C_4 , CAM) have dramatically different $\delta^{13}\text{C}$ values; (ii) $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values distinguish plants and lemurs from moist and dry habitats; and (iii) plant and lemur $\delta^{15}\text{N}$ values are strongly correlated [15]. Accordingly, lemurs that live in cool, moist localities and consume C_3 plants have lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than those inhabiting hot, dry localities or those consuming CAM plants [15]. We can therefore use the isotopic distributions of

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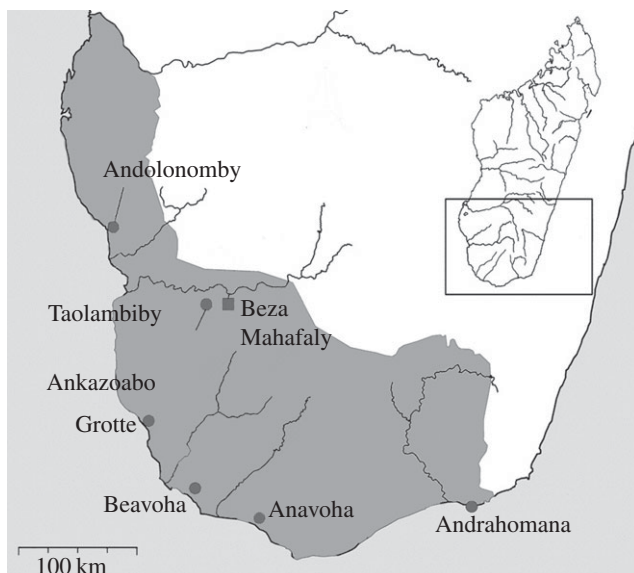


Figure 1. Localities in this study: subfossil localities (circles) and Beza Mahafaly (squares). The Spiny Thicket Ecoregion [16] is highlighted in grey.

each species to distinguish populations feeding predominantly on C_3 , CAM or C_4 resources, and those living in drier versus moister habitats.

(a) Research strategy

We report carbon and nitrogen isotope data from bone collagen for four living species (ring-tailed lemurs, *Lemur catta*; sportive lemurs, *Lepilemur leucopus*; mouse lemurs, *Microcebus griseorufus*; and sifakas, *Propithecus verreauxi*), as well as eight extinct species (*Archaeolemur majori*, *Daubentonia robusta*, *Hadropithecus stenognathus*, *Megaladapis edwardsi*, *Megaladapis madagascariensis*, *Mesopropithecus globiceps*, *Pachylemur insignis* and *Palaeopropithecus ingens*) from six subfossil localities in the Spiny Thicket Ecoregion (STE) of southern Madagascar [16] (figure 1). The term subfossil describes Late Pleistocene or Holocene bones with reduced collagen content but minimal permineralization. In addition, we included isotope data from fur and bone from each of the modern species from a single inland locality, the Beza Mahafaly Special Reserve (BMSR), an inland riparian forest located 17 km to the east of one of our six subfossil localities.

The advantages of comparing past lemurs in the STE with modern lemurs at BMSR are twofold. First, lemur population density today in the STE is highest in riparian forests [17–19]. Rich riparian forests, such as BMSR, are considered the most favourable habitats for lemurs in the south. They differ from drier localities in having higher mean ratios of protein to fibre, as well as more fruiting trees and higher canopy [20,21]. Second, precisely because of these associations, long-term ecological studies of extant lemurs in the STE have focused largely on populations inhabiting riparian forests [22–24]. The rarity of modern STE lemurs away from riparian forests and their sparse history of study make it difficult to sample these subpopulations.

The observed or inferred body sizes and diets of the lemur species included in our analysis are provided in the electronic supplementary material, table S2. We compare extant species with extinct species with broadly

similar dietary adaptations, which are often also their closest extinct relatives. Surviving species are considerably smaller than extinct lemurs. Such differences in body size might be expected to correspond with dietary difference (e.g. increased folivory in larger species), yet Madagascar has a large number of extant small-bodied folivorous lemur taxa. Moreover, anatomical and other lines of evidence indicate that several of the large extinct species were highly frugivorous [25]. In general, body size does not correlate tightly to inferred diet (see electronic supplementary material, table S2) and so it is unlikely to bias our comparisons of extant versus extinct lemur taxa.

The STE was largely devoid of large-bodied lemurs by 900 calendar years (Cal) BP [5]. We compared data from three time bins: pre-900 Cal BP, post-900 Cal BP and modern. Extant lemurs occurred in both of the older bins. We used three complementary methods to examine the isotopic niche space for each lemur species and for each species assemblage: (i) pairwise comparisons of both Euclidean distances and density overlap scores (ω) between extinct species and extant species in subfossil deposits before and after 900 Cal BP; (ii) the means, ranges and variances calculated for all pairwise Euclidean distances between species centroids of community members in each time bin; and (iii) comparisons of $\delta^{13}C$ and $\delta^{15}N$ values over time for each extant species. Pairwise Euclidean distances and ω scores can elucidate potential competitive interactions in two-isotope niche space. The means, variances and ranges calculated for pairwise Euclidean distances within each time bin illuminate species dispersion, niche diversification and overall niche breadth at the community level [26,27]. Finally, mean and variance for $\delta^{13}C$ and $\delta^{15}N$ values provide information about actual diet and habitat preferences through time.

Under competitive release, the isotopic niches of extant lemurs are expected to converge on those of extinct taxa with similar morphological dietary adaptations [10,25], resulting in decreased pairwise Euclidean distances and increased niche density overlap scores after 900 Cal BP [26,27]. For example, the isotopic niche of *Lemur catta*, an extant frugivore [28], is predicted to converge on those of extinct frugivores such as *Pachylemur insignis* or *A. majori* [29]. Similarly, *Lepilemur leucopus*, an extant folivore [30], is expected to shift towards the extinct folivores *Megaladapis edwardsi* and *Megaladapis madagascariensis* [29,31], which have very similar dental relief and complexity [25]. Finally, the isotopic niche of *Propithecus verreauxi*, a folivore/frugivore [28], might converge on the isotopic niche of the closely related *Palaeopropithecus ingens* [31].

2. MATERIAL AND METHODS

(a) Sample collection and preparation

In total, we included 117 subfossil bones and 207 modern bone and fur samples. We sampled 12 bone specimens of modern *Propithecus verreauxi* and *Lemur catta* from the osteological collection at BMSR. All remaining isotopic data for modern lemurs (195 fur specimens) were compiled from the literature; they pertain to individuals sampled from the 50 ha riparian forest at BMSR [15,30,32]. Raw data for all subfossils are provided in the electronic supplementary material, table S1, and species means for each time bin are provided in table 1. We analysed 108 subfossil specimens

Table 1. Descriptive statistics for all extant and extinct genera from the Spiny Thicket Ecoregion before and after 900 Cal BP. Subfossil $\delta^{13}\text{C}$ values account for changes in atmospheric CO_2 over the past 150 years. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for modern *Lemur*, *Lepilemur* and *Microcebus* fur have been made comparable with collagen by adding $0.9 \pm 1.1\text{‰}$ and $0.8 \pm 0.9\text{‰}$, respectively [28]. The error associated with this conversion has been propagated in quadrature.

genus	isotope	inland						coastal						inland		
		>900 Cal BP			<900 Cal BP			>900 Cal BP			<900 Cal BP			modern		
		<i>n</i>	mean (‰) ± 1 s.d.	mean (‰) ± 1 s.d.	<i>n</i>	mean (‰) ± 1 s.d.	mean (‰) ± 1 s.d.	<i>n</i>	mean (‰) ± 1 s.d.	mean (‰) ± 1 s.d.	<i>n</i>	mean (‰) ± 1 s.d.	mean (‰) ± 1 s.d.	<i>n</i>	mean (‰) ± 1 s.d.	
extant																
<i>Lemur</i>	carbon	1	-20.8		2	-21.3 ± 0.1	4	-20.4 ± 1.2	11	-19.5 ± 1.0				32	-23.3 ± 1.1	
	nitrogen	1	9.7		2	6.1 ± 2.6	4	12.1 ± 1.8	11	11.7 ± 0.6				32	7.7 ± 1.6	
<i>Lepilemur</i>	carbon	2	-22.3 ± 0.1	1	-20.0								2	-22.9 ± 0.9	9	-20.3 ± 1.4
	nitrogen	2	9.6 ± 0.4	1	8.6	1	9.9						2	9.6 ± 1.5	9	6.5 ± 1.3
<i>Microcebus</i>	carbon												3	-18.9 ± 1.2	156	-21.9 ± 1.4
	nitrogen												3	11.4 ± 0.3	156	8.8 ± 1.3
<i>Propithecus</i>	carbon	4	-21.6 ± 1.4	4	-21.6 ± 1.5	1	-20.9								10	-21.5 ± 1.0
	nitrogen	4	8.2 ± 0.9	4	9.9 ± 2.6	1	8.3								10	7.2 ± 1.3
extinct																
<i>Archaeolemur</i>	carbon	2	-21.8 ± 0.7													
	nitrogen	14	12.0 ± 1.4													
<i>Daubentonia</i>	carbon															
	nitrogen															
<i>Hadropithecus</i>	carbon															
	nitrogen															
<i>Megaladapis</i>	carbon	8	-21.4 ± 0.9													
	nitrogen	7	10.5 ± 0.9													
<i>Mesopropithecus</i>	carbon															
	nitrogen															
<i>Pachylemur</i>	carbon	5	-22.0 ± 1.4													
	nitrogen	5	12.2 ± 0.5													
<i>Palaeopropithecus</i>	carbon	8	-21.9 ± 0.3													
	nitrogen	7	12.1 ± 0.7													

from six localities in the STE for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values. Five of these subfossil localities are on or near the coast (figure 1). The only inland locality, Taolambiby, lies 17 km west of the research station at BMSR. Radiocarbon dates are available for the majority of these subfossils [5]. We augmented this sample with published isotope and radiocarbon data for nine additional subfossil bones [1,3]. Only $\delta^{13}\text{C}$ values were previously published for most of these additional specimens [3]. D. A. Burney provided us with unpublished $\delta^{15}\text{N}$ values for some, but not all, of these specimens. We therefore have a mismatch between the number of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in our dataset.

Collagen samples were prepared for isotopic analysis following the protocol of Crowley *et al.* [33]. The surfaces of fragmentary but diagnostic specimens were cleaned, and around 200 mg of bone flakes were removed, placed in 0.5 M EDTA (pH 8.0), sonicated and allowed to decalcify over four weeks (two weeks at 4°C and two weeks at room temperature). Once decalcified, the collagenous residue was rinsed in ultrapure water 10×, and gelatinized in 0.01 N HCl at 57°C. The gelatin solution was filtered using a Whatman 1.5 µm glass-fibre filter and dried under vacuum.

(b) *Sample analysis*

Approximately 700 µg of collagenous extracts were weighed into tin boats, combusted and analysed for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values on a Finnigan ThermoElectron Delta+XP continuous flow system (Breman, Germany) connected to a Carlo Erba Elemental Analyzer (Milan, Italy) at the University of California, Santa Cruz Stable Isotope Laboratory. Precision (± 1 s.d.) based on 24 IAEA acetanilide replicates was 0.1‰ for both carbon and nitrogen. Sample preservation was assessed using sample yield, atomic C:N ratios, and carbon and nitrogen isotope values [34]. For samples with questionable C:N, filtrate was eluted in 0.01 N HCl a second time and ultrafiltered with retention of the greater than 30 kDa fraction [35].

(c) *Data corrections and calibrations*

We combined data from *Megaladapis madagascariensis* and *Megaladapis edwardsi* because ^{14}C ages, and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for the two species did not differ ($p > 0.05$).

To compare isotope ratios from fur and bone, we corrected for the small apparent isotopic enrichment between bone collagen and fur keratin by adding $0.9 \pm 1.1\%$ and $0.8 \pm 0.9\%$ to keratin $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively [36]. These values are based on the mean apparent enrichment values calculated for a broad spectrum of primate taxa. Assuming a reproducibility error of 0.1‰ for measured $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, propagating these error values in quadrature leads to an uncertainty of 1.1‰ for converted keratin $\delta^{13}\text{C}$ values and 0.9‰ for converted keratin $\delta^{15}\text{N}$ values. We propagated the error associated with converting keratin isotope values into the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for modern *Lemur catta*, *Lepilemur leucopus* and *Microcebus griseorufus*. Incorporating this error into our statistical analyses did not affect the significance of our results (the pooled group error is substantially larger than the propagated error).

We corrected all subfossil $\delta^{13}\text{C}$ values to account for $\delta^{13}\text{C}$ shifts in atmospheric carbon dioxide owing to anthropogenic burning of fossil fuels, using 2005 as the modern target year. The initial timing of ^{13}C shifts is similar in the Northern and Southern Hemispheres [37,38]. However, because annual atmospheric $\delta^{13}\text{C}$ changes following the Industrial Revolution

are not well constrained, particularly for the Southern Hemisphere, and because there is a lag in the carbon pool of the Southern Hemisphere relative to the Northern Hemisphere [39], we used correction curves that were slightly modified from those for the Northern Hemisphere [40]. We applied a conservative time-dependent correction of -0.004% per year between 1860 and 1965 AD, and -0.02% per year between 1965 and 2005 (modern). All subfossil lemurs older than 150 Cal BP were corrected by -1.2% [5,41]. We did not correct for pre-industrial fluctuations in atmospheric $\delta^{13}\text{C}$ values because atmospheric $\delta^{13}\text{C}$ values were remarkably stable prior to the Industrial Revolution. Antarctic carbon isotope records vary only by 0.2‰ between 1000 and 5000 Cal BP [42]. This amount of variability is negligible compared with the post-industrial increase in atmospheric $\delta^{13}\text{C}$ values, for which we did correct. Conventional ^{14}C ages were calibrated to Cal BP using a 20-year moving average and the Southern Hemisphere calibration curve SHCal04 in CALIB v. 6.0 [39,43] (see electronic supplementary material, table S1). We used mean-calibrated calendar years in all statistical analyses.

(d) *Hypothesis testing*

If two lemur species have similar isotopic niches, the pairwise Euclidean distance between the two species should be small and substantial isotopic overlap for the two species should lead to ω scores close to 1.0 (ω scores range from 0 to 1.0, indicating no overlap and complete overlap, respectively). Furthermore, if all lemur species within a community have similar isotopic niches, then the mean, range and variance of pairwise Euclidean distances between species should be small and ω scores should again be close to 1.0. Finally, if two communities of lemur species (e.g. subfossil lemurs before and after 900 Cal BP) occupy similar isotopic niche space, then the means should be similar and the variance and range of pairwise Euclidean distances between the two communities should be small.

To test if competitive release occurred, we used paired-sample *t*-tests to compare the mean Euclidean distances between each extinct species and each extant species (with extant species treated independently before and after 900 Cal BP). Owing to isotopic differences among coastal and inland localities, we considered coastal and inland animals separately for pairwise comparisons (see justification for pooling data in electronic supplementary material, appendix S1). All individuals of *Propithecus verreauxi* and *Lepilemur leucopus* that yielded ^{14}C dates are from inland Taolambiby, and 15 of the 16 dated subfossil *Lemur catta* are from coastal localities. We lack isotope data for extinct *Daubentonia robusta*, *Hadropithecus stenognathus* and *Mesopropithecus globiceps* at inland localities, and we found significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ among the subset of subfossil extinct species occurring at both inland and coastal localities (carbon: pooled $t = -2.13$, d.f. = 111, $p = 0.034$; nitrogen: pooled $t = -4.36$, d.f. = 104, $p < 0.0001$; table 1). We therefore examined only Euclidean distances between coastal extinct species and subfossil coastal *Lemur catta*, and between inland extinct species and subfossil inland *Lepilemur leucopus*, and *Propithecus verreauxi*. Likewise, we calculated density overlap between subfossil coastal *Lemur catta* and coastal extinct species, and inland *Propithecus verreauxi* and inland extinct species. We did not have sufficient dated *Lepilemur leucopus* individuals to calculate and compare density overlap before and after 900 Cal BP (ω can be calculated only between groups composed of three

Table 2. Euclidean distances and niche density overlap (ω) between each of the extant and extinct taxa before and after the decline in extinct species (*ca* 900 Cal BP). Blank cells indicate insufficient data for comparisons. Small sample sizes prohibited niche overlap calculations for *Lepilemur*. Bold numbers identify comparisons between taxa with similar dietary adaptations [29,31,44].

extinct genus	<i>Lemur catta</i> (coastal)				<i>Lepilemur leucopus</i> (inland)				<i>Propithecus verreauxi</i> (inland)			
	pre-900 Cal BP		post-900 Cal BP		pre-900 Cal BP		post-900 Cal BP		pre-900 Cal BP		post-900 Cal BP	
	distance	ω	distance	ω	distance	distance	distance	distance	distance	ω	distance	ω
<i>Archaeolemur</i>	0.71	0.75	1.68	0.46	2.45		3.85		3.81	0	2.83	
<i>Daubentonia</i>	2.93		2.15									
<i>Hadropithecus</i>	10.60	0	9.91	0								
<i>Megaladapis</i>	1.50	0.36	2.42	0.18	1.27		2.36		2.31	0.17	1.62	0.22
<i>Mesopropithecus</i>	3.01	0	2.42									
<i>Pachylemur</i>	2.19	0.43	3.14	0.05	2.62		4.12		4.02	0	3.11	0.11
<i>Palaeopropithecus</i>	2.03	0.53	2.90	0.13	2.53		3.98		3.91	0.002	2.97	0.02
average	3.28	0.55	3.52	0.42	2.22		3.58		3.51	0.06	2.63	0.15

individuals or more). Calculations were also not possible for subfossil *Microcebus griseorufus* because we had data only for individuals younger than 900 Cal BP (table 1).

To test whether niche contraction occurred, we compared the niche breadth (mean Euclidean distance between all species pairs) for the entire subfossil community before and after 900 Cal BP (pooling data from coastal and inland sites; see electronic supplementary material, tables S3 and S4). To test for ecological retreat, we compared the niche breadth, $\delta^{13}\text{C}$ values and $\delta^{15}\text{N}$ values for the entire subfossil extant community (pooling all subfossil samples from all four extant species from before and after 900 Cal BP, from undated specimens and from coastal and inland sites) with modern taxa from Beza Mahafaly (see electronic supplementary material, appendix S1, tables S5 and S6). We then compared isotope values for modern and subfossil individuals from each extant species (see electronic supplementary material, table S7). We also compared isotope values for modern individuals and subfossil individuals for the three extant taxa from the inland site, Taolambiby, to check for potential biases in comparing coastal with inland data (see electronic supplementary material, table S8).

Species mean isotope values and variances are useful when examining both interspecific and intraspecific isotopic variation. However, when comparisons are made of whole community characteristics, unequal representation of individuals in each species can bias comparisons. On the other hand, Euclidean distances between species pairs are unbiased by the number of individuals in each species because they are based on the isotopic centroids for each species. Furthermore, niche density overlap takes the overlap of distributions and the covariance of isotopic values for each species into account. This combination of approaches is particularly useful for comparing niche differentiation and overlap among species, and for quantitatively characterizing community-wide niche breadth [26,27].

Euclidean distances between species pairs were calculated using dissimilarity matrices. We used independent and paired-sample *t*-tests and one-way ANOVA with Tukey's tests of honestly significant differences to test for differences among species and among radiocarbon age groups. When variances between groups were found to be unequal, we report results from unpaired variance *t*-tests. Density overlap

scores between species pairs were calculated using Pianka's measure of density overlap [27]. We calculated density overlap scores using a program written by J. D. Yeakel for R v. 2.11.1. We used Student's *t*-tests to compare $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values among groups, and tested for unequal variances using Levene's tests. When the assumptions of normality or homoscedasticity of variances were not met, we used Wilcoxon signed-rank tests and Welch's unpaired variance *t*-tests, respectively. With the exception of ω scores, all statistical analyses were conducted using JMP v. 7.0 and SPSS 14. Significance was set at $\alpha = 0.05$.

3. RESULTS

We found no evidence of competitive release for subfossil *Lemur catta*. The mean Euclidean distance between isotopic centroids for *Lemur catta* and extinct lemurs in coastal sites did not change after 900 Cal BP (paired $t = -0.72$, d.f. = 6, $p = 0.50$), and species-specific pairwise Euclidean distances shifted in a direction contrary to our expectations (table 2). Niche density overlap decreased from before to after 900 Cal BP between coastal *Lemur catta* and each coastal extinct species, including its most likely competitors, *Archaeolemur* and *Pachylemur* (table 2). Similarly, we found no evidence of competitive release for *Lepilemur leucopus*. The mean Euclidean distance between centroids for *Lepilemur leucopus* and inland extinct lemurs increased after 900 Cal BP (paired $t = -14.61$, d.f. = 3, $p = 0.001$; table 2). The isotopic centroid for *Lepilemur leucopus* shifted away from the centroids for all inland extinct species, including *Megaladapis* spp. *Propithecus verreauxi* shows a different pattern, with decreased mean pairwise Euclidean distances between its centroids and those of inland extinct lemurs before and after 900 Cal BP (paired $t = 13.91$, d.f. = 3, $p = 0.001$; table 2). After 900 Cal BP, its density overlap with extinct species also increased. These results lend only weak support for competitive release, however, because average ω scores remained small throughout and showed no disproportionate convergence towards its extinct relative *Palaeopropithecus* (table 2).

In general, our results refute competitive release, but agree well with a sharp contraction in the isotopic niche breadth of the entire STE lemur community after 900

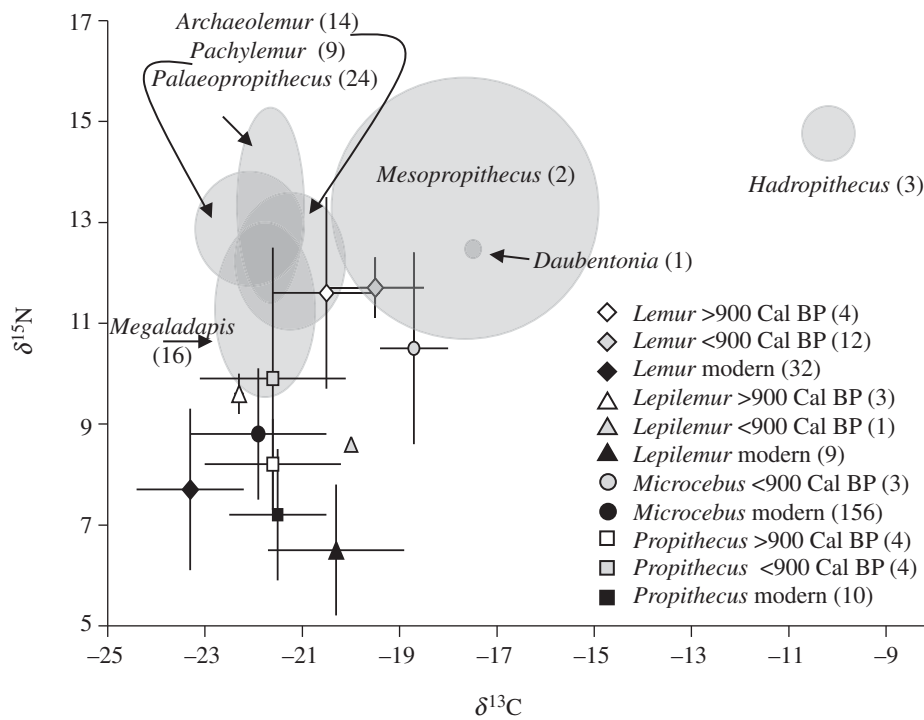


Figure 2. Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (± 1 s.d.) values for all STE extinct lemur taxa (shaded areas, $n = 69$) and extant lemur taxa before 900 Cal BP (white symbols, $n = 11$), after 900 Cal BP (light grey symbols, $n = 20$) and modern (dark grey symbols, $n = 207$). n -values for each taxon are indicated in parentheses. Data include both coastal and inland localities. Subfossil carbon data have been corrected for historical changes in atmospheric ^{13}C . Isotope data for modern *Lemur*, *Lepilemur* and *Microcebus* fur have been made comparable with collagen by adding $0.9 \pm 1.1\text{‰}$ and $0.8 \pm 0.9\text{‰}$ to fur $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively [36]. Raw subfossil data are reported in electronic supplementary material, table S1.

Cal BP (figure 2). The mean Euclidean distance between all species pairs before 900 Cal BP (4.8 ± 1.9 , range 0.6–13.4) was significantly greater than after 900 Cal BP (1.9 ± 0.7 , range 1.3–3.1; unpooled $t = 4.54$, d.f. = 41.88, $p < 0.001$; figure 2; electronic supplementary material, tables S3 and S4).

Comparing isotopic data for the entire subfossil community of extant lemurs and those same species at BMSR, we found stability of community niche breadths (electronic supplementary material, tables S5 and S6). There are no detectable differences in either the variance ($F_{1,11} = 0.018$, $p = 0.90$) or mean pairwise Euclidean distance (pooled $t = 0.48$, d.f. = 10, $p = 0.64$) between modern and subfossil extant lemur communities. Nevertheless, the isotopic niches of modern lemurs differ from those of the subfossil taxa. Modern species evince lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than do their subfossil counterparts (figure 2; table 1; carbon: Welch's $t = 7.34$, d.f. = 44.72, $p < 0.0001$; nitrogen: Welch's $t = 5.71$, d.f. = 42.82, $p < 0.0001$). Although $\delta^{13}\text{C}$ values do not differ for subfossil and modern *Lepilemur leucopus* or *Propithecus verreauxi*, both modern *Lemur catta* and *Microcebus griseorufus* have significantly lower $\delta^{13}\text{C}$ values than subfossils, and modern individuals belonging to all four extant species have significantly lower $\delta^{15}\text{N}$ values than subfossils (table 1; electronic supplementary material, table S7).

This pattern remains robust if we compare only modern lemurs from Beza Mahafaly and the inland site of Taolambiby, located 17 km west of BMSR. Again, there are no detectable differences in either the variance ($p = 0.37$) or mean pairwise Euclidean distance (pooled $t = 0.52$, d.f. = 25, $p = 0.61$) between the modern and

subfossil extant lemur communities, but modern lemurs have significantly lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than subfossil individuals (carbon: $t = -3.95$, d.f. = 65, $p = 0.0002$; nitrogen: $t = -3.44$, d.f. = 65, $p = 0.001$). Modern *Lepilemur* has lower $\delta^{15}\text{N}$ values than the subfossil *Lepilemur* from Taolambiby, but $\delta^{13}\text{C}$ values do not differ (see electronic supplementary material, table S8). Results for *Propithecus* do not change (all subfossil individuals are from Taolambiby). Modern *Lemur catta* have lower $\delta^{13}\text{C}$ values than subfossil individuals, but $\delta^{15}\text{N}$ values do not differ significantly (see electronic supplementary material, table S8).

4. DISCUSSION

The shift in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for extant species conforms to the expectations of classic niche contraction [14], although with a crucial addition—the shift is towards an isotopic space that was largely unoccupied by STE lemurs in the past (figure 2). This pattern supports the expectations of ecological retreat. The observed contraction in the isotopic niche breadth of the STE lemur community following the demise of the extinct taxa may reflect the loss of distinct niches that cannot be exploited by small-bodied surviving taxa. The overall decrease in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values between past and modern individuals indicates an increasing reliance on moister environments with denser canopies from the past to the present (see electronic supplementary material, table S7). The inverse relationship between carbon and nitrogen isotope values and moisture is well documented [45–47]. This relationship is evident in Madagascar, where mouse

lemurs living in moist, dense forest have lower $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than mouse lemurs living in drier, more open habitat [15]. Island-wide, mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values vary by 3.5‰ and 10‰, respectively. On a local scale, mouse lemurs living in the riparian forest at BMSR have $\delta^{13}\text{C}$ values roughly 1.5‰ lower and $\delta^{15}\text{N}$ values roughly 2‰ lower than individuals living in spiny forest at the same reserve [15].

Our data demonstrate that dry forest or spiny scrub habitats were important to lemurs in the past. Even at a site such as Taolambiby, which is (i) close to BMSR (where living lemurs appear to prefer habitats close to the Sakamena River) and (ii) characterized by a seasonal stream and year-round spring, subfossil lemurs have elevated $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values when compared with modern lemurs at BMSR. No lemurs at any STE subfossil locality, inland or coastal, evince a riparian signal and none of the subfossil lemurs (whether extinct or still extant) have isotopic values resembling those of modern lemurs at BMSR. Isotopic values for surviving lemur species 900 years ago or earlier are significantly ^{15}N - and ^{13}C -enriched relative to the same species from BMSR, suggesting that the subfossil conspecifics were feeding in more xeric, open habitats that cover the majority of southwestern Madagascar today. This result is perhaps unsurprising. The fact that the majority of subfossil lemurs have been found at localities that are distant from rivers suggests that these primates were probably able to exploit dry habitats.

There is considerable recent evidence that modern lemurs in southern Madagascar are concentrating in riparian forests [17–19]. The reasons behind this increased reliance on riparian habitat are uncertain, although relatively low hunting and logging pressures in riparian reserves are probably contributing factors. Whereas human disturbance at modern riparian forests such as BMSR has been well documented [19,48], even greater disturbance has been documented in unprotected dry forests in the STE [7,19]. Our point, however, is not to explain the modern distribution of lemurs in southwestern Madagascar, but to explore how extinction affects remaining survivors. Neither competitive release nor niche contraction can adequately explain the striking difference in both carbon and nitrogen isotope values that we have documented.

Our alternative explanation—ecological retreat—may be expected when the loss of certain species and the introduction of new ones have resulted in major vegetation changes in formerly preferred habitats [49], when formerly preferred habitats are no longer available, or when predation pressure is lower in the ‘novel’ habitat. Regarding the case at hand, we are not arguing that lemurs were averse to riparian forests in the past, nor are we arguing that modern lemurs in the STE live only in riparian habitats. However, our data do suggest that in the past, lemurs were very common in dry habitats, and not reliant on resources from riparian forests. Contrary to the long-held belief that lemur population density is highest in riparian habitats because those habitats harbour the best lemur resources, modern lemurs may prefer these habitats simply because they offer the greatest protection. Riparian forests may thus function more as refugia, raising the possibility of a mismatch between the anatomical adaptations of lemurs and their observed behaviours [24,50].

The STE was recently listed as one of the 200 most important ecological regions in the world [51]. Isotopic data suggest that prior to extensive human disturbance, many STE lemurs foraged in more open habitats, such as wooded savannah and spiny thicket [33]. *Lemur catta*, *Lepilemur leucopus*, *Microcebus griseorufus* and *Propithecus verreauxi* still occur in dry spiny forest and scrub [2], but these habitats are under-protected and rapidly shrinking [17,52]. Community response to extinction is complex, and inadequately described under the theoretical umbrella of competitive release and niche contraction alone. Ecological retreat is underappreciated, but it appears to describe changes in the primate communities of southern Madagascar. It may also explain historical isotope shifts in ratites, proboscideans and pinnipeds [13,53,54]. The ecological consequences of retreat may be considerable. Retreat can result in the widespread establishment of both new selective pressures and new ecological interactions that may increase the extinction risk of survivors, potentially creating an extinction cascade [50,55].

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ENDNOTE

¹Isotope ratios are presented as δ values, where $\delta = [(R_{\text{sample}}/R_{\text{standard}}) - 1] \times 1000$, and $R = {}^{13}\text{C}/{}^{12}\text{C}$ or ${}^{15}\text{N}/{}^{14}\text{N}$. Standards are Pee Dee belemnite for C and AIR for N. The units are parts per thousand (per mil, ‰) deviations from the standard.

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