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Strontium Isotopes Support Small Home Ranges for Extinct Lemurs

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Among mammals, including anthropoid primates, the primary factors that affect mobility are body size (larger-bodied species move more than smaller ones), diet (frugivores and trophic omnivores are more mobile than folivores), and habit (terrestrial taxa have larger home ranges than arboreal ones). If similar factors hold for Lemuriformes, we would expect large-bodied (particularly frugivorous) extinct lemurs to have been more mobile than smaller-bodied (particularly folivorous) extant species. Yet multiple lines of evidence (e.g., low Retzius Periodicities, small semicircular canal size, small relative brain size) suggest that extinct lemurs were relatively inactive. If so, they may have had relatively small home ranges, perhaps on par with smaller-bodied extant lemurs. We used strontium isotopes (^{87}Sr/^{86}Sr), which vary spatially primarily as a function of geology, to compare mobility for eight lemur genera: *Eulemur*, *Lemur*, *Lepilemur,* and *Propithecus* (extant), and *Archaeolemur*, *Megaladapis*, *Pachylemur,* and *Palaeopropithecus* (extinct). Subfossils came from two sites: Ankilitelo/Mikoboka, a series of sinkholes in a limestone plateau, and Ampasambazimba, a wetland underlain by a variety of igneous and metamorphic rocks. Within either site, we expected more mobile taxa to exhibit more variable ^{87}Sr/^{86}Sr, reflecting larger movement across a diversity of geologies. We found no differences in median ^{87}Sr/^{86}Sr or variance between extinct and extant lemurs at either site (Wilcoxon and Bartlett $p > 0.05$ for all comparisons). There were apparent but insignificant differences among genera (Kruskal-Wallis and Bartlett $p > 0.05$). Isotopic variability was greater at Ampasambazimba than at Ankilitelo/Mikoboka, reflecting differences in the underlying geology. One *Palaeopropithecus* from Ankilitelo/Mikoboka and one *Eulemur* from Ampasambazimba had unusually elevated ^{87}Sr/^{86}Sr. Both of these individuals could have been deposited at their respective sites by a predatory bird. These results demonstrate the value of ^{87}Sr/^{86}Sr for testing hypotheses related to the behavior of now-extinct species. Strontium isotopes support low mobility for extinct lemurs, and suggest that Lemuriformes as a whole differ from anthropoids in having relatively depressed basal metabolic rates and reduced activity levels. These traits reduce energetic expenditure, and likely developed in response to Madagascar's harsh environments. However, small home ranges also make lemurs more vulnerable to extinction.

Keywords: ^{87}Sr/^{86}Sr, mobility, energy conservation, seed dispersal, Madagascar

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INTRODUCTION

Madagascar is well-known for its diversity of plants and animals, including its endemic primates, the lemurs. Over 100 living species of extant lemur are now recognized, and an additional 17 species went extinct in the Late Holocene (Burney et al., 2004; Crowley, 2010). Thanks to decades of multi-disciplinary research, a wealth of information is now available for Madagascar's extinct lemurs. All were larger-bodied than their extant relatives (ca. 12 to >100 kg vs. <100 g to <8 kg; Smith and Jungers, 1997; Jungers et al., 2008; Mittermeier et al., 2008), and we have a reasonably good understanding of what they ate and the kinds of environments that they inhabited (e.g., Jungers et al., 2002; Schwartz et al., 2002; Godfrey et al., 2006, 2012, 2016a; Crowley et al., 2012). However, we do not yet have a clear idea of how much they may have moved among habitats or across landscapes. Gaining further insight into movement patterns for these species would contribute to our understanding of ecological roles (e.g., their importance as seed-dispersers), which in turn could help inform conservation and biodiversity management decisions on Madagascar.

Among mammals, including anthropoid primates, there are a number of factors that affect home ranges. The primary control appears to be body size; smaller-bodied species tend to have smaller home ranges than larger-bodied species (Milton and May, 1976; Harvey and Clutton-Brock, 1981; Lindstedt et al., 1986; Ofstad et al., 2016; Crowley et al., 2017). Beyond this, terrestrial taxa tend to have larger home ranges than arboreal ones, frugivores tend to have larger home ranges than folivores, omnivores and faunivores have larger home ranges than herbivores, and animals living in open habitats tend to have larger home ranges than those living in denser habitats (Milton and May, 1976). These variables are correlated; for example, body size and diet are both tied to metabolism, and range size is related to the distribution and abundance of preferred resources, in addition to body size (Milton and May, 1976). On the basis of this evidence, we might expect the large-bodied (particularly frugivorous and terrestrial) extinct lemurs to have been more mobile than smaller-bodied (particularly folivorous and arboreal) extant species. This would be especially true for *Archaeolemur*, which has been reconstructed as one of the most terrestrial and frugivorous of the extinct lemurs (e.g., Tattersall, 1973; Jungers et al., 2002; Godfrey et al., 2005).

Yet multiple lines of evidence suggest that the extinct lemurs were relatively inactive. First, none of the giant lemurs have postcranial characteristics suggestive of high agility. Most were arboreal with adaptations for deliberate climbing, and some had adaptations for below-branch suspension (converging on sloths); none were saltatory and none were cursorial (Walker, 1974; Jouffroy and Lessertisseur, 1978; Godfrey et al., 1997; Jungers et al., 2002; Shapiro et al., 2005). Second, small semicircular canals, which are balance organs within the inner ear, also suggest low agility for all of the extinct taxa (Walker et al., 2008). Third, periodicity in the striae of Retzius is low in all measured extinct lemurs (Hogg et al., 2015; Schwartz and Rahantaharivao, unpublished data on *Pachylemur*). These striae are lamellar growth bands in tooth enamel related to biological rhythms, such as the Havers-Halberg Oscillation (HHO), which modulate life-history related traits like brain and body size, age at first reproduction, and activity levels (Bromage et al., 2012). Because Retzius Periodicity (RP) intervals correlate strongly with body size in most mammals, including anthropoid primates, we would expect the larger-bodied extinct taxa to have longer intervals than smaller-bodied extant lemurs. However, this is not the case; all lemuriforms, including the giant lemurs, have relatively low values for RP (Hogg et al., 2015). *Archaeolemur* has a slightly higher RP value than other taxa (4 vs. 2 or 3), but this value is still quite low in comparison to anthropoids of similar body size, such as *Theropithecus*, the gelada (RP = 7), with which *Archaeolemur* has been compared. Hogg et al. (2015) hypothesized that low RP relates to constraints on energy expenditure in lemurs (i.e., selection for risk-averse life histories), which could impact mobility and thus home-range size. Lastly, extinct lemurs had relatively small brains (Catlett et al., 2010), which further suggests low basal metabolic rate, low energy expenditure, and in turn low activity levels. On the basis of this collective body of evidence, we might expect that extinct lemurs had relatively small home-ranges, perhaps as small as those of much smaller-bodied extant lemurs.

Strontium isotope ratios (^{87}Sr/^{86}Sr) in tooth enamel and bone may be able to detect mobility differences among co-occurring extinct and extant taxa. Strontium ions leached from rocks are taken up by plants, and subsequently into animal tissues with negligible fractionation (Capo et al., 1998; Bentley, 2006; Lewis et al., 2017). Because biologically available (bioavailable) ^{87}Sr/^{86}Sr is closely tied to geology, it varies spatially. Madagascar is well-suited for this type of geochemical approach. Its rocks preserve nearly three billion years of our planet's history (reviewed in Crowley and Sparks, 2018), and consequently, the island's geology is extraordinarily diverse (Roig et al., 2012). Within any given site, more mobile taxa should exhibit more variable ^{87}Sr/^{86}Sr, reflecting larger movement across a diversity of geologies.

We used strontium isotopes to compare mobility for extant and extinct lemur genera that are reasonably well-represented in subfossil deposits and fill much of the spectrum of variation in diet and locomotor habits (**Table 1**): *Eulemur*, *Lemur*, *Lepilemur* and *Propithecus* (extant), and *Archaeolemur*, *Megaladapis*, *Pachylemur,* and *Palaeopropithecus* (extinct). *Eulemur* is one of the more frugivorous of extant lemurids and an important seed disperser, *Lemur* is more folivorous but still an important seed disperser, *Propithecus* is yet more folivorous and more of a seed predator than a seed disperser, and *Lepilemur* is a specialized folivore. These taxa vary in their preferred locomotor habits; *Eulemur, Lemur,* and *Propithecus* spend time both on the ground and in the trees while *Lepilemur* is primarily arboreal. The extinct genera that we sampled also run the gamut from the frugivorous and seed dispersing *Pachylemur* to the specialized folivore *Megaladapis*. *Archaeolemur* and *Palaeopropithecus* had more intermediate diets and were likely seed predators (especially *Archaeolemur*). *Pachylemur*, *Megaladapis* and *Palaeopropithecus*

TABLE 1 | Body mass, diet, and locomotion, for taxa included in this study.

Genus	Body Mass Range (kg)	Sources[a]	Diet	Sources[b]	Locomotion	Sources[c]	SCR (mm)[d]	RP (days)[e]	ECV (cc)	Sources[f]
EXTANT										
Eulemur	1.1–2.4	1–3	Primarily fruit	1, 2	Arboreal, quadrupedal, climbing, and leaping	1	2.2–2.3	3	20.17–26.23	1
Lemur	2.2	1	Primarily fruit	1–3	Primarily arboreal, quadrupedal with some leaping	1	2.1	2–3	22.90	1
Lepilemur	∼0.5–1.0	1	Leaves	1, 2	Vertical clinging and leaping	1	1.8	–	6.87–9.56	1
Propithecus	3.0–6.3	1, 2	Primarily leaves	1, 2	Vertical clinging and leaping, some hanging	1	2.3–2.7	2–3	26.21–39.80	1
EXTINCT										
Archaeolemur	18.2–26.5	4	Primarily fruit, seeds, hard objects	2, 4–6	Semi-terrestrial. non-cursorial	1–3	3.0	4	93	2
Megaladapis	46.5–85.1	4	Leaves	2, 4–6	Primarily arboreal, likely slow, and deliberate vertical climbing	1–3	2.3	3	137	2
Pachylemur	11.5–13.4	4	Primarily fruit	2, 6	Primarily arboreal quadruped, some hind-limb suspension	1, 3	–	3	40–46	3
Palaeopropithecus	25.8–45.8	4, 5	Primarily leaves	2, 6, 7	Primarily arboreal and suspensory	1–3	1.9	2	80	2

[a] *Body Mass Sources: 1, Smith and Jungers (1997); 2, Gordon (2006); 3, Isler et al. (2008); 4, Jungers et al. (2008); 5, Jungers et al. (2002).*

[b] *Diet Sources: 1, Godfrey et al. (2004a); 2, Godfrey et al. (2012); 3, Gould (2006); 4, Godfrey et al. (2005); 5, Scott et al. (2009); 6, Muchlinski et al. (2011); 7, Godfrey et al. (2004b).*

[c] *Locomotion Sources: 1, Walker (1974); 2, Jungers et al. (2002); 3, Shapiro et al. (2005).*

[d] *All semicircular canal radius (SCR) data are from Spoor et al. (2007). Measurements for Archaeolemur and Palaeopropithecus are based on single species (A. edwardsi and P. ingens, respectively).*

[e] *All Retzius periodicity (RP) data are from Hogg et al. (2015) with the exception of Pachylemur; unpublished Pachylemur data from Noromamy Rahantaharivao and Gary Schwartz (personal communication).*

[f] *Endocranial volume (ECV) sources: 1, Isler et al. (2008); 2, Catlett et al. (2010); 3, unpublished data for Pachylemur from Noromamy Rahantaharivao (personal communication). Measurements for extinct taxa are based on single species (Archaeolemur majori, Megaladapis edwardsi, Palaeopropithecus ingens, and Pachylemur insignis).*

have anatomical adaptations suggesting they were primarily arboreal while *Archaeolemur* was likely semi-terrestrial.

MATERIALS AND METHODS

Site Description

Because bioavailable ^{87}Sr/^{86}Sr is spatially variable, differences in mobility among taxa can only be examined within single sites or regions (i.e., among co-occurring taxa exposed to the same baseline conditions). We sampled Holocene subfossil material from two localities that have relatively abundant and robust preservation: Ankilitelo/Mikoboka and Ampasambazimba (Crowley, 2010; Muldoon, 2010; Crowley et al., 2012, 2017; Goodman et al., 2013; Godfrey et al., 2016a; **Figure 1**). Ankilitelo/Mikoboka is a series of sinkholes in a plateau in southwestern Madagascar composed of Eocene limestone, oolitic limestone, and sandstone (Roig et al., 2012). Ampasambazimba is a wetland in Central Madagascar underlain by a variety of

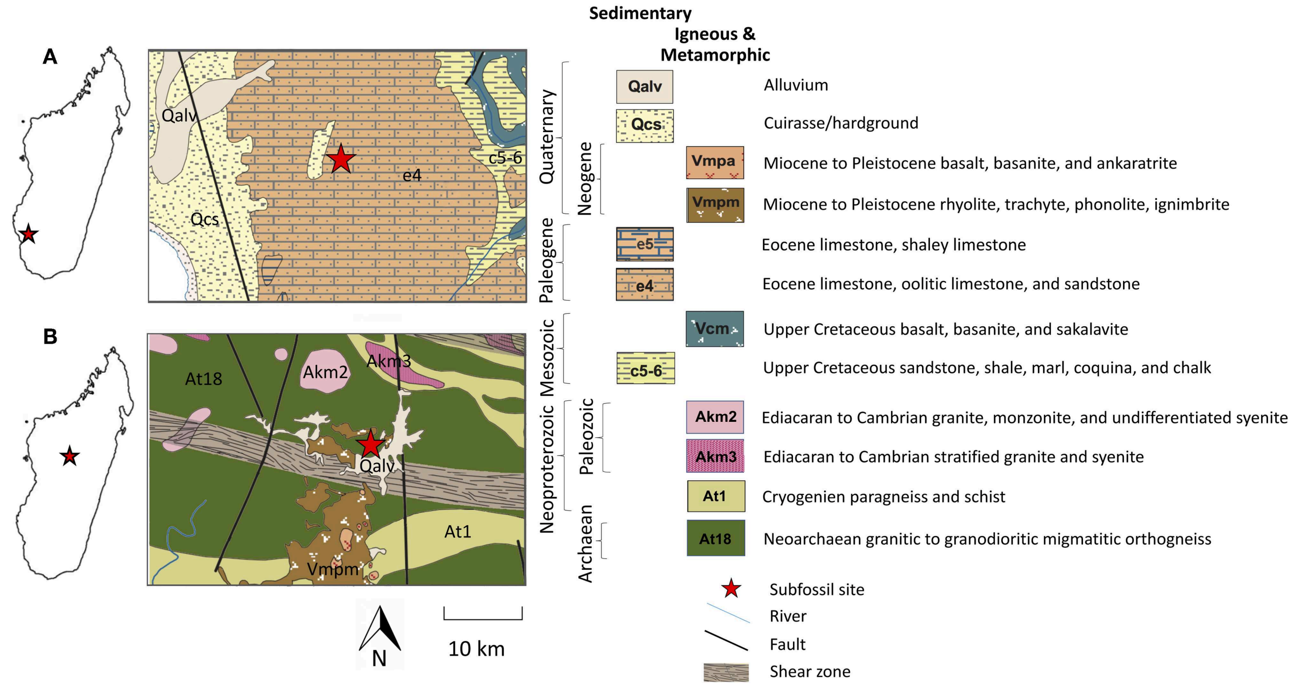

FIGURE 1 | Maps showing the location of our two study sites in Madagascar, as well as the geology at Ankilitelo/Mikoboka **(A)**, and Ampasambazimba **(B)**. Geologic maps were modified from Roig et al. (2012).

igneous and metamorphic rocks dating to the Neoarchean through the Tertiary (Roig et al., 2012).

Sample Acquisition, Preparation, and Analysis

We acquired bones and teeth from previously collected, curated material housed at a variety of museum and university collections, including the University of Antananarivo, the University of Massachusetts Amherst, and the Division of Fossil Primates at the Duke Lemur Center (**Supplementary Table 1**). In total, we were able to include 25 specimens from Ampasambazimba and 30 specimens from Ankilitelo/Mikoboka.

Specimen surfaces were cleaned using a tooth brush or a rotary Dremel tool equipped with a dental drill bit. We then removed 10–20 mg of powder from each sample using the Dremel or by pulverizing fragments with an agate mortar and pestle. Bone and enamel carbonate were isolated chemically (following Crowley and Wheatley, 2014; Baumann and Crowley, 2015; Crowley et al., 2018). Organics were removed by soaking samples in 30% H_2O_2 at room temperature. Enamel samples were soaked for 24 h; bone samples were allowed to react for 72 h, and liquid was replaced between 24 and 48 h. Samples were rinsed 5x with ultrapure water and then reacted for 24 h in 1 M calcium-buffered acetic acid at 4°C. They were again rinsed 5x with ultrapure water, and freeze dried. During both chemical pretreatment steps, samples were agitated regularly to help ensure consistent reaction.

Pretreated samples were sent to the Multicollector Inductively Coupled Plasma Mass Spectrometry (MC-ICPMS) Laboratory in the Geology Department at the University of Illinois Urbana-Champaign for $^{87}Sr/^{86}Sr$ analysis. Three to five mg of each sample were dissolved in 3N HNO_3 and filtered through 0.2 mL of Eichrom Sr spec resin (100–150 mm) packed into Teflon ion-exchange columns. Samples were then eluted with a combination of ultrapure water and 0.05 N HNO_3 into 4-mL Teflon autosampler vials for analysis. Samples were analyzed on a Nu plasma High Resolution MC-ICPMS (Nu Instruments Ltd, Wrexham, Wales, UK). Data were normalized using SRM-987 (accepted $^{87}Sr/^{86}Sr = 0.710255$), and the quality of resulting corrected data was checked using two independent internal standards—South China Sea Coral ($^{87}Sr/^{86}Sr = 0.70918$) and "E&A" ($^{87}Sr/^{86}Sr = 0.70804$). Reported precision for the lab is ± 0.00005.

Data Analysis

At each site, we compared strontium isotope ratios among genera and between extinct and extant lemurs (combining genera). Because we have small and uneven sample sizes, we used non-parametric Wilcoxon and Kruskal-Wallis analyses. We assessed homoscedasticity using Bartlett tests. For all analyses, we used JMP Pro 14.0 with significance set at $\alpha = 0.05$.

One *Palaeopropithecus* from Ankilitelo/Mikoboka and one *Eulemur* from Ampasambazimba had unusually elevated $^{87}Sr/^{86}Sr$ compared to other individuals at the same sites

(**Figures 2**, **3**). The *Palaeopropithecus* was not a statistical outlier for extinct lemurs but was a statistical outlier for this genus at Ankilitelo/Mikoboka. Conversely, the *Eulemur* was a statistical outlier for extant lemurs but was not an outlier for this genus at Ampasambazimba. There was nothing unusual about either of these samples (either in terms of preservation or analysis), which suggests that these data are real. We ran all statistical analyses both including and excluding these two individuals.

RESULTS

There were no differences in median $^{87}Sr/^{86}Sr$ or isotopic variance between extinct and extant lemurs at either Ankilitelo/Mikoboka or Ampasambazimba (**Figures 2**, **3**). These results were consistent whether or not we included the outliers at each site (Wilcoxon and Bartlett $p > 0.05$ for all comparisons). There were small apparent differences in median $^{87}Sr/^{86}Sr$ among individual genera at both sites, but these were not significant (Kruskal-Wallis $p > 0.05$; **Figures 2**, **3**). Likewise, differences in variance among genera at either site were insignificant (Bartlett $p > 0.05$; **Figure 4**). Excluding the outlier individuals, variance was reasonably consistent among taxa at both sites, although *Palaeopropithecus* had considerably smaller variability in $^{87}Sr/^{86}Sr$ than other taxa at both Ankilitelo and Ampasambazimba (**Figure 4**). Including the outliers did not affect the significance of these results, although there were some apparent changes. Specifically, *Palaeopropithecus* had apparently larger variance than all other taxa, including *Eulemur*, at Ankilitelo/Mikiboka, while variance for *Eulemur* was roughly two times larger than *Archaeolemur*, and four times larger than *Palaeopropithecus* at Ampasambazimba (**Figure 4**).

DISCUSSION

We set out to compare mobility of sympatric extinct and extant lemurs using strontium isotopes. Variability in $^{87}Sr/^{86}Sr$ exhibited by both extant and extinct lemurs was greater at Ampasambazimba than at Ankilitelo/Mikoboka (**Figures 2–4**). This likely reflects differences in the underlying geology of the two regions (**Figure 1**; Crowley et al., 2015). While Ampasambazimba is situated in Quaternary sediments, it is surrounded by Neogene volcanics. There also outcrops of Ediacaran to Cambrian granites, and very old metamorphic complexes in close proximity to the site, including both Cryogenian paragneiss and schist and Neoarchaean orthogneiss (Roig et al., 2012). Typically, geologic heterogeneity is beneficial for detecting differences in mobility among individuals; however, this degree of geologic complexity may, in fact, hamper our ability to identify differences in mobility among taxa at Ampasambazimba (**Figures 2**, **4**). Even the *Eulemur* with an elevated Sr isotope ratio could easily have spent much of its life foraging on one or more of these older geologies before meeting its demise at Ampasambazimba. It may have moved to the site on its own, or have been deposited by a predator, such as the crowned eagle (*Stephanoaetus mahery*), which has previously been implicated in the accumulation of lemur remains at the site (Goodman, 1994).

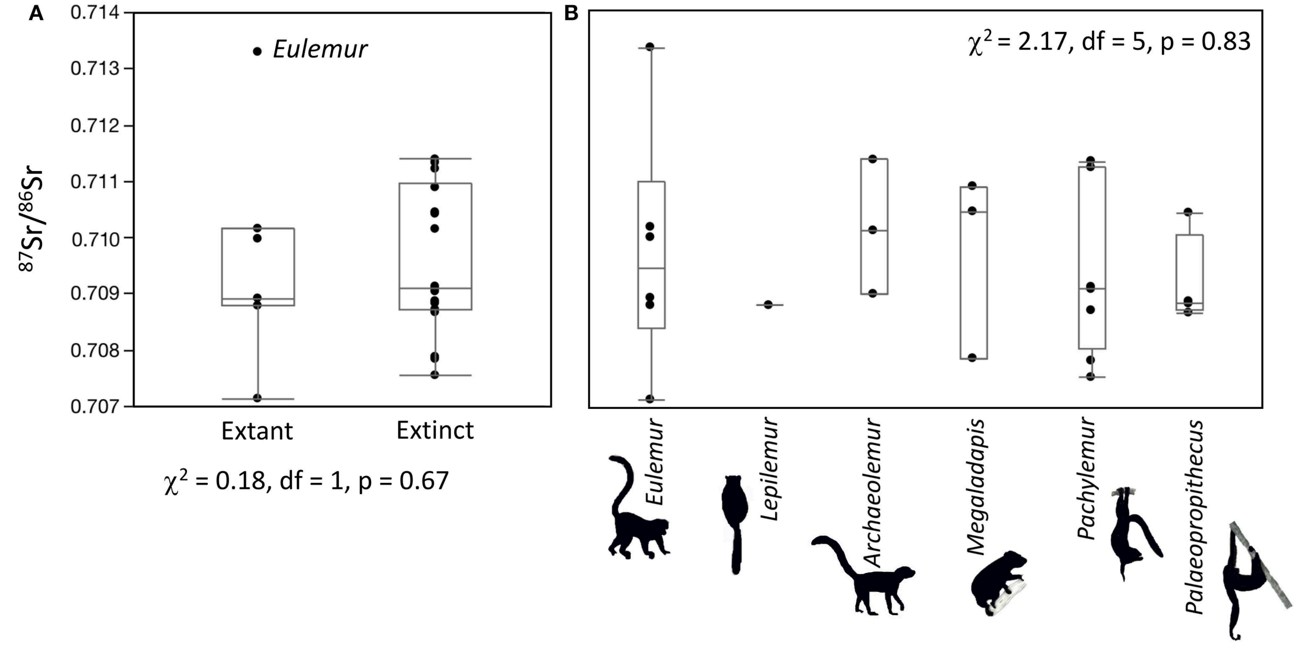

FIGURE 2 | Box plots comparing extinct and extant lemurs **(A)** and all genera **(B)** at Ampasambazimba. Statistical results do not change if the outlier *Eulemur* is excluded ($\chi^2 = 0.51$, df = 1, $p = 0.47$, and $\chi^2 = 9.75$, df = 6, $p = 0.14$, respectively).

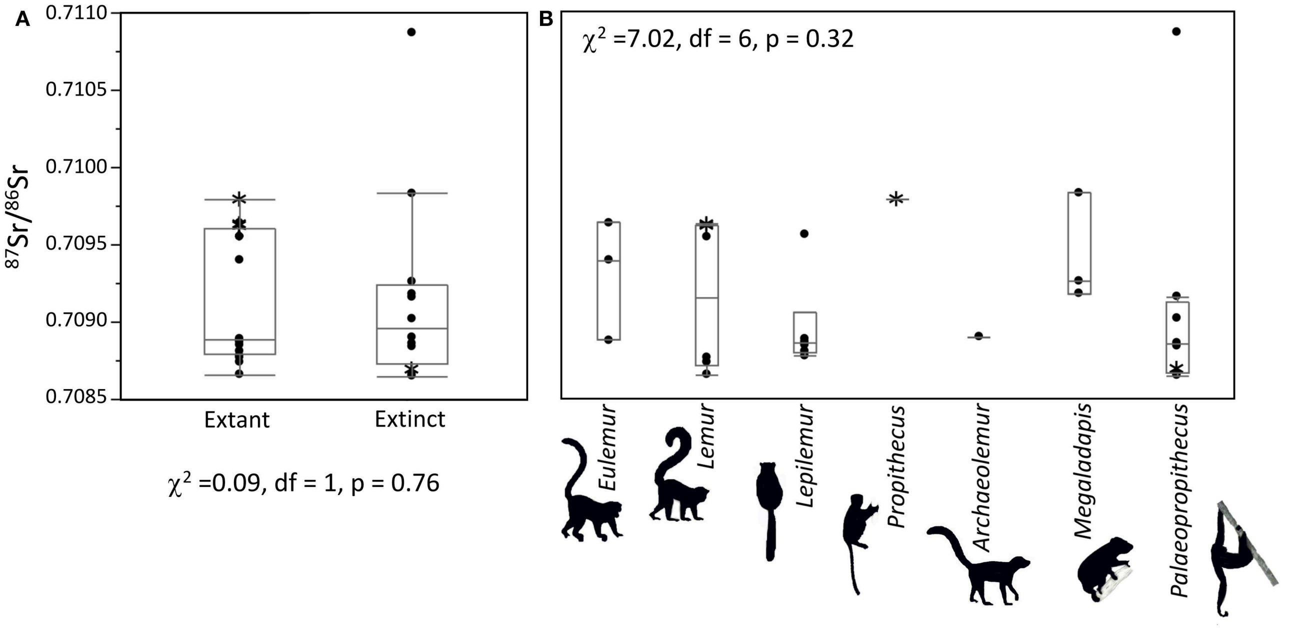

FIGURE 3 | Box plots comparing extinct and extant lemurs **(A)** and all genera **(B)** at Ankilitelo/Mikoboka. Statistical results do not change if the outlier *Palaeopropithecus* is excluded ($\chi^2 = 1.14$, df = 1, $p = 0.29$, and $\chi^2 = 2.95$, df = 5, $p = 0.71$, respectively). Asterisks (*) indicate material from non-Ankilitelo sinkholes on the Mikoboka plateau.

The story at Ankilitelo/Mikoboka is rather different. Here, the geology is much more homogenous, and overall variability in ^{87}Sr/^{86}Sr is quite low (**Figures 3**, **4**). Curiously, the distribution of strontium isotope ratios at Ankilitelo/Mikoboka is apparently bimodal. This is most obvious for extant lemurs, but it also holds for *Megaladapis* and *Palaeopropithecus*. Small apparent isotopic differences may reflect resource partitioning. Extant sympatric lemurs do this by feeding at different times or heights within the forest canopy, or targeting different species of plants (e.g., Ganzhorn, 1988; Wright et al., 2011). Today the habitat surrounding both Ankilitelo and Ampasambazimba is degraded and ruderal vegetation dominates. However, this is likely a relatively recent phenomenon. On the basis of faunal comparisons, Muldoon (2010) argued that vegetation at Ankilitelo during the Late Holocene was similar to succulent woodland or spiny thicket (both of which are native biomes in the region today; Burgess et al., 2004). This type of vegetation would have made it challenging for larger-bodied arboreal folivores, like *Megaladapis* and *Palaeopropithecus*, to feed at different canopy heights. However, it seems quite likely that they would have targeted different food species, as extant folivores do today (Ganzhorn, 1988; Warren, 1997; Thalmann, 2006). They may also have spatially segregated where they foraged. Either of these scenarios could result in isotopic differences between lemur taxa. First, co-occurring species of trees may have slightly different ^{87}Sr/^{86}Sr due to differences in rooting depth and nutrient cycling (Poszwa et al., 2004). Second, although the geology of the Mikoboka Plateau is relatively homogenous, there is still some lithologic variability. For example, the primary geology is Eocene limestone ("e4"; **Figure 1**), but sandstone is also present within this stratigraphic unit (Roig et al., 2012). Moreover, there is a mapped outcrop of Quaternary hardground (Qcs) not far from Ankilitelo (**Figure 1**), and it is highly likely that additional unmapped smaller outcrops are present in the vicinity of the sinkholes. Both sandstone and Qcs would be expected to have higher ^{87}Sr/^{86}Sr than Eocene limestone given that they are comprised of sediments derived from a variety of sources (Crowley et al., 2015). Strontium isotope ratios <0.708 would be consistent with foraging on Eocene limestone (Mcarthur et al., 2001), while ratios larger than this likely reflect input from either sandstone or Quaternary deposits.

Given that multiple lines of evidence suggest sloth lemurs had small ranges, it seems unlikely that the individual *Palaeopropithecus* with an elevated ^{87}Sr/^{86}Sr moved a great distance before meeting its demise at Ankilitelo. There are at least two explanations that would not necessarily require long distance ranging for this individual. First, the ratio for this individual (0.71085) could be consistent with foraging on local Quaternary sediments (e.g., Qcs). Yet if this were the case, we might expect at least some other individuals to also have similarly elevated ^{87}Sr/^{86}Sr. Second, like the *Eulemur* from Ampasambazimba, it is possible that this *Palaeopropithecus* was transported to Ankilitelo by a predatory bird. Raptors are among the most common taxa represented in the subfossil material from Ankilitelo, and it has been suggested that the sinkhole was used as a roosting and nesting location (Goodman et al., 2013). Most of the remains recovered belong to smaller-bodied hawks, kites, and owls that would not be able to carry a

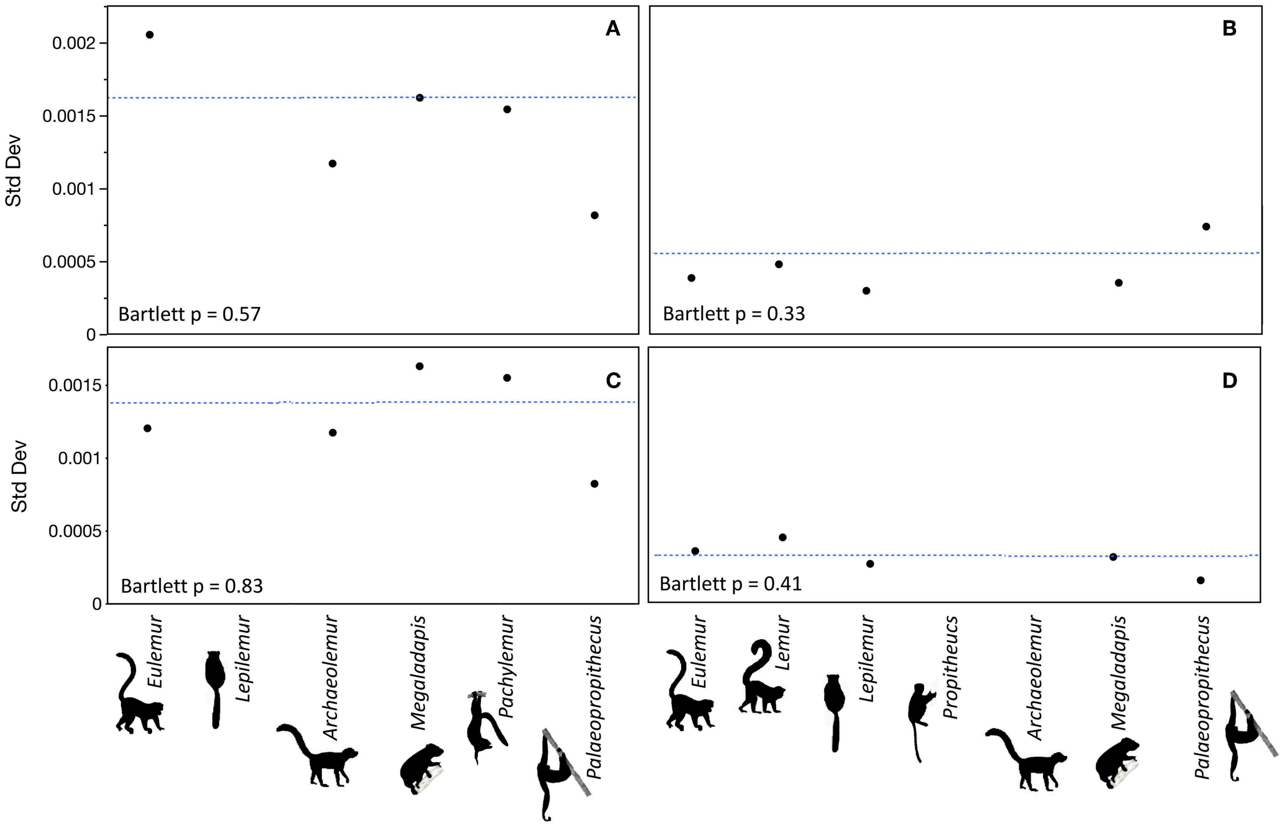

FIGURE 4 | Standard deviations of ^{87}Sr/^{86}Sr for each genus at Ampasambazimba **(A)** and **(C)** and Ankilitelo/Mikoboka **(B)** and **(D)**. The dashed blue lines in each panel indicate the average for all taxa. Outliers are included in **(A)** and **(C)** and excluded in **(B)** and **(D)**.

quarry as large as *Palaeopropithecus*. However, remains of at least one extinct crowned eagle (*Stephanoaetus mahery*) have also been recovered from Ankilitelo (Goodman and Muldoon, 2016). This species was considerably larger than still-extant raptors, and likely larger than its living congener, the African crowned eagle, which regularly predates primates up to ca. 12 kg (Goodman, 1994; Mitani et al., 2001; Mcgraw, 2006). Although *S. mahery* likely preferred taxa <25 kg, taphonomic evidence indicates that it was capable of eating extinct lemurs as large as *Megaladapis edwardsi* (the second largest extinct lemur; Meador et al., 2019).

In summary, ^{87}Sr/^{86}Sr data support comparable mobility for extinct and extant lemurs. This finding contradicts expectations based on body size, but is compatible with other lines of evidence that suggest these extinct taxa were relatively anchored (e.g., Walker et al., 2008; Hogg et al., 2015). Compared to like-sized anthropoids, the extinct lemurs have considerably smaller semi-circular canals, endocranial volume, and lower Retzius Periodicity (Walker et al., 2008; Catlett et al., 2010; Hogg et al., 2015).

Palaeopropithecus, in particular, is thought to have been very slow and sloth like (reviewed in Walker et al., 2008). Elongated forelimbs and curved phalanges demonstrate that it was skilled at below-the-branch quadrupedal suspension (Jungers et al., 2002; Godfrey et al., 2016b) and its semicircular canal radius is comparable to *Lepilemur* (an animal that weighs ∼1 kg). If we exclude the single *Palaeopropithecus* at Ankilitelo/Mikoboka with an elevated ^{87}Sr/^{86}Sr, we note that this genus has apparently smaller variance than co-occurring taxa at both sites, perhaps on par with *Lepilemur* (**Figures 2**, **3**).

What Are the Consequences of Small Home Ranges?

Both living and extinct Lemuriformes appear to differ from anthropoid primates in their relatively depressed basal metabolism, small brains, low Retzius Periodicity, and reduced activity levels. Collectively, this suite of traits serves to reduce energetic expenditure, and likely developed so lemurs can cope with living in the harsh environments that characterize Madagascar (Wright, 1999; Godfrey et al., 2006; Hogg et al., 2015).

Unfortunately, these same traits may make lemurs more vulnerable to extinction. Home range size is often used as a parameter in evaluating extinction risk for a species. Specifically, species with limited mobility are more threatened by habitat fragmentation than species with greater mobility, and large-bodied species are more threatened by habitat fragmentation than small-bodied ones (Haskell et al., 2002). However, diet, resource density and resource distribution also play a role. Frugivores are more vulnerable than folivores because of differences in the distribution of preferred food resources; indeed, folivore population density may even increase following low- or medium-level disturbances such as cyclones, because young foliage tends to increase as pioneer species fill light gaps caused by the destruction of older fruit-producing trees (Johns and Skorupa, 1987).

Given this, it is, perhaps, unsurprising that larger-bodied and frugivorous lemurs are the ones to have disappeared first. Unfortunately, their extinction has reverberating consequences. Globally, the loss of large-seed dispersal services is one of the most challenging problems facing conservationists in the wake of recent megafaunal extinctions (Corlett, 2013), and this is particularly challenging in places like Madagascar, where these services may have been marginal prior to the loss of the largest-bodied species. The size of the primate frugivore guild on Madagascar is small (Fleagle and Reed, 1996; Goodman and Ganzhorn, 1997). Climatic unpredictability and hypervariability have been posited as contributing to this (Wright, 1999; Wright et al., 2005; Dewar and Richard, 2007). Madagascar also has extended dry or lean seasons which can result in erratic fruiting, and a high frequency of cyclones, which can be extremely destructive to older fruiting trees. Furthermore, at any single point in time, fruit is generally less abundant in Madagascar than it is in other places that are home to many primate species (Federman et al., 2017). Additionally or alternatively, it appears that low levels of fruit nitrogen are responsible for the poor representation of frugivores in Madagascar's primate community (Ganzhorn et al., 2009; Donati et al., 2017; Federman et al., 2017). This argument is grounded in the observations, not merely that the fruits of Madagascar have low nitrogen content, but also that such fruits cannot meet the protein requirements of primates during critical times of the year such as the reproductive season.

What is less clear is the extent to which large, fruit-bearing trees and their seed dispersers were better represented in the recent past, the degree to which they face disproportionate extinction risk in the future, and the degree to which that risk depends on the survival of primates. Although Madagascar today has an unusually low number of plant species that disperse their seeds via endozoochory, most of those that do rely on endozoochory have adaptations to attract primates rather than birds (Albert-Daviaud et al., 2018). This is particularly the case for trees with large seeds (Razafindratsima et al., 2018). Thus, the primate frugivore guild plays a very important role in seed dispersal. Threats to plant communities in Madagascar are compounded by the facts that: (1) the primate frugivore guild on Madagascar is increasingly dominated by species too small to disperse large seeds (Richard and Dewar, 1991; Federman et al., 2016); and (2) still-extant seed-dispersing lemurs (i.e., those more likely to pass seeds whole and undamaged through the gut; Dew and Wright, 1998; Razafindratsima and Martinez, 2012) have small seed-dispersal distances in comparison to like-sized frugivores on other continents (Razafindratsima et al., 2014). When seed dispersers have limited home ranges, the plant community as a whole may be more vulnerable to habitat disturbance, and therefore at greater risk of entering into an extinction vortex. The problem is not merely that the loss of key seed dispersers may result in an increase in the number of "orphaned" plants (those lacking seed dispersers; Bollen et al., 2004; Godfrey et al., 2008; Crowley et al., 2011; Buerki et al., 2015; Albert-Daviaud et al., 2018), but also that the plant species most likely to become orphaned are the trees with the highest above-ground biomass, and therefore the greatest capacity to store carbon. They are precisely the trees that contribute the most to climate stability and the health of the entire ecosystem (Razafindratsima et al., 2018). With this in mind, it is imperative that remaining forest cover be protected and that connectivity among fragments be improved.

DATA AVAILABILITY STATEMENT

The dataset analyzed for this study can be found in **Supplementary Table 1**.

AUTHOR CONTRIBUTIONS

BC and LG conceived of the project. BC prepared samples and conducted the data analysis. Both authors wrote the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2019.00490/full#supplementary-material

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