EARLY HUMAN COLONIZATION OF REMOTE INDIAN OCEAN ISLANDS AND ITS ECOLOGICAL IMPACTS

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EARLY HUMAN COLONIZATION OF REMOTE INDIAN OCEAN ISLANDS AND ITS ECOLOGICAL IMPACTS

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EDITORIAL
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Editorial: Early Human Colonization of Remote Indian Ocean Islands and Its Ecological Impacts

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Keywords: migration, colonization, biodiversity, environmental change, human habitation

Editorial on the Research Topic

Early Human Colonization of Remote Indian Ocean Islands and Its Ecological Impacts

The remote islands of the tropical Indian Ocean (Madagascar, Comoros, Mascarenes, Seychelles, Chagos, Maldives, Cocos, and Christmas Island) lie >250 km from continental shores. As a result, their systematic colonization required offshore seafaring that began 4,000 bp. Despite this capability, many islands remained uninhabited 500 years ago, and histories of habitation and environmental change upon others remain conspicuously uncertain among those of oceanic islands generally (Anderson et al., 2018a). Our topic considered the relationships of colonization timing and substantial ecological change. The conjunction of these highlights the fundamental issue of distinguishing natural from cultural causation in ancient sedimentary, ecological and taphonomic phenomena.

Insular distribution of commensal animals can elucidate sources of human migration. Rocha et al. used historical records and DNA from modern and museum samples to explore the distribution and dispersal patterns of house geckos. Their results demonstrate how animals can be used as proxies to identify possible pre-European migration routes. Thomson et al. found that black rats of historical age on Christmas Island were from Southeast Asia, while those on the Cocos Islands had widespread origins. Multiple and continuing introductions of rats and geckos, however, have obscured older patterns require additional research. Recurrent human colonization of Mauritius discussed by Seetah et al. showed how colonialism drove demographic and ecological processes of environmental degradation. Albert et al., compared historical vertebrate extinction between Mauritius and Reunion and found greater extinction on Reunion was associated with faster loss of lowland forest.

Most contributions focused upon Madagascar, where the age (or ages) of human colonization have profound implications for understanding trajectories of anthropogenic ecological change there, and for the timing of maritime migration and colonizing horizons elsewhere in the Indian Ocean. On the basis of archaeological evidence, human genetics and historical linguistics, habitation of Madagascar began around 1,400 bp with a predominantly Austronesian population of agriculturalists. In palaeoecological rainforest data extending to 3,000 bp in NW Madagascar, Reinhardt et al., found no evidence of cultural intervention before 1,350 bp (cf. Tofanelli et al.). Domic et al. showed that forest loss and megafaunal extinctions in SW Madagascar, 1,150–550 bp were associated with intensified burning that reflected a drying climate and pastoral activities. Hixon et al. dissected the pastoral impact with respect to introduced dogs that competed with endemic predators and were used in cultural hunting.

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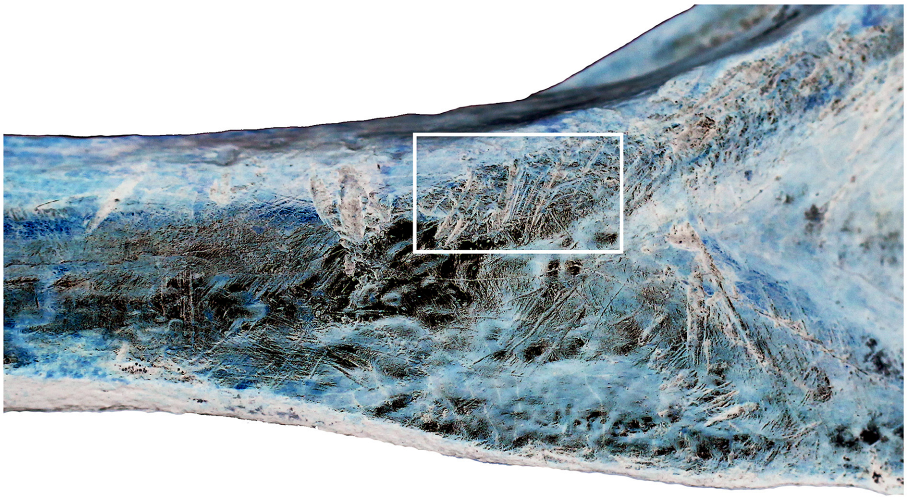

FIGURE 1 | OUM 14342A, *Palaeopropithecus ingens* distal humerus (L) adjusted in Adobe Photoshop to highlight areas with bone damage. Perez et al. (2005) "cut marks" enclosed by white rectangle, but note similar and extensive damage elsewhere that is probably non-cultural (Copyright Anderson and Clark).

An alternative scenario envisages early Holocene occupation of Madagascar by African foragers, as proposed by Godfrey et al., although they considered late Holocene megafaunal losses in the southwest to be drought-associated, and attributed the island-wide collapse of endemic vertebrates at 1,200–900 bp to the advent of agropastoralism. Possible areas of transient occupation in SW Madagascar, identified by remote sensing, were considered by Davis and Douglass as up to 3,000 years old, although they acknowledged the difficulty of identifying foraging in a scarcity of direct evidence (see also Reinhardt et al.). Madagascan colonization much earlier than 2,000 bp, was argued partly from landscape and ecological changes, but based most problematically upon radiocarbon-dated megafaunal bones exhibiting bone damage assumed as anthropogenic.

Potential cut-marks on *Aepyornis* (elephant bird) bones dated 10,000 bp (Hansford et al., 2018) were on facets almost inaccessible during articulation and it is unlikely that, after butchery, the bones were replaced in association as found. Moreover, the clearest marks cut through a surficial stain profile into cleaner bone beneath, indicating damage that could not have been perimortem and must have occurred much later. In this case, and others where local people were employed to excavate, their customary use of sharp implements was the most plausible explanation. Mitchell (2020) pointed to additional flaws in the ancient butchery hypothesis. In the largest systematic study of newly-excavated megafaunal bone in Madagascar, Anderson et al. (2018b) found abundant evidence of taphonomic damage by trampling, scavenging and other agencies but an extremely low incidence of possible butchery and no older than the late first millennium AD. Earlier analysis of Madagascan megafaunal samples (e.g., Perez et al., 2005) had seldom identified the full extent and variety of bone damage on specimens believed to be cut-marked (**Figure 1**). Better identification of bone-damage origins is an important problem in archaeology and paleontology and currently under technical review (e.g., Cifuentes-Alcobendas and Domíngez-Rodrigo, 2019).

Competing hypotheses of relatively early or late human colonization of islands, with premises based alternatively upon archaeological or palaeoenvironmental data, have arisen in the North Atlantic, Caribbean, and East Polynesia. Interdisciplinary research in those regions has substantially reduced chronological spans in dispute, and contributions included here form part of an analogous endeavor for the Indian Ocean.

AUTHOR CONTRIBUTIONS

AA conceived and led this publication. GC, SH, GL, and KS provided intellectual contributions and reviewed the manuscript. All authors approved it for publication.

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Ecological Consequences of a Millennium of Introduced Dogs on Madagascar

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Introduced predators currently threaten endemic animals on Madagascar through predation, facilitation of human-led hunts, competition, and disease transmission, but the antiquity and past consequences of these introductions are poorly known. We use directly radiocarbon dated bones of introduced dogs (*Canis familiaris*) to test whether dogs could have aided human-led hunts of the island's extinct megafauna. We compare carbon and nitrogen isotope data from the bone collagen of dogs and endemic "fosa" (*Cryptoprocta* spp.) in central and southwestern Madagascar to test for competition between introduced and endemic predators. The distinct isotopic niches of dogs and fosa suggest that any past antagonistic relationship between these predators did not follow from predation or competition for shared prey. Radiocarbon dates confirm that dogs have been present on Madagascar for over a millennium and suggest that they at least briefly co-occurred with the island's extinct megafauna, which included giant lemurs, elephant birds, and pygmy hippopotamuses. Today, dogs share a mutualism with pastoralists who also occasionally hunt endemic vertebrates, and similar behavior is reflected in deposits at several Malagasy paleontological sites that contain dog and livestock bones along with butchered bones of extinct megafauna and extant lemurs. Dogs on Madagascar have had a wide range of diets during the past millennium, but relatively high stable carbon isotope values suggest few individuals relied primarily on forest bushmeat. Our newly generated data suggest that dogs were part of a suite of animal introductions beginning over a millennium ago that coincided with widespread landscape transformation and megafaunal extinction.

Keywords: radiocarbon dating, δ15N, δ13C, exclusion competition, predation, fosa, extinction, bushmeat

INTRODUCTION

Madagascar is a biodiversity hotspot that has repeatedly faced a variety of biological invasions over the past millennium (Middleton, 1999; Kolby, 2014; Hixon et al., submitted). A debate regarding when humans first arrived on Madagascar is ongoing, with some researchers favoring early human arrival 10,000–4,000 years ago based on rare stone tools and cutmarks on ancient elephant bird bone (Dewar et al., 2013; Hansford et al., 2018), and other researchers favoring recent arrival 1,600–1,000 years ago based on broader cultural considerations (Anderson et al., 2018). Endemic vertebrates >10 kg declined by ∼950 years ago (Crowley, 2010), and over half of the island's surface is currently dedicated to pastoralism that involves introduced zebu cattle (Anonymous, 2003). Hunting, deforestation, and regional aridification help explain aspects of past extinctions (Burney et al., 2004; Virah-Sawmy et al., 2010; Crowley et al., 2017; Anderson et al., 2018; Hixon et al., 2018; Godfrey et al., 2019; Faina et al., 2021; Godfrey and Douglass, 2021), and interactions with introduced species (e.g., livestock, rodents, and predators) could have exacerbated these stressors (Dewar, 1997; Hixon et al., submitted). Globally, changes in human land use (i.e., the spread of pastoralism and commensal species) generally coincide with past environmental transformations (Stephens et al., 2019) that contribute to biotic homogenization (McKinney, 1997; McKinney and Lockwood, 1999). As part of this transformation, introduced predators can disrupt island ecosystems by facilitating human hunting, creating novel predation pressure, and competing with other predators (e.g., competition between dingoes and red foxes in Australia; Cupples et al., 2011), yet we know very little about the antiquity of introduced predators on Madagascar.

We use radiocarbon (^{14}C) and stable isotope (δ^{13}C and δ^{15}N) data from bone collagen to test the following hypotheses: (1) introduced dogs (*Canis familiaris*) preyed on lemurs, and (2) dogs competed with the island's largest endemic carnivores (*Cryptoprocta* spp., the fosa). Limited chronological overlap (as inferred from directly ^{14}C-dated dog and lemur bones) would reduce the potential for dogs to have aided hunting of extinct lemurs, and lack of isotopic niche overlap among dogs and *Cryptoprocta* spp. would diminish the potential for direct forms of competition. However, lack of dietary overlap would not necessarily exclude the possibility that dogs interacted aggressively with *Cryptoprocta* spp. or facilitated human-led hunts of prey that *Cryptoprocta* spp. also hunted. This work expands our understanding of both past megafaunal extinction and modern functional diversity of predators on Madagascar.

Madagascar's endemic family of carnivorans (Eupleridae) includes ten extant species that range in size from the ∼550 g broad-striped vontsira (*Galidictis fasciata*) to the ∼8.5 kg fosa (*Cryptoprocta ferox*, Wampole et al., 2021). The so-called "cave" fosa (*Cryptoprocta spelea*, thought to be extinct) was likely double the size of *C. ferox* (Goodman et al., 2004) and may still exist in remote parts of northern Madagascar (Nomenjanahary et al., 2021). All members of Eupleridae are currently threatened, and the IUCN red list currently includes *C. ferox* as vulnerable due to rapid population decline (Hawkins and Racey, 2008). Introduced mammalian predators include dogs, cats (*Felis* spp.), and the small Indian civet (*Viverricula indica*, **Figure 1**), yet only relatively large predators (dogs and *Cryptoprocta* spp.) are reasonably well represented in Madagascar's subfossil record (Rakotozafy and Goodman, 2005; Crowley, 2010). It is not known when dogs first colonized the island (**Figure 2**, Crowley, 2010; Douglass et al., 2019), and traces of predation by dogs on subfossil bones (e.g., gnaw marks) are understudied and possibly cryptic (Brockman et al., 2008). A rare set of cave rock drawings in western Madagascar may depict a hunting scene that includes dogs, an extinct sloth lemur, and symbols that have parallels from around the Indian Ocean, but the age of these drawings is uncertain (Burney et al., 2020). Madagascar's modern dogs have primarily African ancestry (Ardalan et al., 2015), which is consistent with the Bantu origin of the most common Malagasy word for dog (amboa, Blench, 2008).

Dog diet on Madagascar is poorly characterized. Modern and historic surveys suggest dogs rely heavily on plant and animal scraps in human derived food waste (Decary, 1939; Kshirsagar et al., 2020). Yet dogs are also known to stalk lemurs (Brockman et al., 2008) and help humans hunt a variety of bushmeat (**Supplementary Dataset 2**, Decary, 1939; Garcia and Goodman, 2003; Gardner and Davies, 2014). Dogs in at least SW and NW Madagascar currently subsist largely on food scraps, and people often feed hunting dogs the innards of bushmeat (Godfrey et al., submitted, Thompson and Borgerson, pers. comm.). Dogs are popular protection animals around Ranomafana National Park, in central Madagascar (Kshirsagar et al., 2020). However, dogs can also transmit rabies and form a general nuisance while they scavenge (Rajeev et al., 2019). Some dog owners have reported that their dogs harass and kill *C. ferox* around Ranomafana (Valenta et al., 2016; Kshirsagar et al., 2020). Data from live traps and camera traps suggest that *C. ferox* avoids dogs in several national parks (**Figure 1**), which may follow from a combination of aggressive interactions and disease transmission (Dollar et al., 2007; Barcala, 2009; Gerber et al., 2012; Farris et al., 2015; Pomerantz et al., 2016; Rasambainarivo et al., 2017; Merson et al., 2019a). For example, *C. ferox* is typically cathemeral, yet individuals around Ankarafantsika in the NW and Masoala–Makira in the east tend to be primarily nocturnal, where dogs are active during the dawn and day (Farris et al., 2015; Merson et al., 2019a). Additionally, *C. ferox* captures increased following the euthanasia of dogs at Ankarafantsika (Barcala, 2009), which suggests that interactions involving dogs affect both *C. ferox* abundance and activity patterns.

Madagascar's modern dogs have at least some dietary overlap with *C. ferox* that creates potential for exploitation competition (Farris et al., 2017; Merson et al., 2019a). Data from modern kill sites and *C. ferox* scat from multiple ecoregions in Madagascar indicate that they are opportunistic predators with the potential for heavy reliance on lemurs (**Supplementary Dataset 3**, Rasoloarison et al., 1995; Wright et al., 1997; Goodman et al., 1997; Dollar et al., 2007; Hawkins and Racey, 2008). Modern *C. ferox* and dogs are both known to consume sifakas (e.g., *Propithecus verreauxi*), tenrecs, rodents, birds (e.g., chicken and coua), frogs, snakes, and scraps of bushpigs and

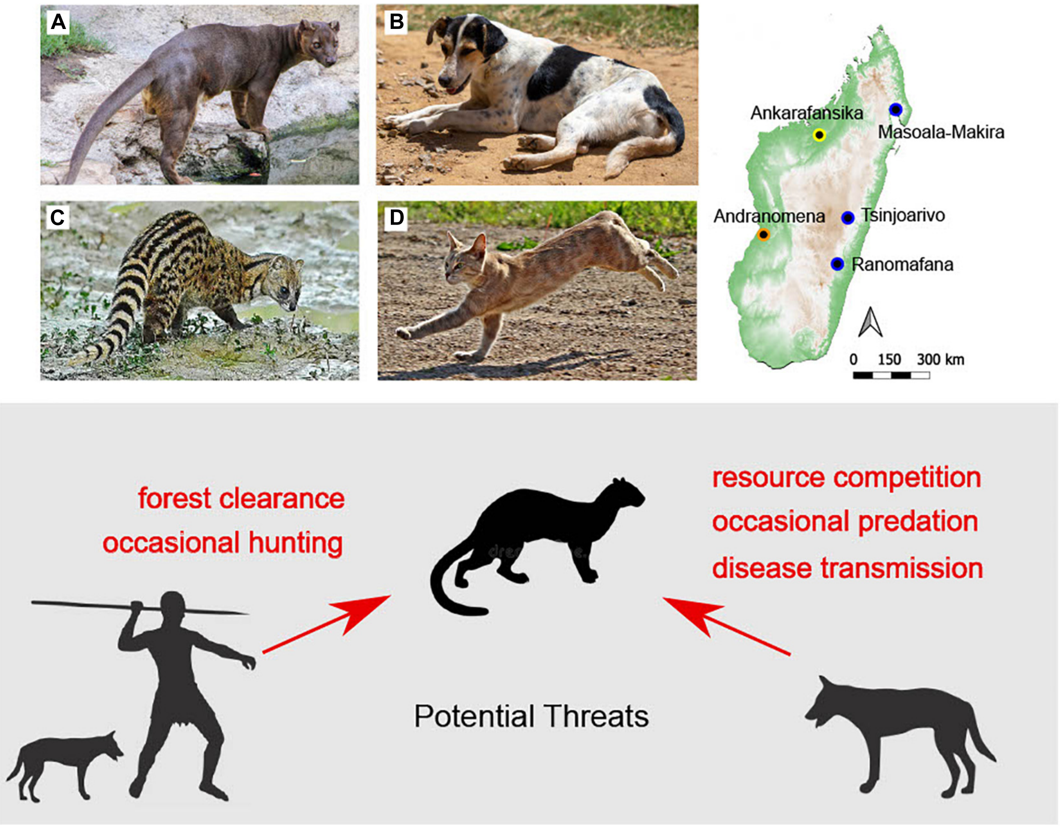

FIGURE 1 | Endemic fosa (**A**, *Cryptoprocta ferox*) may interact with introduced dogs (**B**, *Canis familiaris*), Indian civets (**C**, *Viverricula indica*), and cats (**D**, *Felis* sp.). National parks discussed in the text where antagonistic interactions between introduced and endemic predators have been observed are shown in the map at right. The ecoregion for each park is denoted using colors (orange = succulent woodland, yellow = dry deciduous forest, blue = central highlands and humid forest). Human and introduced predator threats to *C. ferox* are summarized in shaded area below.

zebu cattle (**Figure 2**, Decary, 1939; Rasoloarison et al., 1995; Goodman et al., 1997; Brockman et al., 2008; Hawkins and Racey, 2008; Gardner and Davies, 2014; Valenta et al., 2016). There is no published evidence for omnivory by *C. ferox* beyond possible occasional fruit consumption as a source of water during the dry season (Hawkins and Racey, 2008). Dogs raid bird and reptile nests and can engage in devastating amounts of surplus killing. Though they are typically more inefficient hunters than wild canids (Butler et al., 2004; Serpell and Barrett, 2017), their impacts can still be considerable. For example, a single stray dog killed hundreds of North Island brown kiwis (*Apteryx mantelli*, >50% of the local population) in New Zealand within a couple of months (Taborsky, 1988). The dramatic impact that dogs can have on their prey may diminish prey for *C. ferox*.

Exclusion competition between dogs and *C. ferox* follows from the potential for aggressive encounters and occurs regardless of impacts on prey populations. Dogs are avid chasers that contribute to habitat fragmentation by inducing fear and avoidance in a wide range of animals (Lenth et al., 2008; Young et al., 2011; Ritchie et al., 2014). Dogs associated with human hunters increase the potential for exclusion competition with native predators throughout Madagascar. Some evidence of the past association of dogs with human hunters (Burney et al., 2020) suggests that there may be a history of exclusion competition between dogs and *Cryptoprocta* spp.

Radiocarbon and stable isotope data from bone collagen can give a long-term perspective on predator interactions and clarify past and ongoing processes that influence endemic biodiversity. Based on the potential association of dog bones with extinct megafauna from paleontological sites (Douglass et al., 2019), we expect some chronological overlap among these animals. We also expect some overlap in dog and *Cryptoprocta* spp. isotope values. Animals with similar diets that forage in similar habitats have tissues with similar $\delta^{13}C$ and $\delta^{15}N$ values (reviewed in Crawford et al., 2008). Carbon isotope values predominantly reflect the plants at the base of the food web (Farquhar et al., 1989; Marshall et al., 2007). Plants that use the C_3 photosynthetic pathway (primarily trees, shrubs, and herbs) tend to be depleted in ^{13}C by over 10‰ relative to plants that use the C_4 pathway (primarily grasses) or the CAM pathway (primarily succulents). Data from sympatric C_3, C_4, and CAM plants from SW Madagascar reflect this difference, with combined CAM and C_4 plant tissue ($\delta^{13}C$ $\mu \pm \sigma = -12.8 \pm 1.6$‰) enriched in ^{13}C by ~15‰ relative to C_3 plant tissue ($\mu \pm \sigma = -27.2 \pm 2.3$‰, Hixon et al., submitted). To a lesser extent, plant $\delta^{13}C$ values also depend on variables such as canopy cover, moisture availability, salinity, and soil microbe

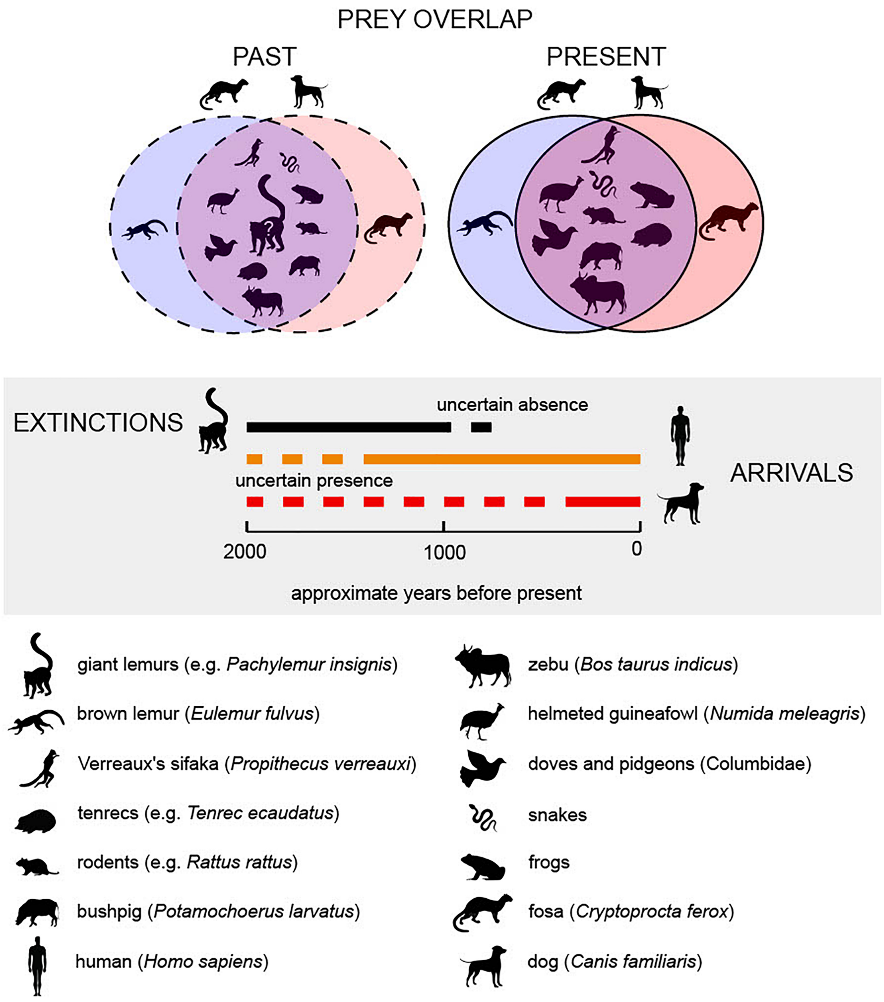

FIGURE 2 | Overlaps in dog and *C. ferox* diet (top) and chronology of extinctions and arrivals as understood before the present study (center, shaded, with uncertain occurrence prior to this publication marked with dashed lines). The spread of dogs (red bar) to Madagascar before European contact (~500 BP) has been poorly documented, and it is unknown whether they overlapped chronologically with extinct megafauna such as giant lemurs (black bar). Dogs and *C. ferox* currently scavenge and prey on many of the same animals (see inexhaustive list at bottom), but the antiquity of this dietary overlap is unknown (dashed lines). Before the present study, it was unknown whether past dogs preyed on extinct giant lemurs, yet there are abundant traces of human and mammalian carnivoran predation on extinct giant lemurs. Note that examples of exclusively dog or *C. ferox* prey are token and do not represent the diversity of predator-specific diets (see **Supplementary Datasets 2, 3**).

respiration (reviewed in Farquhar et al., 1989). These patterns are passed on to herbivores and higher order consumers over time. If both dogs and *Cryptoprocta* spp. consumed forest-dwelling herbivores (such as most of the island's extinct megaherbivores), then we would expect overlap in collagen δ^{13}C values among these groups (Godfrey and Crowley, 2016). Alternatively, if dogs regularly consumed scraps of introduced grazers (e.g., zebu cattle and ovicaprids), then we would expect dogs to have relatively high collagen δ^{13}C values and minimal overlap with *Cryptoprocta* spp.

We also expect overlap in collagen δ^{15}N values among co-occurring dogs and *Cryptoprocta* spp. Consumer tissues tend to be enriched in ^{15}N relative to diet such that each increase in trophic level corresponds to a 3–5‰ increase in collagen δ^{15}N values (Cleland, 2001; McCutchan et al., 2003; Hyodo et al., 2010). As secondary consumers, dogs and *Cryptoprocta* spp. should have comparable δ^{15}N values, though omnivory or the preferential consumption of certain prey tissue (e.g., intestines) may reduce dog δ^{15}N values relative to *Cryptoprocta* spp. δ^{15}N values (Reid and Koch, 2017). Soil nitrogen cycling also strongly influences ecosystem δ^{15}N values and is sensitive to moisture availability (Austin and Vitousek, 1998), so both plant and consumer δ^{15}N values vary considerably among ecoregions in Madagascar (Crowley et al., 2011). Specifically, values are highest in the xerophytic spiny thicket in SW Madagascar and lowest in the humid forests in the east and north. There can also be pronounced differences among microhabitats in the same region (Crowley et al., 2012, 2014; Heck et al., 2016). Plants and animals living on saline coastal soils that are influenced by marine-derived nitrates may also have higher δ^{15}N values than those that live inland (Heaton, 1987; Sparks and Crowley, 2018; Mosher et al., 2020; Hixon et al., submitted). Thus, only in comparable environments can consumer δ^{15}N values be interpreted primarily in terms of diet.

MATERIALS AND METHODS

Specimen and Site Selection

Sampled dog bones come from 13 sites spread throughout Madagascar (**Figure 3** and **Supplementary Datasets 1, 4**). We sampled all available bones from existing collections ($n = 16$ subfossils + 3 modern dog bones). Most specimens ($n = 12$) are housed at the University of Antananarivo; others are curated at the National Museum of Natural History, Paris as well as Yale University, the University of Massachusetts, Amherst, and the University of California at Santa Barbara (**Supplementary Dataset 1**). These bones were collected from both archeological sites (Rezoky, Andranosoa, and Lakato'ni Gavin) and paleontological sites (e.g., Andolonomby and Tsirave) that span four of Madagascar's five major ecoregions but are concentrated in the spiny thicket and succulent woodland of the southwest (**Figure 3**). We also analyzed two subfossil *C. ferox* bones from Taolambiby that are currently housed at the Australian National University (ANU). To augment these datasets, we compiled previously published data from five dogs (includes two modern bones, Crowley, 2010; Douglass et al., 2019), nine subfossil *C. ferox* (Crowley, 2010; Crowley and Godfrey, 2013; Crowley et al., 2017; Anderson et al., 2018), and three subfossil *C. spelea* (Crowley, 2010). Note that all subfossil *Cryptoprocta* spp. come from paleontological sites and that all but one of the previously published predators (a subfossil *C. ferox*, OxA 27174) have both δ^{13}C and δ^{15}N data.

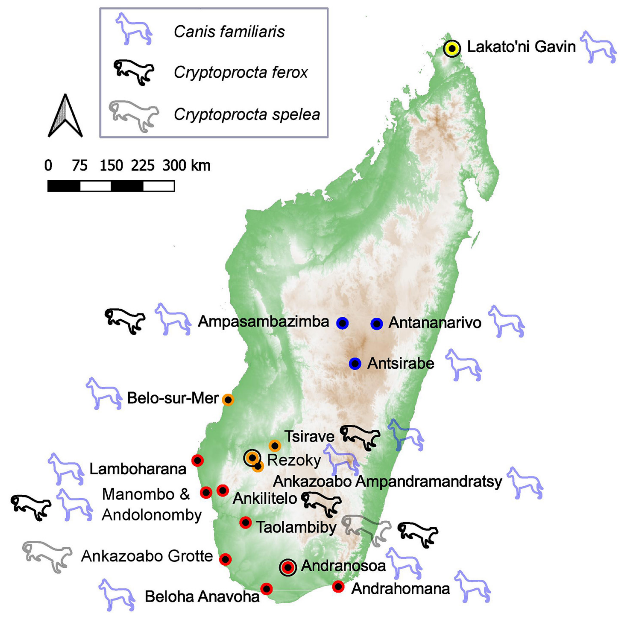

FIGURE 3 | Collection sites of dog and *Cryptoprocta* spp. bones considered in this study, with archeological sites (Lakoto'ni Gavin, Rezoky, and Andranosa) circled and sites colored according to ecoregion (red = spiny thicket, orange = succulent woodland, blue = central highlands, yellow = dry deciduous forest).

To compare an estimated time of dog introduction with hunting and extinction chronologies (see section "Data Analysis" below), we also compiled previously published ^{14}C data from butchered bone of multiple endemic taxa from SW Madagascar (extinct giant lemurs, an extant lemur consumed by *C. ferox* (*P. verreauxi*), elephant birds, and pygmy hippo, (**Supplementary Dataset 1**) and three species of giant lemurs with relatively large sample sizes ($n \geq 20$ each, *Pachylemur insignis*, *Archaeolemur majori,* and *Palaeopropithecus ingens*, all from SW Madagascar, **Supplementary Dataset 1**). We focus on the arid SW, because each ecoregion has its own chronology of species introductions and extinctions, and most existing ^{14}C datasets come from this ecoregion (Crowley, 2010; Douglass et al., 2019). We focus on comparing dog and *Cryptoprocta* spp. data with those from extinct giant lemurs, because (1) there is widespread evidence that at least *Cryptoprocta* spp. and humans preyed on these animals (Meador et al., 2019; Godfrey et al., submitted), and (2) these taxa have robust ^{14}C chronologies that suggest they disappeared at approximately the same time as other megafauna such as pygmy hippos and giant tortoises (Crowley, 2010; Hixon et al., submitted). To help infer past dog and *C. ferox* diet, we compiled published lists of prey species from across the island (**Supplementary Datasets 2, 3**). We make stable isotope comparisons involving prey taxa within the arid SW (**Supplementary Dataset 1**), and we also focus on subfossil bone, because few of our sampled specimens are modern, and some extant and introduced taxa likely shifted their diet and habitat use in response to the recent expansion of grasslands on the island (Crowley and Samonds, 2013). The previously published literature includes 298 potential prey individuals with stable isotope data from the SW, and we include unpublished records from 11 individuals in our dataset (analyzed previously by B.E.C. using approach from Sparks and Crowley, 2018). We further expanded this dataset by sampling bones from an additional 13 potential prey individuals from Taolambiby and Lamboharana/Lamboara in SW Madagascar, which brings the potential prey total to 311 individuals. During analyses, we excluded 21 previously published data from specimens that (1) lack explicit reference to bone collagen purification protocols or (2) include signs of contamination (i.e., atomic C:N > 3.5, Brock et al., 2010).

^{14}C and Stable Isotope Analyses

Pretreatment of the 31 subfossil and three modern specimens took place in the Human Paleoecology and Isotope Geochemistry Laboratory at Pennsylvania State University (PSU). Prior to demineralization, bones sampled from museum collections suspected of using ink labels and conservants/consolidants such as polyvinyl acetate must go through solvent rinses to remove exogenous carbon with distinct ^{14}C content and δ^{13}C values (France et al., 2011). We sonicated museum specimens in sequential washes of methanol (MeOH), acetone, dichloromethane (DCM), and nanopure water. Samples were sonicated in 20 mL of each fluid for 20 min. For the three modern bone samples, we removed lipids using 3× sonication in 2:1 DCM:MeOH followed by 3× rinsing in nanopure water (modified from Guiry et al., 2016).

All bones were mechanically cleaned, demineralized in 0.5 N hydrochloric acid (HCl) under refrigeration, and gelatinized in 0.01 N HCl at 60°C. Collagen from the bone of subfossil individuals was purified through ultrafiltration (14 samples, Beaumont et al., 2010; Fernandes et al., 2021) or purification with XAD resin (17 samples, **Supplementary Dataset 1**, Stafford et al., 1988, 1991; Lohse et al., 2014). When collagen is relatively intact and yields are high, ultrafiltration can purify a sample by mechanically removing the smaller (<30 kDa) fraction, which includes degraded collagen and exogenous contaminants (Higham et al., 2006). When collagen is stained or degraded, the relatively less polar contaminants (humates, in particular) can be separated chromatographically by passing the hydrolyzed sample through a column filled with XAD resin (Stafford et al., 1988).

Stable isotope data were obtained at Yale University's W.M. Keck Biotechnology Resource Laboratory, the University of Cincinnati's Stable Isotope Laboratory, and the University of New Mexico's Center for Stable Isotopes (**Supplementary Dataset 1**). Secondary standards from each lab were used to correct data using two-point normalization, and the mean accuracy of $\delta^{13}C$ and $\delta^{15}N$ measurements across runs was $\leq 0.3‰$. Standard quality assurance data indicate that the mean precision of $\delta^{13}C$ and $\delta^{15}N$ measurements across runs was ≤ 0.3 and $\leq 0.2‰$, respectively.

We confirmed sample quality and collagen preservation using percent collagen yield, atomic C:N, $\delta^{13}C$ values, and $\delta^{15}N$ values prior to AMS ^{14}C measurement (DeNiro, 1985; Van Klinken, 1999; Beaumont et al., 2010; Kennett et al., 2017). Residual contaminants can have distinct C:N and stable isotope values, and this was the case for one sample (a dog from Rezoky, sample ID "615," which was not dated and not further considered; see **Supplementary Dataset 1**). We graphitized collagen from the remaining 30 subfossil specimens at PSU and submitted graphite for ^{14}C analysis at the Pennsylvania State University AMS facility and UC Irvine's W.M. Keck Carbon Cycle AMS (**Supplementary Dataset 1**).

Data Analysis

We calibrated radiocarbon dates in OxCal 4.4 using the Southern Hemisphere calibration curve SHCal20 (Hogg et al., 2020), or the post-bomb atmospheric SH3 curve (Hua et al., 2013) for three dogs that yielded > ^{14}C modern ages (**Supplementary Dataset 1**). We used both classical frequentist and Bayesian statistical approaches to event estimation to compare estimated times of dog introduction and lemur extinctions (Buck and Bard, 2007; Bradshaw et al., 2012).

Our Bayesian approach starts with the assumption that dateable material was deposited uniformly during the past several thousand years. This assumption is conservative and underestimates the true degree of temporal overlap between introduced and extinct taxa. Extinctions actually involve a period of declining population (and decreasing rate of deposition), while introductions tend to involve a period of expanding population (and increasing rate of deposition). Both approaches produce confidence/credible intervals for extinction and introduction events. Note that, in the case of an extinction event, the Bayesian credible interval represents the posterior probability that a species is extinct at a certain time given that it was not sampled, while the extinction confidence interval produced through the classical approach reflects the probability that a species was not sampled at a certain time because it was no longer present. We used the package "rcarbon" in R to create summed probability distributions for calibrated dates from extinct and extant fauna, and each distribution was normalized such that it integrates to one (Crema and Bevan, 2020). Note that all confidence/credible intervals for event estimation are sensitive to outliers (such as rare late occurrence data), and numerous historical accounts suggest that relict populations of extinct species may have survived until recent centuries (Godfrey, 1986; Flacourt, 1995; Burney and Ramilisonina., 1998; Nomenjanahary et al., 2021).

We follow the approach of Crowley and Godfrey (2013) to correct collagen $\delta^{13}C$ values for the Suess effect (recent enrichment of atmospheric CO_2 in ^{13}C due to the burning of fossil fuel). Specifically, we made modern and subfossil collagen $\delta^{13}C$ values comparable by adding 0.004‰ to modern data for each year that passed from 1860 to 1965 AD and 0.02‰ for each year that passed from 1965 to the time of death (if known) or sample collection (2019 most recently).

We used general linear models (GLMs, R package "glmulti," Calcagno and de Mazancourt, 2010) with corrected data to identify which variables drive variation in predator $\delta^{13}C$ and $\delta^{15}N$ values (i.e., taxon, time, and location, **Supplementary Tables 1, 2**). Sites with data from both dogs and *Cryptoprocta* spp. (**Figure 3**, Andolonomby, Tsirave, and Ampasambazimba) are ideal for stable isotope comparisons. For example, Tsirave dog and *C. ferox* $\delta^{15}N$ values are comparable (dog $n = 4$, $\bar{x} = 10.6‰$, *C. ferox* $n = 3$, $\bar{x} = 11.5‰$), yet Tsirave dog $\delta^{13}C$ values ($n = 4$, $\bar{x} = -9.4‰$) tend to be ∼10‰ higher than *C. ferox* $\delta^{13}C$ values from this site ($n = 3$, $\bar{x} = -19.6‰$). Unfortunately, most sites include data from less than five specimens. Given limited site-specific sample sizes, we classified site location of dogs, *C. ferox*, and *C. spelea* according to coastal proximity and ecoregion. We defined coastal sites as those ≤ 10 km from the coast and inland sites as those >10 km from the coast.

We simplified ecoregion data into two groups: SW Madagascar (including the spiny thicket and succulent woodland), and North-Central Madagascar (including the dry deciduous forest and central highlands). We combined data from the spiny thicket and succulent woodland ecoregions because they have similar climate and are both dominated by relatively xerophytic vegetation. Plants and animals from these two ecoregions have similar $\delta^{13}C$ and $\delta^{15}N$ values, and are isotopically distinct from those of the relatively mesic central highlands and humid forest (Crowley et al., 2011). For similar reasons, we combine the single dog from the dry deciduous forest (PSUAMS 7663 from Lakato'ni Gavin in the far north) with the group from the central highlands. Note that only in our GLMs do we consider the limited stable isotope dataset for predators from North-Central Madagascar ($n = 5$). The rest of our analyses are focused exclusively on the SW.

We also compared δ^{13}C and δ^{15}N values for dogs from archeological and paleontological sites in inland SW Madagascar using t-tests. Sample sizes in these comparisons are small (archeological $n = 5$, paleontological $n = 6$), but neither δ^{13}C nor δ^{15}N values within these groups violate the t-test assumptions of normality (Shapiro-Wilk $p \geq 0.06$) or equal variance (Brown-Forsythe $p \geq 0.23$).

Uneven sampling of individuals through space and time influences the observed variance in stable isotope values for dogs and *Cryptoprocta* spp. We used Stable Isotope Bayesian Ellipses in R (SIBER) to visually inspect the breadth of δ^{13}C and δ^{15}N data from SW Madagascar (combining spiny thicket and succulent woodland) and also compare isotopic overlap between predator genera in a way that is unbiased by sample size (Jackson et al., 2011). We consider both standard ellipse areas (SEAs, which contain ∼40% of the data from each group) and ellipses that include 95% of the data from each group. Because our sample of *C. spelea* includes fewer than the recommended five specimens, we combined data from *C. spelea* and *C. ferox*. We feel this is reasonable because, within SW Madagascar, the two species have indistinguishable δ^{15}N values (**Figure 6**, *C. spelea* $n = 3$, $m = 14.0‰$; *C. ferox* δ^{15}N value: $n = 9$, $m = 13.9‰$, Mann-Whitney $U = 12.00$; $p = 0.85$), and δ^{13}C values (*C. spelea* $n = 3$, $m = -19.3‰$; *C. ferox* $n = 10$, $m = -18.6‰$, Mann-Whitney $U = 8.50$, $p = 0.31$). Note that the similar stable isotope values of *C. spelea* and *C. ferox* do not exclude the possibility that these species preyed on different taxa that were isotopically similar. Before analysis with SIBER, we used Shapiro-Wilk tests to confirm that *Cryptoprocta* spp. and dog δ^{13}C and δ^{15}N values from SW Madagascar are normally distributed ($p \geq 0.67$).

Lastly, we plotted stable isotope data from predators and potential prey from SW Madagascar on the same graph to visually assess the potential for different patterns of predation. In this graph, we shifted predator δ^{13}C and δ^{15}N values by –0.5 and –3‰, respectively, to account for estimated offsets in stable isotope values between trophic levels (McCutchan et al., 2003), and we grouped prey species at different taxonomic levels (family and above). Large, species-specific lemur datasets are grouped according to family due to relatively similar isotopic niche spaces occupied by different species. We use higher level classification for other prey types (e.g., all birds grouped in Aves) due to limited sample sizes.

RESULTS

Chronological Data

Directly ^{14}C-dated bones suggest a brief period of overlap between dogs and extinct giant lemurs in SW Madagascar and that dogs could have been present at kill sites during times that humans butchered extinct megafauna and an extant lemur (*Propithecus verreauxi*). Limited sample sizes prevent us from meaningfully considering differences in introduction and extinction timing in different ecoregions. However, our results suggest that dogs were widespread on Madagascar by ∼900 calibrated years before present (cal BP, **Figure 4**). The oldest ^{14}C-dated dog comes from the far northern archeological site of Lakato'ni Gavin (**Figure 3**, PSUAMS 7663, 1,035 ± 15 ^{14}C BP, 960–810 cal BP) and is roughly contemporaneous with a dog from the archeological site of Andranosoa in the far south (PSUAMS 7623, 1,010 ± 15 ^{14}C BP, 930–800 cal BP). The calibrated 95% age ranges of these two individuals overlap with those of five subfossil butchered extant lemurs (*Propithecus verreauxi*) from Taolambiby and with the three youngest ^{14}C-dated extinct giant ruffed lemurs (*Pachylemur insignis*) from Tsirave (**Figure 5**). The youngest dated *P. insignis* from Tsirave (UCIAMS 167930, 940 ± 20 ^{14}C BP, 900–740 cal BP) postdates the two earliest dogs by less than a century, and predates the oldest dog from Tsirave by ca. 80 years (CAMS 142889, 860 ± 30 ^{14}C BP, 790–670 cal BP).

Conservative estimates for SW Madagascar suggest the introduction of dogs (approximately 1,000 years ago) roughly coincided with the population collapse and possible extinction of *Palaeopropithecus ingens*, *Archaeolemur majori*, and *P. insignis* (between about 1,100 and 700 cal BP; **Figure 5**). The classical 95% confidence interval for dog introduction (1,120–870 cal BP) also overlaps with the calibrated 95% age ranges for all 26 of the dated butchered bones in **Figure 5**. These include bones of extant *P. verreauxi* ($n = 15$), as well as extinct giant lemurs [*P. insignis* ($n = 7$) and *A. majori* ($n = 1$)], elephant birds [*Aepyornis maximus* ($n = 1$) and *Mullerornis modestus* ($n = 1$)], and a pygmy hippo [*Hippopotamus* sp. ($n = 1$)].

Stable Isotope Data

Predator collagen δ^{13}C and δ^{15}N values suggest dietary flexibility for dogs and some limited dietary overlap between *Cryptoprocta* spp. and dogs (**Table 1** and **Figure 6**). All included predictor variables (i.e., taxon, ecoregion, coastal proximity, and time) contribute to the best fit GLMs (**Supplementary Table 1**) that explain variation in predator δ^{13}C values (Model 1, $n = 37$, AIC = 170.84) and δ^{15}N values (Model 2, $n = 36$, AIC = 142.04). Model 1 suggests that both *C. spelea* and *C. ferox* had low δ^{13}C values relative to dogs (**Supplementary Table 2**, $p = 0.007$ and $p = 0.02$, respectively). It also suggests that predator δ^{13}C values in general tend to be relatively high in SW Madagascar ($p = 0.0002$) and that they also tend to be higher at coastal sites ($p = 0.02$). Overall, predator δ^{13}C values may have decreased through time (Model 1 $p = 0.04$, **Figure 7**), primarily among the three *C. spelea* ($p = 0.006$). However, the model also suggests that combined predator δ^{13}C increased through time both in SW Madagascar ($p = 0.03$) and at inland sites island-wide ($p = 0.04$). Model 2 suggests that *C. ferox* have high δ^{15}N values relative to dogs (**Supplementary Table 2**, $p = 0.002$) and that *C. ferox* from coastal sites tend to have higher δ^{15}N values than those from inland sites ($p = 0.02$). It also suggests that both *C. spelea* and *C. ferox*δ^{15}N values increased through time ($p = 0.05$ and $p = 0.009$, respectively, **Figure 7**).

Standard ellipse areas (SEAs which encompass 40% of a group's data) are nearly twice as large for dogs ($9.6‰^2$) as they are for *Cryptoprocta* spp. in SW Madagascar ($5.2‰^2$; **Figure 6**). While the SEAs do not overlap, ellipses that contain ∼95% of the data from each group do overlap (**Figure 6**). The area of overlap between the 95% ellipses accounts for ∼34% of the isotopic

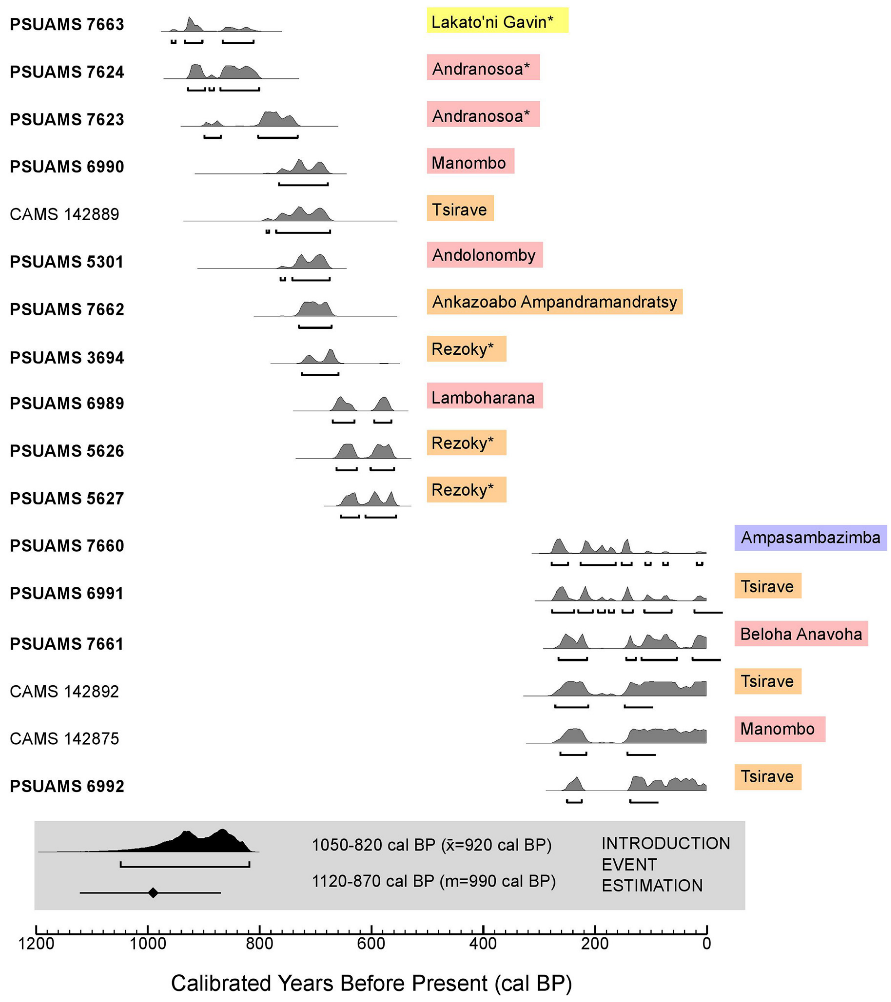

FIGURE 4 | Dog collagen ^{14}C dates calibrated in OxCal 4.4 with SHCal 20 (Hogg et al., 2020). Previously unpublished dates are bolded, sites are colored according to ecoregion (red = spiny thicket, orange = succulent woodland, blue = central highlands, yellow = dry deciduous forest), and archeological sites are marked with asterisks. Shaded box includes results from two approaches to introduction event estimation: The bracket under the Bayesian posterior probability distribution spans 95.5% of the distribution, and the diamond and associated line marks the median and 95% confidence interval estimate from the classical frequentist approach.

niche space of *Cryptoprocta* spp. but only ~16% of the isotopic niche space of dogs. Samples of dog and *Cryptoprocta* spp. bones integrate different amounts of time and space, but these variables alone cannot explain the relatively large isotopic niche space occupied by dogs. Specifically, the range of dates for *Cryptoprocta* spp. is about twice as great as that for dogs (**Figure 7**). Also, although dogs from SW Madagascar come from a greater number of sites than *Cryptoprocta* spp. (n = 8 vs. n = 4), these sites represent similar geographical spread and include both inland and coastal sites (**Figure 3**).

Dogs generally tend to have higher δ^{13}C values and lower δ^{15}N values than *Cryptoprocta* spp., but dogs from inland archeological sites in SW Madagascar (Rezoky & Andranosoa) tend to have δ^{13}C and δ^{15}N values that are relatively comparable with those of *Cryptoprocta* spp. (**Figures 6**, **7**). Specifically, the mean (±1 SD) δ^{13}C value for dogs from inland archeological sites in SW Madagascar ($n = 5$, $\bar{x} = -14.9 \pm 1.4$‰) is significantly lower than the mean value for dogs from inland paleontological sites in this region [$n = 6$, $\bar{x} = -11.1 \pm 3.3$‰, $t(9) = 2.42$, $p = 0.04$]. However, limited sample sizes and limited contemporary samples from archeological and paleontological sites may confound this comparison, since dog δ^{13}C values across inland SW sites significantly increased during the past millennium ($n = 11$, $r_{Spearman} = 0.60$, $p = 0.05$, **Figure 7**). Additionally, the mean δ^{15}N value for dog collagen from archeological sites in this region ($n = 5$, $\bar{x} = 13.3 \pm 0.8$‰) is apparently, yet insignificantly, higher than the mean value for dogs from inland paleontological sites [$n = 6$, $\bar{x} = 11.9 \pm 2.4$‰, $t(9) = 1.26$, $p = 0.24$].

DISCUSSION

Brief overlap in directly dated introduced dogs and extinct megafauna means that we cannot reject the hypothesis that dogs could have helped humans hunt giant lemurs and possibly other megafauna at least ~1,000 years ago. Dogs have had diverse diets that are largely distinct from *Cryptoprocta* spp. diets and

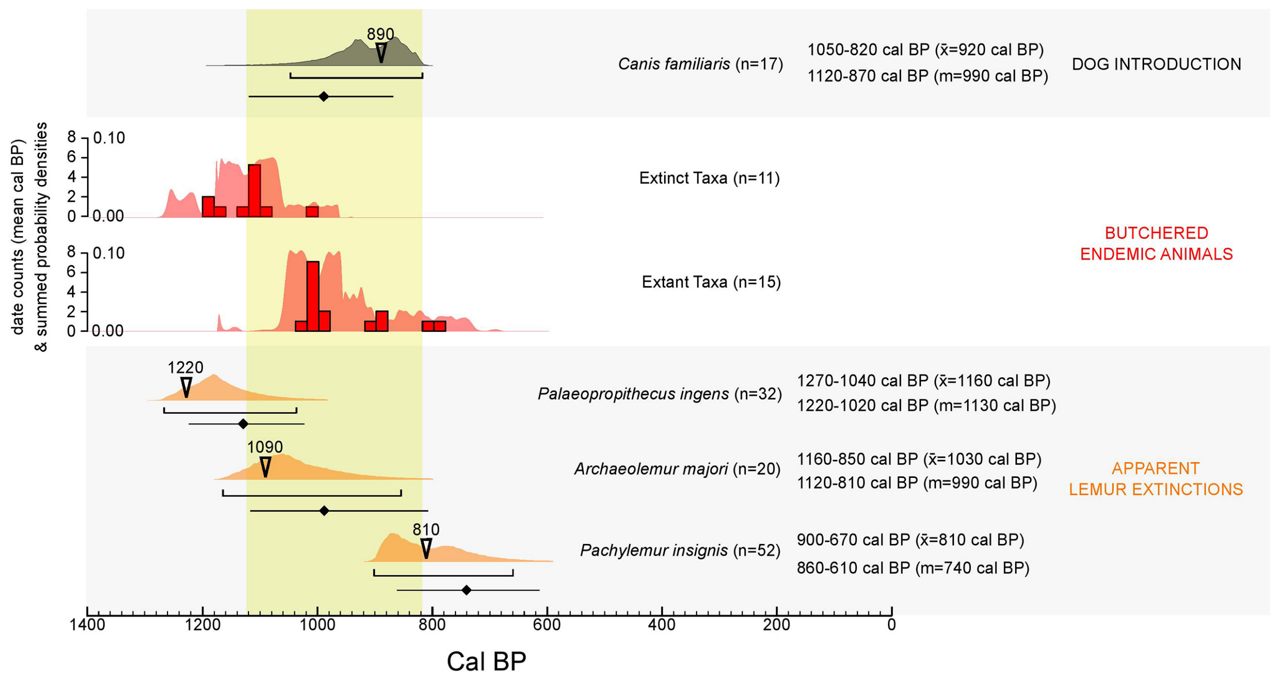

FIGURE 5 | Dog introduction event estimate compared to dates from butchered endemic animal bone and giant lemur extinction event estimation. Numbered arrowheads mark the mean calibrated date from the oldest recognized dog and youngest recognized giant lemur belonging to each taxon. See **Figure 4** for explanation of confidence intervals for event estimation. Note that extinction confidence intervals consider only data from purified collagen. Dates from butchered animal bone are binned in 20-year intervals (saturated color) and are also displayed through summed probability distribution overlays (unsaturated color). Butchered extinct taxa represented in the histogram include *Pachylemur insignis*, *Archaeolemur majori*, *Hippopotamus* sp., *Aepyornis maximus*, and *Mullerornis modestus*. All of these taxa disappear from the subfossil record by ~800 cal BP (Crowley, 2010). Butchered extant taxa in the histogram include only *P. verreauxi*.

TABLE 1 | Descriptive statistics for island-wide *Canis familiaris* and *Cryptoprocta* spp. $\delta^{13}C$, $\delta^{15}N$, and age data.

Taxon	n	x̄	*SD*	Range	[min, max]
$\delta^{13}C$ (‰, VPDB)					
Canis familiaris	23	−13.5	3.0	12.4	[−20.4,−8.0]
Cryptoprocta spp.	14	−18.9	1.1	4.0	[−21.0,−17.0]
$\delta^{15}N$ (‰, AIR)					
Canis familiaris	23	12.3	1.8	6.6	[9.1, 15.7]
Cryptoprocta spp.	13	13.6	1.6	5.1	[11.2, 16.3]
Age (mean cal BP)					
Canis familiaris	23	NA	NA	959	[890, −69]
Cryptoprocta spp.	14	NA	NA	2,280	[3,280, 1,000]

Note that the range within each group includes both spatial and temporal variability (Figures 6, 7), and the $\delta^{13}C$ values for the six modern dogs were corrected for the Suess Effect (following Crowley and Godfrey, 2013) so that they are comparable with subfossil collagen values.

include only minor inputs from forest-dwelling species, which is inconsistent with the hypothesis that dogs competed with *Cryptoprocta* spp. (**Figures 6**, **8**). Nevertheless, dogs could have contributed to interference competition with endemic predators.

The introduction of dogs coincided with expanding human presence on Madagascar, which included the significant growth and movement of Malagasy populations (Pierron et al., 2017), the rise of the island's earliest urban center (Radimilahy, 1998), and the expansion of trade down the west coast of the island (Dewar and Wright, 1993; Boivin et al., 2013). Early trade connections between East Africa and Madagascar are consistent with the primarily African ancestry of Madagascar's dogs (Ardalan et al., 2015). However, given that the earliest directly ^{14}C-dated dog (from Lakato'ni Gavin) slightly preceded the appearance of SE Asian rice and cotton in the region (Crowther et al., 2016), the potential for multiple past dog introductions should be considered through analysis of ancient DNA, if possible.

Early introduced dogs could have aided past human-led hunts of extant lemurs like *P. verreauxi* and megafauna that went extinct within the past millennium (Crowley, 2010; Hixon et al., submitted), but isotope data suggest that these kills did not form the bulk of dog diet (**Figure 8**). Most extinct megafauna browsed woody C_3 vegetation (Crowley and Samonds, 2013; Godfrey and Crowley, 2016; Crowley et al., 2021; Hixon et al., submitted). A modern dog from Antsirabe does have an exceptionally low $\delta^{13}C$ value (−20.4‰) and relatively high $\delta^{15}N$ value (15.7‰), which may indicate that it relied heavily on forest bushmeat. However, the wide range of dog $\delta^{13}C$ values likely reflects a continuum of reliance on agropastoralist-supplied foods (based on C_4 or CAM plants), which is also observed in modern free-roaming dogs (Valenta et al., 2016). Consumption of scraps from butchered grazing livestock (e.g., zebu cattle) could have contributed to relatively high dog $\delta^{13}C$ values (**Figure 8**), particularly at archeological sites that include bones of dogs as

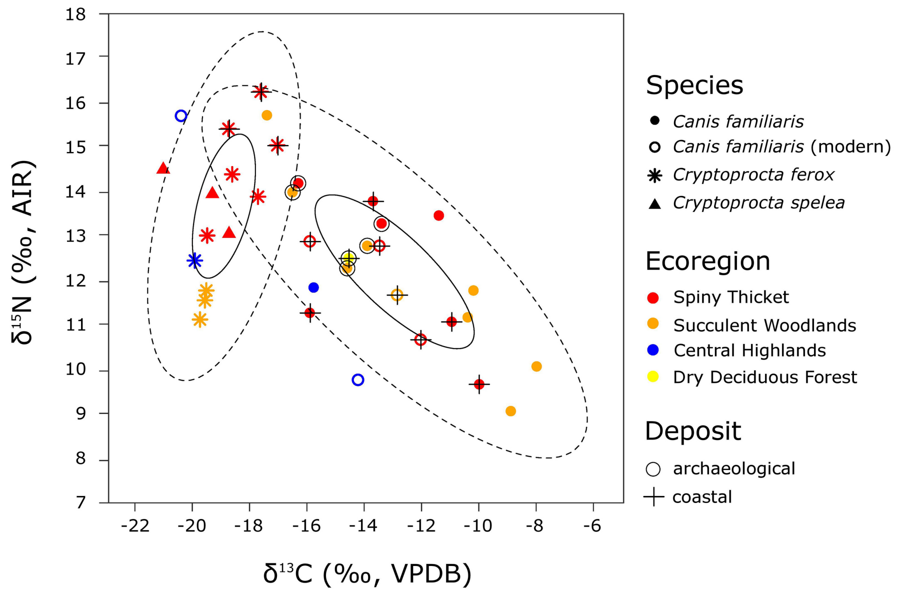

FIGURE 6 | Stable carbon and nitrogen isotope data for bone collagen from dogs (both modern and subfossil) and members of *Cryptoprocta* (all subfossil), with points colored according to ecoregion, shaped according to taxon, and marked according to deposit type (n = 36). For each genus, ellipses outline approximately 95% of the data (dashed) and 40% of the data (solid) from only the SW ecoregions (spiny thicket and succulent woodlands, *Canis* n = 19, *Cryptoprocta* n = 12). Island-wide, average calibrated dates for *C. spelea* specimens (n = 3) range from 3,280 to 1,760 cal BP, those for *C. ferox* (n = 10) range from 2,900 to 1,010 cal BP, and those for dogs (n = 23) span from 890 cal BP to the present. The six modern dogs have δ^{13}C values that are corrected for the Suess Effect (following Crowley and Godfrey, 2013) so that they are comparable with subfossil collagen values.

well as livestock (Vérin and Battistini, 1971; Rasamuel, 1984; Hixon et al., submitted). However, rather counterintuitively, dogs from inland archeological sites in the arid SW tend to have lower δ^{13}C values than those from inland paleontological sites where they were less likely to be associated with pastoralists. The relatively low δ^{13}C values of dogs from archeological sites could be explained by reliance on provisioned scraps from ovicaprids that browsed on a wide range of vegetation (Hixon et al., submitted) or from endemic, forest-dwelling game hunted by humans in forests dominated by C_3 plants (**Figure 8**; Decary, 1939). Archeological bone deposits in SW Madagascar tend to be highly fragmentary and may include traces of scavenging (Vérin and Battistini, 1971; Douglass et al., 2018). There are abundant marks of mammalian carnivoran predation and scavenging on the bones of extinct giant lemurs at paleontological sites (Meador et al., 2019, also at Taolambiby, Clark, pers. comm.), and the possibility that both *Cryptoprocta* spp. and dogs contributed to these patterns of gnaw marks on relatively recent bones cannot be excluded.

Past exploitation competition between dogs and *Cryptoprocta* spp. seems unlikely given that isotope data suggest ancient *Cryptoprocta* spp. consumed mostly forest dwelling animals (e.g., lemurs), while dogs have relied more heavily on prey from relatively open habitats (e.g., scraps from the food of agropastoral communities). Dogs may be replacing endemic predators around human communities today (Farris et al., 2016), but the distinct diets of dogs and *Cryptoprocta* spp. suggest that dogs are not fulfilling the ecological role of *Cryptoprocta* spp. In particular, the distinct isotopic niches of dogs and *Cryptoprocta* spp. suggest that any past antagonistic relationship between these predators did not follow from predation or competition for shared prey. Instead, dogs could have antagonized *Cryptoprocta* spp. through exclusion competition by chasing shared prey, creating a landscape of fear, and thus contributing to habitat fragmentation (Laundré et al., 2010). The directly ^{14}C-dated subfossil record for *C. spelea* is sparse (n = 3), yet recent accounts of what may be *C. spelea* still living in the far north of Madagascar (Nomenjanahary et al., 2021) suggest that there may be a history of interaction between dogs and *C. spelea*. Dogs may occasionally prey on *C. ferox* (Valenta et al., 2016), yet comparable δ^{15}N values for dogs and *C. ferox* suggest that dogs have not routinely consumed endemic predators, such as *C. ferox*, or other introduced predators, such as cats, during the past millennium (**Figure 8**). The observation that dogs rarely prey on cats is consistent with the modern observation that both exotic predators are often simultaneously abundant (Farris et al., 2014).

Although there was limited dietary overlap between *C. ferox* and dogs ~1,000 years ago, this may have expanded during the past millennium as *C. ferox* came into more frequent contact with human modified landscapes that tend to have higher plant and animal δ^{13}C values. Palynological and geochemical records from much of Madagascar document the expansion of grasslands favored by livestock and dogs during the past millennium (Burney, 1987; Crowley and Samonds, 2013; Burns et al., 2016; Virah-Sawmy et al., 2016; Domic et al., 2021). Future stable isotope work with modern and subfossil *C. ferox* individuals that span the past millennium can test this possibility. *C. ferox* continues to hunt in shrinking forest fragments but may partly

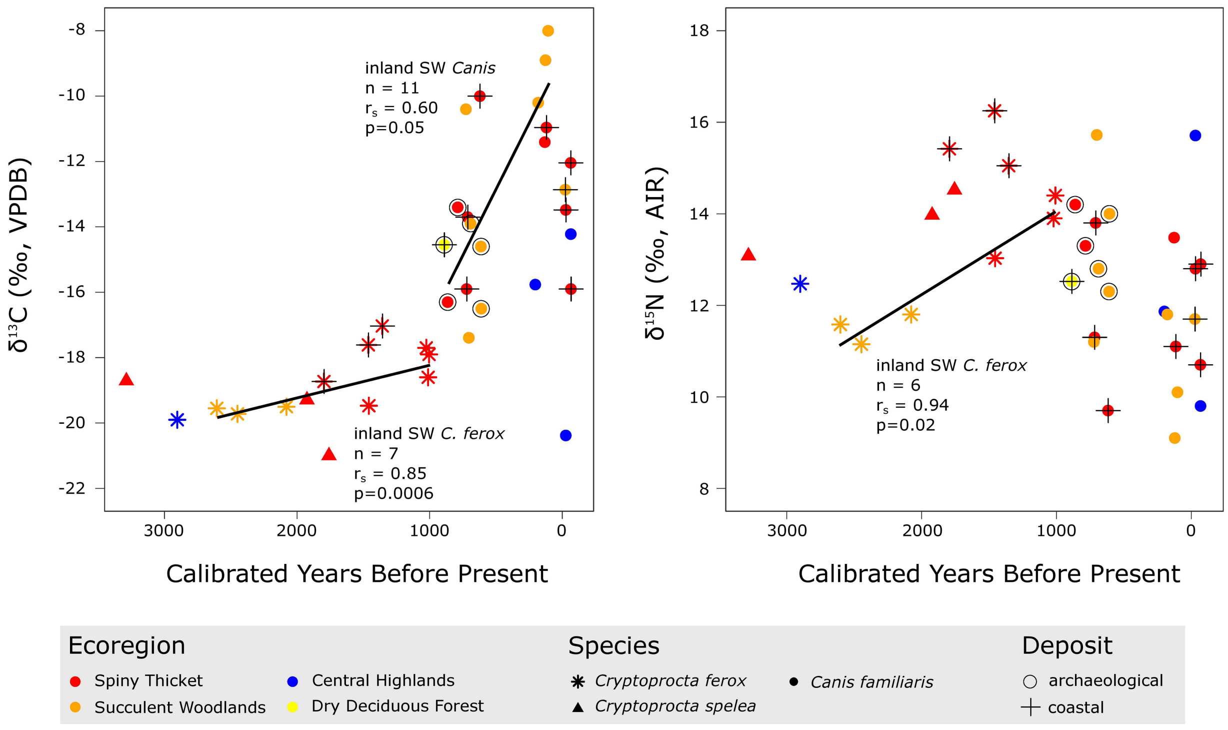

FIGURE 7 | Temporal trends in stable carbon and nitrogen isotope data for bone collagen from dogs (both modern and subfossil) and members of *Cryptoprocta* (all subfossil), with points colored according to ecoregion, shaped according to taxon, and marked according to deposit type ($\delta^{13}C$ $n = 37$, $\delta^{15}N$ $n = 36$). The six modern dogs have $\delta^{13}C$ values that are corrected for the Suess Effect (following Crowley and Godfrey, 2013) so that they are comparable with subfossil collagen values. Trend lines illustrate the only significant temporal trends when controlling for region and coastal proximity: In inland SW Madagascar (including both spiny thicket and succulent woodlands), dog and *C. ferox* $\delta^{13}C$ values and *C. ferox* $\delta^{15}N$ values significantly increased through time, yet these trends could be explained by uneven sampling across archeological versus paleontological deposits in the case of dogs or by uneven sampling between the spiny thicket and succulent woodlands in the case of *C. ferox*.

exploit the expanding anthropogenic niche, as documented in other taxa such as vervet monkeys (*Chlorocebus pygerythrus*) on mainland Africa (e.g., Loudon et al., 2014). *Cryptoprocta ferox* is known to navigate deforested areas (Wyza et al., 2020), and there are numerous recent accounts of *C. ferox* raiding poultry and controlling introduced rat populations (Merson et al., 2019b).

Ongoing efforts try to control dog populations, yet dogs are only part of the picture. A growing body of directly ^{14}C-dated specimens of introduced animals suggests that dogs became established on Madagascar at approximately the same time as introduced herbivores (zebu cattle and ovicaprids, Hixon et al., submitted) and at possibly the same time as cats (Sauther et al., 2020). Genetic data from Madagascar's modern cats indicate that their ancestors colonized the island from the Arabian Sea region within the past millennium (Sauther et al., 2020). Similar to dogs, cats are a successful invasive predator on numerous islands (Medina et al., 2011; Nogales et al., 2013). However, unlike dogs, cats may be a closer functional replacement for *Cryptoprocta* spp. since they also climb trees. Cats successfully prey on a large variety of endemic species on Madagascar (Brockman et al., 2008; Merson, 2017) and are difficult for endemic predators to avoid (Gerber et al., 2012). Existing $\delta^{13}C$ data from four cats in SW Madagascar (**Figure 8**) could suggest that they consumed different prey than *Cryptoprocta* spp., but the available sample size is quite small. Though cats are well-represented in archeological deposits of ~1,000 years ago on the island of Mayotte (~330 km NW of Madagascar), subfossil felid remains are unfortunately very scarce in Madagascar's paleontological and archeological deposits (Petit, 1933; Chanudet, 1975). The analysis of additional cat remains would better clarify when cats arrived on Madagascar and how their diets compared to those of other predators.

Madagascar's ecosystems continue to face new species introductions (e.g., Asian toads; Kolby, 2014) and shifts in land use (e.g., cash cropping; Réau, 2002) that threaten endemic biodiversity. The suite of past animal introductions that included dogs and livestock coincided with a pulse of megafaunal extinction and constituted an early turning point in Malagasy socio-ecological history. This situation is analogous to the colonization of Remote Oceania by people with a "transported landscape" that included dogs, pigs, rats, and chickens (Anderson, 2009). During the brief co-occurrence of dogs, introduced livestock, and endemic megafauna on Madagascar, pastoralists both relied on their livestock and opportunistically hunted endemic animals (Vérin and Battistini, 1971; Rasamuel, 1984). Introduced animals compounded negative impacts of humans on endemic fauna. Livestock provided a reliable food supply for growing human

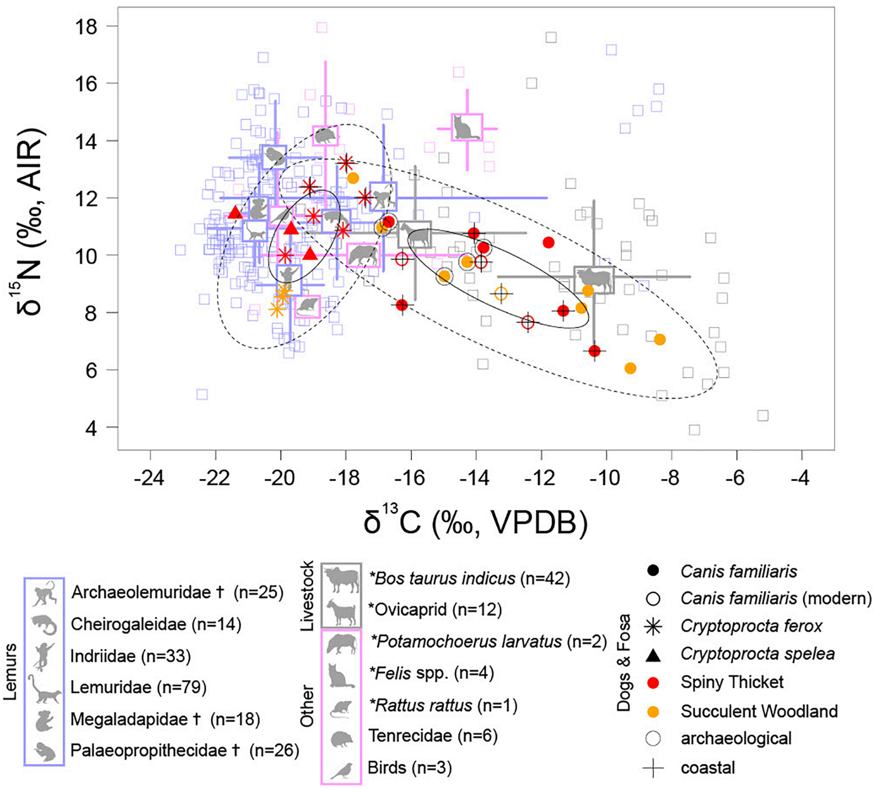

FIGURE 8 | Stable carbon and nitrogen isotope data for bone collagen from dogs (both modern and subfossil) and members of *Cryptoprocta* (all subfossil) collected in SW Madagascar, with points colored according to ecoregion, shaped according to taxon, and marked according to deposit type (n = 36, see **Figure 5** explanation of ellipses fitted to dog and *Cryptoprocta* spp. data). Stable isotope data from the bone collagen of lemurs, livestock, and other animals collected in SW Madagascar are plotted for reference, with icons marking means and lines marking standard deviations in $\delta^{13}C$ and $\delta^{15}N$ values. Note that extinct families of giant lemurs are marked with (†), introduced taxa are marked with (*), and modern individuals (including six modern dogs) have $\delta^{13}C$ values that are corrected for the Suess Effect (following Crowley and Godfrey, 2013) so that they are comparable with subfossil collagen values. Also note that dog and *Cryptoprocta* spp. $\delta^{13}C$ and $\delta^{15}N$ values are shifted by –0.5 and –3‰, respectively, to account for estimated offsets in stable isotope values between trophic levels (McCutchan et al., 2003). Thus, the dog and *Cryptoprocta* spp. points approximate the isotopic composition of their diet.

populations (Pierron et al., 2017), and we have shown here that dogs could have aided human-led hunts and contributed to habitat fragmentation during the past millennium. However, forest-dwelling endemic animals contributed relatively little to dog diet. The colonization of Madagascar by pastoralists and introduced predators likely had dramatic environmental consequences and formed what can be considered the first step in the biotic homogenization of the island.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because the work focuses on ancient vertebrates.

AUTHOR CONTRIBUTIONS

SWH, DK, KD, BC, LG, LR, and HW designed the research. SWH, KD, LE, and BC performed the analyses. SWH, KD, LG, BC, LR, GC, AA, SH, and HW aided sample collection and identification. SWH and DK wrote the manuscript. All authors edited 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.2021.689559/full#supplementary-material

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Forests Without Frugivores and Frugivores Without Forests – An Investigation Into the Causes of a Paradox in One of the Last Archipelagos Colonized by Humans

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The Mascarenes are sadly famous worldwide for the massive extinction of their native vertebrates since recent human colonization. However, extinction patterns show astonishing disparities between the two main islands and between lineages of forest vertebrates. On Réunion (2,512 km^2, 3,070 m) where about a third of native habitats remains, most large-bodied vertebrates, especially frugivores, collapsed by the first half of the 18th century, while several have survived longer and some still exist on Mauritius (1,865 km^2, 828 m) where more than 95% of native habitats have been transformed. Considering lineages of forest vertebrates shared by both islands (23 genera, 53 species), we test the hypothesis that differing patterns of lowland suitable habitat destruction is the main cause behind this paradox. Before that, we assess the potential impact of other major drivers of extinctions since first contact with humans. Firstly, Mauritius shows earlier and more numerous introductions of mammal predators known for their devastating impact (except northern islets which have thus become important sanctuaries for several squamates). Secondly, settlers were inveterate hunters on both islands, but while Réunion was overhunted before Mauritius, the burst of human population in the latter in late 18th century has not led to the rapid extinction of all large native vertebrates. These two factors alone therefore cannot explain the observed paradox. Rather, the early destruction of lowland habitats (<400 m) on Réunion is concomitant with most extinctions of forest vertebrate, notably frugivores that rapidly lost most lowland habitats dominated by large fleshy-fruited plants. Moreover, landform-induced fragmentation has likely decreased the ability of adjacent habitats to act as effective refuges. Conversely, Mauritius retained suitable low-fragmented habitats until the late 19th which probably allowed, at least for a time, several native vertebrates to escape from multiple human-induced disturbances. Despite the almost total destruction of native habitats since then on Mauritius, conservation actions have saved several threatened vertebrate species that play a fundamental role in the functioning of native ecosystems. The fact that there are now more favorable habitats on Réunion than on Mauritius argues for the rewilding of Réunion with these extant large vertebrates.

Keywords: biodiversity loss, biological invasion, elevational gradients, habitat destruction and fragmentation, Mascarene archipelago, overhunting

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INTRODUCTION

The Dodo of Mauritius became one of the most emblematic species of human-induced extinction but this species is only a symbol among numerous other insular species that constitute the bulk of documented extinctions at the Holocene (Steadman, 1995; Alcover et al., 1998; Blackburn et al., 2004; Whittaker and Fernandez-Palacios, 2007; Kier et al., 2009). Islands show indeed a more pronounced extinction rate than mainland ecosystems, which often leads to the global extinction of species due to high endemism. The primary drivers of vertebrate extinction, all induced by human colonization, are the destruction and fragmentation of habitats, the introduction of predators and competing vertebrate species, as well as overhunting (Blackburn et al., 2004; Cheke and Hume, 2008; Triantis et al., 2010; Duncan et al., 2013; Heinen et al., 2017; Osuri et al., 2020). However, biogeographic factors such as high isolation, small area or high elevation, have also been shown to increase vertebrate extinction risk on islands (Blackburn et al., 2004; Duncan et al., 2013; Heinen et al., 2017).

Habitat destruction is a major cause of global diversity loss (Tilman et al., 1994; Triantis et al., 2010). It results in small and isolated populations, susceptible to stochastic factors such as erosion of genetic diversity or random fluctuation in demography, and can lead these populations to extinction in a few generations. These populations are, however, also vulnerable to other human-induced factors. For example, the introduction of invasive predators has been a major cause of vertebrate extinctions on oceanic islands worldwide, because most islands have few native predators (Blackburn et al., 2004; Doherty et al., 2016). Invasive mammals are particularly damaging, having contributed to considerable species decline and extinction. Introduced rodents and cats have for instance been listed as causal factors in 44% of modern species extinctions of bird, mammal, and reptile (Doherty et al., 2016). In addition, non-predator introduced vertebrates can also negatively impact native vertebrates by competing for resources and nest sites, or being reservoirs of exotic diseases (Jones, 1996; McClure et al., 2020).

Among biogeographic factors, island isolation increases the risk of vertebrate extinction (Heinen et al., 2017). Indeed, isolation may cause exaggerated ecological release, resulting in traits such as flightlessness, which make species more vulnerable to extinctions (MacArthur and Wilson, 1967). Smaller islands are also more prone to vertebrate extinctions because resources as well as refuges from anthropogenic overhunting or deforestation are more limited (Blackburn et al., 2004; Duncan et al., 2013; Heinen et al., 2017). Although montane areas were also expected to act as refuges from anthropogenic disturbances, greater extinction risks are nevertheless associated with island maximum elevation (Blackburn et al., 2004; Heinen et al., 2017). Heinen et al. (2017) suggested this might be explained by the great heterogeneity of habitat suitability along elevational gradients, making species more vulnerable to the destruction of lowland habitats. This "habitat suitability" hypothesis was first proposed by Cheke and Dahl (1981) who discussed a striking paradox in the Mascarenes. Despite the almost total destruction of native habitats, one of the two native species of fruit bats survived on Mauritius whereas they have long gone extinct on Réunion, where vast areas of native habitats remain. Thiollay and Probst (1999) made a comparable observation concerning the two extant Mascarene cuckoo-shrikes: the species confined to native remnants on Mauritius is doing better than the sister species on Réunion, where major conservation efforts are hardly succeeding in significantly increasing its population size in montane forest (see Salmona et al., 2012). In West Indies and Hawai'i, where similar patterns exist, it has been postulated that the loss of dry lowland habitats long before the arrival of Europeans might have caused the extinction of numerous vertebrates (Olson and James, 1989). Yet it has never been tested on oceanic islands, where historical contingency is generally poorly known.

Here, we use the Mascarene archipelago as a study system to test the "habitat suitability" hypothesis. It is probably one of the only archipelagos worldwide where natural history has been so well documented since first human settlement both in terms of historical accounts (Lougnon, 2005; Cheke and Hume, 2008) and paleontological works on extinct vertebrates (Cheke and Dahl, 1981; Hume, 2007, 2011, 2013, 2014, 2019; Arnold and Bour, 2008; Rijsdijk et al., 2009). With a very low filter effect (*sensu* Blackburn et al., 2004), we have a unique opportunity to study the main drivers of a paradoxical vertebrate extinction pattern: among the 23 forest vertebrate genera shared by Réunion and Mauritius, 12 genera (55.2% of species involved) went extinct on Réunion that still harbors 35% of native habitats (Strasberg et al., 2005), while five genera (31.4% of species involved) went extinct on Mauritius that retains less than 5% of native vegetation (Hammond et al., 2015; **Figure 1** and **Table 1**). This contrast between the two islands is all the more puzzling since the extinction of vertebrates on Réunion has been staggering (Lougnon, 2005; Cheke and Hume, 2008). To decipher this paradox, we study the three main drivers of extinction, i.e., introduction of non-native vertebrates, overhunting and deforestation of suitable habitats, and compare the associated timeline on Réunion and Mauritius. To better characterize changes in habitat suitability since human colonization, we focus on an important guild of forest vertebrates, the frugivores of which spatial distribution is globally associated with the distribution of fleshy-fruited plants (Dehling et al., 2014; Ferger et al., 2014; Correa et al., 2015; Hazell, 2020).

MATERIALS AND METHODS

Study Site

Réunion (2,512 km^2) and Mauritius (1,865 km^2) are the two main islands of the Mascarenes (**Figure 1**). Rodrigues (109 km^2), the smallest and easternmost island, was not included in this study. Indeed, the natural history of this island provides little information to disentangle the different drivers of extinctions due to the early and almost complete destruction of native habitats. Mauritius and Réunion have very different topographical characteristics. The first one is a shield volcano that peaks at 3,070 m asl with 50% of areas located above 770 m. The island is marked by a very

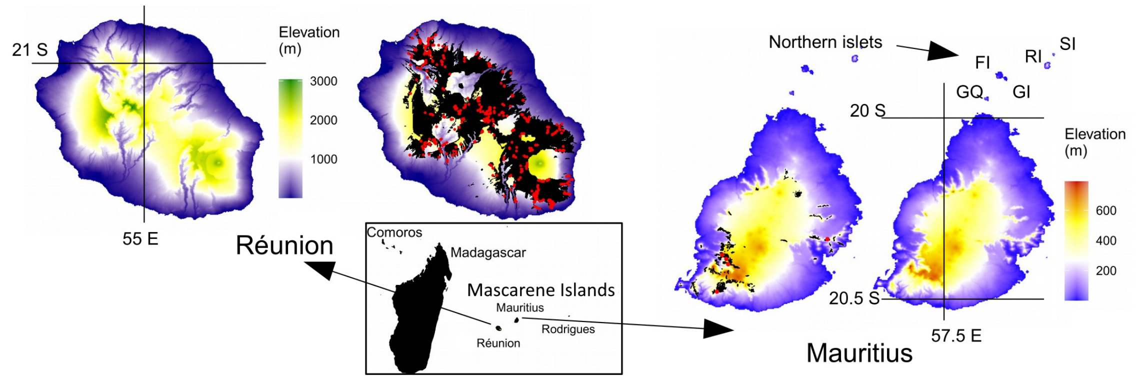

FIGURE 1 | Topography and native forest remnants of the two main islands of the Mascarenes. Réunion is a relatively recent high-elevation island with only one tiny islet, while geologically older Mauritius shows a much less rugged topography and a large number of islets. The northern islets that have played an important role for the conservation of several endemic reptiles are indicated by letters: from South to North, "GQ" Gunner's Quoin, "GI" Gabriel Island, "FI," Flat Island," "RI" Round Island and "SI" Serpent Island. The small Pigeon House Rock is not visible on the map. These six islets are located between 4 km (Gunner's Quoin) and 24 km (Serpent Island) from the mainland. Extant native forests and shrublands are shown in black. On both islands, they are mainly located at the highest elevations, but two native forest corridors between sea level and montane habitats still persist in the South-East and North on Réunion. Red points display the location of historical surveys used for analyses of plant diversity (430 and 5 plots on Réunion and Mauritius, respectively).

rugged relief that induces strong geographical barriers, e.g., the Northwest/Southeast diagonal, the *Cirques* and other radially deep valleys (**Figure 1**). Conversely, 50% of areas are located under 161 m on Mauritius. Even if the island has some steep massifs that peak above 800 m asl, they are located in a rather lateral position, the center of Mauritius being occupied by a large, relatively flat plateau (**Figure 1**). Both islands experience a tropical oceanic climate, but the relief on Réunion induces far greater variations in terms of temperature and rainfall. Frost can appear above 1,500 m and is frequent above 2,000 m in winter, and the windward and leeward coasts, respectively, record the maximum (11,000 mm) and minimum (450 mm) annual rainfall in the archipelago (Réchou et al., 2019). The result is a zoning of habitats that has been the subject of various typological works (Cadet, 1977; Dupouey and Cadet, 1986; Strasberg et al., 2005). On Mauritius, an elevational zoning of habitats has also been described although the whole island is included in the megathermic domain (Vaughan and Wiehe, 1937; Page and D'Argent, 1997).

Extinct and Extant Forest Vertebrates

Until the 17th century, Réunion and Mauritius were almost totally wooded (except at high elevations on Réunion) and were home to a particularly abundant and relatively diverse fauna for oceanic islands. Here, we focus on vertebrates that are (were) closely dependent on forest habitats, so that we excluded seabirds and vertebrates dependent on wetlands. Both islands shared 23 genera of forest vertebrates (14 birds, one chelonian, three mammals, five squamates, **Table 1**). However, 15 genera of forest vertebrates were not found on the sister island. Réunion had other endemic bird species such as the *Solitaire* (*Threskiornis*), the *Oiseau bleu* ("*Cyanornis*"), the Mascarin parrot (*Mascarinus*), the Hoopoe starling (*Fregilupus*) and the Réunion stonechat (*Saxicola*), but also insectivorous bats, i.e., the Pale house bat (*Scotophilus)* and the Bory's white bat *(Boryptera*). Mauritius sheltered endemic flightless birds, the Dodo (*Raphus*) and the Red hen (*Aphanapterix*), but also the Raven parrot (*Lophopsittacus*), the Wood pigeon (*Columba*) and the Mauritius starling (*Cryptopsar*) (Hume, 2013, 2014). More surprisingly, Mauritius also had several endemic snakes: the Keel-scaled boa (*Casarea)*, the Burrowing boa *(Bolyeria)* and the Carié's blind-snake *(Typhlops*). All these vertebrates went extinct since human colonization, except the Stonechat on Réunion and the Keel-scaled boa that survives on the northern islets of Mauritius (Cheke and Hume, 2008). Here, we studied the genera present both on Mauritius and Réunion, assuming that they shared intrinsic characteristics to allow a direct comparison of extinction factors.

Data Collection and Analyses

The chronology of extinctions of forest vertebrates was documented on the basis of a literature review. Most of the data regarding the dates of extinction were drawn from the appendices of Cheke and Hume (2008) and relative updated publications (**Table 1**). We also compiled the body sizes of focal species and assessed changes in median body size of forest vertebrates since first contact with humans.

Introduction of Exotic Vertebrates

We established a chronological overview of terrestrial vertebrate naturalizations on Réunion and Mauritius since the beginning of human colonization. We characterized their introduction date on Réunion, Mauritius mainland or Mauritius islets, as well as their diet. The aim was not to provide a complete picture of vertebrate introductions on both islands, but to present all those that potentially negatively impacted the native fauna or have impacted the extant fauna. This impact may be directly mediated *via* predation or indirectly *via* competition, sometimes between related lineages. We also presented vertebrates that potentially contribute to alter the structure of native habitats. Most of the data regarding vertebrate introductions were drawn from the

TABLE 1 | Overview of forest vertebrate lineages shared by Réunion and Mauritius in the pristine Mascarenes.

	Taxonomy					**Réunion**		**Mauritius**	
	Genus	**Species**	**Common name**	**Diet**	**Body size (g)**	**Extinct**	**Extant**	**Extinct**	**Extant**
Aves	*Aerodramus*	*francicus*	Mascerene swiftlet	I	8.9		VU		DD
	Alectroenas	*nitidissima*	Pigeon Hollandais	**F**	170			1835	
		sp	Réunion blue pigeon	**F**	170	1715			
	Circus	*maillardi*	Réunion harrier	R	1000		EN	1630	
	Dryolimnas[1]	*chekei*	Sauzier's wood rail	I	300			1695	
		augusti	Réunion wood rail	I	300	1695			
	Falco	*punctatus*	Mauritius kestrel	R	350				EN
		duboisi	Réunion kestrel	R	350	1675			
	Foudia	*rubra*	Mauritius fody	f G	15				EN
		delloni	Réunion fody	f G	15	1675			
	Hypsipetes	*olivaceus*	Mauritius bulbul	**F**	55				VU
		borbonicus	Réunion bulbul	**F**	55		LC		
	Lalage	*typica*	Mauritius cuckoo-shrike	f I	32				VU
		newtoni	Réunion cuckoo-shrike	f I	32		CR		
	Mascarenotus	*sauzieri*	Commerson's lizard-owl	R	370			1860	
		grucheti	Gruchet's lizard-owl	R	370	1675?			
	Nesoenas	*mayeri*	Mauritius pink pigeon	f G H	300				VU
		duboisi	Réunion pink pigeon	f G H	300	1705			
		cicur	Mauritius turtle dove	f G H	300			1730	
		aff. picturata	Réunion turtle dove	f G H	300	1720?			
	Phedina	*borbonica*	Mascarene swallow	I	23.9		VU		DD
	Psittacula	*eques*	Echo parakeet	**F** G	220	1755			VU
		bensoni	Thirioux's gray parrot	**F** G	180	1735		1760	
		borbonicus[2]	Réunion red and green parrot	**F** G	300	1675			
	Terpsiphone	*bourbonnensis*	Mascarene flycatcher	I	11		LC		LC
	Zosterops	*mauritianus*	Mauritius gray white-eye	**F** I N	9				LC
		borbonicus	Réunion gray white-eye	**F** I N	9		LC		
		chloronothos	Mauritius olive white-eye	**F** I N	10				CR
		olivaceus	Réunion olive white-eye	**F** I N	10		LC		
Chelonii	*Cylindraspis*	*inepta*	Mauritius domed tortoise	**F** H	50000[3]			1850[4]	
		triserrata	Mauritius high-backed tortoise	**F** H	50000[3]			1850[4]	
		indica	Réunion giant tortoise	**F** H	50000[3]	1760[4]			
Mammalia	*Mormopterus*	*acetabulosus*	Mauritius free-tailed bat	I	7				EN
		francoismoutoui	Réunion free-tailed bat	I	7		LC		
	Pteropus	*rodricensis*	Golden bat	**F** N	254			1745	
		niger	Black-spined flying-fox	**F** N	450	1775[5]	(CR)		EN
		subniger	Rougette	**F** N	250[3]	1860		1865	
	Taphozous	*mauritianus*	Gray tomb bat	I	28		NT		NT
Squamata	*Cryptoblepharus*	*boutonii*	Bouton's skink	I	1.7		CR[6]		DD
	Gongylomorphus	*bojerii*	Bojer's skink	I	3.9	1865			CR[7]
	Leiolopisma	*mauritiana*	Didosaurus	**F** I	1120			14th–15th?	
		telfairii	Telfair's skink	**F** I	68				VU
		ceciliae	Arnold's skink	**F** I	130[3]	1665?			
	Nactus	*serpensinsula*	Mauritius night-gecko	I	5.8				VU
		coindemirensis	Lesser night-gecko	I	0.8				VU
		soniae	Réunion night-gecko	I	2.1	1665?			
	Phelsuma	*cepediana*	Blue-tailed day-gecko	f I	4.6				LC
		rosagularis	Upland forest day-gecko	f I	3.4				DD
		ornata	Vinson's day-gecko	f I	3.7				DD
		guimbeaui	Guimbeau's day-gecko	f I	7.1				DD
		guentheri	Günther's day-gecko	f I	74.6				VU
		borbonica	Réunion forest day-gecko	f I	10		EN		
		inexpectata	Manapany day-gecko	f I	6		CR		
	Number of species					16	13	11	24

For each species, diet, body size, and status are given ("extinct" with the date of extinction or "extant" with the IUCN status).
Red colors indicate when extant species on Mauritius are confined to northern islets.
Diet: ***F****, frugivore; f, occasionally frugivore; G, granivore; H, herbivore; I, insectivore; N, nectarivore; R, raptor.*
?, putative date of extinction; 1, only flightless taxon shared by both islands; 2, species of which genus remains unclear (formerly Necropsittacus); 3, rough approximate value because substantial differences were found depending on the sources; 4, isolated individuals probably survived beyond this date on Réunion, and populations have survived between 1740 and 1850 on the northern islets on Mauritius; 5, a small population has been rebuilding in the East since the beginning of the 21st century; 6, several individuals recently observed, but this species has long been presumed extinct; 7, one of the two subspecies went extinct on Mauritius mainland.
Source: Dunning (2007); Hume (2007, 2011, 2013, 2019); Arnold and Bour (2008); Cheke and Hume (2008); Cheke (2013); Slavenko et al. (2016); Heinen et al. (2017); and Fourasté et al. (2019); https://www.iucnredlist.org.

appendices of Cheke and Hume (2008) and relative updated publications (see **Supplementary Appendix 1**).

Overhunting

Overhunting is primarily related to human demography, and this was especially the case in the Mascarenes where the first settlers were described as inveterate hunters on both islands (Lougnon, 2005; Cheke and Hume, 2008). Using data available for Mauritius in Cheke and Hume (2008) and for Réunion in INSEE (2014), we compared the demography on Réunion and Mauritius since the beginning of human colonization. We also tried to document the extent to which marooning, i.e., slaves fleeing their captive terrible condition, might have contributed to overhunting on both islands.

Deforestation

We assessed the destruction of native forest habitats since the beginning of human settlement on Mauritius using digitized maps of native forest clearings in 1773, 1835, 1872, 1935 and 1997 available in Norder et al. (2017). For Réunion, we created digitized maps of native forest clearings based on Selhausen's maps of 1793 and 1818. Earlier maps were not used because they were far too inaccurate regarding forest clearings (Germanaz, 2016). We also produced a map of native forest clearings in 1925 (J.-C. Notter, unpublished data), which marked the end of the *Pelargonium* cropping (Cheke and Hume, 2008), and used the recent work of Strasberg et al. (2005) as the most recent assessment of habitat transformation (**Supplementary Appendix 2**).

By cross-referencing the current habitat maps with maps of the clearing progress since the beginning of human colonization, we assessed the chronology of the destruction of native habitats. Habitat maps were based on common elevational zoning: 0–400 m, lowland; 400–850 m, mid-elevation; 850–1,200 m, submontane; 1,200–2,000 m, montane; 2,000–3,070, subalpine. This zoning generally follows elevational boundaries classically described for the two islands. The "lowland" area here is close to the definition of Dupouey and Cadet (1986) on Réunion and the elevational boundary between the so-called humid and subhumid forests was probably a bit below on Mauritius (Vaughan and Wiehe, 1937). The elevation of 850 m corresponds more or less to the upper limit of the megathermic area (Cadet, 1977) and to the top of Mauritius. Numerous lowland woody species occur up to 1,200 m in the "submontane" area on Réunion (Strasberg et al., 2005). The "montane" area then extends up to the average elevation of the trade-wind inversion (Cadet, 1977; Strasberg et al., 2005). The "subalpine" area also includes elevations above 2,700 m which are in an "alpine" environment.

Finally, given the importance of frugivores among forest vertebrates in the Mascarenes, we focused on the spatial distribution of fleshy-fruited plants that provide(d) crucial resources for these vertebrates. In particular, we studied the influence of elevation on the proportions of fleshy-fruited plants and large fleshy-fruited plants (i.e., mean fruit diameter > 13 mm) within woody plant communities. On Réunion where sampling is substantial, we used spatial statistics for modeling (for more details, see **Supplementary Appendix 3**; Albert et al., 2018). Such modeling could not be performed on Mauritius because extant forests are too scarce and do not currently display sufficient environmental heterogeneity (**Figure 1**). Nevertheless, Florens (2008) surveyed native forest remnants, which enabled to roughly characterize the proportions of (large) fleshy-fruited plants on Mauritius. We then cross-referenced the spatial distribution of fleshy-fruited plants with land clearing maps at studied dates.

RESULTS

Human-induced extinctions within taxa of forest vertebrates shared by Réunion and Mauritius might have begun in the 14th century on Mauritius mainland after the arrival of Arab traders (Hume, 2013; **Figure 2A** and **Table 1**). Several reptile species may have survived only on the northern islets from that time. Most extinctions occurred from the beginning of permanent human colonization, i.e., 1638 on Mauritius and 1665 on Réunion. Shared lineages of forest vertebrates were dominated by frugivores in terms of body mass (**Figure 2B**). Frugivores went extinct more often than other vertebrates and this phenomenon was much more marked on Réunion which lost a large part of its large frugivores as early as 1750. Most large-bodied frugivores were present until the middle of the 19th century on Mauritius: giant tortoises went extinct on the northern islets in 1850 and the *Pigeon Hollandais* and the *Rougette* around 1870 on Mauritius mainland. The balance of extinctions, i.e., 16 and 11 species extinct on Réunion and Mauritius, respectively, remains unchanged since that time and Mauritius still has 68% of its native forest vertebrates (**Figure 2A** and **Table 1**). The largest surviving native frugivore on Réunion for more than 150 years is the Réunion bulbul (the only larger extant forest vertebrate is the Réunion harrier). The median body size of frugivores remains much larger on Mauritius compared to Réunion due to the extant Black-spined flying-fox, Echo parakeet and Telfair skink (on northern islets only for the latter; **Figure 2B**).

Introduction of Vertebrates

Réunion and Mauritius have experienced the naturalization of about 50 vertebrate species that have potentially impacted native terrestrial biota (**Supplementary Appendix 1**), excluding the two species of non-native tortoises voluntarily introduced on Round Island as taxon substitutes of native giant tortoises (Griffiths et al., 2011; Cole, 2012). Mauritius mainland showed earlier introductions of vertebrates than Réunion, especially predators such as the Ship rat introduced in the 14th century, the Crab-eating macaque and the Pig in the 16th century (Hume, 2013; **Figure 2C**). Potentially harmful birds and reptiles were introduced late except the Common myna in the mid-18th century (**Supplementary Appendix 1**). Hence, the main vertebrates involved in early extinctions were land mammals that were introduced before or at the beginning of permanent settlements on Réunion and Mauritius (**Figure 2C**).

The early introduction of predators such as the Ship rat, the Pig and especially the Cat, caused a carnage among flightless birds, e.g., Wood rails (*Dryolimnas*), but also among other ground nesting birds (Cheke, 2013) and giant tortoises,

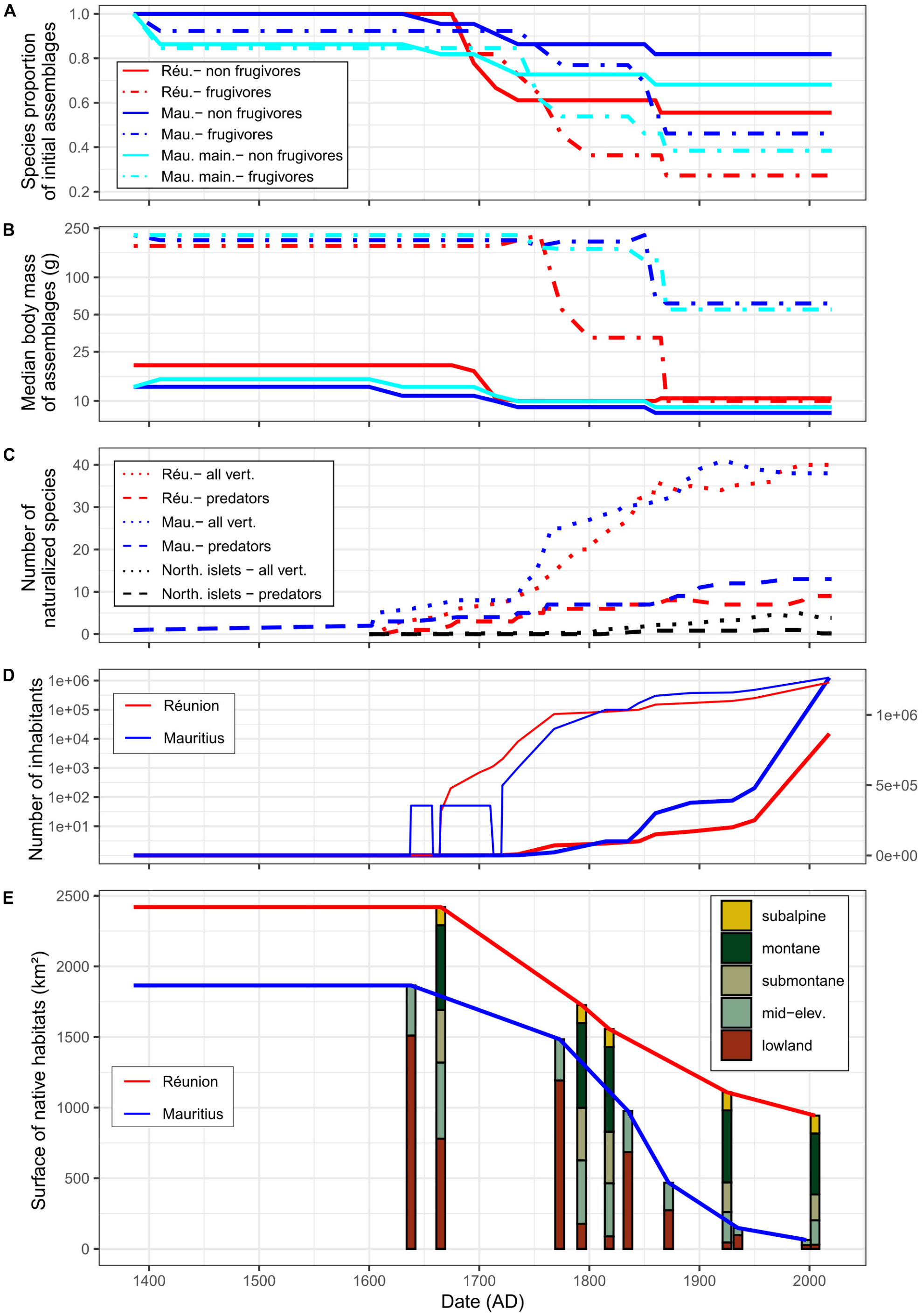

FIGURE 2 | Chronology of extinctions of native forest vertebrates in lineages shared between Réunion and Mauritius **(A,B)** and of main extinction factors **(C–E)** since first human arrival. Islands are displayed by colors: Réunion in red, Mauritius in blue (i.e., considering mainland and the northern islets), Mauritius mainland in cyan [panels **(A,B)** only], northern islets in black [panel **(C)** only]. **(A)** Changes in species richness of native frugivores (dotdash lines) and non-frugivores (solid lines) due to extinctions as proportions of initial species assemblages. **(B)** Changes in median body mass of native assemblages of frugivores and non-frugivores [same legend as in panel **(A)**]. Note the log-scale for the y-axis. **(C)** Changes in the number of vertebrate naturalizations: all land vertebrates (dotted lines) and predators (dashed lines). For the northern islets, the mean number is given. Note the non-monotonicity of the curves which reflects extinctions (for more details, see **Supplementary Appendix 1**). **(D)** Human population size (bold lines: arithmetic scale on right y-axis, thin lines: log-scale on left y-axis). There are no accurate estimate of the number of Dutch settlers who occupied Mauritius more or less permanently during the 17th century. Similarly, after the abandonment of Mauritius by the Dutch, the human population officially fell to zero even though there is evidence of maroons persistence before the French took possession. **(E)** Changes in areas of native habitats; for all habitats (solid lines) and elevational habitats (colored bars: lowland, 0–400 m; mid-elevation, 400–850 m; submontane, 850–1,200 m; montane, 1,200–2,000 m; subalpine, 2,000–3,070 m). For Réunion, approximately 100 km^2 of unfavorable areas (mostly bare lava flows in the caldera) have been excluded from analyses.

as reported many times by settlers and travelers (Lougnon, 2005; Cheke and Hume, 2008). Moreover, the absence of any mention in the historical literature of the world's greatest skink on Mauritius is likely the direct result of the early introduction of the Ship rat (Hume, 2013). As stated by Blackburn et al. (2004), species most susceptible to introduced mammals probably went extinct rapidly on both islands, i.e., before 1750 (**Figure 2C**). However, several large vertebrates were able to survive on Mauritius until now despite the persistence of mammal predators, sometimes at high density, while the Pig went extinct in the meantime on Réunion (**Table 1**). Even taxa such as fruit pigeons (*Alectroenas*) that went extinct on both islands have lasted longer on Mauritius mainland than on Réunion (**Table 1**). This is all the more puzzling since several mammal species known for their severe impact, such as the Crab-eating macaque and the Indian mongoose, have been introduced on Mauritius, but never on Réunion (**Supplementary Appendix 1**). The northern islets experienced few introductions of vertebrates, and especially few and relatively late introductions of predators (**Figure 2C**), which is probably the main reason for the capacity of the Telfair skink and several endemic geckos to persist until now (**Figure 2A** and **Table 1**). Thus, although introduced vertebrates have had a major impact on the native fauna of the archipelago, apart from the northern islets which shelter several endemic reptiles, this factor cannot explain alone why all large forest vertebrates went extinct so quickly on Réunion compared to Mauritius.

Overhunting

The Dutch claimed Mauritius in 1598 and occupied the island between 1638 and 1710, with a pause between 1657 and 1664. During this period, the European population of Mauritius never numbered more than 50 according to Hume (2013). When the French actually took control of Mauritius in 1721, Réunion already had about 2,000 inhabitants (**Figure 2D**). On that date, flightless birds were extinct on both islands and many forest vertebrate populations were already strongly reduced or were collapsing, especially on Réunion where increasing demography led to a strong demand for meat. The local authorities actually early realized how quickly the populations of large vertebrates were collapsing, which particularly worried them because the French East India Company was using the native fauna to supply its ships free of charge (Lougnon, 2005). Large frugivores were particularly prized because they were, by necessity, large body-sized game (**Figure 2B**). Settlers were literally obsessed with the areas that were still home to abundant wildlife at the beginning of the 18th century, areas known as "the land of food" (Defos Du Rau, 1960). Attempts to legally regulate hunting on Réunion proved totally unsuccessful (Cheke and Hume, 2008). The arrival of the governor Mahé de La Bourdonnais in 1735 coincided with strong economic development based on sugar production and a sharp increase in the number of inhabitants on Mauritius (**Figure 2D**). In 1768, the number of inhabitants was still three times larger on Réunion than on Mauritius, but the balance was reversed in the last decades of the century (**Figure 2D**). The number of inhabitants on Mauritius has remained higher since that date. Settlers were known as active and efficient hunters on both islands (Lougnon, 2005; Cheke and Hume, 2008), deer hunting has for instance remained an institution on Mauritius since that time (Cheke and Hume, 2008). However, the sharp increase in inhabitants on Mauritius has surprisingly not led, as on Réunion, to the rapid extermination of all large native frugivores.

Marooning may have significantly contributed to vertebrates being overhunted in the archipelago. Indeed, maroons have early taken refuge in the remote forests of Réunion and Mauritius, and lived largely on the fauna of both islands between the 17th and 19th centuries (Lougnon, 2005; Cheke and Hume, 2008; Dijoux, 2013). We do not have accurate estimates of the number of maroons on both islands (**Figure 2D**). The phenomenon was quite intense in the first half of the 18th century on Réunion where small villages of maroons may have existed in the *Cirques* before the settlers launched man-hunts that gradually pushed the maroons back up to the highlands (Dijoux, 2013). Marooning was also prominent in the early phases of the colonization of Mauritius (Hume, 2013) and succeeded in posing severe difficulties to the first French settlers (Cheke and Hume, 2008). The phenomenon then seems to have been essentially confined to south-western Mauritius where large native forests have belatedly remained. On both islands, marooning probably contributed to increased pressure on wildlife in remote areas that could act as refuges. However, while overhunting has played an important role in the extinction of vertebrates on both islands, it fails to explain alone why the native fauna that had survived the arrival of introduced predators went rapidly extinct on Réunion compared to Mauritius.

Deforestation

Before permanent colonization, lowland forests (under 400 m asl) represented 31.8 % of total area on Réunion against 81% on Mauritius (**Figure 2E**). On Réunion, the belt of lowland habitats was rapidly cleared which generated large-scale fires on the leeward as reported by La Houssaye in 1698 (Lougnon, 2005). During the 18th century, deforestation eventually affected almost all lowlands that could be cultivated on the windward. Despite the intense exploitation of ebony trees on Mauritius by the Dutch and the early use of fires (Gosling et al., 2017), the island was still largely wooded when the French took control in 1721 (**Figure 2E**). The permanent colonization of Mauritius led to intense deforestation that has not stopped until the 20th century. Around 1800, 610 km^2 of native forests have been cleared on Réunion and Mauritius, which represented *ca* 87% and 40% of lowland habitats, respectively (**Figure 2E**). Hence, Réunion lost its overall tropical lowland forest in less than 135 years of settlement, which probably had dramatic functional consequences for native forest vertebrates, notably for frugivores.

On Réunion, fleshy-fruited plants overwhelmingly dominated woody plant communities at sea level (estimated proportion $>80\%$) and were dominant up to 1,400 m asl (**Figure 3**). The estimated proportion of large fleshy-fruited plants was *ca* 25% at sea level and sharply decreased with elevation ($<10\%$ in submontane habitats and $<3\%$ in montane habitats). The early destruction of the lowland belt has thus led to the rapid loss of highly favorable areas for frugivores (**Figures 2E**, **3**). Moreover, due to belt structuring, favorable

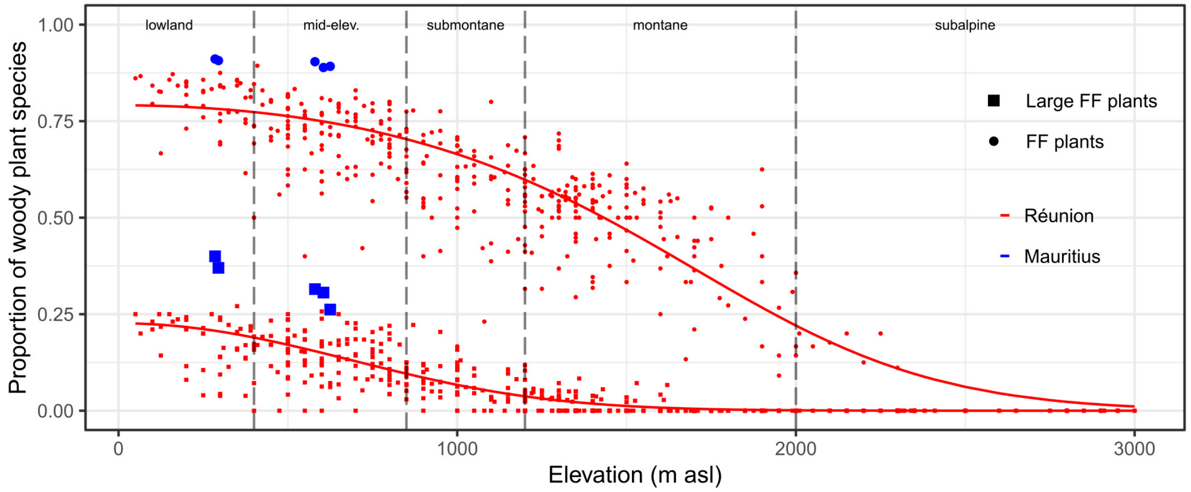

FIGURE 3 | Proportion of (large) fleshy-fruited plants within woody plant communities depending on elevation on Réunion and Mauritius. The x-axis is divided according to the typology of elevational habitats (dashed vertical lines). Dots and squares symbolize the proportions of fleshy-fruited (FF) and large fleshy-fruited plants, respectively. Sampling plots on Réunion and Mauritius are displayed by red and blue colors, respectively. For Réunion, predicted probabilities are displayed by solid lines (spatial modeling is visible at **Supplementary Appendix 4**).

remnants were systematically adjacent (i) at lower elevations, to cleared areas (and subsequently subject to high hunting pressure), and (ii) at higher elevations, to (sub)montane habitats where proportions of (large) fleshy-fruited plants rapidly decreased with elevation (**Supplementary Appendix 4**). Thus, effective refuges were rare on Réunion, not only because the original area of favorable habitats was relatively small, but also because the relief accentuated the fragmentation of potentially suitable remnants (**Supplementary Appendix 5**).

On Mauritius, fleshy-fruited plants dominated woody plant communities in the lowlands even more than on Réunion (**Figure 3**). This was mainly due to higher proportions of large-fruited plants with up to 40% of woody plants on Mauritius. Hence, native forest habitats are supposed to have been formerly highly favorable to native frugivores throughout the island. This high suitability implies that, with a comparable level of deforestation in 1800, native forests probably remained much more favorable to native frugivores on Mauritius than on Réunion (**Figures 2E**, **3**). Finally, native areas have belatedly persisted on the central plateau of Mauritius as a compact habitat (**Supplementary Appendix 5**), with the possibility for native vertebrates to better escape, at least for a time, from the multiple human-induced disturbances.

DISCUSSION

Behind This Faunal Paradox, the Rapid Deforestation of Suitable Habitats on Réunion

The majority of native forest vertebrates in the Mascarenes has disappeared since human colonization, but this phenomenon nevertheless shows important disparities in the archipelago (Cheke and Dahl, 1981; Cheke and Hume, 2008; Hume, 2013). Considering vertebrates from lineages shared by Réunion and Mauritius, we sought to understand why the former island, which still hosts 35% of native habitats, has lost all of its large forest vertebrates (except the Réunion harrier, *Circus*) while the latter, whose habitats have been almost completely destroyed, has retained a greater diversity of squamates (*Gongylomorphus*, *Leiolopisma*, *Nactus*), birds (*Falco*, *Foudi*, *Nesoenas*, *Psittacula*) and mammals (*Pteropus*). With the exception of the northern islets where squamates avoided extinction thanks to low densities of introduced predators (Cheke and Hume, 2008; Cole, 2012), this paradox cannot be explained by differential pressures of mammal introduction and overhunting. On the contrary, Mauritius experienced a greater number of introductions of predators known for their negative impact on native vertebrates (Florens, 2013; Reinegger et al., 2021). Meanwhile, although overhunting likely impacted more Réunion during early human colonization, it has not spared Mauritius, where the number of inhabitants has been higher than on Réunion since the late 18th century. The introduction of invasive vertebrates and overhunting being put aside, the major explanatory difference between the two islands is the rate of deforestation of lowland habitats since human colonization. While on Mauritius, low-fragmented favorable forests have long persisted, lowland habitats on the leeward coast of Réunion had disappeared as soon as the early 18th century and were massively destroyed along the century course on the windward coast. The suitability of mid-elevation remnants on Réunion has probably also been reduced due to the fragmentation induced by landform configuration. Montane habitats, especially in steep places, may have acted as inhospitable refuges from overhunting, but not from introduced mammal predators (Thiollay and Probst, 1999; Pinet et al., 2009). In fact, there may be a critical size/configuration of suitable home-range for a given level of disturbance. This was demonstrated on Mauritius after the disappearance of *Les Mares* in 1975 with the sharp decline of the populations of the Pink pigeon, the Echo parakeet and the Mauritius olive white-eye which had resisted well until 1950 (Jones, 1987; Jones et al., 1998). Additional drivers, beyond the scope of this study, may also have played a role in the extinctions observed. For example, avian malaria has been mentioned as a possible cause of extinction of the Hoopoe starling on Réunion in the 19th (Cheke, 2013). However, vector-borne diseases seem unlikely to have decimated focal vertebrates on Réunion, but not on Mauritius, where introductions of potential host vertebrates have been more massive and where there is no elevational escape from *Culex pipiens fatigans* (see Peirce et al., 1977).

We show that large frugivores are more prone to extinction than other forest vertebrates in the Mascarenes, as already demonstrated elsewhere (Steadman, 1995). Their extinction has been especially rapid and massive on Réunion where the lowland belt rich in large fleshy-fruited plants was concomitantly destroyed. These plants probably provided crucial resources for frugivores and their spatial distributions may have coincided, as already demonstrated in the tropical Andes (Dehling et al., 2014; Correa et al., 2015), on Mount Kilimanjaro (Ferger et al., 2014) or in Papua New Guinea (Hazell, 2020). All forests on Mauritius were probably widely dominated by fleshy-fruited species with an even higher proportion of large fleshy-fruited plants than on Réunion. Therefore, the long-standing persistence of low-fragmented suitable forests probably played a key role in the survival of the *Pigeon Hollandais* until 1850 (see Morante-Filho et al., 2018) and in the maintenance of the Black-spined flying-fox and the Echo parakeet until today. Even introduced *Coracopsis* parrots from Madagascar that naturalized in the 1790s on Réunion failed to survive in lowland forest remnants, while the Ring-necked parakeet has naturalized in Mauritius native forests since its introduction in the 19th century (Cheke and Hume, 2008). Hence, in regards to the strong modulation by elevation of suitable surfaces observed in the Mascarenes, it is not surprising that high-elevation oceanic islands, all subject to strong environmental gradients (Irl et al., 2016), experience globally higher rates of frugivore extinctions (Heinen et al., 2017). In all these islands, the systematic destruction and fragmentation of lowland native forests by humans have led to the early destruction of the most suitable habitats for frugivores.

Because of the assumed overlap of spatial distributions of fleshy-fruited plants and frugivores in the Mascarenes, it is more convenient to study changes in habitat suitability for frugivores compared to vertebrates with different diets. However, the study of habitat suitability goes beyond food availability and encompasses a panel of biotic and abiotic conditions to maintain a population. Although belonging to radiated lowland lineages (Cheke and Hume, 2008; Kehlmaier et al., 2019), several extinct vertebrates were sometimes described as frequenting montane habitats on Réunion, which fueled the idea that these habitats may have acted as effective refuges. Yet, these vertebrates may have been unable to breed and/or to feed all year long there. The case of giant tortoises is emblematic, as they were observed in steep and cool montane slopes (Lougnon, 2005), but probably lacked suitable nesting localities without the possibility of returning to the coast (Hume et al., 2021). Likewise, vertical migrations were attributed to several bird species, of which passerines, pigeons and parrots (Lougnon, 2005). As suggested by fruit pigeons *Alectroenas* in Madagascar, vertical migrations of pigeons on the leeward were probably seasonal, descending in the lowlands during the wet season, and returning in winter to the mid-elevations, probably because of food availability (Hume, 2011). Hence, these forest vertebrates were capable of adapting to heterogeneous insular contexts, but they probably remained highly dependent on lowland habitats. In this respect, the South-West Indian Ocean islands offer interesting perspectives to understand the distribution of extinct vertebrates. For example, four sympatric pigeons and doves related to the extinct Mascarene columbids have persisted in the Comoros where forests still remain along elevational gradients (Hume, 2011). Recent deforestation in this archipelago thus provides a clinical case to better understand the capacity of these species to adapt to montane conditions that are presumed to be much less favorable.

Need for Paleoecological Works, Especially on Réunion

Paleontology plays a central role in the knowledge of extinct fauna and extinction factors. In the Mascarenes, Réunion paleoecosystems remain the less well investigated (Hume, 2013). The main reasons are geomorphological as the island has few favorable sites (but see Mourer-Chauviré et al., 1999) compared to Mauritius and Rodrigues where caves, limestone deposits and Lagerstätte as *La Mare aux Songes* have yielded numerous subfossil bones (Griffiths and Florens, 2006; Cheke and Hume, 2008; Rijsdijk et al., 2009, 2015; Hume, 2013; Hume et al., 2021). Due to the lack of osteological material, several emblematic vertebrates have not yet been described and remain poorly known, such as the Réunion blue pigeon, the Réunion turtle dove or the Réunion red and green parrot (Hume, 2011, 2013). The existence of certain species remains putative, e.g., the Réunion wood pigeon (*Columba*) (Hume, 2011), and Mourer-Chauviré et al. (1999) stated that the near absence of flightless birds on Réunion might be a sampling bias. Moreover, osteological details allow us to better understand the ecology of extinct species of which we usually have very sketchy accounts. For example, the extinct Mauritius turtle dove differs from the Madagascar turtle dove in a number of osteological details, which shows that this subspecies was probably more terrestrial than the introduced Madagascar turtle dove (Hume, 2011). Finally, osteological material can also be used to better trace the chronology of native vertebrate extinction. For example, the first material evidence of contact between the Mascarenes and the Arab traders was obtained by dating a mandible of ship rat collected from *La Mare aux Songes*, which provided at the same time a credible explanation for the early extinction of several endemic animals on Mauritius mainland (Hume, 2013).

Lowland leeward habitats have been completely transformed and may have been the richest in large vertebrates such as giant tortoises or skinks in the Mascarenes (Cheke and Hume, 2008), as elsewhere (Olson and James, 1989). Our analyses, based on extrapolation of statistical estimators (**Supplementary Appendix 6**), suggest that the lowlands on Réunion leeward were rich in large fleshy-fruited plants and that ecosystems more complex than a latan/benjoin savanna were probably encountered there. Our work therefore supports the hypothesis that the structure and composition of the whole coastal dry forest have been early altered and the leeward lowlands early savannised [in Lougnon (2005), Houssaye reported large areas of recently burned land in 1689, while stating that the dry *Pointe des Galets* was forested]. Moreover, Mourer-Chauviré et al. (1999) excavated a great amount of large seeds belonging to *Latania, Terminalia*, *Cassine, Foetidia*, *Pandanus*, or *Sideroxylon* among giant tortoise bones in the swamp of l'Ermitage (D. Strasberg, personal communication). These findings suggest that plant community composition might have been relatively close to what was revealed by Rijsdijk et al. (2009) at *La Mare aux Songes* on Mauritius. Hence, we need a thorough paleoecological work on Réunion to better understand what may have been the likely main habitat of the largest forest vertebrates.

Concern for Extant Forest Vertebrates and the Functioning of Native Forests

While the majority of native forest vertebrate species are extinct, the situation is highly contrasted regarding extant ones. There is little doubt that many of them would have gone extinct if the conservationists had not taken action on both islands to face the extinction debt. While clearings no longer seem to occur, conservationists have focused on improving the quality of native remnants that are often severely degraded by exotic plants, on combating poaching and introduced predators, while attempting to control the introduction of new harmful organisms (Cheke and Hume, 2008; Sanchez and Probst, 2016). At the same time, concerns about the impact of vertebrate loss on the functioning of tropical forests have globally grown and recent studies with dramatic results for the regeneration of Mascarene tropical forests have shown the urgency of restoring plant-vertebrate interactions.

Some vertebrates were able to adapt to disturbances induced by human colonization in the Mascarenes. For example, the Réunion gray white-eye is able to colonize all kinds of habitats (Barré et al., 2005; Cheke and Hume, 2008). Likewise, the Mascarene swiftlet or microbats such as the Réunion free tailed bat, hold up well as long as breeding and roosting sites are preserved, especially caves and lava tunnels. Bourbon gecko's and Réunion passerines (except the cuckoo-shrike) are widely distributed where native forest still remain, even though the size of populations is sometimes much smaller than what it used to be, e.g., the Réunion bulbul (Cheke, 1987). However, most extant vertebrates are threatened and subject to considerable conservation effort, especially on Mauritius. The reintroduction of individuals of the Pink pigeon and the Echo parakeet reproduced in captivity has recently allowed to significantly increase their population size. Likewise, the Réunion harrier and the Mauritius kestrel have recolonized a large part of their initial range in their respective island. The rescue of the latter is regarded as a tremendous success story in conservation biology. Populations of native reptiles have reached satisfactory sizes on northern islets of Mauritius since the extirpation of all non-native mammals in the 1990s (Cheke and Hume, 2008). Some actions, however, are currently unable to enhance populations of threatened species, for example for the Mauritius olive white-eye, the Manapany gecko or the Réunion cuckoo-shrike. The latter, which previously had a wider range including the lowlands, is now confined to montane habitats to northern Réunion (Barré et al., 2005). The impressive efforts to control introduced predators into a specially created reserve have been unsuccessful to downlist the species from the "Critically Endangered" category. Hence, this species may be a lowland species which survives in sub-optimal habitat (Thiollay and Probst, 1999). In light of our results, the establishment of a second population at lower elevations should be reconsidered.

Among forest vertebrates, the guild of frugivores plays a crucial role in the functioning of tropical forests by ensuring seed dispersal of most woody plants. Building on works showing the negative impact of the extirpation of large frugivores in continental forests (Terborgh et al., 2008; Effiom et al., 2013; Harrison et al., 2013), recent studies have investigated the consequences of their massive defaunation on the regeneration of Mascarene forests. They showed that primary succession has been profoundly disturbed on Réunion for several centuries with a dramatic loss of native plant diversity on historical lava flows (Albert et al., 2020), but also that numerous tree species show a worrying lack of recruitment in old-growth forests, particularly on Réunion where all large frugivores went extinct (Albert et al., 2021). In contrast, the regeneration success for many small- and medium-seeded plants in Mauritian remnants is probably due to the extant Black-spined flying-fox and Echo parakeet (Florens et al., 2017). While experimental direct sowing on Réunion has already shown that the recruitment of large-seeded trees can be restored (Albert, 2020), the future should focus on rewilding ecosystems to restore processes across space and time. From this point of view, the situation is contrasted on Mauritius. On the one hand, the Black-spined flying-fox is facing a massive slaughter for demagogic reasons instead of being protected (Florens et al., 2017). On the other hand, the population of the Echo parakeet has reached a threshold which may coincide with the carrying capacity of native remnants (S. Henshaw, personal communication); rewilding with substitute giant tortoises has also been undertaken to restore seed dispersal and herbivory on northern islets and *Ile aux Aigrettes* (Griffiths et al., 2011; Cole, 2012), which are now formidable labs for ecological restoration. The most promising possibilities may be found on Réunion where there are now more suitable areas than on Mauritius and where the need to restore plant-animal interactions in native ecosystems should be a high-rank priority (Albert et al., 2021). The Echo parakeet being rescued on Mauritius, it is now possible to consider its reintroduction on Réunion, where populations could reach even higher levels than on Mauritius. French and Mauritian stakeholders are currently reflecting on the feasibility of this project (K. Leclerc, personal communication). Finally, the Black-spined flying-fox is back to Réunion after more than two centuries of absence (Fourasté et al., 2019). If the embryonic population is not hunted and/or persecuted, this species may be able to recolonize native forests where it has a crucial role to play as double mutualist vertebrate (Florens et al., 2017; Albert et al., 2021). Needless to say, this will depend on the ability of conservationists to learn from the socio-ecological context and create the conditions for consent.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

SA, OF, CA-P, and DS developed the ideas for the research. SA and DS collected the data. SA analyzed the data. All authors contributed critically to the drafts of the article and have given their approval for publication.

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Remote Sensing Reveals Lasting Legacies of Land-Use by Small-Scale Foraging Communities in the Southwestern Indian Ocean

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Archaeologists interested in the evolution of anthropogenic landscapes have productively adopted Niche Construction Theory (NCT), in order to assess long-term legacies of human-environment interactions. Applications of NCT have especially been used to elucidate co-evolutionary dynamics in agricultural and pastoral systems. Meanwhile, foraging and/or highly mobile small-scale communities, often thought of as less intensive in terms of land-use than agropastoral economies, have received less theoretical and analytical attention from a landscape perspective. Here we address this lacuna by contributing a novel remote sensing approach for investigating legacies of human-environment interaction on landscapes that have a long history of co-evolution with highly mobile foraging communities. Our study is centered on coastal southwest Madagascar, a region inhabited by foraging and fishing communities for close to two millennia. Despite significant environmental changes in southwest Madagascar's environment following human settlement, including a wave of faunal extinctions, little is known about the scale, pace and nature of anthropogenic landscape modification. Archaeological deposits in this area generally bear ephemeral traces of past human activity and do not exhibit readily visible signatures of intensive land-use and landscape modification (e.g., agricultural modifications, monumental architecture, etc.). In this paper we use high-resolution satellite imagery and vegetative indices to reveal a legacy of human-landscape co-evolution by comparing the characteristics – vegetative productivity and geochemical properties – of archaeological sites to those of locations with no documented archaeological materials. Then, we use a random forest (RF) algorithm and spatial statistics to quantify the extent of archaeological activity and use this analysis to contextualize modern-day human-environment dynamics. Our results demonstrate that coastal foraging communities in southwest Madagascar over the past 1,000 years have extensively altered the landscape. Our study thus expands the temporal and spatial scales at which we can evaluate human-environment dynamics on Madagascar, providing new opportunities to study early periods of the island's human history when mobile foraging communities were the dominant drivers of landscape change.

Keywords: foraging, landscape archaeology, remote sensing, niche construction, ecological legacies, Madagascar

INTRODUCTION

Among archaeologists, the identification and quantification of feedbacks between past human activities and landscape-scale transformations have historically focused on economies of scale that generate highly visible changes to landscapes (e.g., monumental architecture, intensive agriculture, shifts from forests to grasslands, etc.). In contrast, activities associated with small-scale mobile foraging economies have generally been portrayed as "low impact" (Smith, 2001; Stephens et al., 2019). In regions around the world, like the Amazon, this line of thought has been compounded by legacies of settler colonialism and the processes of industrialization of land and resource use, resulting in narratives that downplay, obscure, or erase earlier (and subtler) traces of human landscape use (Heckenberger and Neves, 2009; Douglass and Cooper, 2020). Uses of remote sensing technology (i.e., satellite images) in such contexts have successfully identified these "low-impact" signatures of human action on large geographic scales (Lombardo and Prümers, 2010). While predictive models have been used around the world to narrow the search for ephemeral archaeological deposits (McMichael et al., 2014; Kirk et al., 2016; Davis et al., 2020a), the use of automated remote sensing in archaeology remains skewed toward landscape modifications that are easy to identify because of their lasting marks and effects (Tarolli et al., 2019; Davis, 2021).

Prior remote sensing analyses on Madagascar have focused on the drivers of settlement and mobility (e.g., resource availability and social aggregation) using predictive models based on satellite-derived environmental information and statistical modeling (Davis et al., 2020a,b). To fully understand settlement patterns, however, we must also look at the ecological effects of human occupation (**Figure 1**). Therefore, in this paper, we focus on identifying and characterizing legacies of forager activities and coastal settlement on the landscape of the Velondriake Marine Protected Area of southwest Madagascar, a region with a history of coastal foraging that extends back at least to 2,000 cal year BP (**Figure 2**; Douglass et al., 2019). The climate of southwest of Madagascar is defined by a wet season and a dry season. The region is extremely arid, receiving less than 50 cm of rainfall annually, and is home to highly endemic flora and fauna which varies according to the underlying geology (Douglass and Zinke, 2015). The Velondriake region sits on a Quaternary dune system composed of sandy-shell and limestone coastal rock outcrops, while further inland the geology is characterized by Pleistocene and Eocene geological systems (Besairie, 1964). Vegetation in Velondriake is largely xerophytic and classified as a "spiny thicket" ecoregion, which contains some of the highest levels of endemic flora on the island (Gautier and Goodman, 2003). The people living in coastal Velondriake today primarily identify as *Vezo* (roughly translated as "to paddle") and center their livelihood on the sea (Astuti, 1995). The area has been inhabited for thousands of years by communities practicing foraging and fishing, as well as agropastoralism over the past several 100 years (Douglass et al., 2018; Hixon et al., 2021).

In this article, we investigate whether the ancient communities inhabiting the Velondriake region in southwest Madagascar significantly modified their landscape in ways that persist into the present. Specifically, we hypothesize that lasting changes in vegetative communities and soil chemistry are legacies of fitness-enhancing activities that have landscape-scale effects. We further demonstrate that these legacies can be systematically characterized using remote sensing and machine learning techniques. Machine learning, specifically probability-based methods (e.g., Breiman, 2001; Malley et al., 2012), allow us to systematically evaluate the likelihood of anthropogenic disturbance across large geographic spaces based on the geophysical properties identified in remotely sensed data. We look at geophysical properties of vegetation and soil as a palimpsest resulting from movement, settlement, and resource use over thousands of years. We then compare these landscape signatures between locations with and without material culture surface scatters to assess cumulative anthropogenic effects on the landscape. Our expectation is that places where people settled or engaged in sustained land-use will exhibit significantly different patterns in vegetative and soil properties when compared to locations with no evidence of archaeological settlement.

While the exact timing of the initial peopling of Madagascar is hotly debated (e.g., Anderson et al., 2018; Douglass et al., 2019; Hansford et al., 2020; Mitchell, 2020), coastal foraging has a long history on the island (e.g., Barret, 1985; Rakotozafy, 1996; Dewar et al., 2013; Douglass, 2016; Douglass et al., 2018), and predates evidence for the introduction of farming and herding lifeways (Domic et al., under review; Godfrey et al., 2019; Hixon et al., 2021). The debate over Madagascar's human settlement has been central to questions of anthropogenic impact on the island, notably *via* activities that may have contributed to the extinction of endemic fauna (Godfrey and Douglass, in press). Theories regarding anthropogenic drivers of extinction include potential overhunting, habitat modification, and forms of direct or indirect competition between endemic and introduced animals (Dewar, 1984, 1997; Burney, 1997, 1999; Hixon et al., 2018; Godfrey et al., 2019). Teasing apart drivers of extinction requires further clarification of anthropogenic landscape change, including in regions with long histories of foraging and the management of wild resources. Madagascar is also known for its long history of climatic variability

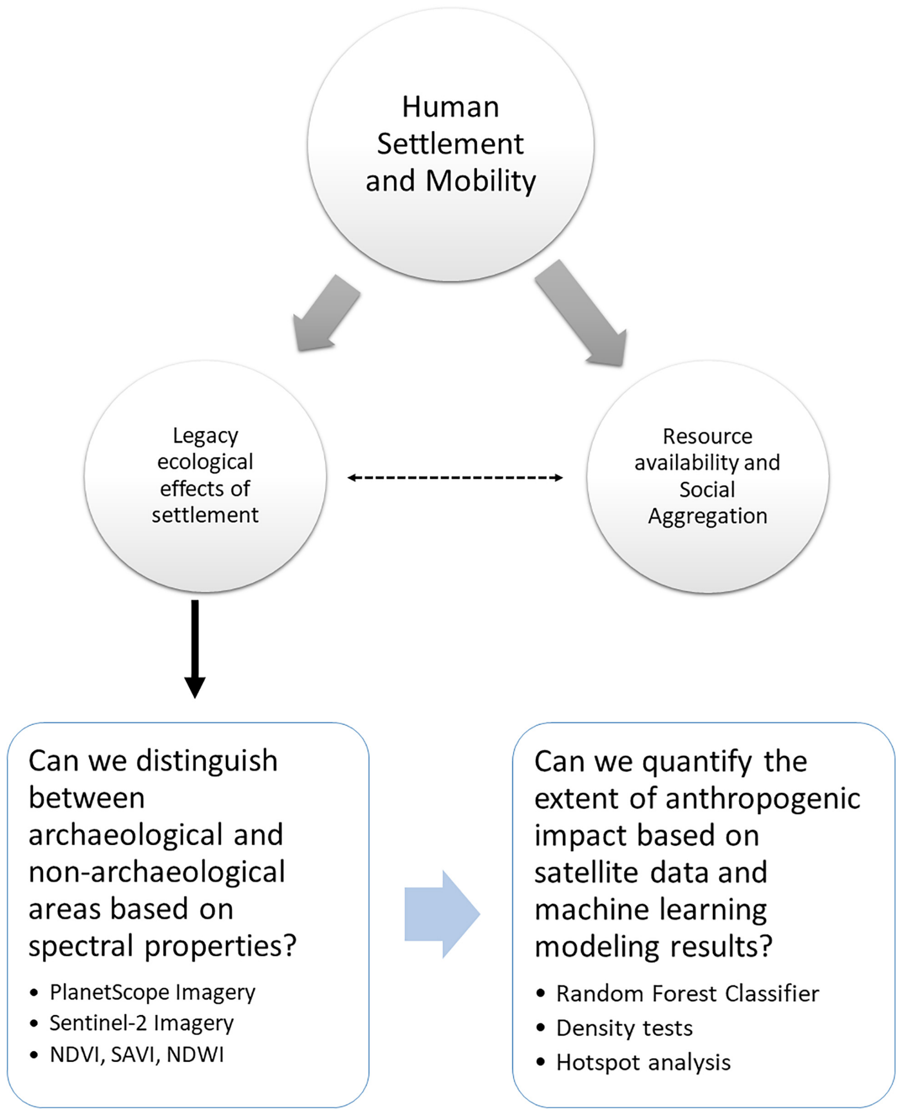

FIGURE 1 | Illustrates the methodological workflow presented in this article. The central question of human settlement and mobility patterns has been investigated previously by Davis et al. (2020a,b) as a consequence of resource availability and social aggregation. The results of this prior work feed directly into this article, and vice versa (indicated by dashed arrow). Within this paper we evaluate whether we can distinguish between archaeological and non-archaeological areas recorded in our previous work based on spectral properties (including vegetative indices). Then, we use these results to train a machine learning classifier to quantify the extent of anthropogenic impacts.

(e.g., Dewar and Richard, 2007; Douglass and Zinke, 2015). As climate change impacts intensify today, studies of how past populations modified landscapes to mitigate the impacts of resource scarcity and climate variability are vital for promoting sustainability (Razanatsoa et al., in press; Douglass and Cooper, 2020; Douglass and Rasolondrainy, 2021). However, most archaeological sites that retain information about resource use and adaptation by early mobile communities of foragers and herders consist of ephemeral artifact surface scatters and are actively disappearing due to erosion and development (Parker Pearson, 2010; Davis et al., 2020b). Innovative approaches are thus particularly needed to clarify human-environment dynamics during the earliest phases of Madagascar's human settlement and in regions vulnerable to loss or erosion of cultural landscapes.

NICHE CONSTRUCTION AND THE LEGACY OF LAND-USE PRACTICES

Anthropologists interested in the effects that humans have on their environment and the two-way feedbacks in socio-ecological systems have productively integrated Niche Construction Theory (NCT; Laland and O'Brien, 2010; Fuentes, 2016; Zeder, 2016). NCT, which stems from evolutionary biology, stresses that organisms actively modify the selective pressures in their

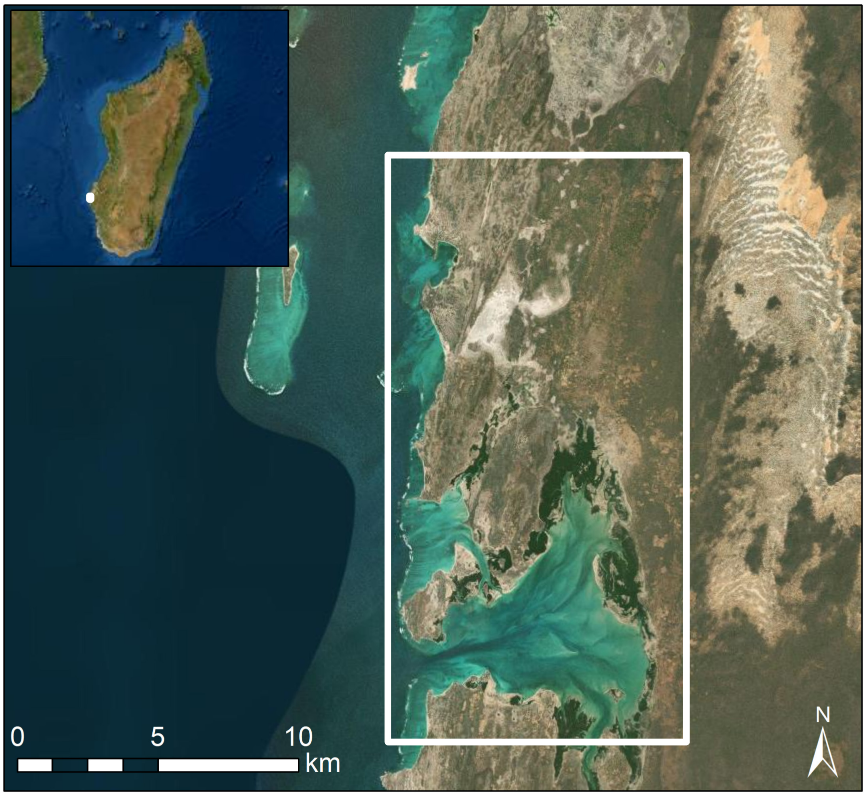

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FIGURE 2 | Map of the study region (white box).

environment in order to increase their fitness. In doing so, all organisms contribute to feedbacks that influence and alter the niches of other organisms that share those same spaces (Odling-Smee et al., 2003; Laland and O'Brien, 2010). It should be emphasized that many of the concepts of NCT borrow from related concepts previously described by evolutionary biologists (see Spengler, 2021), such as environmental engineering (e.g., Jones et al., 1994, 2010) – central to the work presented here. NCT has guided investigations of how "low impact" human activities create niches by altering the distribution and abundance of flora and fauna in ways that enhance human livelihoods (Rowley-Conwy and Layton, 2011). Prior work shows that many such niche construction activities are identifiable through soil changes (Smith, 2001) and alterations to vegetation (e.g., modification of trees) (Mobley and Eldridge, 1992; Oliver, 2007). Investigations of cultural landscapes further demonstrate how humans intentionally manipulate soil chemistry and vegetative growth patterns (Lightfoot et al., 2013). Such niche construction activities have landscape-scale effects that are difficult to assess using site-based approaches alone. Furthermore, taphonomic processes and other destructive forces can disproportionately affect the remains of ephemeral sites (i.e., foraging camps) and evidence for landscape management by "low impact" communities with high levels of mobility (Iovita et al., n.d.; Smith, 2001). Applications of NCT and related evolutionary frameworks to landscapes shaped by foraging economies have also revealed feedbacks between human use of fire, biodiversity, and resilience to climate change (Bliege Bird et al., 2008, 2020; Bird et al., 2016; Bliege Bird and Bird, 2020). This work demonstrates the vast spatial extent and persistence through time of legacies of landscape management by foragers, including through innovative use of historical aerial photographs that permit landscape-scale analysis of the effect of previous fire regimes on contemporary settlement and land-use patterns (Bliege Bird et al., 2020).

Our paper aims to build on this previous work by combining archaeological satellite-based remote sensing and innovative computational automation approaches to reveal legacies of forager land-use in coastal Madagascar. Prior remote sensing studies of archaeological foraging societies (and recently paleoanthropological sites) have taken place around the world, and many have relied on unsupervised land-cover classifications and environmental proxies to narrow down survey areas to where ephemeral cultural deposits are likely to exist (Keeney and Hickey, 2015; Davis et al., 2020a; d'Oliveira Coelho et al., 2021; Lim et al., 2021). Here, we attempt to use multispectral satellite data to directly pinpoint ecological changes associated with archaeological activity. Innovating and expanding the use of approaches that can effectively reveal "low-impact" signatures of human-environment dynamics is critical for developing more holistic understandings of the contributions of diverse communities – including highly mobile foraging communities – to shaping landscapes (Crumley, 1979).

In leveraging NCT, we are also engaging principles of relocation and perturbation (**Figure 3**), wherein relocation refers to the movement of certain ideas and resources, and perturbation refers to the subsequent adaptation and changes to both human populations and environments over time (Odling-Smee et al., 2003; Quintus and Cochrane, 2018). Signatures of a modified niche include changes to biotic, abiotic, and artifactual components of the environment, and must be related to intentional, non-random processes (Odling-Smee et al., 2013; also see Jones et al., 2010). In order for remote sensing tools to identify niche construction, we must be able to recognize instances of both perturbation (to quantify landscape modifications, themselves) and relocation (to identify different kinds of niche construction and the potential movement of people across a landscape). Relocation and perturbation should be traceable *via* similarities in material culture between sites, but also *via* patterns in vegetative and soil properties; i.e., archaeological niche construction will display perturbations in the form of distinct geophysical characteristics related to vegetative and soil characteristics and these differences will be relocated as communities migrate between places.

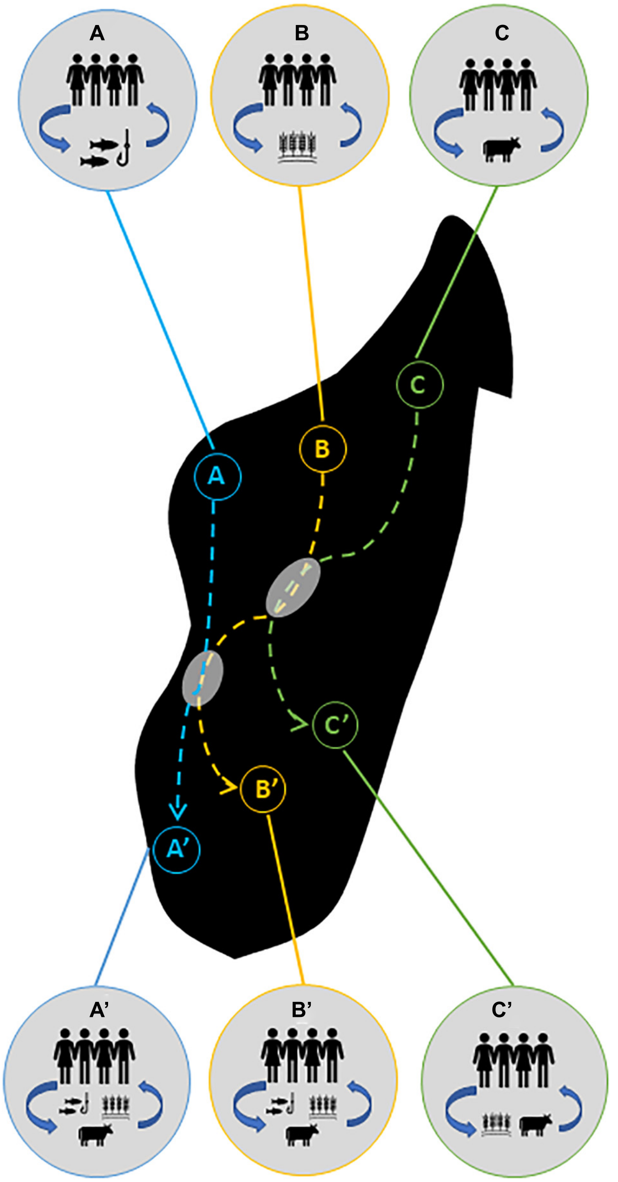

FIGURE 3 | Illustration of perturbation and relocation components of Niche Construction Theory (NCT). Each population **(A–C)** performs specific activities which create feedbacks (blue arrows) between themselves and their surrounding environments. This constitutes a cultural "niche." Relocation is represented by the dashed arrows, in which people move throughout a landscape and take their practices with them. In addition, ideas and adaptations can be spread from one community to another (gray circles) when different groups overlap in time and space, leading to the adoption of new behaviors and the formation of new niches **(A'–C')**.

In this study, we focus primarily on perturbation effects. Relocation will be the focus of future work and will require a robust radiocarbon dataset to evaluate settlement chronologies and temporal shifts in settlement. Nonetheless, our present study has ramifications for how archaeologists reconstruct and understand the impacts of foraging societies on a global scale, as the methods proposed here can be widely applied. It also contributes new insights into longstanding questions regarding the consequences of human colonization of the unique insular environments of the southwestern Indian Ocean, and Madagascar specifically.

MATERIALS AND METHODS

Previous studies, using traditional ground-based and remote sensing survey (Douglass, 2016; Davis et al., 2020a,b), have expanded our understanding of Late Holocene (~3,000 cal year B.P.) settlements on Madagascar's southwest coast. This work assessed whether settlement was affected by resource availability and used satellite-derived information about environmental factors (e.g. proximity to important resources) to generate a probability model to locate archaeological settlements. This work documented hundreds of new archaeological deposits and indicated that freshwater availability, marine resources, and defensibility are among the primary drivers of settlement choice and mobility in this region since the Late Holocene. Additionally, this work suggested the presence of Allee effects, or positive density dependence, wherein settlement actively modifies surrounding environments and results in improvements to habitat suitability (Fretwell and Lucas, 1969; Angulo et al., 2018).

In this paper, we are addressing whether ecological legacies of landscape modification exist and whether these constructed niches – primarily in the form of soil and vegetative properties – can allow us to predict ancient settlement locations and provide insight as to the extent of anthropogenic landscape modifications (**Figure 1**). In order to do this, we must first determine whether available satellite data have the spectral resolution needed to discern between known archaeological sites and places that do not contain material culture deposits (**Figure 1**). We use high-resolution PlanetScope satellite imagery (Planet Team, 2020) with 3 m spatial resolution and multispectral capabilities to calculate vegetative productivity and soil moisture content in surveyed areas with known archaeological sites (n = 340). In total, we averaged 6 PlanetScope images taken between 2018 and 2020 during the wet and dry seasons to create a 3-year average of the study region (**Supplementary Table 1**). The years chosen experienced climatic conditions within the typical range for the region (Andavadoaka Monthly Climate Averages, n.d.). We supplemented PlanetScope images with multispectral bands available from Sentinel-2 to provide additional assessment of moisture retention properties of soils and vegetation (see below). We then compared these values with ground-tested locations without any evidence of archaeological materials based on absence of surface deposits (i.e., ceramics, shells, charcoal, etc.; n = 80). Sites in this region tend to feature single occupation horizons and relatively shallow cultural deposits that are typically indicated by the presence of surface scatters (Douglass, 2016). All archaeological and non-archaeological datapoints were recorded during systematic survey operations between 2011 and 2020 (Douglass, 2016; Davis et al., 2020a).

Machine Learning Algorithm

We used PlanetScope imagery and compiled 3-year averages for the dry and wet seasons between 2018 and 2020. Seasonal differences are extreme in this region (Jury, 2003), and thus we need to account for these variations and how they affect our ability to discern archaeological materials in satellite data. As such, we conducted a pixel-by-pixel comparison in R (R Core Team, 2020) between the 3-year averaged PlanetScope images to highlight differences in environmental geophysical properties between the wet and dry season using the equation:

$$\triangle_r = D - W$$

Where Δ_r, difference between images; D, the dry season image, and W, the wet season image.

Next, we assessed the spectral characteristics of a sample of known archaeological (n = 340) and non-archaeological (n = 80) deposits throughout the study area to determine their degree of separability between different image bands. Some prior studies have chosen non-archaeological sites randomly, but here we used ground-tested locations to alleviate potential errors in sample creation (Sonnemann et al., 2017). We drew 10 m buffers around each data point and the average value for each band was calculated in R (R Core Team, 2020). Then we statistically compared archaeological and non-archaeological sites using different bands of PlanetScope imagery (see **Supplementary File**).

Next, we used Google Earth Engine (GEE; Gorelick et al., 2017), following Orengo et al. (2020), to train a random forest (RF) probability algorithm to identify archaeological deposits in southwest Madagascar. Because the archaeological deposits in this area are primarily ephemeral artifact scatters, high resolution data are required to attempt any sort of automated identification. We ran a RF probability algorithm using 128 trees and three iterations [which were deemed optimal for archaeological purposes by Orengo et al. (2020)] to locate artifact scatters (code can be found in the **Supplementary document**). The RF procedure outputs a raster of values ranging from 0 to 1, wherein 1 is a perfect match to an archaeological deposit. To evaluate accuracy and performance of this model, we withheld 40 archaeological points and 17 non-archaeological points (~12% of the training data) for validation. Then we calculated the precision (Equation 1), recall (Equation 2), and F1 (Equation 3) scores for the training and test data using thresholds of 0.60, 0.65, and 0.70.

$$\text{Precision} = \frac{\text{True Positives}}{\text{True Positives} + \text{False Positives}} \tag{1}$$

$$\text{Recall} = \frac{\text{True Positives}}{\text{True Positives} + \text{False Negatives}} \tag{2}$$

$$\text{F1} = 2 \times \frac{\text{Precision} \times \text{Recall}}{\text{Precision} + \text{Recall}} \tag{3}$$

A perfect result would have precision, recall, and F1 scores of 1.

Vegetative Indices

To evaluate ecological signatures between archaeological and non-archaeological areas, we used vegetative indices, which are mathematical formulas that provide indications of biomass and plant health/stress. First, we measured vegetative productivity using normalized difference (NDVI) and soil adjusted (SAVI) vegetative indices (Jensen, 2007). NDVI is calculated using the formula:

$$\text{NDVI} = \frac{\text{NIR} - \text{RED}}{\text{NIR} + \text{RED}}$$

SAVI is calculated using the formula:

$$\text{SAVI} = \frac{\text{NIR} - \text{RED}}{\text{NIR} + \text{RED} + \text{L}} \times (1 + \text{L})$$

Where L is a soil adjustment factor. An optimal value for L has been demonstrated at L = 0.5 and was used here (Huete, 1988).

NDVI is one of the most commonly employed vegetative indices and measures vegetation based on a ratio of reflectance values in the near infrared (NIR) and Red wavelengths. However, NDVI has accuracy issues when faced with ecologically and geologically heterogeneous areas and high soil reflectance. The SAVI is an adjusted version of NDVI which corrects for reflectance caused by soil diversity, making it useful for geographically expansive studies with high rates of ecological diversity (Huete, 1988). Both NDVI and SAVI relay information pertaining to water absorption and retention in vegetation. After calculating vegetative index values, we extracted the average values from a 20 m buffer around each archaeological and non-archaeological datapoint used for training the RF algorithm (discussed above). Then we assessed the difference between archaeological and undisturbed locations using non-parametric tests of association (see **Supplementary File**). We conducted all calculations in R v. 4.0.2 (R Core Team, 2020) using the *raster* (Hijmans, 2019) and *rgdal* (Bivand et al., 2019) packages.

Next, we evaluated Sentinel-2 imagery, which contains short-wave infrared (SWIR) bands, in the same manner as described above. We compiled 5 years of Sentinel-2 imagery by month using GEE (Gorelick et al., 2017; also see **Supplementary File**). SWIR has increased sensitivity to moisture content and can be used to distinguish mineral compositions of soils (Davis, 2017; Thabeng et al., 2020). One limitation of the Sentinel-2 data is that it has much lower spatial resolution (20 m). The only high-resolution SWIR satellite currently available is Maxar's Worldview-3 satellite (which has shown promise for archaeological purposes, see Davis, 2017). We did not have access to these particular data, however. To improve the utility of the Sentinel-2 SWIR, we used a pansharpening procedure – a form of data fusion whereby lower-spatial resolution imagery is enhanced using a higher-resolution dataset (Garzelli et al., 2004) – to resample the SWIR data from 20 to 3 m using PlanetScope imagery (see **Supplementary Figure 1**). Pan-sharpening followed a principle-component analysis (PCA) method using the RStoolbox package in R (Leutner et al., 2019). PCA pansharpening is appropriate because PlanetScope imagery is spectrally compatible with Sentinel-2 sensors (Ichikawa and Wakamori, 2018).

Using this pansharpened SWIR data, we calculated a Normalized Difference Water Index (NDWI; Gao, 1996), which is a vegetative index that reflects the biochemical metrics of plants (Sun et al., 2019). Such metrics can be used to distinguish different taxa, in addition to assessing the water content of leaves (Gao, 1996; Sun et al., 2019). NDWI uses the NIR and SWIR spectrum to measure the liquid water molecules contained within vegetative canopies (Gao, 1996). It is calculated using the formula:

$$\mathrm{NDWI} = \frac{\mathrm{NIR} - \mathrm{SWIR1}}{\mathrm{NIR} + \mathrm{SWIR1}}$$

Where NIR is the near-infrared band and SWIR1 corresponds to the first shortwave-infrared band of Sentinel 2 (1,610 nm).

Finally, to assess the potential bias in our samples of archaeological and non-archaeological points, we generated 1,000 random points within the study area and compared vegetative index and SWIR reflectance values between them and our ground-tested data (**Supplementary Figure 2**). If people have fundamentally changed the geophysical and/or geochemical properties of the landscape, we hypothesized earlier that the random locations will express different vegetative and soil properties than areas with archaeological surface scatters. Conversely, if people merely settled in areas with specific geochemical characteristics that are distributed throughout the landscape, random locations should show some similarities with archaeological areas.

Spatial Analysis

In order to quantify the impact of niche construction on different parts of the study area, we ran several spatial analyses to determine the amount of land area impacted by legacy effects and the distribution of niche construction activities across the landscape. Settlements in this region are non-randomly distributed (Davis et al., 2020b), as are niche construction activities more generally (Odling-Smee et al., 2013). Thus, anthropogenic niche construction on Madagascar should also be non-random, and likely clusters in particular places that have been used repeatedly over time. After assessing the results of the RF algorithm, the locations identified as archaeological sites with the threshold with the highest accuracy scores were converted to polygons. We calculated the area of these polygons to generate an assessment of the extent of archaeological activity within the study region. Next, we analyzed the spatial distribution of these points using the Getis–Ord General *G* test to compare the distribution of areas identified as archaeological by the RF algorithm with random patterns (Getis and Ord, 1992). Then we converted the polygons of anthropogenic locations into points and computed kernel density estimations for these locations. We conducted all spatial tests in in ArcGIS 10.7.1 (ESRI, 2020).

RESULTS

Assessments of training datasets and PlanetScope imagery resulted in clear distinctions between archaeological and non-archaeological points in all four electromagnetic bands (Blue, Green, Red, and NIR; **Figure 4B**). The differences between the samples are also statistically significant (see **Supplementary File**). The RF classifier was trained using 300 archaeological points and 63 non-archaeological points and resulted in strong performance on both the training data and test data (see **Figure 4** and **Table 1**).

Analyses of annually averaged NDVI and SAVI show a significant difference ($W = 8639$, $p < 0.05$) between vegetation in archaeological and non-archaeological contexts, where archaeological sites have higher mean vegetative index values than locations without archaeological activity (**Figure 5**; mean of -0.02 and -0.03, respectively). NDWI results show the same pattern ($W = 8468$, p-value $= 0.042$). This suggests that archaeological sites exhibit vegetative index values that are distinct from non-archaeological areas. Furthermore, archaeological sites are noticeably different in their vegetative index value distribution from randomly generated points throughout the study region (see **Supplementary Figures 2–5**).

SWIR analysis indicates that there is a tendency for areas surrounding archaeological sites to have slightly higher reflectance values in the SWIR spectrum (SWIR1: $W = 12713$, p-value < 0.002; SWIR2: $W = 11999$, p-value $= 0.024$). Most archaeological deposits express higher reflectance in the SWIR spectrum, indicating mineralogical differences and vegetation that might be distinct from surrounding non-archaeological areas.

Seasonally, we find that NDVI and SAVI values during the wet season, show a significant difference ($W = 8282$, $p < 0.02$) between vegetation in archaeological and non-archaeological contexts, where archaeological sites have higher mean vegetative index values than locations without archaeological activity (mean of -0.005 and -0.008, respectively; see **Supplementary Figure 2**). During the dry season, however, there is no significant difference ($W = 10230$, $p = 0.925$) between locations.

Using the RF results with a threshold of 0.65, we calculated the area of all identified potential archaeological deposits within the study region. Approximately 38.6 km^2 ($\sim$17%) of the study region exhibits differences in soil and vegetative properties

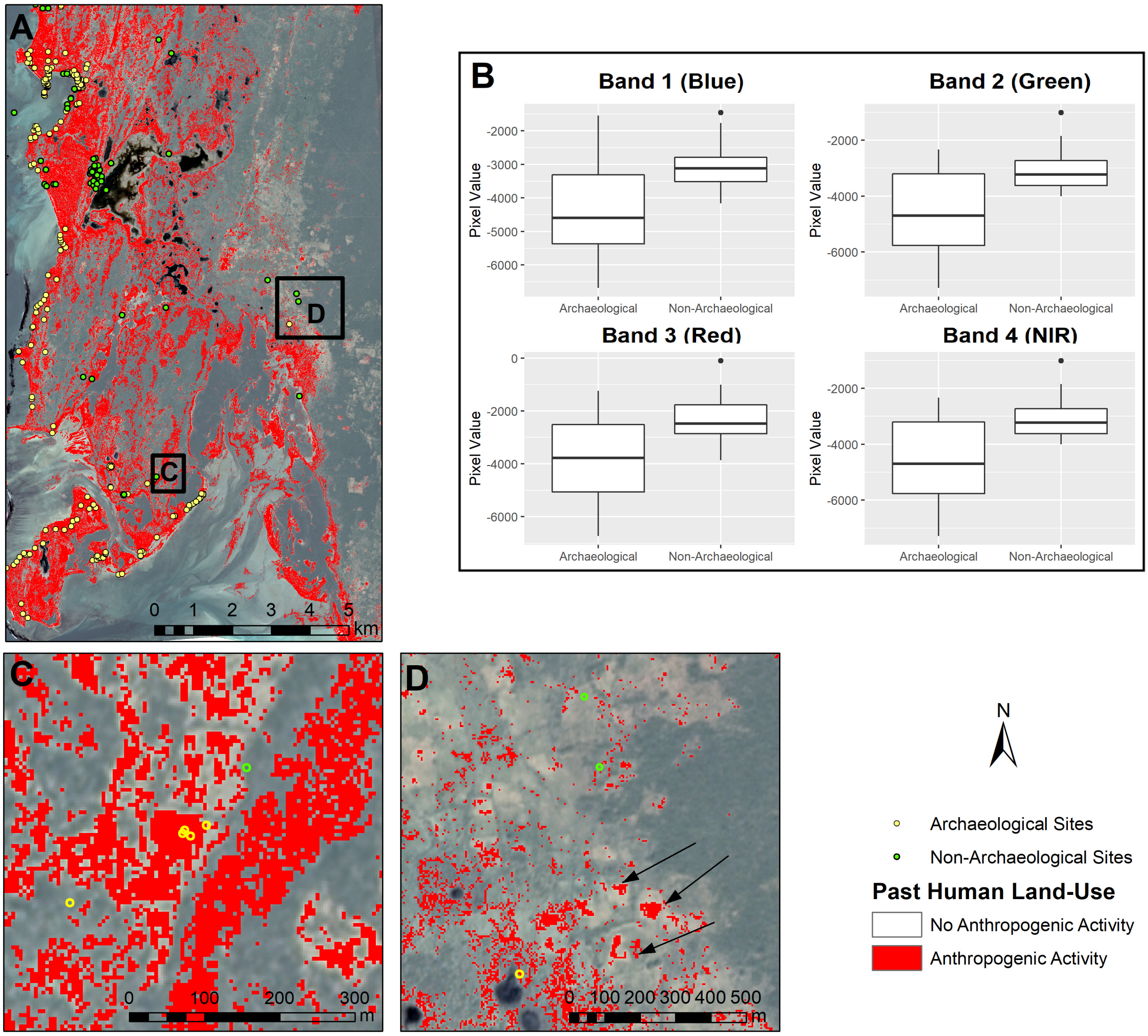

FIGURE 4 | (A) Results of random forest (RF) algorithm (red) using a threshold of 0.7 compared with known archaeological deposits (yellow circles) and non-archaeological areas (green circles). **(B)** Visualization of band separability between archaeological and non-archaeological training data. All band differences are statistically significant ($p < 0.001$). **(C)** Close up of known archaeological and non-archaeological sites. All but one are correctly identified. **(D)** Another area with anthropogenic activity (forest clearings indicated by arrows) and known archaeological sites. Imagery © 2020 Planet Labs. Inc.

TABLE 1 | Accuracy assessment of random forest algorithm.

Threshold	Precision (Validation)	Recall (Validation)	F1 (Validation)	Precision (Training)	Recall (Training)	F1 (Training)
0.7	0.972	0.875	0.921	0.976	0.963	0.969
0.65	0.973	0.900	0.935	0.977	0.973	0.975
0.6	0.947	0.900	0.922	0.964	0.977	0.970

which are likely linked to human activities. Spatial analyses demonstrate that anthropogenic areas are clustered and non-randomly distributed throughout the landscape ($p > 0.0001$; **Supplementary Figure 6**). The density of anthropogenic areas appears highest 3–5 km inland from the coast (**Figure 6**), where there are known to be an abundance of seasonal freshwater ponds.

DISCUSSION

The results of this analysis suggest that ancient coastal communities in southwest Madagascar – including highly mobile foraging and herding populations – have contributed to shaping the modern landscape in important ways. Our previous work contributed directly to this present study by allowing us to

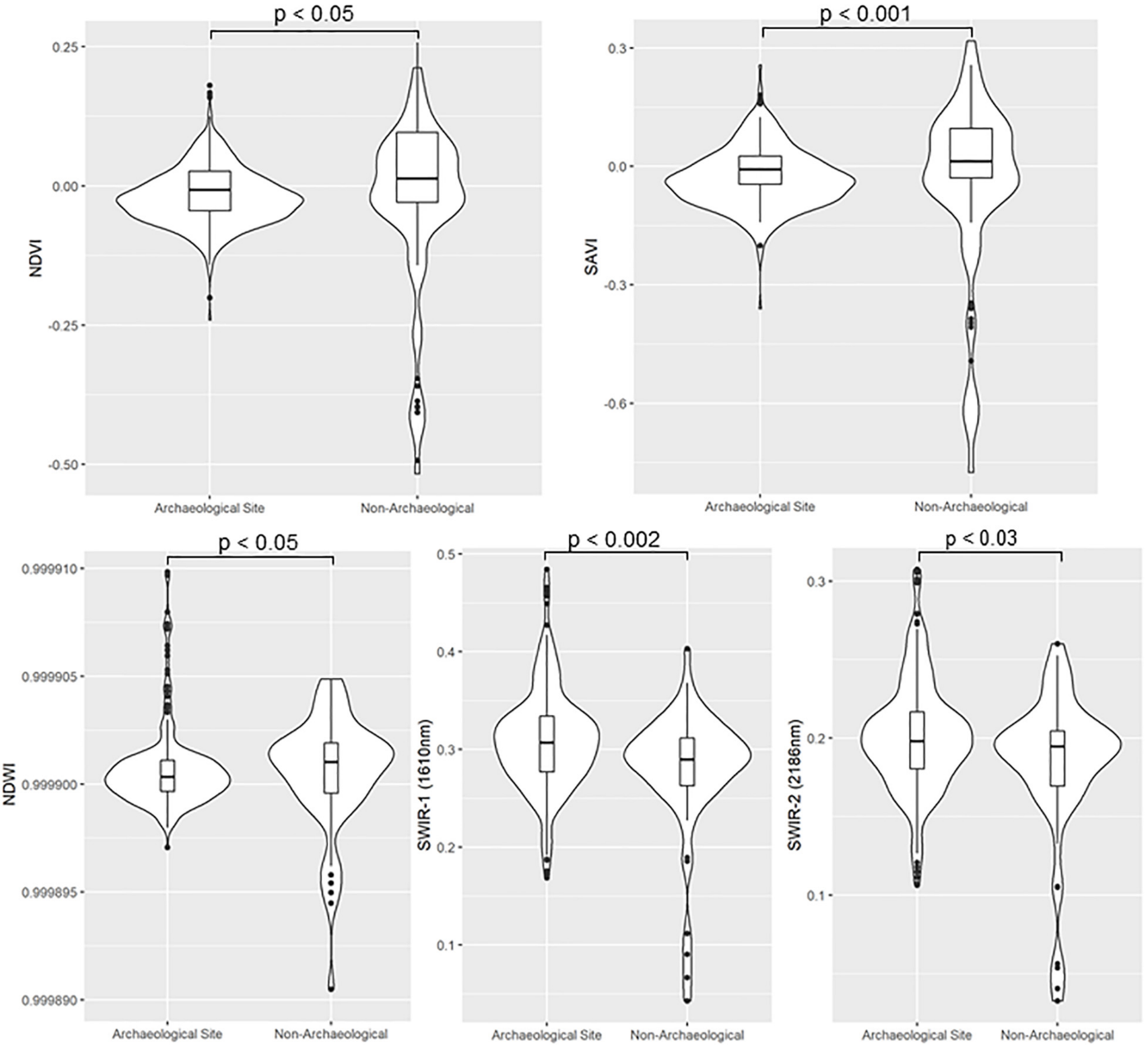

FIGURE 5 | Vegetation index values for archaeological and non-archaeological locations. NDVI and SAVI are annual averages over 3 years of PlanetScope imagery (Planet Team, 2020). Normalized Difference Water Index (NDWI) uses the annually averaged PlanetScope and Sentinel-2 short-wave infrared (SWIR) bands.

investigate settlement patterns and landscape change from two different, but complementary, angles. Our prior investigations focused on the factors that influence settlement choice (e.g., resource availability and social cohesion), while this study focuses on the long-lasting, landscape-scale effects of settlement. In fact, prior work (Davis et al., 2020a,b) indicated the presence of Allee effects, which suggests that ancient communities actively modified their ecological surroundings in ways that increased the suitability of previously settled areas. Here, we used machine learning and vegetative indices to further investigate the possibility that Allee effects were present in coastal Madagascar and resulted in legacy effects *via* cultural niche construction. The results of this study largely complement earlier investigations, pinpointing specific areas that contain landscape modifications, many of which overlap with previous predictive modeling results (**Figure 7**). Archaeological deposits exhibit significantly different spectral characteristics when compared to non-archaeological locations. While the potential of multispectral and hyperspectral imagery has long been established for archaeology, the detection of scant artifact scatters is not the norm (c.f., Orengo and Garcia-Molsosa, 2019). Rather, most literature focuses on the detection of highly visible landscape modifications, like architecture and remains of intensive agricultural activity (e.g., Tarolli et al., 2019; also see Davis, 2021). As such, this work suggests that the development of machine learning and cloud-based computational processing provides the ability to detect even the most ephemeral archaeological deposits and use these to reveal patterns of human activity and impact on the wider landscape.

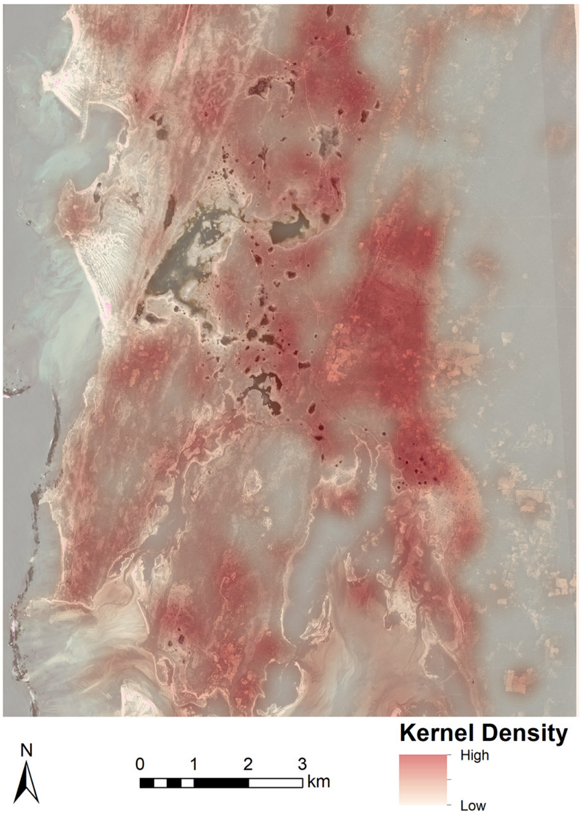

FIGURE 6 | Density of anthropogenic modifications within the study region identified by the machine learning algorithm. Imagery © 2020 Planet Labs. Inc.

Our analysis shows that the overall health and abundance of extant vegetation (defined by vegetative index scores) on and around archaeological deposits exhibits a statistically significant different when compared to areas lacking any archaeological materials. The exact difference is not clear, however, as assessments of median values suggest vegetative values are higher in non-archaeological locations while evaluations of mean values suggest that vegetative values are higher in archaeological locations. The contrast between these two averages may be indicative of the wide range of environmental contexts within the study area and could suggest that non-archaeological localities exhibit wider range of environments while archaeological areas are more limited in their vegetative diversity. This, itself, could be the result of active settlement choices or the effects of human landscape modification. This hypothesis is supported by **Figure 5**, which shows a larger range of values among non-archaeological areas compared with archaeological locations.

The difference in vegetative index scores is statistically significant in the wet season ($p = 0.01$). Additionally, the SWIR wavelength displays differences in the soils around archaeological sites and non-archaeological locations, suggesting that there are underlying differences in the mineralogical composition and moisture retention properties between areas with and without archaeological surface materials. NDWI index assessments further demonstrate that areas with archaeological materials have vegetation with different water retention properties than non-archaeological or random locations. This may signal healthier vegetation, overall, or might relate to the presence of introduced taxa that are not xerophytic and thus retain more water than endemic taxa. Because this region is arid and rainfall is highly variable (Jury, 2003), even small increases in vegetation moisture content could have significant implications for human livelihoods and the biota that sustain them. This, coupled with spatial tests of identified archaeological deposits, indicates the presence of a distinctive human niche on Madagascar resulting from a variety of economic activities – ranging from foraging to pastoralism and agriculture – since the Late Holocene. The inland areas of the study area may have been preferred by pastoralists who have been present for the past several 100 years (Parker Pearson, 2010), and the anthropogenic signatures found here may therefore reflect the activities of pastoral and foraging community activities. While the precise geochemical composition of soils requires further ground-based studies, human activity has likely played a role in changing these components of the landscape.

Some caution is necessary in interpreting these results, however. While it is possible that these distinctive differences between archaeological and non-archaeological locations are due to human activities (e.g., Storozum et al., 2021), it is also possible that these soils were inherently different prior to human occupation. Our prior work demonstrates that human settlement choice is not random in this region (Davis et al., 2020a,b), and thus communities may have chosen areas already possessing specific soil and vegetation properties. To definitively establish the nature of human impact on soil chemistry, and to understand the feedbacks between soil and vegetation dynamics in this region, future studies will need to evaluate stratigraphic and geochemical changes in soil composition through time at archaeological and non-archaeological localities. This will involve ground-based survey as well as a program of radiometric dating to improve settlement chronologies.

Nonetheless, based on this analysis, we can definitively state that archaeological deposits in southwest Madagascar have distinct geophysical and vegetation profiles compared with non-archaeological locations. Likewise, the difference in vegetation between archaeological and non-archaeological areas is inherently linked to the geochemical properties of these locations, as well as to modern ecological variables. Because the primary difference between our study locations is the presence or absence of archaeological deposits, vegetative differences are likely linked to human activity (Lasaponara and Masini, 2007; Bennett et al., 2012). Furthermore, our results indicate that ephemeral archaeological deposits composed of artifact scatters can be distinguished from surrounding environments using high-resolution multispectral imagery and machine learning. Thus, we can conclude that underlying differences in geophysical properties of the landscape and vegetative composition are impacted by a legacy of human landscape use over the past several 1,000 years. The results presented here demonstrate that archaeological sites dated to as early as ca. 3,000 cal year B.P. by Douglass (2016) are identifiable based on their ecological impact. However, a robust settlement chronology for the study region is needed to investigate whether the age of

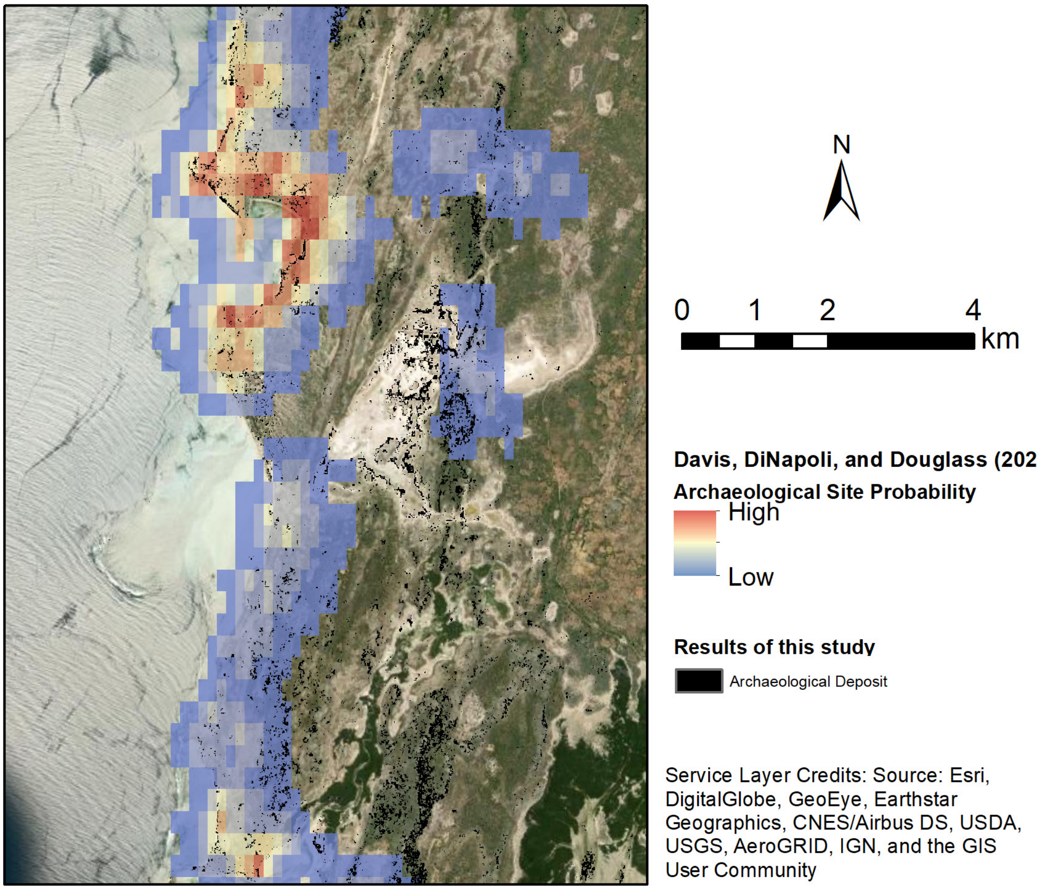

FIGURE 7 | Comparison between predictive modeling results of Davis et al. (2020b) and this study. The previous study investigated settlement distribution *via* environmental and social drivers, while this study looked at long-term ecological effects of settlement activity. Notice that both models detect or predict archaeological activity in many of the same locations. The areas ranked with the highest likelihood by Davis et al. (2020b) also contain some of the oldest recorded evidence of human occupation in this region (∼2,500–3,000 cal year B.P.).

archaeological deposits impacts their signature or detectability *via* multispectral remote sensing.

More broadly, we demonstrate how a focus on areas with "low-impact" human activities can facilitate greater understanding of the extent of human occupation and land-use on a landscape shaped by diverse socioeconomic systems and exhibiting an ephemeral archaeological record (Parker Pearson, 2010; Douglass and Zinke, 2015). The impacts of early communities of foragers on Madagascar's diverse ecosystems is widely debated, but more evidence of the (in)direct effects of human settlement are needed (Davis et al., 2020a; Domic et al., under review; Douglass et al., 2019). The same can be said for many regions around the world where the availability and quality of archaeological data is lower for periods of time when foraging was the dominant livelihood strategy shaping landscapes (Stephens et al., 2019). By extending our focus to these understudied components we can re-evaluate and more fully appreciate the extent to which diverse peoples have modified the Earth's environments.

A shift in research attention toward understanding the environmental impacts of small-scale and mobile subsistence communities can also fundamentally change how we approach sustainability and conservation. One of anthropology's longstanding goals has been to understand the dynamics between human and environmental systems (Steward and Setzler, 1938; Steward, 1955; Carneiro, 1970; Davis, 2020). Long-term perspectives on human-environment dynamics offered by archaeology provide context for understanding contemporary land-use and sustainability issues. A goal of historical ecology and ecological anthropology is to derive lessons from these long-term perspectives and eco dynamics to inform present and future management decisions (Altschul et al., 2017, 2020; Rick and Sandweiss, 2020). By viewing anthropogenic landscape modifications at multiple scales and levels of intensity, as well as *via* a range of (in)direct impacts, we can improve our understanding of human niche construction in diverse societies, ranging from small-scale, mobile communities to large urban centers.

This paper makes contributes to Malagasy archaeology by illuminating the scale and extent of human traces on the landscape, in a way that is time and cost-effective, allowing us to lay the critical foundation needed for further work on coupled human-natural systems. The archaeological data contained within this space has implications for our understanding of human niche construction on Malagasy landscapes over time. Beyond Madagascar, this study also holds importance for studying the ecological legacies of foraging societies and detecting ephemeral archaeological sites in semi-arid environments using high resolution satellite images and machine learning techniques.

DATA AVAILABILITY STATEMENT

The PlanetScope imagery analyzed for this study is proprietary and unfortunately cannot be shared. However, access to PlanetScope imagery is free for educators and researchers via Planet's Education and Research Program: https://www.planet.com/markets/education-and-research/. The datasets generated from PlanetScope image analysis (i.e., density tests) for this study can be found in Penn State's ScholarSphere Repository at https://doi.org/10.26207/zmsr-tc92. Data can also be replicated using GEE. Compilation of Sentinel data in GEE can also be run using the following link: https://code.earthengine.google.com/67eeee7b0e7cb49beac1237aff1f5f53 and the Random Forest analysis can be run in GEE using the following link: https://code.earthengine.google.com/99ccb498ea588d44a0b3300841163405.

AUTHOR CONTRIBUTIONS

DD designed and performed the research. DD and KD analyzed data, wrote and revised the manuscript, and acquired the funding. Both the authors contributed to the article and approved the submitted version.

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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.2021.689399/full#supplementary-material

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Teasing Apart Impacts of Human Activity and Regional Drought on Madagascar's Large Vertebrate Fauna: Insights From New Excavations at Tsimanampesotse and Antsirafaly

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Madagascar experienced a major faunal turnover near the end of the first millenium CE that particularly affected terrestrial, large-bodied vertebrate species. Teasing apart the relative impacts of people and climate on this event requires a focus on regional records with good chronological control. These records may document coeval changes in rainfall, faunal composition, and human activities. Here we present new paleontological and paleoclimatological data from southwestern Madagascar, the driest part of the island today. We collected over 1500 subfossil bones from deposits at a coastal site called Antsirafaly and from both flooded and dry cave deposits at Tsimanampesotse National Park. We built a chronology of Late Holocene changes in faunal assemblages based on 65 radiocarbon-dated specimens and subfossil associations. We collected stalagmites primarily within Tsimanampesotse but also at two additional locations in southern Madagascar. These provided information regarding hydroclimate variability over the past 120,000 years. Prior research has supported a primary role for drought (rather than humans) in triggering faunal turnover at Tsimanampesotse. This is based on evidence of: (1) a large freshwater ecosystem west of what is now the hypersaline Lake Tsimanampesotse, which supported freshwater mollusks and waterfowl (including animals that could not survive on resources offered by the hypersaline lake today); (2) abundant now-extinct terrestrial vertebrates; (3) regional decline or disappearance of certain tree species; and (4) scant local human presence. Our new data allow us to document the hydroclimate of the subarid southwest during the Holocene, as well as shifts in faunal composition (including local extirpations, large-vertebrate population collapse, and the appearance of introduced species). These records affirm that climate alone cannot have produced the observed vertebrate turnover in the southwest. Human activity, including the introduction of cattle, as well as associated changes in habitat exploitation, also played an important role.

Keywords: megafaunal collapse, climate change, human impacts, southwest Madagascar, Late Holocene

INTRODUCTION

The literature on humans versus climate shifts as triggers for extinction of Madagascar's megafauna has grown enormously over the past few years, but no consensus has emerged. There are cultural sites where humans have been present over extended periods of time with little impact on megafauna (e.g., Douglass et al., 2018). Likewise, climate fluctuations in the Late Quaternary have been documented from northern to southern Madagascar (Scroxton et al., 2017, 2019; Voarintsoa et al., 2017; Wang et al., 2019; Railsback et al., 2020) with little apparent impact on the fauna; large-vertebrate extinctions are well represented at a range of sites from the very late Holocene (Crowley, 2010; Godfrey et al., 2019; Hansford et al., 2021). The notion that neither climate nor humans alone, but the combination of the two, was responsible for the megafaunal crash of the Late Holocene has gained broad acceptance in recent years (e.g., Burney et al., 2003, 2004; Goodman and Jungers, 2014), but no single hypothesis appears to apply across the island.

The problem of understanding endemic vertebrate decline is perhaps most vexing for the subarid region of Tsimanampesotse National Park (hereafter TNP) in southwestern Madagascar, where very different interpretations of past events have been proposed. MacPhee (1986), for example, was reluctant to attribute the disappearance of large vertebrates from this part of Madagascar to climate change. He argued on the basis of the xerophytic plants and microfauna endemic to the region that conditions in southwestern Madagascar have been dry over a long period of time, and that we cannot assume the hydroclimate of the subarid south prior to large vertebrate extinctions was markedly different than it is today. He further maintained that even in dry regions, wet microhabitats may be sufficient to support species dependent on moist conditions. In contrast, Goodman and Jungers (2014) defended a primary role for aridification in triggering local species extirpation and extinction. They hypothesized that the climate of the southwest was wetter and less seasonal when now-extinct vertebrates were present, and that wetter habitats likely persisted up to around 1000 years ago when conditions became too dry to sustain now-extinct species, both large and small, including certain freshwater birds.

Developing an understanding of extinction across Madagascar demands that we first focus on changes with good chronological resolution at the local area or ecological levels, and then gradually build broader regional chronologies. Here we present paleontological and paleoclimatological data from a multiyear, collaborative project focusing on a part of Madagascar that is exceptionally dry today – the southwestern coastal region south of the Onilahy River. Our team is the first to document this region's changes in hydroclimate through the Holocene based on stalagmites collected from several caves at TNP as well as caves to the north and northeast of the park. Our team is also the first to explore subfossils preserved in the underwater deposits of the flooded caves of TNP. Our paleontological mission focused mainly on retrieving bones from flooded as well as dry caves within the park, but we also collected bones from lacustrine deposits at Antsirafaly, ∼45 km north of TNP.

Our goal in this paper is to provide an overview of our work and place our results within a broader regional context. We describe: (1) changes in hydroclimate or rainfall of southern Madagascar over the past 25,000 years; (2) vertebrate taxa found in subfossil cave deposits at TNP and lacustrine deposits at Antsirafaly; and (3) the chronology of local decline of endemic vertebrate taxa. We also document evidence, direct and indirect, of past human presence at TNP. We then address the following four questions: (1) Is today's hydroclimate in southwestern Madagascar significantly drier than the hydroclimate several thousand years ago, when there were numerous large-bodied endemic vertebrate species in this region? (2) What triggered local extirpation of vertebrate species at TNP and Antsirafaly? (3) How does the local extirpation of vertebrate species at TNP and Antsirafaly relate to their regional decline at other sites in southern Madagascar? (4) What, ultimately, caused the extinction of the large-bodied vertebrates in Madagascar's southwest?

MATERIALS AND METHODS

Collection Sites

Geographic Locations of Collection Sites

We collected stalagmites and subfossils in southern Madagascar over the course of four field seasons. In **Figure 1** we show the locations of the limestone caves that yielded stalagmites covering the period covering the Last Glacial Maximum (LGM, 22.9-19.4 kyr BP) and onward, and the sites at which we obtained subfossils. All collection sites are in the subarid "spiny thicket" terrestrial ecoregion, with the exception of Andranomilitsy Cave, which is located in the southern part of the subhumid "central highland" terrestrial ecoregion. Ecoregions are geographic units that share environmental features and characteristic species; the major ecoregions of Madagascar have been described by Burgess et al. (2004).

Stalagmites were collected at two of the three major caves of the TNP karst system that are now phreatic (i.e., largely below the water table): Mitoho and Vintany. We also collected stalagmites at four dry caves within the park (Soarano, Andriamaniloke, Esajo, and Fihamy), as well as two dry caves well outside the park (Andranomilitsy and Asafora). Andranomilitsy Cave is located 300 km northeast of Tsimanampesotse, off Route National 7 in the southcentral portion of the subhumid Central Plateau and near the town of Ihosy and the Isalo National Park. Given its position in the interior of the island and given the dual east-west and north-south precipitation gradients in Madagascar, this site can be expected to have been consistently wetter than sites south of Toliara on or near the west coast. Asafora Cave is in the Morombe District, 130 km north of Toliara, 200 km north of Tsimanampesotse, and ~10 km from the coast. It also can be expected to have been slightly wetter than the region of Tsimanampesotse (including Antsirafaly) due to the north-south precipitation gradient.

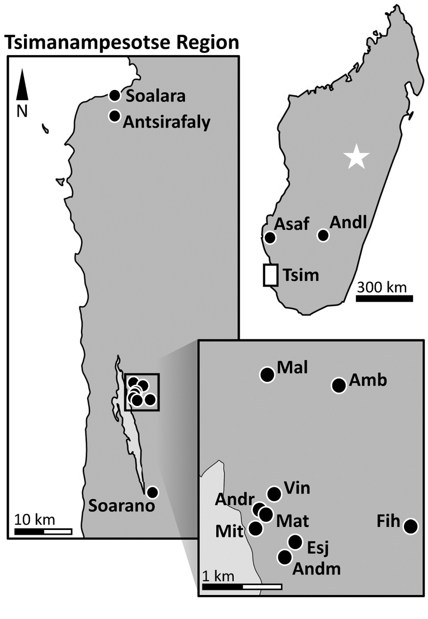

FIGURE 1 | Fossil and stalagmite site names and abbreviations. Map of Madagascar: Asaf, Asafora Cave; Andl, Andranomilitsy Cave; Tsim, region of the Tsimanampesotse National Park. The star represents the capital of Madagascar, Antananarivo. Vertical rectangular blowout box: Town of Soalara and nearby lacustrine site Antsirafaly; Soarano Cave is indicated near the southernmost end of Lake Tsimanampesotse. Square blowout box: Amb, Ambolely Sinkhole; Andm, Andriamaniloke Cave; Andr, Andranohilova Cave; Esj, Esajo Cave; Fih, Fihamy Cave; Mal, Malazamanga Cave; Mat, Maty Cave, or Anjohimpaty Rock Shelter; Mit, Mitoho Cave; Vin, Vintany Cave.

We collected subfossils at all three phreatic caves of the karst system at TNP: Vintany, Mitoho, and a cave called Malazamanga (literally "famous blue"). Subfossils were also collected at four dry sites within TNP, two of which (Anjohimpaty and Andranohilova) are part of the Mitoho Cave system. Anjohimpaty (or Maty Cave, literally "cave of the dead") is a rock shelter with cave art (anthropomorphic images and graffiti). Andranohilova (literally "at the water our descendants will inherit, where the drongo drinks") is a small, shaft-like dry cave that opens into the main portion of Mitoho Cave. The other two dry subfossil collection sites at TNP were Ambolely sinkhole and Soarano Cave. Finally, we also collected subfossils at Antsirafaly (literally "place of the sacred salt"), a lacustrine site near the coastal town of Soalara, ~45 km north of TNP. We collected plant material (seeds, bark, twigs) in association with subfossils from sediments in two caves at TNP (five locations from Vintany and one from Malazamanga).

Exploration History

Exploratory paleontological missions to Tsimanampesotse began in the 1930s when Perrier de la Bâthie (1934) and Petit (1935) reported fragmentary subfossil remains of crocodiles (*Voay robustus*) and giant tortoises (*Aldabrachelys grandidieri*) at the main entrance to Mitoho Cave. Three decades later, Ravelonanosy and Duflos (1964) explored Andranohilova Cave, which was much later discovered by us to be one of several entrances into the Mitoho flooded cave system. MacPhee (1986) conducted a survey of the dry deposits at the entrances to TNP caves, including Mitoho as well as Anjohimpaty where he reported seeing human bones. He also compared the subfossils he found at the various caves to those reported by Lamberton (1937) at Ankazoabo Cave, almost 60 km south of Mitoho Cave. In 2001, a team led by Karen Samonds visited Andranohilova Cave while prospecting for Cenozoic fossil-bearing sediments, and collected some reference specimens from the floor of this cave.

Our paleontological mission began in 2014 with an initial exploration and survey of both TNP (Rosenberger et al., 2015) and Antsirafaly. Limited collection of subfossil bones from the surface of the submerged floor of Vintany Cave to determine underwater preservation of organic material began in 2015.

Our first large-scale effort to collect subfossils was launched in 2016, when team divers collected bones from the floors of all three flooded caves. We did no underwater excavation of sediments at that time so we did not know the degree to which the sediment might be fossiliferous. In addition to doing surface collection under water, we collected bones from three dry sites within the park: Soarano, Anjohimpaty, and Ambolely (**Figure 1**).

In 2018 and 2019, we followed different collection methodologies for each TNP locality, and, for the first time, targeted selected locations within Vintany Cave for careful manual excavation by divers, down to a maximum of one foot below the sediment surface. We found that Vintany Cave sediments preserved abundant subfossils, and we mapped and recorded all collection localities within the cave. We further noted whether each specimen came from excavated sediment or from the surface of the submerged cave floor (i.e., on top of rocks or sediment).

In the Mitoho Cave system, we collected microfaunal bones (rodents, bats, and birds) from eolian deposits on the floor of Anjohimpaty Rock Shelter. In the flooded cave passages of the Mitoho system, divers collected bones underwater from: (1) the surface of the cave floor, (2) between large rocks, (3) on the surface of a massive bat guano mound, (4) in the crevices and on the shelves that lined the walls of a vertical "chimney," and (5) in a deep horizontal passage at the chimney floor. The top of the vertical chimney is close to Andranohilova. Given the proximity of this entrance to the underwater chimney, it is clear that Andranohilova was the original source of the subfossil remains that accumulated within, and below, the vertical chimney passage. The narrow, open-air entrance of Andranohilova leads to a wide chamber that we called the "bat cave room"; this room has a pool of water at its floor and a low ceiling where bats roost today. Beneath the water is the flooded portion of the Mitoho Cave system. Directly below the bat cave room there is a very large, now entirely submerged, guano mound which spans the floor of this chamber. The periphery of the southwestern chamber floor is marked by a series of boulders, a gap among which forms the entrance to the vertical chimney passage to the deeper sections of the cave.

We spent limited time exploring Malazamanga Cave. Access to this flooded cave is precarious because it is situated at the bottom of a dry and deep, collapsed sinkhole, and navigation of the underwater passages requires technical skills. On the floor of the sinkhole there is a wide rock shelter visible in the northern wall that narrows to a dark passage about 5–6 m wide and 2.5 m tall and ends at a small pool only about 1 m deep. Below the water's surface, a small "duck-under" opening leads to a circuitous underwater passage, marked by small (garage-sized) rooms that ultimately lead to a series of chambers more comparable in size to basketball courts. Divers found partially buried subfossils in only one of the small rooms, approximately 400 m from the entrance at the shallow pool, shortly before reaching the larger chambers. The bones likely washed in from an overhead fissure that was open for a limited period but is now closed, and invisible to divers from the inside.

In 2019, our team returned to Antsirafaly where we extracted subfossils from an isolated dried pond. In the region there are multiple such features, which appear to have been part of an extensive fluvial-lacustrine system that may have produced isolated oxbow lakes and ponds as it dried. Subfossils had been retrieved at this site previously by local villagers (which we designated "Soalara" to distinguish them from bones we collected ourselves). Some of these bones articulated with the bones that we collected, suggesting that they belonged to the same individuals.

Within the perimeter of the former pond, we dug pits at 14 locations, searching for subfossil bones. We also dug two pits outside its perimeter (one to a depth of 113 cm and the other to a depth of 80 cm) to build a stratigraphic profile of the site. Our profile-pit sediments transitioned gradually from sand at the top to clay at a depth of 30 cm from the top. The color of the clay transitioned from red to gray from 50 to 73 cm below the surface. There was a light gray indurated layer between 73 and 80 cm, possibly indicative of drying, below which the sediment was composed entirely of gray clay. This clay also became wetter with depth, and we reached the current water table at 113 cm depth. These profile pits contained gastropod shells but no vertebrate bones.

In contrast, the 14 pits we dug within the perimeter of the pond yielded abundant bones of now-extinct species, beginning at slightly different depths (from 65 to 76 cm, depending on the pit) and continuing to below the water table in at least one pit (Pit H, GPS coordinates –23.62959 S, 43.71833 E). Most subfossils were found in moist clay, below the indurated layer. Because of the disturbed nature of this site, we selected many specimens for radiocarbon dating to establish a chronology, taking precautions not to sample different bone elements that could belong to the same individual.

Analytical Methods

Stalagmite Age Determinations

Of the stalagmites that we collected, 27 were amenable to U-Th disequilibrium dating, producing stratigraphically sequential dates. Twenty-three stalagmites came from six caves within the boundaries of TNP, one from Andranomilitsy Cave, and three from Asafora Cave. From these 27 stalagmites we conducted 131 U-Th individual age determinations; 120 came from the Tsimanampesotse stalagmites, 10 from Asafora stalagmites, and one from the single Andranomilitsy stalagmite. Our U-Th disequilibrium dating methods follow Hellstrom (2003) and Cheng et al. (2013), with half-lives from Jaffey et al. (1971) and Cheng et al. (2013). All dates were generated at the Department of Earth, Atmospheric and Planetary Sciences, Massachusetts Institute of Technology, Cambridge, MA, United States. Seventeen U-Th disequilibrium dates have not been previously published; 33 are in Scroxton et al. (2019), two are in Faina et al. (in press), and 79[1]. All use the same chronological scale as radiocarbon (^{14}C), where 1950 CE = 0 calendar years before present (yr BP) and subsequent years are given negative numbers. Additionally, Faina et al. (in press) used 10 radiocarbon dates in the age model of stalagmite AF2. These extend the growth period of AF2, and at Morombe in general, to 3.5 kyr BP.

Identifying Taxa and Documenting Traces of Human Activity

Genus and species identifications of subfossils were made by team members with appropriate expertise for particular orders or

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[1] Burns, S. J., McGee, D., Scroxton, N., Kinsley, C. W., Godfrey, L. R., Faina, P., et al. (submitted). Southern Hemisphere controls on ITCZ variability in southwest Madagascar over the past 117,000 years.

families. When needed, we used comparative collections housed at the Université d'Antananarivo, Madagascar; the University of Massachusetts, Amherst, MA, United States; Midwestern University, Glendale, AZ, United States; the Field Museum of Natural History, Chicago, IL, United States; the Duke University Division of Fossil Primates, Durham, NC, United States; and the American Museum of Natural History, New York, NY, United States. We examined bone specimens for any traces of human butchery (following the methods of Hansford et al., 2020) and we documented additional signs of past human presence at bone collection sites.

Radiocarbon Dating and Date Calibration for Vertebrate and Plant Remains

Subfossil specimens selected for dating were processed at the University of Cincinnati, OH, United States. From each specimen, we removed approximately 250 mg of bone with tin snips or a rotary Dremel tool equipped with a saw blade. Samples were coarsely chopped or crushed into ∼1–3 mm fragments and demineralized in 0.5 N hydrochloric acid (HCl) under refrigeration for 5–10 days. HCl was refreshed every 3–5 days until samples were completely demineralized. Samples were rinsed five times in ultrapure water, with agitation (vortexing) and centrifugation steps occurring with each rinse. Samples were then soaked in 0.01 N sodium hydroxide (NaOH) for 4 h at room temperature to remove humic acids, rinsed with ultrapure water five times (as described above), and freeze dried. Lastly, samples were gelatinized in 0.01 N HCl at ca. 75°C overnight and passed through 1.5 μm glass fiber filters under vacuum. Samples were again dried down via lyophilization.

After we confirmed sufficient preservation of organic content using collagen yield, atomic C:N, and stable carbon and nitrogen isotope values (e.g., Ambrose, 1990; van Klinken, 1999), we sent aliquots of dried collagenous residue to the Center for Accelerator Mass Spectrometry at Lawrence Livermore National Laboratory (Livermore, CA, United States) for radiocarbon dating. Plant samples from sediment in flooded caves were dried, packaged in plastic bags and sent to the Beta Analytic Testing Laboratory (Miami, FL, United States).

We calibrated individual conventional ^{14}C ages to 2σ calendar years before present (Cal yr BP) using the Southern Hemisphere calibration curve SHCal20, in Calib 8.2 (Hogg et al., 2020; Stuiver et al., 2021). Calibrated age ranges (min and max) were rounded to the nearest 5-year intervals. All radiocarbon dates (vertebrate and plant) reported herein are calibrated ages (with the exception of conventional ^{14}C dates also provided in **Tables 3**, **4**). We report them as mean values in yr BP $\pm$ 1σ.

In total, we obtained ^{14}C dates from 65 bones (32 from TNP and 33 from Antsirafaly) and six plant remains. All samples from Antsirafaly yielded sufficient organic material for direct dating but the same was not true for TNP, where we needed to process many more than 32 samples to obtain 32 dates. While all TNP botanic samples were datable, many vertebrate specimens from the flooded caves could not be directly dated. This is not peculiar to the flooded caves of Tsimanampesotse; other researchers have noted that bones that are continually immersed in water tend to have low protein content (e.g., Nielsen-Marsh and Hedges, 2000; Bailey and Flemming, 2008; Stinnesbeck et al., 2017).

For Vintany Cave, our overall failure rate for obtaining sufficient organic material was 68.4% for bones of extinct animals and 51.7% for bones of extant animals. We failed to extract sufficient collagen for radiocarbon dating from any of the sampled extinct animal specimens that we collected from the top of the cave floor. However, our failure rate was much lower (25%) for bones of extinct animals excavated from within sediment. For much smaller-bodied extant species at Vintany, a different pattern held, probably because many individuals died so recently that their bones had not lost much organic content. In contrast to the extinct animals sampled, over 80% of the bones of extant animals sampled from the cave floor yielded good collagen, while our success rate for buried bones was much lower (presumably because many are considerably older). These discrete trends in collagen preservation for buried bones are unsurprising given expected differences in protein loss due to microbial activity in buried bones of small versus large diameter (Pfretzschner, 2004).

Reconstructing Hydroclimate

To develop a long-term record of pluvial versus interpluvial conditions in southwestern and southcentral Madagascar, we used U-Th disequilibrium dating of growth phases of speleothems. In semiarid and arid environments, this tool can be used as a paleoclimate indicator of pluvial conditions (Ayliffe et al., 1998; Vaks et al., 2010). To grow, speleothems require calcium ion supersaturation in percolating drip waters (White, 1976). To achieve supersaturation, sufficient precipitation must fall to allow for soil development, soil respiration and high soil CO_2 concentrations. This results in sufficiently strong percolating carbonic acid to dissolve the carbonate host rock and redeposit the calcium carbonate upon degassing of CO_2, which occurs in the lower-CO_2 concentration atmospheres of cave environments. The amount of rainfall necessary for speleothem growth to occur is estimated to be approximately 250–300 mm per year, but this is also highly dependent on evaporation and the seasonality of rainfall (Vaks et al., 2010). For southwest Madagascar, with annual rainfall near the minimum required for speleothem growth, periods of stalagmite deposition and non-deposition can be used to infer pluvial versus arid climate. The difference in rainfall amount between pluvial and interpluvial periods need not be large.

One hundred and seventeen of the 120 TNP stalagmite dates were used to generate a summary of stalagmite growth periods in southern Madagascar between 125,000 and 0 years BP (one U-Th date that was older than 125,000 years and two that were younger than 0 were not used). Seventy-two dates from stalagmites from all sites (TNP, Asafora and Andranomilitsy) provided a detailed record of the past 25,000 years (i.e., LGM onward), the period of primary interest to us.

We plotted date "density" curves to determine the probability of wet versus dry hydroclimate at any point in time. Probability density plots are created by summing assumed Gaussian distributions for each individual age with attendant error at regular intervals and normalizing the distribution so that the integral equals 1. Kernel density estimates are like probability density plots except that a constant Gaussian width is used for all ages. This prevents individual precise ages from dominating the plot, but also underplays the spread of low-precision ages.

Because some stalagmites were sampled more than others, the dates cannot be considered independent of one another, and therefore the relative heights of the peaks are as much a function of sampling density as a natural indicator of relative wetness.

Reconstructing the History of Cave Flooding

In addition to the 117 dates from stalagmites mentioned above, a small number of stalagmites (notably stalagmite AV2 from Vintany Cave) revealed significant age reversals. We excluded these ages from our reconstruction of past hydroclimate, but as these stalagmites still provided an approximate indication of growth timing, they were nevertheless capable of providing geochronological constraints on, for example, the timing of cave flooding.

Stalagmites from coastal caves can be used, along with global records of the rise in sea level, to reconstruct the history of cave flooding (Dumitru et al., 2021). This history can in turn be used to determine a minimum age for bones that must have accumulated in certain locations prior to when the water table reached their top depths within the caves. This method for inferring minimum age for extinct animals is particularly useful when bones lack collagen and cannot be dated directly.

The Tsimanampesotse flooded cave network is low lying and only a few kilometers from the sea; thus, the local water table is closely tied to sea level. The lower parts of these caves have been alternatively phreatic (when sea level is high, as it is now) or vadose (when sea level was lower). Because speleothem growth is almost always subaerial, the fact that stalagmites exist in now-flooded portions of the caves is evidence of a much lower water table at times in the past. As sea level rose during the last deglaciation and into the Early Holocene, the freshwater lens would have been pushed up until it intersected with the caves. Cave flooding would have been gradual, progressing from bottom to top. Stalagmites that were actively growing when the water level reached their tops would have ceased growing at that time; their top dates would thus provide a record of when they became submerged. It is therefore possible to extract a maximum age for the timing of the last rise of the water table from the top dates of submerged stalagmites, combined with information on submerged stalagmite distribution and depths. This is a maximum age for flooding because stalagmites could have stopped growing earlier due to arid conditions.

RESULTS

Stalagmites

Glacial and Post-glacial Climate Inferred From Growth Periods of Stalagmites

Eleven of the 23 stalagmites that we collected at TNP cover portions of the LGM and/or the last deglaciation (**Table 1**) and allow us to affirm pluvial conditions at TNP between 25.8 and 11.7 thousand years before present (kyr BP). The wettest interval was the LGM itself, judging from the large number of stalagmites showing growth at that time and their widespread distribution within the park (**Table 1**); however, this pluvial period can be described broadly as having lasted until stalagmite MT1 stopped growing at 11.7 kyr BP. This was synchronous with the end of the Younger Dryas, the terminal cold event of both the last deglaciation period and the Late Pleistocene.

TABLE 1 | Youngest and oldest age determinations for Tsimanampesotse stalagmites that cover the Last Glacial Maximum (which peaked between 22,900 and 19,400 yr BP), the last deglaciation, and the Holocene (beginning 11,700 yr BP).

Cave	Stalagmite ID	Top age		Bottom Age	
		yr BP*	± 2σ	yr BP*	± 2σ
Andriamaniloke	AD5	60	38	279	94
	AD6	–36	49	*Single age only*	
	AD7	*Modern (Active)*		322	12
Fihamy	F1	1,360	670	*Single age only*	
Andriamaniloke	AD1	18,080	120	19,810	140
	AD4	15,550	140	19,220	140
	AD10	17,000	120	21,200	110
Esajo	E1	20,930	490	*Single age only*	
Fihamy	F1	19,170	190	23,110	160
Mitoho	MT1	11,730	170	22,700	1,000
	MT2	16,590	110	17,170	110
	MT4	14,380	120	19,800	2,400
Soarano	SR1	22,590	310	23,650	380
	SR2	11,762	67	23,700	170
	SR3	17,900	5,100	*Single age only*	

**BP notation uses the ^{14}C convention that 1950 CE = 0 yr BP.*

Other stalagmites collected at Tsimanampesotse covered much earlier time intervals. Together, stalagmites from southwest Madagascar document an alternating wet/dry pattern. The pattern holds for at least the last six summer insolation peaks extending back to 120,000 yr BP and follows the ∼19–23 kyr precession cycle (**Figures 2**, **3**; see text footnote 1). In general, periods of stalagmite growth coincide with local summer insolation above the mean.

Our data show that the Holocene falls largely within an interpluvial. From the beginning of the Holocene until only several hundred years ago, we have almost no record of speleothem growth at TNP. The sole exception is a single short record of growth around a millenium ago. This implies that, despite almost-certain fluctuations in the hydroclimate of TNP over the Holocene, annual rainfall in this region was never sufficient to trigger stalagmite growth, likely remaining below ∼300 mm/yr. Southern Madagascar is approaching peak summer insolation once again. Thus, taking sufficient rainfall for stalagmite growth as the measure of pluvial conditions, we infer that southern Madagascar is currently at the beginning of a pluvial period. This is consistent with current average annual rainfall at TNP of 389 mm/year (1981–2017; Goodman et al., 2018), which is above the minimum necessary for stalagmite growth. The current pluvial period should last until summer insolation declines sufficiently, depending on current and future anthropogenic forced changes.

Four stalagmites from TNP (stalagmites F1, AD7, AD6, and AD5) record the beginning of the current pluvial period in this region (**Table 1**). The first (F1) is from Fihamy Cave. This

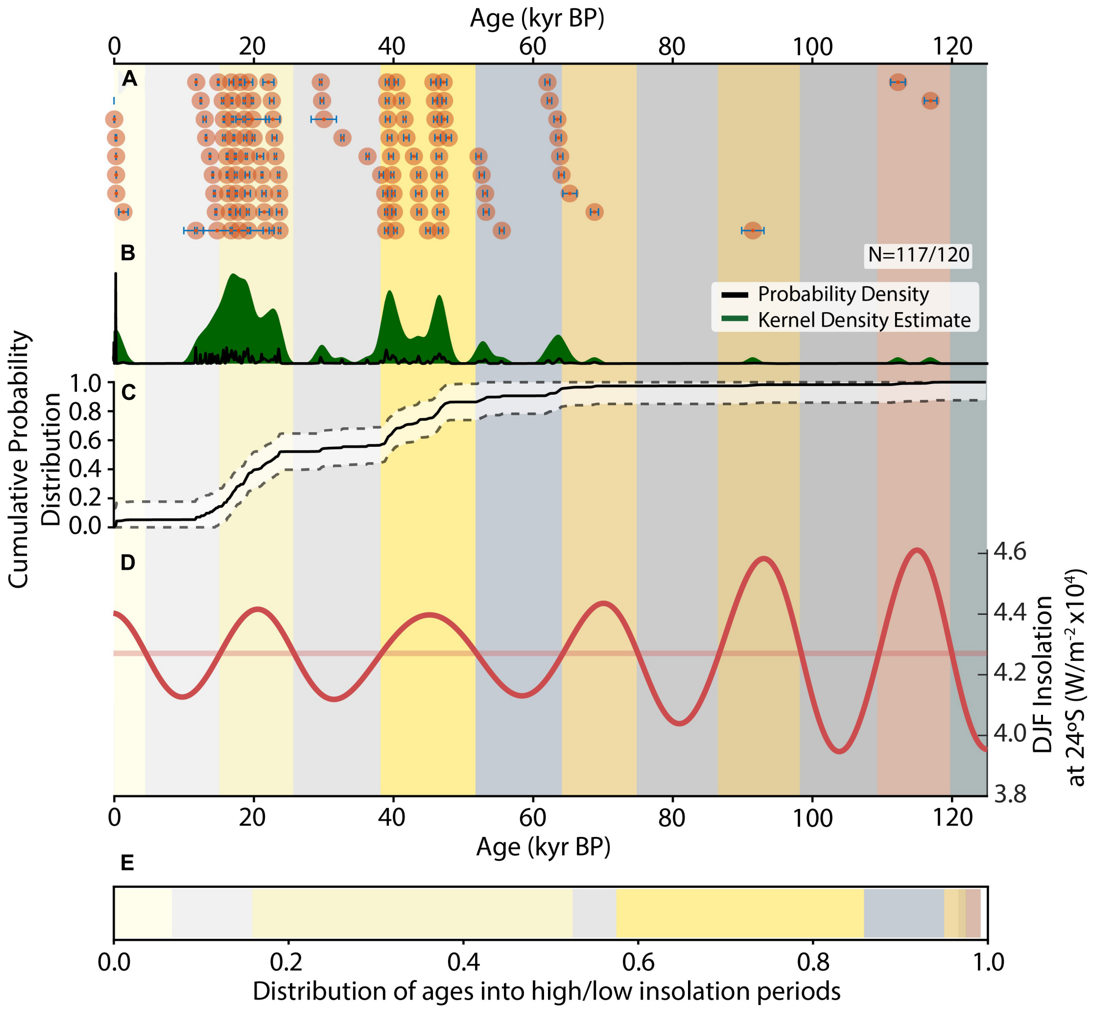

FIGURE 2 | Age distribution of stalagmites from TNP through time. **(A)** Individual U-Th ages (red dots) and 2σ uncertainty (blue bars) based on 117 of 120 dated samples, **(B)** Probability density function of age distributions (black line) and kernel density estimate (green shading). **(C)** Cumulative probability distribution of U-Th age distributions with error. The fluctuating gradient highlights relative periods of excess and deficient speleothem growth relative to the idealized smooth exponential distribution of stalagmite age distributions with time (Scroxton et al., 2016). **(D)** Integrated summer (December–January–February, or DJF) insolation at 24°S (bold red line), and mean value (pale red line). Vertical color bars indicate periods with higher than mean insolation (yellows, darkening with time), and lower than mean insolation (grays, darkening with time). **(E)** Distribution of ages into high/low insolation periods following the color scheme above. Probability Density and Kernel Density Estimate curves determined using the detritalPy Python package (Sharman et al., 2018), with a fixed optimized kernel bandwidth and Dvoretsky-Kiefer-Wolfowitz inequality error estimates on the cumulative probability function. Insolation curves from The Climate Data Toolbox for MATLAB (Greene et al., 2019) using the daily insolation function originally by Eisenman and Huybers (Huybers, 2006).

stalagmite grew through much of the LGM, and stopped growing at 19,172 yr BP. After a long hiatus, growth resumed. Regrowth is represented by a small segment (30 mm) at the top of this stalagmite; a sample from the middle of this small segment is dated to 1360 ± 670 yr BP. The large confidence limit on this date allows us to infer only that this date fell sometime between 2,000 and 700 years ago. More precisely dated speleothem growth occurred during the past millennium at Andriamaniloke Cave: AD5 (279 to 60 yr BP), AD7 (322 yr BP to the present day), and AD6 (modern) (**Table 1**).

Late Holocene stalagmite growth, and the current pluvial period, likely began earlier to the north and east of TNP and Antsirafaly. At Asafora Cave, speleothem growth began as early as 3500 yr BP (**Figure 3**; Faina et al., in press). At Andranomilitsy Cave, speleothem growth began by at least 1274 ± 35 yr BP. These dates indicate that the modern north-south rainfall gradient was manifested in the past, with the isohyet that triggers stalagmite growth tracking north to south following the precession cycle.

Age of Cave Flooding Inferred From Top Dates of Submerged Stalagmites, Combined With Submerged Stalagmite Distributions and Depths

At present the cave network at Tsimanampesotse is flooded by a lens of fresh to slightly saline water (typically less than 1500 mg/l total dissolved solids; Rasoloariniaina et al., 2015), with the current water table approximately 10 m above sea level.

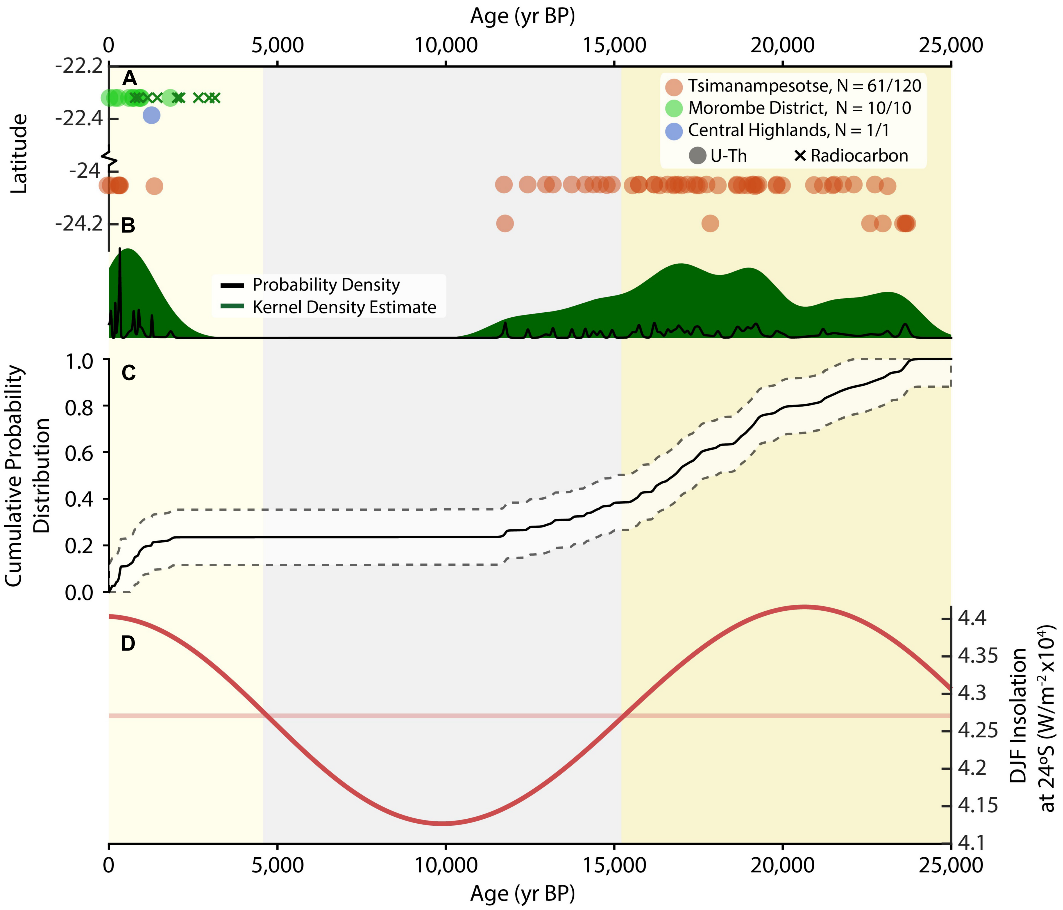

FIGURE 3 | Age distribution of stalagmites from southern Madagascar caves through time (see **Figure 1** for map and **Table 1** for full cave list). **(A)** Individual age determinations against latitude from caves within the TNP (red dots, based on 61 of 120 U-Th dated samples), Asafora Cave, Morombe District (green dots, based on all 10 U-Th dated samples, and green crosses based on 9 radiocarbon ages), and Andranomilitsy in the southernmost part of the Central Plateau, near Isalo (blue dot, based on a single U-Th dated sample). **(B)** Probability density function of age distributions (black line) and kernel density estimate (green shading). **(C)** Cumulative probability distribution of U-Th age distributions with error. The fluctuating gradient highlights relative periods of excess and deficient speleothem growth relative to the idealized smooth exponential distribution of stalagmite age distributions with time (Scroxton et al., 2016). **(D)** Integrated summer (DJF) insolation at 24°S (bold red line), and mean value (pale red line). Vertical color bars indicate periods with higher than mean insolation (yellows), and lower than mean insolation (gray).

The freshwater lens extends to at least the deepest explored cave section (>60 m maximum depth at Malazamanga Cave, i.e., over 50 m below sea level). During the last glacial, sea level off southwestern Madagascar would have been approximately 120 m below present day and the caves were subaerially exposed, as evidenced by the abundant speleothem growth in currently flooded sections. As sea level rose during the last deglaciation, the caves would have gradually flooded as the top of the water table intersected them. The timing of flooding may not have perfectly followed global, or local, sea-level curves as the freshwater lens can vary in thickness with the attendant climatic conditions. Nevertheless, stalagmite growth phases, which must be subaerial, can be used to date cave flooding.

Owing to logistical challenges, stalagmites were not recovered from underwater depths greater than 20 m, and the ages and depths of most stalagmites that we did recover from flooded caves do not meet the conditions required to test reasonable last deglaciation flooding hypotheses. However, the analysis of one stalagmite from Vintany, AV2, reveals that, at ∼8.3 kyr BP, the caves were still subaerial at 14 m below the current water table. This depth is important because it is also the depth of the entrance to the fossiliferous vertical chimney at Mitoho that we described above. Prior to its filling with water during the last deglaciation, this chimney would have functioned like a water chute during storms, carrying sediment, bones and carcasses into it from the guano mound, which would have been at that time subaerial. This would explain the concentration of fossils in the horizontal passage at the floor of the vertical chimney and in bends or ledges within the vertical passage, all of which likely predate the flooding of the chimney.

We consider the 8.3 kyr date uncertain due to age reversal of two dates in this stalagmite (hence its exclusion from our overall date compilation), but the date is consistent with inferences drawn from data on global sea-levels, which would have reached −22 masl at 9,000 years ago, −13 masl about 8,000 years ago and −5 masl around 7,000 years ago (Fleming et al., 1998). Therefore, the freshwater lens cannot have been substantially thicker than present in the Early Holocene and the water table in the karst system, and presumably local sea-level, could only have reached present levels at 8.3 kyr BP or afterward.

Subfossils

Taxonomic Identifications

Although separated by only ∼45 km direct distance, the deposits of the Antsirafaly pond and TNP caves show striking differences in faunal composition (**Table 2**). In total, we found 16 extinct species, eight at Antsirafaly and 13 at Tsimanampesotse, with five species occurring at both sites. At Antsirafaly, we only recovered extinct species. These included three primates (*Megaladapis edwardsi*, *M. madagascariensis*, and *Archaeolemur majori*), two elephant birds (*Mullerornis modestus* and the largest-bodied species, *Vorombe titan*), two reptiles (*Voay robustus* and *Aldabrachelys* sp.), and a hippo (*Hippopotamus lemerlei*). Delicate bones of small vertebrates were either not preserved or may have been missed because we did no fine sieving of sediments.

At TNP, the extinct species included three primates (*Pachylemur insignis*, *Mesopropithecus globiceps*, and *Megaladapis edwardsi*), two euplerid carnivorans (*Cryptoprocta* new sp. and *C. spelea*), an artiodactyl (*Hippopotamus lemerlei*), an elephant bird (*Mullerornis modestus*), four volant birds (*Alopochen sirabensis*, *Coua* cf. *berthae*, *Coua* cf. *primaeva*, and *Vanellus madagascariensis*), a tortoise (*Aldabrachelys grandidieri*), and the horned crocodile (*Voay robustus*).

Comparing the extinct taxa at Antsirafaly and TNP, the two extinct primate species most common at TNP (*Pachylemur insignis* and *Mesopropithecus globiceps*) are notably absent at Antsirafaly. Crocodiles are much more common at the TNP sites than at Antsirafaly. In contrast, the extinct *Megaladapis*, which is relatively common at Antsirafaly, is extremely rare at TNP. *Megaladapis edwardsi* is represented by a single skull at Malazamanga Cave and two specimens found at the entrance to Mitoho Cave by MacPhee (1986); *M. madagascariensis* is absent entirely at TNP. Similarly, *Hippopotamus* is extremely rare at TNP, being represented by just two (likely associated) specimens from Malazamanga Cave, and found under the *Megaladapis* skull. Elephant birds are far more common at Antsirafaly than at TNP.

We recovered bones from over 40 endemic extant taxa at TNP (**Table 2**). Many of these still live within the park, but five are locally extirpated. The latter include a rare and poorly known nesomyid rodent (*Macrotarsomys petteri*, Petter's big-footed mouse), a Vulnerable euplerid (*Fossa fossana*, the fanaloka), and three Endangered or Critically Endangered birds (*Ardea humbloti*, Humblot's heron, *Threskiornis bernieri*, the Madagascar sacred ibis, and *Haliaeetus vociferoides*, the Madagascar fish-eagle). *Fossa fossana* subfossils have never previously been collected in the dry west or subarid southwest; this euplerid is restricted today to the humid eastern rainforest and parts of the Central Plateau. *Haliaeetus vociferoides* is of interest because it would have presumably exploited freshwater fish from Lake Tsimanampesotse, which no longer exist due to the lake's current salinization (Goodman and Jungers, 2014).

Lastly, we found bones of introduced cats, rats, and cows (*Felis catus*, *Rattus rattus*, and *Bos taurus*) at TNP. MacPhee (1986) reported finding multiple suid specimens (probably *Potamochoerus larvatus*, the bushpig) at the main entrance to Mitoho Cave and remains of mice (*Mus*), as well as rats, at Anjohimpaty Rock Shelter.

The Chronology of Change in Faunal Assemblages at Tsimanampesotse and Antsirafaly

Calibrated dates for our animal specimens from TNP range from 2985 ± 285 yr BP to modern (<0 Cal yr BP); those from Antsirafaly range from 1823 ± 73 to 933 ± 133 yr BP. This age range extends back to 4443 ± 208 yr BP if we include an additional single date reported by MacPhee (1986) for elephant bird eggshell. Calibrated dates for plant specimens from Vintany Cave range from 2245 ± 100 to 225 ± 85 yr BP. The more recent plant dates derive from underwater sediments in a "shallow" portion of Vintany with continuing heavy sedimentation today (**Figure 4**, Localities 1 and 2). The older plant dates come from a "deeper" portion of the cave that is largely (but not entirely) blocked from deposition today, and that currently experiences much slower sedimentation[2] (**Figure 4**, Localities 4 and B, the latter locality also called "Bone Soup" because of the thick, gelatinous quality of the sediment). Because the taxonomic composition of the fauna changes dramatically (described below) from before to after 900 yr BP, we present the dates for individual specimens in two tables: **Table 3** for dates earlier than 900 yr BP and **Table 4** for more recent specimens. **Table 5** presents all Vintany plant dates and one from Malazamanga.

When dated individuals are placed on a timeline displaying their current distributional status (extinct, locally extirpated, local extant, or introduced), the profile of faunal change becomes evident (**Figure 5**). The TNP vertebrate assemblage shows a dramatic shift in taxonomic composition ∼2,000 years ago and another at ∼900 years ago (**Tables 3**, **4**). Prior to ∼2000 years ago, the assemblage is comprised of species that are today extinct, locally extirpated, and extant in the park. With one possible exception (*Numida meleagris*; see below), there are no introduced species.

The oldest subfossils we collected at TNP are probably euplerids (*Cryptoprocta spelea* and a new, much larger species of extinct *Cryptoprocta*)[3] that we found in the vertical chimney at Mitoho Cave. These are most likely individuals that sheltered or made birthing dens within Andranohilova. We have no way of knowing exactly how old these bones may be, or whether they date to the LGM pluvial period. None of the fossils from this location (including bats, *Macronycteris commersoni*, *M. cryptovalorona*, and *Triaenops menamena*) could be directly dated; they were all brittle and lacked organic material. As the fossils in the chimney of Mitoho Cave were found between 20 and

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[2] Klukkert, Z. S., Godfrey, L. R., Crowley, B. E., Muldoon, K. M., Burns, S. J., Ranivoharimanana, L., et al. (in prep.). Flooding Vintany; Formation and faunal deposition in an ecologically important sinkhole in southwest Madagascar.

[3] Lewis, M. E., Godfrey, L. R., Rakotondramavo, J.-C., Klukkert, Z., Scroxton, N., Burns, S. J., et al. (Submitted). A new large, extinct fosa (Carnivora: Eupleridae) and other Cryptoprocta from Tsimanampesotse National Park, Madagascar.

TABLE 2 | Vertebrate taxa found in subfossil deposits at Tsimanampesotse and/or region of Antsirafaly.

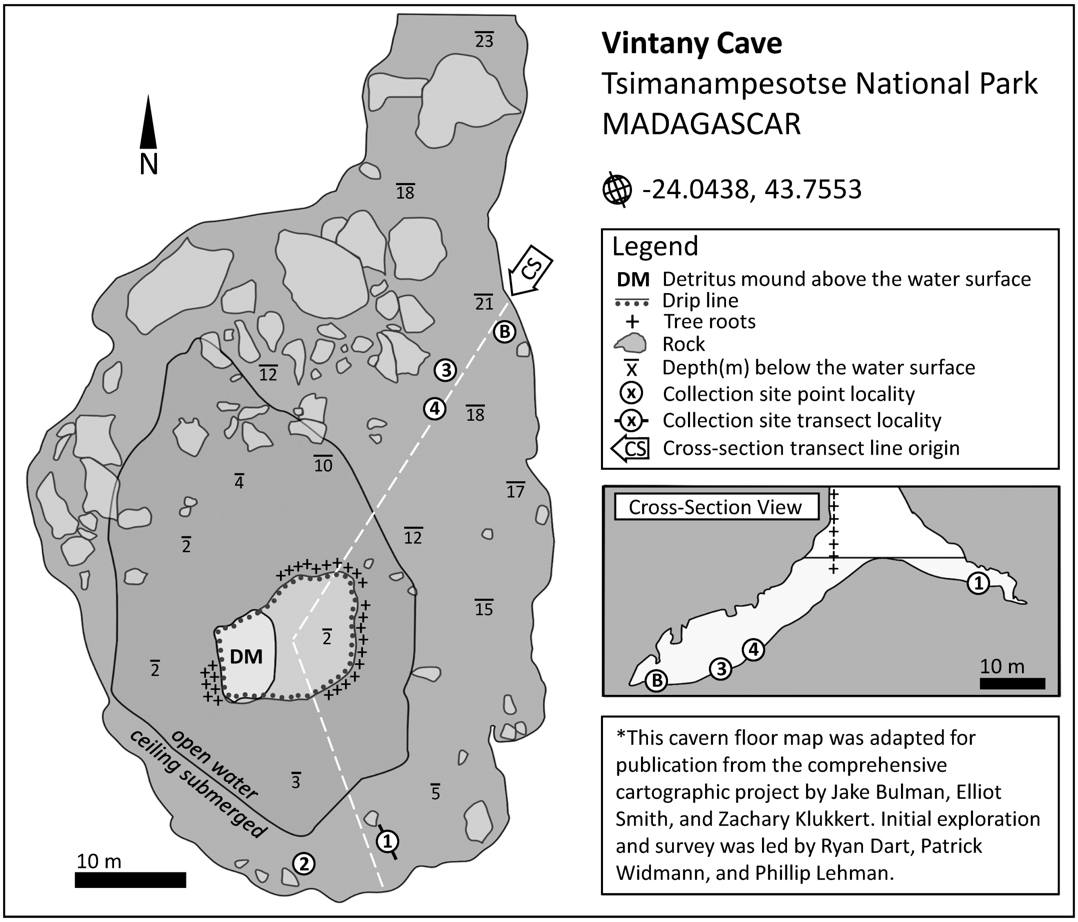
Order	Family	Species	Locality	Conservation status
Class Mammalia				
Afrosoricida	Tenrecidae	*Setifer setosus*	Vin	LC
Primates	Lemuridae	*Lemur catta*	Vin, Mit, Mal	EN
		Pachylemur insignis	Vin	EX
	Cheirogaleidae	*Microcebus griseorufus*	Vin	LC
	Palaeopropithecidae	*Mesopropithecus globiceps*	Vin, Soa	EX
	Megaladapidae	*Megaladapis edwardsi*	Mal, Atsf	EX
		M. madagascariensis	Atsf	EX
	Archaeolemuridae	*Archaeolemur majori*	Atsf	EX
Rodentia	Nesomyidae	**Macrotarsomys petteri*	Vin, Mit	DD
		Eliurus sp.	Vin	–
	Muridae	*+Rattus rattus*	Vin, Mat	–
Chiroptera	Molossidae	*Mormopterus jugularis*	Vin, Mit	LC
	Hipposideridae	*Macronycteris commersoni/ cryptovalorona*	Vin, Mit, Mat	NT
	Pteropodidae	*Eidolon dupreanum*	Vin, Mat	VU
	Rhinonycteridae	*Paratriaenops furculus*	Vin	LC
		Triaenops menamena	Mit, Mat	LC
Carnivora	Eupleridae	*Cryptoprocta* new sp.	Mit	EX
		C. spelea	Vin, Mit	EX
		C. ferox	Mit	VU
		**Fossa fossana*	Vin	VU
	Felidae	*+Felis catus*	Andr	–
Artiodactyla	Hippopotamidae	*Hippopotamus lemerlei*	Atsf, Mal	EX
	Bovidae	*+Bos taurus*	Andr, Mit	–
Class Aves				
Aepyornithiformes	Aepyornithidae	*Mullerornis modestus*	Vin, Atsf	EX
		Vorombe titan	Atsf	EX
Anseriformes	Anatidae	*Alopochen sirabensis*	Vin	EX
		Anas sp.	Vin	LC
Galliformes	Numididae	+?*Numida meleagris*	Vin	LC
Phoenicopteriformes	Phoenicopteridae	*Phoenicopterus roseus*	Vin	LC
Columbiformes	Columbidae	*Oena capensis*	Vin	LC
		Nesoenas picturata	Vin	LC
Pterocliformes	Pteroclidae	*Pterocles personatus*	Vin	LC
Cuculiformes	Cuculidae	*Coua gigas*	Vin	LC
		Coua cristata	Vin	LC
		Coua ruficeps	Vin	LC
		Coua cf. *berthae*	Vin	EX
		Coua cf. *primaeva*	Vin	EX
Caprimulgiformes	Caprimulgidae	*Caprimulgus madagascariensis*	Vin	LC
	Apodidae	*Apus balstoni*	Vin	LC
Gruiformes	Rallidae	*Fulica cristata*	Vin	LC
Charadriiformes	Recurvirostridae	*Himantopus himantopus*	Vin	LC
	Charadriidae	*Vanellus madagascariensis*	Vin	EX
Pelecaniformes	Ardeidae	**Ardea humbloti*	Vin	EN
	Threskiornithidae	*Plegadis falcinellus*	Vin	LC
		**Threskiornis bernieri*	Vin	EN
Accipitriformes	Accipitridae	*Accipiter henstii*	Vin	NT
		cf. *Accipiter henstii*	Vin	–
		Buteo brachypterus	Vin	LC
		**Haliaeetus vociferoides*	Vin	CR
		Milvus aegyptius	Vin	NT
		Polyboroides radiatus	Vin	LC
Strigiformes	Strigidae	*Athene superciliaris*	Vin	LC

(Continued)

TABLE 2 | (Continued)

Order	Family	Species	Locality	Conservation status
		Otus rutilus	Vin	LC
	Tytonidae	*Tyto alba*	Vin	LC
Falconiformes	Falconidae	*Falco newtoni*	Vin, Mat	LC
Psittaciformes	Psittacidae	*Coracopsis vasa*	Vin, Mat	LC
Passeriformes	Ploceidae	*Foudia madagascariensis*	Vin	LC
		Nelicurvius sakalava	Vin	LC
	Hirundinidae	*Phedina borbonica*	Vin	LC
Class Reptilia				
Testudines	Testudinidae	*Aldabrachelys grandidieri*	Vin, Mal, Atsf	EX
		Astrochelys radiata	Mat	CR
Crocodilia	Crocodylidae	*Voay robustus*	Vin, Soa, Atsf, Amb	EX

*Localities: Amb, Ambolely Sinkhole; Andr, Andranohilova Cave; Atsf, Antsirafaly and surrounding region; Mat, Maty Cave (Anjohimpaty Rock Shelter); Mal, Malazamanga Cave; Mit, Mitoho Cave; Soa, Soarano Cave; Vin, Vintany Cave. IUCN Conservation status: EX, Extinct; CR, Critically Endangered; EN, Endangered; VU, Vulnerable; LC, Least Concern; NT, Not Threatened; DD, Data Deficient. *, locally extirpated; +, introduced; +?, perhaps introduced.*



*This cavern floor map was adapted for publication from the comprehensive cartographic project by Jake Bulman, Elliot Smith, and Zachary Klukkert. Initial exploration and survey was led by Ryan Dart, Patrick Widmann, and Phillip Lehman.

FIGURE 4 | Vintany Cave, showing excavation sites in shallow (Localities 1 and 2) and deep (Localities 3, 4, and B = Bone soup) sections of the cave.

32 m below the present water table, we conclude that they were deposited prior to cave flooding (i.e., when the subaerial chimney would have functioned like a water chute during storms). They are likely older than 8,300 yr BP and almost certainly older than 7,000 yr BP.

The next oldest date is from a piece of elephant bird eggshell (likely *Mullerornis*) found by MacPhee (1986) at the main entrance to Mitoho Cave (**Table 3**). Only slightly younger are a series of radiocarbon dates for other TNP extinct species (*Pachylemur insignis*, *Coua* cf. *primaeva*, and *Voay robustus*), as

TABLE 3 | TNP/Antsirafaly specimens with conventional and calibrated ^{14}C dates prior to 900 yr BP.

Taxon	Locality	Catalog #	Conventional age: ^{14}C yr BP ± 1σ	Calibrated age: Cal yr BP ± 1σ	Laboratory #	Source
Order Primates						
†*Pachylemur insignis*	Vin	UABEC 0821	2830 ± 130	2985 ± 285	CAMS 182448	Faina et al., in press
†*P. insignis*	Vin	UABEC 0824	2155 ± 30	2073 ± 68	CAMS 182344	Faina et al., in press
†*P. insignis*	Vin	UABEC 0930	2135 ± 30	2068 ± 68	CAMS 183953	This paper
†*P. insignis*	Vin	UABEC 0924	2135 ± 25	2065 ± 65	CAMS 184645	This paper
Microcebus griseorufus	Vin	UABEC 0744	2325 ± 45	2250 ± 110	CAMS 185375	Faina et al., in press
†*Megaladapis edwardsi*	Atsf	UA 10699	1550 ± 20	1385 ± 40	UCIAMS 167900	Faina et al., in press
†*M. edwardsi*	Atsf	UABEC 1371	1660 ± 25	1498 ± 73	CAMS 183950	Faina et al., in press
†*M. edwardsi*	Atsf	UABEC 1461	1285 ± 30	1168 ± 98	CAMS 184638	This paper
†*M. edwardsi*	Slar	UABEC 1462	1325 ± 25	1228 ± 53	CAMS 184639	This paper
†*M. edwardsi*	Slar	UABEC 1468	1305 ± 25	1178 ± 93	CAMS 184640	This paper
†*M. edwardsi*	Slar	UABEC 1463	1310 ± 35	1178 ± 98	CAMS 184641	This paper
†*M. edwardsi*	Slar	UABEC 1470	1380 ± 25	1240 ± 60	CAMS 184642	This paper
†*M. edwardsi*	Slar	UABEC 1418	1460 ± 25	1270 ± 85	CAMS 184643	This paper
†*Megaladapis madagascariensis*	Slar	UABEC 1471	1315 ± 25	1190 ± 85	CAMS 184636	This paper
†*M. madagascariensis*	Slar	UABEC 1465	1295 ± 25	1170 ± 95	CAMS 184637	This paper
†*Archaeolemur majori*	Atsf	UABEC 1349	1310 ± 25	1185 ± 90	CAMS 183972	Faina et al., in press
†*A. majori*	Slar	UABEC 1469	1090 ± 60	933 ± 133	CAMS 184644	This paper
Lemur catta	Mal	UABEC 0341	1140 ± 40	998 ± 68	CAMS 185378	This paper
Order Rodentia						
**Macrotarsomys petteri*	Vin	UABEC 0427	2210 ± 40	2185 ± 140	CAMS 185383	This paper
Order Artiodactyla						
†*Hippopotamus lemerlei*	Atsf	UABEC 1378	1580 ± 25	1438 ± 78	CAMS 183970	Faina et al., in press
†*H. lemerlei*	Atsf	UABEC 1391	1940 ± 25	1818 ± 73	CAMS 183973	Faina et al., in press
†*H. lemerlei*	Atsf	UABEC 1377	1620 ± 25	1473 ± 63	CAMS 183975	Faina et al., in press
†*H. lemerlei*	Slar	UABEC 1453	1300 ± 25	1173 ± 98	CAMS 184652	This paper
†*H. lemerlei*	Atsf	UABEC 1376	1835 ± 25	1715 ± 105	CAMS 184653	This paper
†*H. lemerlei*	Atsf	UABEC 1429	1535 ± 25	1365 ± 50	CAMS 184654	This paper
†*H. lemerlei*	Slar	UABEC 1455	1390 ± 25	1243 ± 63	CAMS 184655	This paper
†*H. lemerlei*	Slar	UABEC 1472	1265 ± 25	1123 ± 58	CAMS 184656	This paper
†*H. lemerlei*	Atsf	UABEC 1375	1490 ± 25	1138 ± 38	CAMS 184657	This paper
†*H. lemerlei*	Slar	UABEC 1456	1255 ± 30	1120 ± 60	CAMS 184658	This paper
†*H. lemerlei*	Atsf	UABEC 1381	1475 ± 30	1330 ± 40	CAMS 184659	This paper
Order Chiroptera						
Macronycteris commersoni/cryptovalorona	Mit	UABEC 1287b	1525 ± 25	1360 ± 50	CAMS 183971	Faina et al., in press
M. commersoni/cryptovalorona	Vin	UABEC 0901	1950 ± 30	1835 ± 90	CAMS 182449	Faina et al., in press
Order †Aepyornithiformes						
Elephant bird eggshell	Mit	Uncatalogued	4030 ± 70	4443 ± 208	β-16442	MacPhee, 1986
†*Mullerornis modestus*	Atsf	UABEC 1372	1945 ± 25	1823 ± 73	CAMS 183974	Faina et al., in press
†*M. modestus*	Atsf	UABEC 1382	1465 ± 25	1325 ± 35	CAMS 183969	Faina et al., in press
†*M. modestus*	Slar	UABEC 1471	1305 ± 25	1178 ± 93	CAMS 183967	Faina et al., in press
†*M. modestus*	Slar	UABEC 1476	1270 ± 25	1118 ± 53	CAMS 183966	Faina et al., in press
†*M. modestus*	Slar	UABEC 1385	1595 ± 25	1450 ± 75	CAMS 183965	Faina et al., in press
†*M. modestus*	Atsf	UABEC 1380	1560 ± 35	1415 ± 100	CAMS 184633	This paper
†*M. modestus*	Atsf	UABEC 1374	1575 ± 25	1420 ± 65	CAMS 184634	This paper
†*M. modestus*	Atsf	UABEC 1369	1515 ± 25	1358 ± 48	CAMS 184635	This paper
†*Vorombe titan*	Atsf	UABEC 1434	1540 ± 25	1368 ± 53	CAMS 183968	Faina et al., in press
†*V. titan*	Atsf	UABEC 1414	1675 ± 25	1518 ± 68	CAMS 183949	Faina et al., in press
Order Cuculiformes						
†*Coua* cf. *primaeva*	Vin	UABEC 0854a	2190 ± 45	2160 ± 155	CAMS 185377	This paper
Order Crocodilia						
†*Voay robustus*	Soa	UABEC 1358	2340 ± 30	2253 ± 103	CAMS 183952	Faina et al., in press

*UA, Université d'Antananarivo; UABEC, Université d'Antananarivo, Bassins Sédimentaires Evolution et Conservation. Localities: Andr, Andranohilova; Atsf, Antsirafaly; Mal, Malazamanga Cave; Mit, Mitoho Cave; Slar, Soalara; Soa, Soarano Cave; Vin, Vintany Cave; CAMS, Center for Accelerator Mass Spectrometry at Lawrence Livermore National Lab; "β", Beta Analytic; UCIAMS, University of California, Irvine W.M. Keck Carbon Cycle Accelerator Mass Spectrometer Facility. † = extinct; * = locally extirpated. Dates in text are all calibrated ages, but designated "yr BP."*

TABLE 4 | Tsimanampesotse/Antsirafaly specimens with conventional and calibrated ^{14}C dates younger than 900 yr BP.

Taxon	Locality	Catalog #	Conventional age: ^{14}C yr BP ± 1σ	Calibrated age: Cal yr BP ± 1σ	Laboratory #	Source
Order Primates						
Microcebus griseorufus	Vin	UABEC 0431d	^{14}C modern	0	CAMS 185376	This paper
Lemur catta	Mit	UABEC 1314	100 ± 25	Too young to calibrate	CAMS 184646	This paper
Order Rodentia						
+*Rattus rattus*	Mat	UABEC 1352	145 ± 35	135 ± 135	CAMS 185381	This paper
+*R. rattus*	Vin	UABEC 0435A	^{14}C modern	0	CAMS 185379	This paper
+*R. rattus*	Vin	UABEC 0435B	^{14}C modern	0	CAMS 185380	This paper
+*R. rattus*	Vin	UABEC 0940	^{14}C modern	0	CAMS 185382	This paper
Order Chiroptera						
Eidolon dupreanum	Vin	UABEC 0711	150 ± 35	138 ± 138	CAMS 185385	This paper
E. dupreanum	Vin	UABEC 1033	475 ± 35	490 ± 45	CAMS 185384	This paper
E. dupreanum	Mat	UABEC 1329	170 ± 25	138 ± 138	CAMS 184649	This paper
Macronycteris commersoni/cryptovalorona	Andr	UAP-01.158a	135 ± 20	130 ± 125	CAMS 150527	Faina et al. (in press)
M. commersoni/cryptovalorona	Mit	UABEC 1287a	^{14}C modern	0	CAMS 183951	Faina et al. (in press)
M. commersoni/cryptovalorona	Mit	UABEC 0865d	^{14}C modern	0	CAMS 183976	This paper
M. commersoni/cryptovalorona	Mit	UABEC 0865b	^{14}C modern	0	CAMS 183977	This paper
Order Carnivora						
+*Felis catus*	Andr	UAP-01.158i	905 ± 25	763 ± 38	CAMS 148400	Crowley et al. (2017)
+*F. catus*	Andr	UAP-01.158ii	295 ± 25	360 ± 80	CAMS 148401	This paper
Order Falconiformes						
Falco newtoni	Mat	UABEC 1324	850 ± 20	708 ± 33	CAMS 184650	This paper
Order Psittaciformes						
Coracopsis vasa	Mat	UABEC 1330	185 ± 25	140 ± 140	CAMS 184648	This paper
C. vasa	Mat	UABEC 1325	115 ± 25	Too young to calibrate	CAMS 184651	This paper
Order Testudines						
Astrochelys radiata	Mat	UABEC 1321	155 ± 25	133 ± 133	CAMS 184647	This paper
Order Squamata						
Unidentified Snake	Andr	UAP-01.158r	160 ± 25	135 ± 135	CAMS 148385	Faina et al. (in press)

UAP, Université d'Antananarivo Paléontologie; UABEC, Université d'Antananarivo, Bassins Sédimentaires Evolution et Conservation. +, introduced. ^{14}C "modern" specimens were assigned a calibrated age of 0 Cal yr BP for our analysis. Localities: Andr, Andranohilova; Mit, Mitoho Cave; Vin, Vintany Cave; Mat, Anjohimpaty Rock Shelter. Dates mentioned in text are all calibrated ages, designated "yr BP."

TABLE 5 | Plant material from sediments collected from underwater deposits at Vintany and Malazamanga Caves (Tsimanampesotse National Park), AMS-dated at Beta Analytic Laboratories, FL, United States.

Excavation site and description	Conventional age: ^{14}C yr BP ± 1σ	Calibrated age: Cal yr BP ± 1σ	Laboratory #
Vintany Locality 4: In deep section of cave, with low sedimentation rate	2310 ± 30	2245 ± 100	β521009
Vintany Bone Soup: In deep section of cave, with low sedimentation rate	2070 ± 30	1990 ± 70	β521008
Vintany Bone Soup: In deep section of cave, with low sedimentation rate	1900 ± 30	1775 ± 65	β521014
Vintany Locality 2: In shallow section of cave, with high sedimentation rate	310 ± 30	363 ± 83	β521011
Vintany Locality 1 (Square AB): In shallow section of cave, with high sedimentation rate	240 ± 30	225 ± 85	β521010
Malazamanga Cave: Bark associated with bone cluster found 400 m from entrance to cave	1040 ± 30	880 ± 80	β521015

*See **Figure 4** for the locations of Vintany excavation sites.*

well as the locally extirpated *Macrotarsomys petteri*, all falling between 3,000 and 2,000 years ago. We can infer similar ages for additional extinct species (*Mesopropithecus globiceps*, *Coua* cf. *berthae*, and *Mullerornis modestus*) on the basis of depositional association. Specimens belonging to these three species were retrieved from the locality in the deep portion of Vintany Cave known as "Bone Soup" (**Figure 4**, site B). Present in the same deposit are specimens of *Voay robustus* and *Pachylemur insignis*, both of which are known to have survived at TNP until ∼2,000 years ago or later based on dated specimens at other Vintany localities and at another cave within the park. At Bone Soup we found associated bones of a single *Pachylemur* along

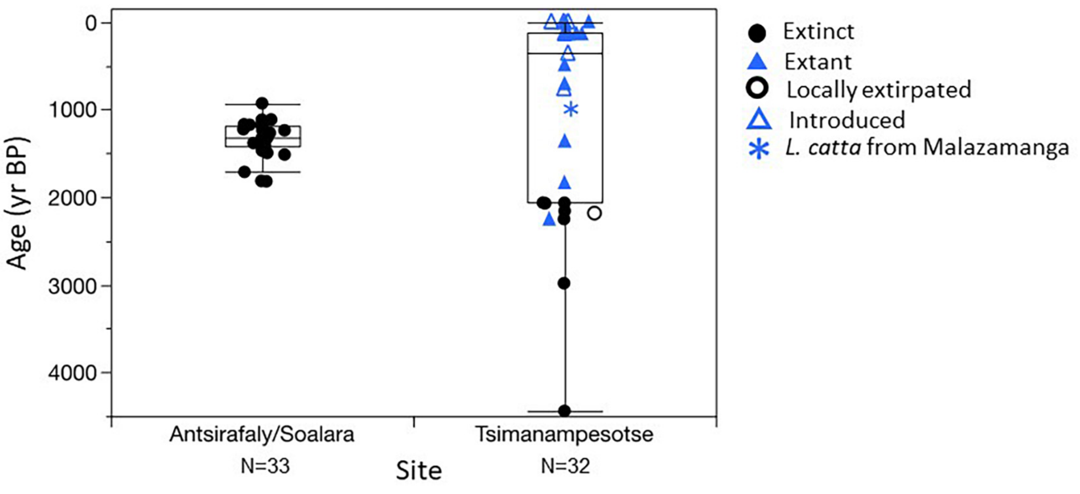


FIGURE 5 | Distribution of calibrated dates for extinct, extant, locally extirpated, and introduced taxa at Antsirafaly and Tsimanampesotse. The date for a humerus of the extant *Lemur catta* at Malazamanga is highlighted (blue asterisk) because of its possible temporal association with several bones of extinct species (*Megaladapis edwardsi*, *Hippopotamus lemerlei*, and *Cryptoprocta spelea*). See text.

with mixed remains of individuals belonging to other extinct species, as well as plant material. None of the bones from Bone Soup were directly datable, but plants from this deposit yielded calibrated dates of 1990 ± 70 and 1775 ± 65 yr BP. Given that these sediments appeared to be little disturbed, one might infer that the entire Bone Soup assemblage could have been slightly under 2,000 years old.

All TNP vertebrate dates between 2000 and 900 yr BP belong to smaller-bodied, endemic species, such as extant lemurs or bats. However, there is some indirect evidence that *Megaladapis edwardsi*, *Hippopotamus lemerlei*, and *Cryptoprocta spelea* were still present at TNP around 1,000 years ago. As mentioned above, divers found these bones in a cluster far from the entrance to Malazamanga Cave. Most were buried in sediment but an undamaged skull of a *Megaladapis edwardsi* was exposed on the cave floor. We did not sample these bones for dating, but we did obtain radiocarbon dates for a piece of bark (880 ± 80 yr BP) (**Table 5**) and a *Lemur catta* humerus (998 ± 68 yr BP) (**Table 3**), both of which were found directly below the *Megaladapis* skull. The overlapping confidence limits of these dates suggest that subfossils and other debris accumulated at this location over a short window of time, most likely through a fissure in the ceiling that was only open for a limited period. This bone cluster is unique in that this was the only place at Malazamanga where bones and other debris from outside were found. Furthermore, the bones showed no evidence of abrasion through water transport. The taxonomic composition of this cluster of bones is strikingly different from that of all other subfossil assemblages at TNP. *Pachylemur* and *Mesopropithecus*, common at nearby Vintany Cave, are both notably absent at Malazamanga. With the exception of *C. spelea*, the extinct species found in the bone cluster at Malazamanga are all also present at Antsirafaly until nearly 1,000 years ago, so survival of these particular species in the region until the beginning of the second millenium is not unexpected.

Finally, after 900 yr BP at TNP, we begin to see introduced taxa (e.g., cats, rats, and cows) alongside endemic extant species (**Table 4**). The date range for bones of introduced taxa at TNP is 763 ± 38 yr BP to modern. The oldest are cat bones from Andranohilova. Cow bone was also present at Andranohilova, but we failed to recover collagen from a specimen that we treated for dating, and thus cannot exclude the possibility that cattle were present prior to 900 yr BP. We found many rat bones at the Anjohimpaty Rock Shelter and in both shallow and deep sections of Vintany Cave, but always exposed on the floor of the flooded cave rather than within the sediments. Most of the *Rattus* specimens we dated are radiocarbon-modern, and none is older than ∼200 years, suggesting recent colonization of natural environments of the southwest.

At Antsirafaly, we see a very different profile of faunal change (**Figure 5**). There was no early first millenium CE crash; instead, the subfossil record ends abruptly ∼1,000 years later, near the end of the first millenium but before the appearance of introduced taxa at TNP (**Table 3**). Only one dated specimen (an *Archaeolemur majori*) was younger than 1118 yr BP (933 ± 133 yr BP), suggesting that, not long after 1100 yr BP, the Antsirafaly pond dried up or became too muddy to support local animals seeking fresh water. We found no bones at this site older than 1823 yr BP; this may simply mean that we did not dig sufficiently deep below the current water table to expose older specimens. However, sites such as Ampoza with similar depositional profiles, have never yielded additional fossils from below the fossiliferous layer despite continued excavation. *Hippopotamus lemerlei*, *Mullerornis modestus*, *Megaladapis edwardsi*, and *M. madagascariensis* were present at Antsirafaly through much of the first millenium CE. We have few dates for *Vorombe titan* and *Archaeolemur majori*, but the dates we have, with the exception of the single dated *A. majori* mentioned above, fall within the temporal range of the other species. Giant tortoises (*Aldabrachelys* sp.) and horned crocodile (*Voay robustus*) bones from the same deposits were not dated. We found no bones of introduced domesticated species at Antsirafaly, suggesting that these animals may have arrived at this locality after the pond dried up.

Evidence of Human Presence in the Region of TNP

Neither TNP nor Antsirafaly was an early human settlement site, nor did we find any evidence at either of large-vertebrate butchery. MacPhee (1986) reported a scattering of elephant bird eggshell on the talus below Anjohimpaty, which may suggest that people used elephant bird eggs to carry water to this site, but this could have happened long after elephant birds were locally extirpated. However, there are clear signs of human presence, minimally over the past ∼800 years, derived from introduced taxa. Our two calibrated radiocarbon dates for introduced *Felis catus* from Andranohilova (763 ± 38 and 360 ± 80 yr BP; **Table 4**) span much of the past millenium. They suggest that feral cats at least occasionally used Andranohilova. This in turn may suggest that *Cryptoprocta spelea* were rarely sheltering in the cave or absent entirely during this period. Modern introduced carnivorans often displace native carnivores (Farris et al., 2015), but cats are much smaller in body size than *C. spelea* and likely would have been displaced by them. The still-extant *C. ferox* is smaller than *C. spelea* and still lives in the park.

We found specimens of *Numida meleagris* (helmeted guineafowl, long assumed to be introduced to Madagascar) in association with nearly 2,000-year-old plant remains and over 2,000-year-old subfossil *Pachylemur* within the sediments of the deep-section of Vintany Cave (Localities Bone Soup and 4). Goodman et al. (2013) reported guineafowl at Ankilitelo in southwest Madagascar over 13,000 years ago, raising the possibility that this species colonized Madagascar from Africa prior to, and independently of, the initial colonization of the island by humans (but see Hansford et al., 2018; Godfrey et al., 2019). Our discovery of *Numida* in 2,000-year-old deposits at Vintany provides indirect support for the prolonged presence of guineafowl in southwestern Madagascar, but not necessarily for human presence at Tsimanampesotse 2,000 years ago. This is because helmeted guineafowl may have colonized Madagascar independently of humans (Goodman et al., 2013), and because, even if they were introduced by humans over 13,000 years ago, we cannot assume that the presence of feral *Numida* at any one locality thousands of years later indicates the local presence of humans.

Cave art (including two graffiti messages using the Roman alphabet and two anthropomorphic figures) at Anjohimpaty Rock Shelter covers much of the northern wall of the shelter (**Figures 6–8**). Both anthropomorphic figures (a possible solitary sorcerer figure, and a very faint combination of seven figures in 'human-pyramid' formation, four in a bottom layer, two in a middle layer, and one on top) show images with down-curved arms. The solitary figure has a pointed head and bowed legs. Finally, at the eastern end of the wall, there is a second graffiti message located above a small cavity where the wall meets the floor (**Figure 8**).

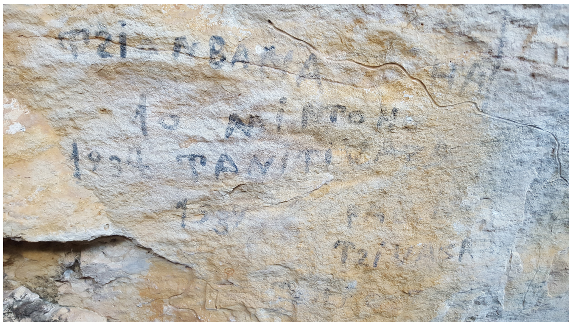


FIGURE 6 | Mahafale graffiti on the western end of the northern wall at Anjohimpaty Rock Shelter.

The graffiti depicted in **Figure 6** dates from 1934. It was written by a Malagasy person using the local Mahafale (primarily) and Central Highlands Merina dialects. Although some of the writing is faded, and although characters may be missing, the general message can be deciphered. The first line, TZI*NBANA (where the asterisk represents a likely missing letter), can be read as 'tsy ombàna.' This is a combination of the Mahafale expression 'tsy ombà' (no trespassing) and the Merina suffix '-na.' Mahafale people would not use the suffix '-na' unless they are trying to communicate with Merina people. This suggests that the person who wrote this inscription was a local Mahafale person (hence the use of 'tsy ombà') who interacted with either a Merina person (from the Central Highlands) or a foreigner (vazaha) who spoke the Merina language (hence the use of the suffix 'na'). The next line appears to read '10 MINTOHO.' If, instead of the number 10, the inscriber intended to write 'IO,' the first word would mean 'here' in the Mahafale dialect. MINTOHO is an alternative spelling of the name of the cave. Taken together, this becomes 'this cave, Mitoho.' The next line reads 1934 TANITIVAZA. 1934 can be easily interpreted as the date the graffiti was written. In the Mahafale dialect, 'TANITIVAZA' should read 'tani'ty vazaha' or 'tane'ty vazaha' which means 'vazaha's land' (foreigner's land). The next portion of this inscription (1934 FA TZIVAZA) could have been written by a second person as a reply to the first person (which might explain the repetition of the date, 1934), or by the first person replying to his or her rhetorical question. 'FA' means 'but' in the Merina dialect ('fe' in Mahafale), but 'fa' means 'already' in Mahafale, and together with the negation 'tsy,' it means 'no longer.' Thus, 'Fa tsy vazaha' means 'it is no longer vazaha's' in Mahafale.

The second graffiti on the eastern end of the northern wall of the shelter appears to be a solitary word, I?)BERTEM(T?Y?I?)OK. It was written above a small arched inner depression, 1 m from the floor of the main shelter (**Figure 8**). This inscription does not resemble Mahafale or any other dialect of Malagasy. We cannot exclude the possibility that it is misspelled Mahafale, or the name of a person – perhaps of someone buried there. There is no reason to believe that the anthropomorphic images or the two graffiti messages are related to one another. Whereas both messages appear to be recent, the anthropomorphic images are faint and may be older. There is evidence of additional, very

FIGURE 7 | Possible anthropomorph **(left)** and human pyramid **(right)** figures on northern wall at Anjohimpaty Rock Shelter.

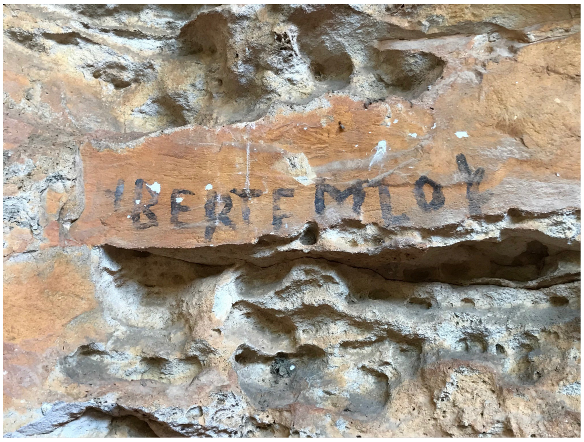


FIGURE 8 | Graffiti on the eastern end of the northern wall of the Anjohimpaty Rock Shelter.

faint, writing. The Anjohimpaty Rock Shelter wall may have been used by people over an extended period, but at present, we have no definitive indication of great antiquity for any particular image or inscription.

DISCUSSION

Is Today's Hydroclimate in Southwestern Madagascar Significantly Drier Than the Hydroclimate of Several Thousand Years Ago, When There Were Numerous Large-Bodied Endemic Vertebrate Species at TNP?

On the basis of evidence presented herein, we conclude that today's hydroclimate in southwest Madagascar is not significantly drier than the hydroclimate of several thousand years ago, when there were numerous large-bodied endemic vertebrate species in this region. To the contrary, our analysis of 23 stalagmites from TNP shows that modern mean annual rainfall at this locality is higher than it was throughout most of the Holocene. Low rainfall would have characterized extended periods during which large-bodied vertebrates thrived in the region, including between 3,000 and 2,000 years ago at TNP and between 2000 and ~1000 yr BP at Antsirafaly. This suggests that the large-bodied vertebrates at TNP and Antsirafaly, like so many plants of the dry southwest (spiny thicket and succulent woodland ecoregions), were likely drought-tolerant.

The hydroclimate of southern Madagascar was characterized by alternating wetter and drier periods. On a coarse scale there were pluvials and interpluvials, each lasting around 10,000 years, but each in turn was characterized by climate fluctuations on a finer, centennial scale. One such drought occurred within the current pluvial, as revealed by a study of stable isotopes in one of our Asafora stalagmites, AF2 (Faina et al., in press). An analysis of stalagmite AF2 indicates a relatively wet period at its base (~3,500 yr BP) with dominant C_3 vegetation. This corresponds to the beginning of the current pluvial at this location. At 3350 yr BP, rainfall began to decline slowly until 1680 yr BP, at which point the decline accelerated markedly. Full drought conditions began ~1560 yr BP and continued until ~880 yr BP, after which wetter conditions resumed. Within this 700-year drought, there were fluctuations in both rainfall and vegetation reflected in the $\delta^{18}O$ isotope records and the $\delta^{13}C$ records respectively. These correlated trends suggest a coupling of changes in rainfall amount and ground vegetation from dominant C_3 to higher representation of CAM and C_4 vegetation (i.e., succulent plants and grasses) and back. Drought conditions at Asafora were most severe between 1100 and 960 yr BP. At TNP, after 880 yr BP, there was likely a gradual increase in rainfall until the threshold of speleothem growth was reached (perhaps as recently as several hundred years ago).

What Triggered Local Extirpation of Species at Tsimanampesotse and Antsirafaly?

We have identified two episodes of local extirpation of a wide variety of vertebrate species that are now extinct: one at TNP (near the beginning of the first millenium CE, i.e., 2,000 years ago) and one at Antsirafaly (near the end of the first millenium CE, i.e., 1,000 years ago). The two were not synchronous, and neither can be linked to human activities. Instead, they appear to be related to climate change. However, a third event clearly related to human activities, i.e., the local arrival of introduced vertebrates in association with the spread across Madagascar of agropastoralism, impacted the southwest not long after the second extirpation event. We will return to this third event later.

At Antsirafaly, a temporal link between peak drought conditions and local vertebrate extirpation can be defended on the grounds that aridification likely caused the small pond at this site to shrink and then disappear entirely. The mean for last-known occurrences for the six dated extinct species at Antsirafaly is 1146 yr BP (range from 1368 ± 53 to 933 ± 133 yr BP; **Table 3**); this mean closely matches the beginning of peak drought at Asafora. Large vertebrates such as hippopotamuses and elephant birds likely simply shifted to nearby bodies of water as smaller ones dried. We do not know the extent to which the drought affected water bodies across the region. Hansford et al. (2021) estimate the time of disappearance of hippopotamuses and elephant birds at other sites in the spiny thicket at between 957 and 911 yr BP.

At TNP, the link between vertebrate species extirpation and arid climate is more tenuous. A lot depends on the precise timing of extirpation at this site: did it begin around 2000 yr BP or several centuries later? Given that the vertebrates living in southwestern Madagascar through the Holocene were drought-tolerant, one might expect that only extreme climate perturbations or large-scale changes in underground freshwater sources would have forced local extirpation. As we have discussed above, radiocarbon dates suggest that local extirpation of *Pachylemur*, *Mesopropithecus*, and other large vertebrate species at TNP occurred shortly after 2,000 years ago, but dates for plants in apparent association with bones of these same vertebrate species suggest that they may have persisted a bit longer. We know from stalagmite records at both TNP and Asafora Cave that the early first millenium was dry at TNP, but it is not clear that it would have been exceptionally dry at around 2,000 yr BP.

One could make a stronger case for aridity being the trigger for vertebrate decline at TNP if vertebrate decline did not commence until around 1700 yr BP or later. As described above, Asafora stalagmite AF2 recorded a sharp decrease in rainfall beginning 1680 yr BP, with drought conditions manifested by 1560 yr BP (Faina et al., in press). Simultaneously, Lake Ihotry, which is located ∼55 km NE of Asafora Cave, underwent salinization beginning around 1600 years ago (Vallet-Coulomb et al., 2006). We know, on the basis of old strand lines and deltaic sediments, that Lake Tsimanampesotse was once of much greater size and depth than it is today (Loewen et al., 2001), and we know on the basis of freshwater mollusks along the old strand lines and waterfowl bones in subfossil deposits that this was once a freshwater lake (Perrier de la Bâthie, 1934; Petit, 1935; Goodman and Jungers, 2014; Rasolonjatovo et al., in press). Assuming that change in local hydroclimate was the primary driver of lake salinization at Tsimanampesotse, Faina et al. (in press) hypothesized that lake salinization may have begun around 1600 years ago at this site (as at Lake Ihotry), coeval with the beginning of the late first millenium CE drought. Lake salinization has been suggested as a proximate cause of local extirpation of freshwater birds at TNP (Goodman and Jungers, 2014; Rasolonjatovo et al., in press).

There are three potential controls on lake size, salinity, and water availability, however, in addition to local rainfall. These are: (1) Changes in rainfall patterns inland impacting groundwater flow through the resurgences and into the lake (Guyot, 2002; Goodman and Jungers, 2014); (2) Geomorphological changes in the capture of overland streams draining to the lake (Loewen et al., 2001); and (3) Changes in evaporation from the lake surface. Only with new coring and detailed study of lake sediments will we be able to piece this all together for TNP.

Guyot (2002) found that inland water sources have direct underground links to the resurgent-artesian water sources at the western foot of the Mahafaly Plateau. These changes may have affected the gallery forest along the resurgent stream margins and the sources of freshwater that fed into Lake Tsimanampesotse and sites such as the ponds and marshes in the region of Antsirafaly. For variation in lake level during the Middle and Late Holocene (once sea levels were high and stable), groundwater flow from inland rainfall is a plausible control on lake level fluctuations. However, the magnitude of such change would likely have been small compared to the influence of sea-level change between glacial and interglacial periods. We consider it unlikely that Lake Tsimanampesotse could have been fed by groundwater resurgences during the last glacial period while the nearby caves remained subaerial, as evidenced by speleothem growth. Local and regional geomorphological changes remain unstudied in the area, preventing greater assessment of their potential impact. Finally, any significant changes in evaporation would have likely followed glacial/interglacial changes in temperature (and therefore have been correlated with sea-level via global climatic change) and/or orbital scale changes in local precipitation.

We emphasize that the driver of early vertebrate extirpation at Tsimanampesotse, excluding freshwater birds, could not have been lake salinization alone. Salinization at Lake Tsimanampesotse would have had minimal effect on species that could easily access the fresh water at sinkholes on the karst, including primates. *Lemur catta* drinks fresh water from sinkholes at Tsimanampesotse today (Gould et al., 1999); its close relative, *Pachylemur*, probably did the same. Others could have avoided drinking water entirely. *Mesopropithecus globiceps* was a palaeopropithecid that, like its close extant relatives, the indriids, likely obtained all the water they required from the foods it consumed (see, for example, Semel et al., 2019, on *Propithecus* from the eastern rainforest; similar behaviors are observed for *Propithecus* in much drier habitats). For primates at TNP, the more critical resources may have been large trees offering preferred foods, nesting sites or protection from large predatory euplerids. At Tsimanampesotse today, big trees and cliff faces serve to protect the extant lemurid, *Lemur catta*, from the extant fosa, *Cryptoprocta ferox* (Sauther et al., 2013). Morphological evidence supports the inference that *C. spelea* was, like its living congener (e.g., Lührs and Dammhahn, 2010; Lührs and Kappeler, 2014), quite capable of climbing trees and hunting on high branches (see text footnote 3), but lemurs may nevertheless use the highest canopy branches of the tallest trees for sleeping or nesting in an attempt to avoid euplerid predation (Sauther et al., 2013; Vasey and Godfrey, in press). Virah-Sawmy et al. (2016) reported an abrupt decline of *Pandanus* trees beginning at 1574 yr BP at Ambolisatra, followed by gradual disappearance of *Pandanus* and other large trees, including palms, over the next ∼600 years, and ending with the local extirpation of these plants. Regardless of whether vertebrate extirpation at TNP began 2,000 years ago or several centuries later, and regardless of specific proximate triggers, we can assert with some confidence that none of the species that disappeared from TNP early in the first millenium CE were threatened with broader regional extinction at that time. *Pachylemur insignis*, for example, is known to have survived in the southwest for another thousand years. There is no reason to believe that it would have disappeared were it not for events that occurred 1,000 years later. We will return to this question below.

There is also no evidence that the large vertebrates at Antsirafaly were adversely affected by dry conditions of the early- or mid- first millenium CE. Hippopotamuses, elephant birds, large-bodied folivorous primates such as *Megaladapis*, and semiterrestrial generalists such as *Archaeolemur*, all larger than 15 kg, were apparently more drought-tolerant than *Pachylemur*, *Mesopropithecus*, and other species that disappeared early from TNP. Drought tolerance in *Megaladapis edwardsi* and *M. madagascariensis* may seem surprising as these animals have clear tree climbing adaptations and have been considered by some to have shunned more open canopy forests. However, we know that *Megaladapis*, like *Palaeopropithecus* and other highly arboreal giant lemurs, were victims of crocodiles (Meador et al., 2019). They must have regularly descended to the ground to cross open spaces or to visit waterholes. *Megaladapis* often occurred at subfossil sites in the southwest in association with *Archaeolemur*, and to the near exclusion of *Pachylemur* (Vuillaume-Randriamanantena, 1982). This holds for coastal dune sites with interdunal pools, lakes, or marshes (e.g., Beloha Anavoha, Beavoha, Ambolisatra, and Manombo-Toliara).

Neither Antsirafaly nor TNP shows evidence that humans triggered local vertebrate extirpation. Indeed, it is possible that no people arrived in the region until after the beginning of the second millenium CE, when we know of their proximity through the presence of introduced taxa at TNP. We found no evidence of megafaunal butchery at TNP or Antsirafaly, despite the fact that megafaunal butchery has been documented elsewhere on the southwest coast during the first millenium CE (Hansford et al., 2018).[4]

Some of the art at Anjohimpaty Rock Shelter may bear testimony to early human presence at TNP, but the graffiti that we documented above is almost certainly recent. The age of the single word on the eastern end of the northern wall of the cave is uncertain, but the inscription regarding foreign versus Malagasy ownership of Mitoho Cave includes a date (1934), and indeed can be understood within the context of events of the 1920s and 1930s. The reserve at Tsimanampesotse was initially established in 1927 under the control of the Muséum National d'Histoire Naturelle in Paris. Henri Perrier de la Bâthie and Georges Petit were two French scientists who surveyed the local wildlife in the early 1930s; both were also complicit in the colonial French campaign to eradicate the prickly pear cactus (*Opuntia*) from the region of Toliara using cochineal insects that parasitize the plant. *Opuntia* was and continues to be an important source of food for both people and cattle (Kaufmann, 2004). The eradication policy had disastrous (both intended and unintended) consequences, affecting the human population of most of southern Madagascar (Middleton, 1999; Kaufmann, 2008). That population had increased to significant size by the early 1900s, but the great famine, precipitated by the eradication of *Opuntia*, resulted in mass starvation and death. For example, in the year 1931 alone, a single district (Tsihombe) of the extreme south was estimated to have lost half of its human population (around 30,000 people; Middleton, 1999). The toll on cattle was said to be much worse. Local anger at Tsimanampesotse over actions of foreigners is easy to understand.

People today do hunt wild animals and similar practices in the past may not have left clear traces. For example, perishable artifacts for trapping bats are sometimes left inside Andranohilova Cave, where the highly sexually dimorphic modern *Macronycteris* bats are hunted during the season of scarce resources. Bat skulls collected from the submerged guano mound under the active bat roost at Mitoho Cave (dating to as old as 1360 ± 50 yr BP) differ cranially from modern individuals roosting at the same cave. Variation in body size and cranial shape in *Macronycteris* spp. is correlated with variation in rainfall across western Madagascar (Ranivo and Goodman, 2007; Alumbaugh et al., 2021). The degree to which variation in the skulls of the guano mound *Macronycteris* bats reflects recent changes in local habitat or recent human activities, such as predation, is currently under study. At present, it appears highly likely that such changes occurred during the second millenium CE.

In summary, aridification remains the most likely explanation for local vertebrate extirpation at TNP and Antsirafaly, but the timing of the two and the proximate causes of extirpation at each differed. In the case of TNP, early local extirpation appears to have resulted from a combination of lake salinization and the loss or decline of tall (likely open canopy) tree species. Much later, at Antsirafaly, aridification appears to have resulted in the drying of the pond we sampled, although we do not know the extent to which other bodies of water in the surrounding wetlands were affected. Habitat changes in the southwest were likely influenced by regional variation in hydroclimate, but perhaps also by shifts in rainfall patterns in the interior to the east of the Mahafaly Plateau that impacted the underground water system

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[4] Godfrey, L. R., Pérez, V. R., Crowley, B. E., Borgerson, C., Bankoff, R. J., Perry, G. H., et al. (Submitted). Giant lemur butchery was widespread in southwestern Madagascar prior to 1000 CE.

and resurged in the immediate vicinity. Two questions remain: first, how do these local extirpation events relate to regional vertebrate decline, and second, what caused so many vertebrate species to go extinct?

How Does the Local Extirpation of Vertebrate Species at Tsimanampesotse and Antsirafaly Relate to Their Regional Decline at Other Sites in Southern Madagascar?

To place local extirpation events at TNP and Antsirafaly within a broader geographic context, we can examine patterns of species decline for now-extinct vertebrate taxa with rich regional radiocarbon records. Of the 16 extinct species we identified from these sites, seven (*Hippopotamus lemerlei*, *Pachylemur insignis*, *Archaeolemur majori*, *Megaladapis edwardsi*, *M. madagascariensis*, *Mullerornis modestus*, and *Aldabrachelys* sp.) are represented by more than 10 dated specimens from the spiny thicket and succulent woodland ecoregions (**Table 6**). An eighth species (*Voay robustus*) has a poor regional radiocarbon record but is richly represented in the recent lore and ethnohistorical records. There is strong evidence (either directly from radiocarbon dates or indirectly from local traditional knowledge and ethnohistoric records) that all eight of these species survived in spiny thicket or succulent woodland ecoregions well into the first millenium CE or beyond (**Table 6**).

It is instructive to examine the decline of each species relative to the time of recent large-bodied vertebrate collapse in southwest Madagascar (i.e., 1200 yr BP; Faina et al., in press). Five of the eight species (*Hippopotamus lemerlei*, *Archaeolemur majori*, *Megaladapis edwardsi*, *M. madagascariensis*, and *Mullerornis modestus*) can be characterized as having: (1) A relatively high percentage (on average, just under 30%) of all dated specimens

TABLE 6 | Endemic vertebrates of the Tsimanampesotse region (now extinct) that likely survived into the last millenium, with last-known radiocarbon date in the spiny thicket or succulent woodland ecoregions, last-known date at Tsimanampesotse/Antsirafaly, survival past regional onset of large-vertebrate population crash.

Last occurrence date Cal yr BP + 1σ (site) [Date source]	**Last occurrence at Tsimanampesotse or Antsirafaly [Date source]**	**Survival in the spiny thicket past regional onset of megafaunal crash (% of all dated specimens younger than 1200 yr BP that derive from the spiny thicket)**
Pachylemur insignis UA 3647 820 ± 85 yr BP (Tsirave) [see text footnote 4]	*P. insignis* UABEC 0924 2065 ± 65 yr BP (Tsimanampesotse: Vintany Cave) [This paper]	9%
Voay robustus AMNH FR-3101 1323 ± 43 yr BP (Ampoza) (Hekkala et al., 2021)	*V. robustus* UABEC 1368 2253 ± 103 yr BP (Tsimanampesotse: Soarano Cave) (Faina et al., in press)	No specimens date to < 1200 yr BP (total sample size < 10)
Megaladapis madagascariensis 590 ± 65 yr BP (Ankilitelo) (Simons, 1997)	*M. madagascariensis* UABEC 1465 1170 ± 95 yr BP (Antsirafaly/Soalara)	100%
Aldabrachelys sp. 665 ± 610 yr BP (Ambolisatra) (Burleigh and Arnold, 1986)	No specimens from Tsimanampesotse or Antsirafaly/Soalara have been dated	40%
Elephant bird (eggshell) 768 ± 138 yr BP (Manambovo)[1] (Battistini et al., 1963)	*Mullerornis modestus* UABEC 1476B 1118 ± 53 yr BP (Antsirafaly/Soalara) [Faina et al., in press]	66.7%
Archaeolemur majori UABEC 1469 933 ± 133 yr BP (Antsirafaly/Soalara) [This paper]	*A. majori* UABEC 1469 933 ± 133 yr BP (Antsirafaly/Soalara) [This paper]	86%
Hippopotamus lemerlei 085c 943 ± 18 yr BP (Lamboharana) (Hixon et al., 2021a)	*H. lemerlei* UABEC 1456 1120 ± 60 yr BP (Antsirafaly/Soalara) [This paper]	100%
Megaladapis edwardsi UA FMG-126 1119 ± 63 yr BP (Anavoha) [This paper]	*M. edwardsi* UABEC 1461 1168 ± 98 yr BP (Antsirafaly/Soalara) [This paper]	100%

AMNH, American Museum of Natural History; UA, Université d'Antananarivo, and UABEC, Université d'Antananarivo, Bassins sédimentaires Evolution et Conservation.
[1] *Date published prior to 1980, not considered reliable by some investigators.*

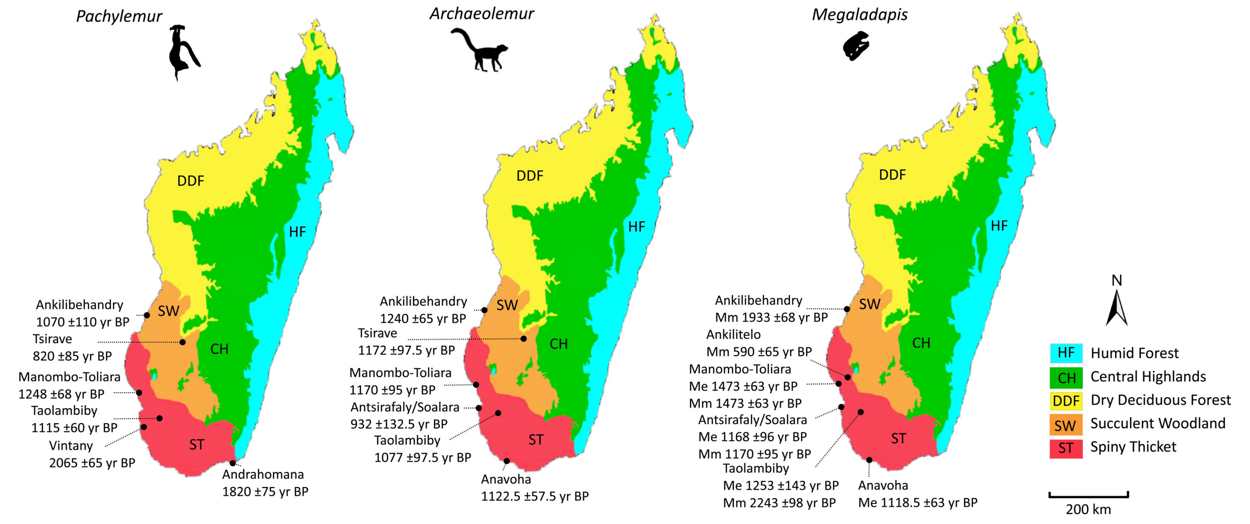

FIGURE 9 | Last occurrence dates for *Pachylemur*, *Archaeolemur*, and *Megaladapis* at sites in the spiny thicket and succulent woodland ecoregions of the dry southwest. For *Megaladapis*, Mm, *M. madagascariensis*, and Me, *M. edwardsi*. All dates are calibrated, and all major terrestrial ecoregions of Madagascar (Burgess et al., 2004) are shown.

from the southwest postdating 1200 yr BP; (2) A much higher percentage (on average, 95%) of the post-1200 yr BP dates for individuals from the spiny thicket rather than the succulent woodland; and (3) Last-known radiocarbon occurrences in the spiny thicket (**Table 6**). Traditional ecological knowledge of the survival well into the last millenium exists for some of these species (**Supplementary Data File**).

Pachylemur insignis shows a distinctly different pattern of regional decline (**Table 6**). This difference is exemplified by comparing *P. insignis* to the other large-bodied lemurs from the region: *Archaeolemur majori*, *Megaladapis edwardsi*, and *M. madagascariensis* (**Figure 9**). Unlike the other three lemur species, *P. insignis* is rare in the spiny thicket after the beginning of the megafaunal crash in the southwest (i.e., 1200 yr BP), and all dated specimens from the coast predate this period. This bears testimony to a possible decline of *Pachylemur* along the southern and southwestern coasts during the early part of the first millenium CE, with retreat to (or survival in) parts of the spiny thicket and succulent woodland to the east (inland) and north of TNP and Antsirafaly. The most recent dated *Pachylemur insignis* specimen from TNP is 1245 years older than the most recent specimen from elsewhere in the southwest. This species survived at Tsirave in the succulent woodland until at least 820 yr BP (**Table 6**). Similarly, *Voay robustus* survived at Ampoza in the succulent woodland for at least another 930 years past its last occurrence date at TNP (**Table 6**).

Regional chronological records are sparse for the other now-extinct species that we found at Tsimanampesotse, such as *Mesopropithecus globiceps*, the larger-bodied *Coua* spp., and *Alopochen sirabensis*; thus, we cannot be confident in reconstructions of their decline in geographic distribution. Published dates for these taxa at other spiny thicket sites all predate 1200 yr BP. This is true, for example, of *M. globiceps* from Tsiandroina at 1520 ± 95 yr BP (Burney et al., 2004); *C. primaeva* from Tsiandroina at 1870 ± 140 yr BP (Goodman and Rakotozafy, 1997); and *A. sirabensis* from Beloha Anavoha at 1233 ± 178 yr BP (Goodman and Rakotozafy, 1997). There are very few dates for species that are locally extirpated at TNP from other sites in the southwest, and all that exist predate 1200 yr BP. *Macrotarsomys petteri* has been dated at Andrahomana in the spiny thicket ecoregion (1620 ± 85 yr BP; Burney et al., 2008). It is possible that these extinct and locally extirpated taxa began declining on the southwest coast early in the first millenium CE, as did *P. insignis*.

Most of the well-dated species that we recovered at Antsirafaly are known to have survived at other sites in the subarid south for centuries past their ages of last-known occurrence at Antsirafaly (see **Figure 9** for examples). This difference ranges from 0 years for *Archaeolemur majori* (Antsirafaly is its most recent last-known occurrence) to 580 years for *Megaladapis madagascariensis*. The average difference for five species is 231 years (**Table 6** and **Figure 9**).

Aldabrachelys sp. and *Voay robustus* may also have survived well into the last millenium in the spiny thicket, but species identifications are often difficult for fragmentary giant tortoise remains, and *Voay* has its last-known radiocarbon occurrence in the succulent woodlands. Only four *Voay* specimens have been dated and its geographic pattern of decline is not well documented.

In summary, despite their geographical proximity, the extirpation episodes we documented at TNP and Antsirafaly differ not merely in timing and apparent proximate causation, but also in how they relate to the regional decline or extinction of the affected species. Local extirpation does not necessarily portend impending extinction. Along the coast at TNP, we observe early first millenium decline of a suite of species, some of which may have simply migrated to more mesic environments. At Antsirafaly, we observe the local extirpation of a suite of species that appears to have been more drought resistant. There is little evidence that these species migrated to more mesic environments either inland or to the north, but they likely sought nearby freshwater bodies that had not yet dried. Their disappearance at Antsirafaly is closer to the time of their eventual extinction.

What, Ultimately, Caused the Extinction of the Large-Bodied Vertebrates in Madagascar's Southwest?

It was not long after vertebrate extirpation at Antsirafaly that island-wide extinction of Madagascar's large-bodied endemic species occurred. Between 1200 and 900 yr BP, populations of the island's largest endemic terrestrial vertebrates collapsed, not merely throughout the subarid southwest but across the island (Godfrey et al., 2019; Faina et al., in press). Large vertebrates disappeared from the wettest as well as the driest ecoregions of Madagascar; wherever subfossil sites exist, their decline can be documented. Species that were not yet extinct by the end of this period were presumably reduced to such small populations that they became paleontologically invisible. The hydroclimate of Madagascar at the time of the crash of megafaunal populations was neither uniformly wet nor dry. At ~1,100 years ago when the local crash at Antsirafaly began, the northwest was wet (Scroxton et al., 2017) and the southwest was dry (Faina et al., in press). As we have shown above, a new pluvial period had swept into portions of the south thousands of years earlier, but it only arrived in the driest parts of the southwest as the regional drought of the late first millenium CE subsided.

It is worth emphasizing that the differences in mean annual rainfall between 'pluvial' and 'interpluvial' periods in the southwest were not necessarily very large, and certainly were smaller than the differences across ecoregions at any single point in time. That said, we can assume that if there is any place in Madagascar where dry climate would have been most likely to trigger the extinction of vertebrate species, it would be the subarid southwest. We have marshaled evidence that, at the end of a long, dry interpluvial, arid conditions did, indeed, impact vertebrate populations. At both TNP and Antsirafaly, local extirpation occurred without evidence for a human trigger. However, our data also suggest that climate alone cannot have caused their extinction. Our profiles of local decline, coupled with regional data, present a picture that is more complex.

We contend that it was the introduction and spread of agropastoralism that transformed what had been a series of local biogeographic shifts into wholesale population collapse and species extinction. Agropastoralism spread to Madagascar during the late first millenium CE with the introduction of domesticated animals and cultivated plants from Asia and Africa (Dewar and Wright, 1993; Boivin et al., 2013; Crowther et al., 2016). Between 1200 and 900 yr BP, it spread across Madagascar. This was long after people had settled on Madagascar; indeed, there is strong evidence that people were present at least intermittently in the southwest during the Early and Middle Holocene and certainly prior to 2,000 years ago (Hansford et al., 2018, 2020; Douglass et al., 2019; Davis et al., 2020). Hunter/forager and fisher/forager impacts on endemic large-bodied vertebrate populations were minimal, however (Douglass et al., 2018; Hansford et al., 2021). Large vertebrates were hunted, but there is little evidence of early megaherbivore population collapse (Godfrey et al., 2019; Faina et al., in press).

Not long after introduced animals appeared in the north, they spread southward. An influx of cattle, dogs, cats and bushpigs to the southwest is documented by a plethora of specimens dating between 900 and 700 yr BP (Hixon et al., 2021a,b). Temporal overlap between large-bodied endemic vertebrates and introduced species can be inferred (Hixon et al., 2021a,b), but what is abundantly clear is that, as populations of introduced species expanded, those of large-bodied endemic species dramatically declined. Bones of introduced species are found in the south and southwest at archeological settlement sites such as Andranosoa and Rezoky and at paleontological sites (lacking human artifacts) such as Lamboharana, Ambolisatra, and Beloha Anavoha as well as Tsimanampesotse. They are found at sites in the spiny thicket and succulent woodland, along the coast and much further inland. And importantly, the rapid increase in the populations of domesticated animals occurred in the southwest precisely when we have documented a shift in hydroclimate to more mesic conditions. We see this sequence of events in the region of Tsimanampesotse and Antsirafaly combined – i.e., with 900 yr BP representing the cut-point for a dramatic change in faunal composition. Now-extinct endemic large vertebrates occur prior to 900 yr BP, and introduced vertebrates appear afterward.

The extinction dynamic in the spiny thicket differed from that in the dry deciduous forest in northwestern Madagascar and likely in other parts of Madagascar. Faina et al. (in press) compared the trajectories of large-vertebrate decline in these two ecoregions; they found that the decline began earlier in the spiny thicket, in concert with drought conditions, whereas it began a century later in the dry deciduous forest, in concert with anthropogenic habitat transformation. In effect, the large-bodied vertebrate species of the southwest were already vulnerable to extinction by the time agropastoralism spread into the region.

There is a growing literature that addresses the reasons why agropastoralists can pose greater danger to endemic species than hunter/foragers. Perhaps counterintuitively, wild-animal hunting is often less sustainable in herder/farmer communities than in hunter/forager communities (Robinson and Bennett, 2000). Extinction of slow-breeding, large-bodied endemic species is more likely in the former because they rely on alternative food sources including cultivated plants and fast-breeding domesticated animals (Belovsky, 1988; Winterhalder, 2001). People are not likely to drive to extinction species on which they depend for sustenance; supplemental sources of food are more expendable.

Modern vertebrate populations may provide some clues regarding the impacts of severe climate events and mechanisms of local vertebrate population recovery. When critical resources decline or disappear at any single locality, populations suffer, but they usually recover (Gould et al., 1999; Ratsimbazafy et al., 2002). The initial stimulus may involve a climate event, but ultimately, extinction occurs because normal population recovery mechanisms are disrupted, particularly for species that have dietary or locomotor specializations. Agropastoralists can disrupt normal population recovery mechanisms by cutting typical dispersal pathways, modifying habitats, competing directly with vulnerable endemic species for resources such as fresh water, competing indirectly by introducing other competitors, and indeed killing endemic wild animals for food or because the latter may pose threats to domesticated animals or crops (e.g., Borgerson, 2016; Borgerson et al., 2019). When humans are present, waterholes that formerly provided sanctuary can pose new risks (Janzen, 1983). Finally, the decline of endemic keystone large-bodied herbivore species (whether from climate change or human impacts) can affect ecosystem functionality, further exacerbating environmental degradation and contributing to the simultaneous disappearance of different vertebrate species. In Madagascar, this happened within a narrow temporal band, regardless of climate conditions (Burney et al., 2003; Hansford et al., 2021).

CONCLUSION

Returning to the prior analyses of MacPhee (1986) and Goodman and Jungers (2014), we see elements of each that can be supported. Goodman and Jungers (2014) were likely correct in highlighting a role for aridification in driving periodic local extirpations, independent of human activities, in Madagascar's southwest. Our data do not support their hypothesis, however, that the climate of the southwest was wetter and less seasonal than it is now until around 1,000 years ago. MacPhee (1986) was correct in asserting that southwestern Madagascar may have been as dry as it is today when now-extinct megaherbivores thrived there. Indeed, our stalagmite growth data demonstrate that, between 3,000 and 2,000 years ago, Tsimanampesotse was drier than it is today. MacPhee was also likely correct that wet microhabitats were key to the local survival of species dependent on wetter conditions in the past. Long-term survival would have depended on the existence of dispersal pathways that allowed populations to track these critical resources.

The late first millenium CE drought resulted in a regional decline in the populations of large-bodied, drought-resistant vertebrates in the southwest but likely did not drive these species to extinction. Indeed, it may have temporarily helped to isolate them from expanding agropastoralist populations. With increasing rainfall, albeit limited, agropastoralists spread into localities that they previously considered too dry for habitation. Thus, ironically, one can make the argument that the *amelioration* of climate contributed to the rapid demise of the large-bodied endemic vertebrates in the southwest. The return to mesic conditions undoubtedly expedited the spread of agropastoralists into the region and prevented the recovery of Madagascar's large endemic vertebrate species.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

LG, BC, KM, SB, NS, and ZK designed the research. LG, BC, KM, SB, NS, ZK, LR, JA, PF, SG, IG, JH, EH, CK, ML, DM, VP, NR, HR, ST, and NV performed the analyses. LG, BC, KM, ZK, LR, JA, MB, RD, PF, SG, IG, JH, EH, PL, ML, NR, HR, KS, ST, and PW aided fossil collection and/or identification. LG, BC, SB, NS, and ZK wrote the manuscript. All the authors edited 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.2021.742203/full#supplementary-material

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Influence of Late Holocene Climate Change and Human Land Use on Terrestrial and Aquatic Ecosystems in Southwest Madagascar

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Madagascar's biota underwent substantial change following human colonization of the island in the Late Holocene. The timing of human arrival and its role in the extinction of megafauna have received considerable attention. However, the impacts of human activities on regional ecosystems remain poorly studied. Here, we focus on reconstructing changes in the composition of terrestrial and aquatic ecosystems to evaluate the impact of human land use and climate variability. We conducted a paleoenvironmental study, using a sediment record that spans the last ∼1,145 years, collected from a lakebed in the Namonte Basin of southwest Madagascar. We examined physical (X-ray fluorescence and stratigraphy) and biotic indicators (pollen, diatoms and micro- and macro-charcoal particles) to infer terrestrial and aquatic ecosystem change. The fossil pollen data indicate that composition of grasslands and dry deciduous forest in the region remained relatively stable during an arid event associated with northward displacement of the Intertropical Convergence Zone (ITCZ) between ∼1,145 and 555 calibrated calendar years before present (cal yr BP). Charcoal particles indicate that widespread fires occurred in the region, resulting from a combination of climate drivers and human agency during the entire span covered by the paleorecord. Following settlement by pastoral communities and the disappearance of endemic megafauna ∼1,000 cal yr BP, grasslands expanded and the abundance of trees that rely on large animals for seed dispersal gradually declined. A reduction in the abundance of pollen taxa characteristic of dry forest coincided with an abrupt increase in charcoal particles between ∼230 and 35 cal yr BP, when agro-pastoral communities immigrated into the region. Deforestation and soil erosion, indicated by a relatively rapid sedimentation rate and high K/Zr and Fe/Zr, intensified between 180 and 70 cal yr BP and caused a consequent increase in lake turbidity, resulting in more rapid turnover of the aquatic diatom community. Land use and ongoing climate change have continued to transform local terrestrial and freshwater ecosystems during the last ∼70 years. The current composition of terrestrial and aquatic ecosystems reflects the legacy of extinction of native biota, invasion of exotic species, and diminished use of traditional land management practices.

Keywords: agro-pastoralists, environmental change, dry deciduous forest, aquatic ecosystems, herbivore introductions, socio-ecological systems

INTRODUCTION

Remote islands of the southwestern Indian Ocean were among the last regions worldwide to be permanently colonized by humans. Human settlement and land use practices, which invariably involve non-native plants and animals, may contribute to loss of endemic biota and transformation of native ecosystems (Douglass and Zinke, 2015; Wang et al., 2019). On Madagascar, people hunted endemic fauna (Perez et al., 2005; Anderson et al., 2018), introduced domesticated animals and plants (Crowther et al., 2016; Hixon et al., 2021a), and promoted the expansion of grasslands (Burney, 1987b; Burns et al., 2016). The timing of human arrival and contribution of hunting to faunal extinctions on Madagascar have received considerable attention (Crowley, 2010; Feranec et al., 2011; Douglass et al., 2019a). The direct and indirect impacts of anthropogenic activities on the composition and function of terrestrial and aquatic ecosystems are a subject of ongoing research. Only recently have studies begun to focus on the long-term consequences of human activities on Madagascar's ecosystems (Virah-Sawmy et al., 2010, 2016; Burns et al., 2016). Integration of paleoecological, archaeological, and historical information provides a long-term perspective to assess the timing and socio-ecological consequences of human disturbance on such insular ecosystems (Douglass and Cooper, 2020).

The timing of the peopling of Madagascar has been widely debated (Crowley, 2010; Anderson et al., 2018; Hansford et al., 2018; Lawler, 2018; Douglass et al., 2019a; Mitchell, 2020; Hixon et al., 2021a). However, a growing body of archaeological research suggests that foraging communities had settled the island permanently by ∼1,500 cal yr BP, several centuries before a pulse of faunal extinctions that included giant lemurs, pygmy hippos, giant tortoises, and elephant birds (Douglass and Zinke, 2015; Douglass et al., 2019a). Human subsistence strategies later diversified, as evidenced by the coincident spread of southeast Asian crops and pastoralism, beginning by around 1,000 years ago (Crowther et al., 2016; Godfrey and Crowley, 2016; Hixon et al., 2021a). The emergence of agro-pastoral economies involved the introduction of animals such as zebu cattle (*Bos taurus indicus*), sheep (*Ovis aries*), and goats (*Capra hircus*), as well as cultigens like rice, greater yam, coconut, and Indian saffron during the last millennium (Burney et al., 2004; Kull et al., 2012; Beaujard, 2017).

Contemporary Malagasy people rely on a range of ecosystems. People typically use grasslands and succulent woodlands to fodder livestock and exploit forests for hunting and as sources of firewood, construction materials, and edible and medicinal plants (Bloesch, 1999; Kaufmann and Tsirahamba, 2006; Kull and Laris, 2009; Fritz-Vietta et al., 2017). Lakes and wetlands also constitute important sources of animal protein and drinking water, and anthropogenic disturbances have degraded these ecosystems and threatened aquatic biodiversity (Bamford et al., 2017). Although fire is the leading cause of past forest degradation and loss (Kull, 2000), paleoenvironmental data suggest that wildfires and fire-adapted vegetation were common even before the expansion of human populations on the island (Virah-Sawmy, 2009; Godfrey and Crowley, 2016). Today, Madagascar's biodiversity is increasingly threatened by intensifying land use practices (*e.g.,* deforestation, charcoal production, shifting cultivation, and industrial mining) and the climate crisis (Spencer et al., 2005; Hannah et al., 2008; Goodman et al., 2018). Interactions between land use and climate change have important socio-ecological impacts, including biodiversity loss, ecosystem degradation, pollution, disruption of traditional lifeways, and conflicts over natural resources (Scott et al., 2006; Virah-Sawmy et al., 2009; Harvey et al., 2014; Douglass and Cooper, 2020).

Climate change and human activities have also shaped Madagascar's vegetation. Paleoecological reconstructions have shown, for example, that *Erica-Myrica* heath/grasslands replaced *Uapaca* woodlands during the last 950 years in coastal southeast Madagascar due to marine surges, reduced precipitation, and anthropogenic fires (Virah-Sawmy et al., 2009). In contrast, the vegetation around Andolonomby/Ambolisatra in the coastal southwest transitioned from a palm-savanna to depauperate, xerophytic bush ∼700 cal yr BP, during a period of intensified burning and a possible drought event (Virah-Sawmy et al., 2016). Multiple studies have shown that (1) northwest Madagascar was wetter and relatively forested during the Early and Middle Holocene, (2) grasslands expanded during the onset of drier conditions ∼1,000 years ago, and (3) human activities promoted the establishment of fire-adapted trees and ruderal herbs ∼500 years ago (Burney, 1987a,b; Matsumoto and Burney, 1994; Burney et al., 1997; Crowley and Samonds, 2013; Burns et al., 2016; Wang et al., 2019).

We assessed the long-term consequences of climate variability and anthropogenic impacts on the composition of terrestrial vegetation and aquatic ecosystems in southwest Madagascar. Specifically, we used a 1,145-year sediment record from a lake in the Namonte Basin to evaluate responses in aquatic and terrestrial ecosystems to Late Holocene drought, the spread of pastoralism, the extinction of endemic fauna, and recent intensification of forest clearance. We examined physical (X-ray fluorescence and stratigraphy) and biotic indicators (pollen, diatoms and micro- and macro-charcoal particles) in the sediment record to explore past terrestrial and aquatic ecosystem change. Integration of paleoecological, archaeological, and historical data is crucial for developing holistic perspectives on the timing and socio-ecological consequences of human land use in insular ecosystems (Braje et al., 2017; Douglass et al., 2019b). The following research questions were tested in this study: (a) Did increasing fire frequency during dry/wet periods induce changes in vegetation composition? (b) How did excess detrital and organic matter, produced by anthropogenic deforestation and forest burning, affect the aquatic ecosystem? and c) What were the impacts of extinction of large seed dispersers on vegetation?

MATERIALS AND METHODS

Study Area

The Namonte Basin (S 22.12513°, E 43.40634°; ∼30 m asl; **Figure 1A**) is comprised of a system of seasonal and permanent lakes and floodplains in the lowlands of the Mangoky-Ihotry complex in southwest Madagascar. The main chain of lake basins has an area of ∼13 km^2 and a catchment area that is ∼2,000 km^2. However, these lake basins are shallow (maximum water depth up to ∼1.4 m deep in September, 2017), and their areas fluctuate considerably with interannual variation in rainfall. For example, during a 1997–98 drought (100 mm total annual precipitation), the lakes approached desiccation, but during a wet interval in 1999–2000 (1,500 mm annual precipitation), the lakes expanded into the surrounding forest (Tucker, 2020). In 2017, the lake was fresh (conductivity of 261 μS/cm) and mesotrophic. The modern climate is semi-arid, with a mean temperature of 23°C and annual precipitation < 400 mm, which falls mostly during the austral summer (November – March) (Dewar and Richard, 2007). The sandy substrate of Quaternary alluvium in this area includes both active and vegetated dunes.

The landscape is generally characterized by a mosaic of wooded grasslands, dry deciduous and riverine forests, and mangroves that grow near estuaries. The dry deciduous forest is dominated by several plant species, including the endemic family Didiereaceae, the fony baobab tree (*Adansonia fony*), several species of *Euphorbia*, and *Pachypodium geayi* (Grubb, 2003; Aronson et al., 2018). The region is also habitat for several endemic primates, including the ring-tailed lemur *(Lemur catta),* Verreaux's sifaka (*Propithecus verreauxi*), and the reddish-gray mouse lemur (*Microcebus griseorufus*). Other endemic species with restricted distributions include Grandidier's mongoose (*Galidictis grandidieri*) and the Madagascar radiated tortoise (*Geochelone radiata*) (Scott et al., 2006). The Mikea Forest is part of a vegetation mosaic in southwest Madagascar that refers specifically to the dry forest between the urban centers of Toliara and Morombe (Seddon et al., 2000). The northern portion of this forest surrounds the Namonte Basin and has been part of the Mikea National Park since 2012.

Mikea people descend from herding clans settled in the area during the 17th century to escape banditry and oppression by the Maroseragna and Andrevola kings (Tucker et al., 2015). In the late 19th century, the area came under French colonial control, and much of the coastal plains to the east have since been used to produce a variety of cash crops such as maize, cotton, and butterbeans (Blanc-Pamard et al., 2005). Currently, most Mikea living in the Namonte Basin reside in villages that are usually located near lake margins, where they fish, cultivate crops, and herd zebu and goats. Mikea complement their diet with a range of forest products, including wild tubers (*Dioscorea, Colocasia, Ipomoea,* and *Tacca*), honey, and wild meat (*e.g.*, birds, tortoises, tenrecs and feral cats; Tucker, 2007; Douglass and Rasolondrainy, 2021). Deforestation has intensified greatly since the 1970s, with ∼55% of the primary forest lost between 1949 and 2004 (Blanc-Pamard et al., 2005).

Sediment Sampling and Processing

In 2017, a 138-cm-long composite sediment core was retrieved in the deepest part of the Namonte basin (**Figure 1B**). A large-diameter (7 cm ID) mud-water interface piston-corer (Fisher et al., 1992) was used for the collection of upper deposits and a Colinvaux-Vohnout-type corer, modified to use clear polycarbonate core barrels (5.4 cm ID), was used for deeper deposits. Unconsolidated upper deposits were maintained in a vertical orientation and extruded in the field at 2-cm intervals. The sediment core was shipped to the University of Florida (UF), where the deeper portion was split lengthwise and photographed. Samples were then shipped to Pennsylvania State University (PSU) for X-ray fluorescence (XRF), pollen, and charcoal analysis, and to the University of Regina (UR) for diatom analysis. The stratigraphy of the sediment core was characterized based on field observations and lab-acquired digital photographs. Elemental data were produced from XRF scans at 3-cm core intervals, using an Olympus DeltaX model X-ray fluorescence core scanner and Geotek MSCL 7.9 Multi-sensor Core Scanner Innoux 1776 at PSU.

A core chronology was constructed using ^{14}C accelerator mass spectrometry (AMS) dates on five samples of terrestrial plant material (*i.e.,* seeds, charcoal fragments and fragments of plant remains). Samples were pretreated following the protocol of Kennett et al. (2014) and dated at the Radiocarbon Laboratory at PSU. Radiocarbon dates were calibrated using the Southern Hemisphere calibration curve SHCAL20 (Hogg et al., 2020). For the topmost (recent) section of the core, ^{14}C ages were calibrated using the post-bomb (SH 1-2 zone) dataset (Hua et al., 2013). Two dates, PSUAMS-6324 and PSUAMS-6325, were excluded from the age-depth model, as they contain modern (post-bomb) carbon and likely indicate translocation of recent plant material to greater depth during the coring process. Radiocarbon dates were used to generate a Bayesian age-depth model with the rbacon package (v. 2 3.3) for R (Blaauw and Christen, 2011), using default parameters [accumulation rate (acc.mean) = 10 year cm^{-1}, shape distribution of accumulation rate (acc.shape) = 1.5, memory mean (mem.mean) = 0.7, memory strength (mem.strength) = 4] to the full depth of the core. The model was built under the assumption that the top of the sequence corresponds to the year of core retrieval (2017 CE).

The sediment core was subsampled for pollen and spores, microcharcoal, and diatom analysis at 4-cm intervals. Pollen, spores, and microscopic charcoal sample preparation followed standard protocols, including treatment with hydrofluoric acid and acetolysis (Faegri and Iversen, 1989). A tablet of exotic *Lycopodium* spores was added to each sample to

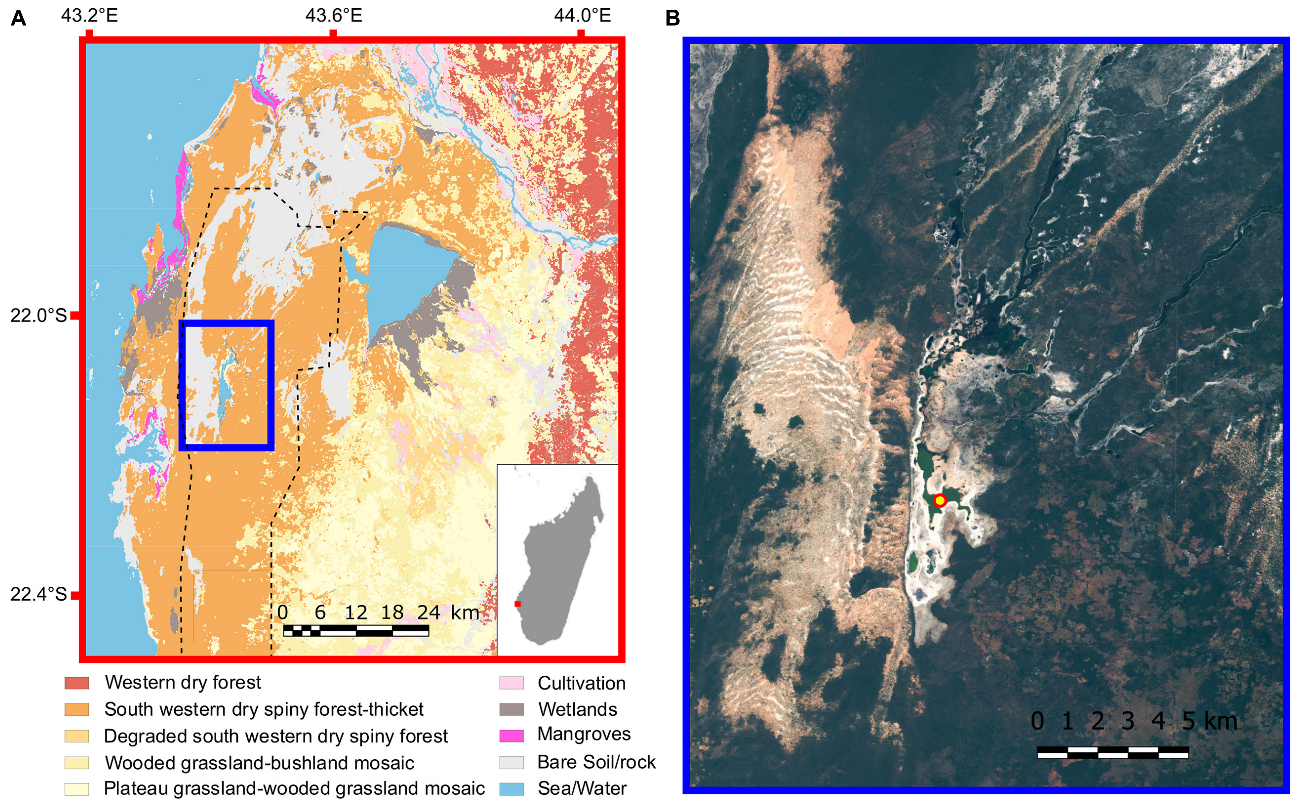

FIGURE 1 | (A) Vegetation map showing the Namonte Basin, circumscribed by the blue rectangle. Inset shows the island of Madagascar, with the red dot in the southwest indicating the study area location. The vegetation map was modified from the Madagascar Vegetation Mapping Project (www.vegmad.org). Extent of the Mikea National Park is marked with a dashed line and includes primarily dry forest (orange). **(B)** Sentinel 2 satellite image of the outlined blue area in **(A)**, showing the region of Namonte, SW Madagascar. The coring site is marked with a red and yellow circle in a portion of the Namonte Basin known as Andramby.

calculate pollen concentration and pollen influx. A total of 36 samples were analyzed for pollen and fungal spores. In each sample, we identified at least 300 pollen grains if possible, excluding aquatic taxa. Pollen grains and fungal spores were identified using the reference collection at PSU and palynological atlases and keys (Gosling et al., 2013; Schüler and Hemp, 2016). To assess temporal changes in pollen taxa that may be correlated with megafaunal extinctions, we assigned a seed dispersal mechanism to each terrestrial pollen taxon as defined by Albert-Daviaud et al. (2020). We grouped plant taxa based on their mode of seed dispersal (*e.g.,* autochorous = self-dispersed by dehiscent fruits, anemochorous = wind-dispersed, or zoochorous = animal-dispersed) (Knowles et al., 1995).

Microcharcoal (15–150 μm) concentrations were determined in the same samples used for pollen analysis. Microcharcoal particles and *Lycopodium* spores were quantified by randomly selecting 200 fields of view in each sample under 40× magnification. Each particle was characterized as woody or herbaceous based on morphology, including presence of stomata, epidermal cells, and an elongated shape (Walsh et al., 2014). Microcharcoal particles are presented as microcharcoal influx, calculated using charcoal concentrations and bulk sedimentation rates derived from the age-depth model.

For macroscopic charcoal analysis from 30 cm to the bottom of the core, continuous sediment subsamples (0.5 cm^3) were retrieved. Samples were processed following the protocol of Mooney and Radford (2001). The remaining fraction was photographed using a digital camera attached to an Olympus microscope. ImageJ software[1] was used to process sample images, quantify the total number of charcoal particles, and estimate total area of each charcoal particle (Halsall et al., 2018). Macrocharcoal was expressed as macrocharcoal influx (particles cm^{-2} yr^{-1}) and macrocharcoal area (mm^2 cm^{-2} yr^{-1}) based on concentration, total area of charcoal particles, and bulk sediment accumulation rate at specific depths.

For diatom analysis, 0.2–0.5 g of dry sediment was processed following the protocol of Battarbee (1986). Permanent slides were mounted in Zrax (RI ~1.7 +). At least 400 valves in each sample were counted. Diatom species were grouped according to ecological guilds and motility into High Profile (HP), High Profile Planktonic (HPP), Low Profile (LP) and Motile Profile (MP), following Passy (2007) and Berthon et al. (2011) (**Supplementary Material 4**). Although most of the studies on diatom functional groups and disturbance have been conducted in rivers and streams, the multi-proxy analyses

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[1] https://imagej.nih.gov/ij/index.html

presented in Velez et al. (2021) showed that they can be used to identify anthropogenic disturbances, including drainage and deforestation, with the consequent changes in water level, water transparency and macrophyte cover. These guilds reflect the forms and life habits of diatoms that are adaptations to particular physical (currents, turbidity) and chemical (nutrients) conditions (Leira et al., 2015; Algarte et al., 2016). Large and colonial forms are included in the HP, short or low-stature species are included in LP, and MP include species that can move. Motile species are very useful to infer physical disturbance such as an increase in water turbidity, shading and burial from excess sediment input (Jones et al., 2014).

Data Analysis

Total pollen sum, excluding aquatics, and total diatom sum were used to calculate the relative abundances of each taxon in each group, respectively, which are presented as percentages. Pollen and diatom diagrams were created using Tilia software (Grimm, 1991). Zones representing thresholds of change in pollen and diatom composition were identified using stratigraphically constrained incremental sum of square clustering (CONISS) (Grimm, 1987). To assess changes in the abundance of plant taxa assigned to a specific seed dispersal mechanism, pollen percentages were normalized by applying a min-max and box-cox transformation and rescaled to z-scores to reduce skewness caused by high variability among samples. Elemental profiles from XRF data were normalized to Zr, because measures of other lithogenic elements Al and Ti were discontinuous due to low abundance. A Principal Component Analysis (PCA) was used to assess changes in XRF data throughout the stratigraphic section. All statistical analyses were performed in R version 3.5.1 (R Core Team, 2013).

RESULTS

Chronology, Lithology and Geochemistry

The sediment core from Namonte is characterized by dark silt (130–0 cm) that overlies primarily medium quartz sand at the base (138–131 cm). The chronology was established based on three AMS radiocarbon ages determined on plant remains. These dates indicate that the sediment record spans ∼1,145 years (**Table 1** and **Figure 2**). Two radiocarbon ages (PSUAMS-6326 and PSUAMS-3520) have relatively wide calibrated 2σ ranges (∼280 and 180 years, respectively), which contributes to high uncertainty in the modeled ages of the lower core section. The distribution of AMS ^{14}C dates with depth suggests two stages of deposition. Continuous deposition occurred from the base of the core at 130 cm to 85 cm depth (0.22 cm yr^{-1} on average between ∼1,145 and 270 cal yr BP). Following this, there was a period of more rapid sedimentation (0.55 cm yr^{-1} on average from ∼270 cal yr BP to present). However, given that the estimated sedimentation rate in the upper section of the core was based on only two AMS dates, we interpreted changes during the recent phase of the chronology with caution.

The evidence suggests no obvious major depositional hiatuses or sediment mixing in the sediment core. The inference is based on observations that (1) the sediment lithology of the core is relatively homogenous throughout the sediment core; (2) pollen preservation is good, as less than 5% broken or shriveled pollen grains were observed in each sample; (3) seeds of *Carex* and other Cyperaceae were common in the core and diatoms were found in all samples, suggesting that the coring site has been continuously covered with water.

Elemental analysis of the Namonte sediment core documents differences between sediments from 129 to 60 cm depth and those from the overlying section (**Supplementary Material 1**). The lower core section possesses relatively abundant Ni and Cd, whereas the overlying section (60–33 cm depth) includes more Ca, K, Cl, Fe, and Zr. The first two principal components of a PCA conducted on the correlation matrix of all elemental profiles explain nearly 65% of the variance and highlight the distinct geochemical compositions of the lower section (129–60 cm) and upper sections (60–33 cm) of the core (**Supplementary Materials 1, 2**). PC1 (46.4% variance explained) values generally increase up-core, despite peaks in S that occur at 91–81 cm and 59–39 cm. The change in sign of PC1 values up-core at ∼60 cm depth coincides with decreases in Ca/Zr and Si/Zr values and increases in Fe/Zr and K/Zr (**Figure 3**). These measures are sensitive to authigenic carbonate precipitation, deposition of biogenic silica, and weathering regime. Specifically, relatively more Ca deposition may have been associated with carbonate precipitation during dry conditions and low lake levels (Haberzettl et al., 2007; Kylander et al., 2011), or associated with higher primary production. Increased runoff could deposit detrital calcite and increase Ca/Zr values, but the alluvium around Namonte is almost entirely quartz sand. Deposition of biogenic silica, with only traces of lithogenic elements such as Zr, can drive increases in Si/Zr values (Agnihotri et al., 2008; Dickson et al., 2010). Here, we consider that changes in Si/Zr are driven mainly by changes in diatom productivity, given that the diatom analysis revealed good diatom preservation and a concomitant shift in the diatom assemblage over time. Mobile elements such as K, and sometimes Fe, are more likely to accumulate and drive high K/Zr and Fe/Zr values during times of relatively greater physical, as opposed to chemical weathering (Piva et al., 2008; Kylander et al., 2011; Aufgebauer et al., 2012). Given that the lake is shallow, we suspect that it has been consistently well-oxygenated and that changes in redox conditions have likely contributed very little to variation in Fe/Zr values.

Microfossil Analysis

Pollen and Microcharcoal

We identified 78 pollen taxa in the sediment core from Namonte. Pollen preservation was good as each sample contained less than 5% damaged or shriveled pollen grains. Pollen concentration was variable throughout the core (mean = 41,800 grains cm^{-3}), likely attributable to depth-associated variability in overall pollen preservation and/or bulk sedimentation rate (Zhao et al., 2009). Cluster analysis identified five major pollen zones (P1, P-2a and 2b, P-3, P-4) within the sequence (**Figure 4**). Poaceae was the most abundant pollen type through the entire record, followed by *Euphorbia* and *Ephedra*, suggesting that grasslands and the

TABLE 1 | AMS Radiocarbon dates used to construct the age-depth model for Namonte core 22-IX-17-1B, southwest Madagascar.

Lab code	Sample ID	Depth (cm)	Material	^{14}C age (BP)	Error	Calibrated age (BP)
*PSUAMS-6324	NA-30	55	Seeds and unidentified plant remains	-20	20	-6
*PSUAMS-6325	NA-33	70	Charcoal and unidentified plant remains	-295	20	-7
PSUAMS-6326	NA-34	85	Seeds and unidentified plant remains	170	20	133
PSUAMS-6327	NA-35	101	Wood	495	25	506
PSUAMS-3520	NA-1	128	Twig	1300	20	1,197

**Dates excluded from the age-depth model.*

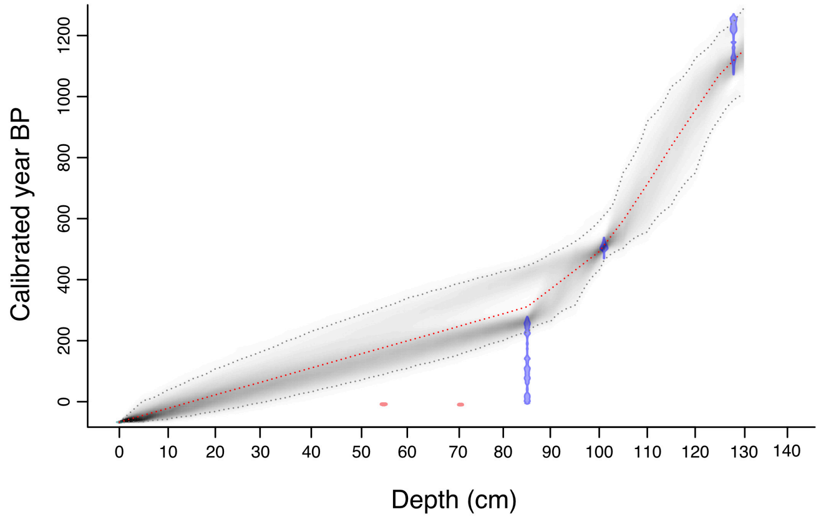

FIGURE 2 | Age-depth model from Namonte sediment core 22-IX-17-1B, southwest Madagascar. All ^{14}C dates pictured in blue were calibrated with SHCAL20 (Hogg et al., 2020), the gray line represents the 95% confidence interval, and the red dotted line is the best-fit model based on a weighted mean. ^{14}C dates indicated in red were excluded from the age-depth model. The sediment surface (-67 cal yr BP) was included in the Bayesian modeling.

dry deciduous forest dominated the landscape for at least the last ~1,145 years (**Figure 4** and **Table 2**). Taxa characteristic of drylands (*Ephedra*, *Uapaca*, Anacardiaceae) were relatively common between ~1,145 and 200 cal yr BP, followed by a transition period, between ~190 and 20 cal yr BP. This transition was characterized by a decline in *Ephedra* and *Euphorbia* and sporadic appearance of Arecaceae, *Ficus,* Ericaceae, *Pandanus,* and *Syzygium*. Most recent zone P-4 is differentiated by a dramatic decrease in abundance of *Ephedra* and an increase in *Prosopis*, an indicator of soil disturbance.

Charcoal particles were found in all the samples analyzed throughout the core, and numerous charcoal peaks were observed, indicating past fire activity (**Figure 5**). A macrocharcoal peak was recorded ~1,040 cal yr BP and a second peak of macrocharcoal area occurred between ~470 and 400 cal yr BP. Between ~240 and 125 cal yr BP, both macrocharcoal influx and macrocharcoal area increased abruptly, followed by sharp decreases between 120 and 70 cal yr BP.

Our analyses also revealed differential trends regarding relative abundances of taxa with distinct seed-dispersal pathways throughout the core. Pollen of plants with wind-dispersed seeds (anemochory) dominate the pollen assemblage and tend to increase over time (**Figure 6**). In contrast, pollen of taxa with seeds dispersed by animals (zoochory) fluctuate over time. Pollen from plant taxa dispersed only by lemurs show a relative decrease in more recent pollen zones P-3 and P-4, in comparison to earlier zones P-1, P-2a, and P-2b. Pollen of plants with seeds dispersed by lemurs and other animals show a relative increase in abundance during pollen P-2a, decreases in P-2a and P-3, and a slight increase in P-4.

Diatom Analysis

We identified 62 diatom species and grouped them according to functional groups. We identified three main diatom zones (D1-3), with zone D1 divided into sub-zones D1-a and D1-b (**Figure 7**) based on the cluster analysis, as described in **Table 3**.

DISCUSSION

This multi-proxy environmental reconstruction enabled us to assess the role of Late Holocene climate change, human occupation, and megafaunal extinctions on terrestrial and aquatic ecosystems of southwest Madagascar (**Figure 8**). The pollen record shows that grasslands and dry deciduous forests dominated the vegetation for at least the last ~1,145 years and that a major turnover in the plant community took place between ~195 and 20 cal yr BP, when grasslands expanded

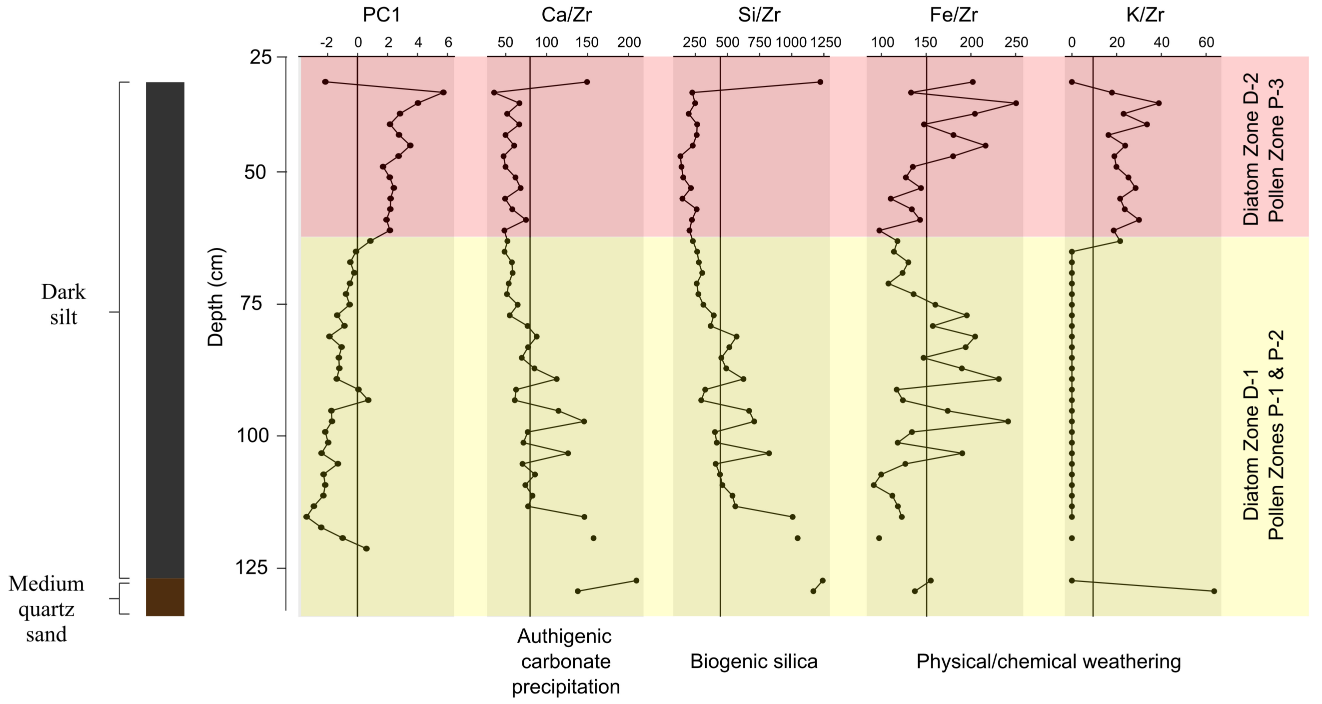

FIGURE 3 | Depth versus XRF-PC1 and XRF-derived element abundances normalized to Zr, from the Namonte sediment core, southwest Madagascar. Mean values are indicated by vertical lines and pollen and diatom zones are marked by different colors.

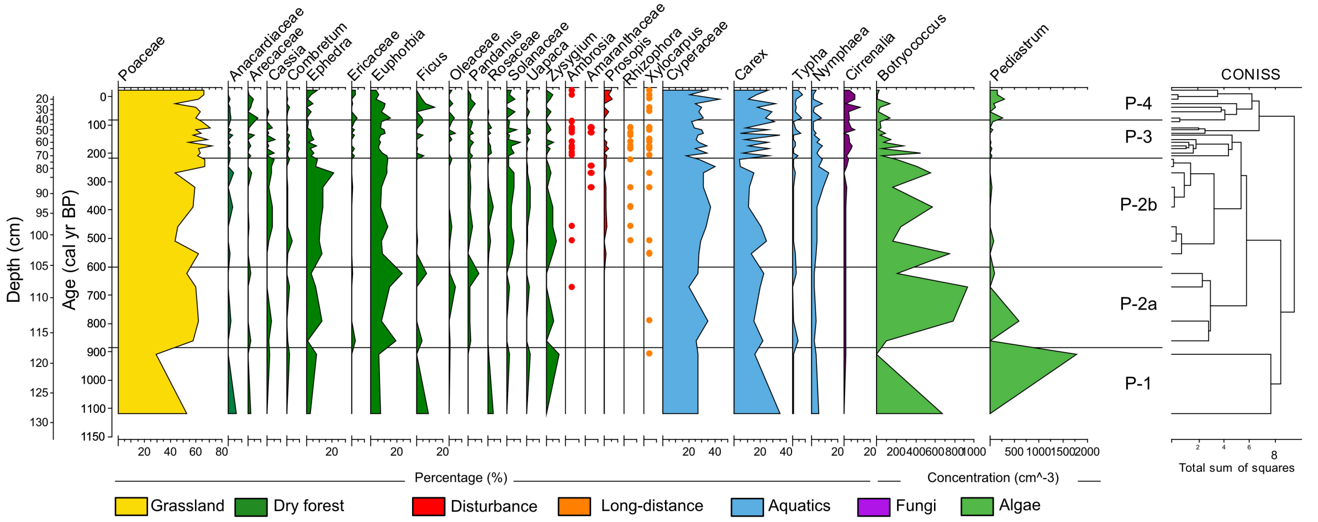

FIGURE 4 | Pollen relative abundance and algae concentration versus depth and calibrated radiocarbon age in the sediment core from Namonte, southwest Madagascar. CONISS analysis on the right side of the diagram shows the four major pollen zones, with zone P-2 divided into two subzones.

and elements of the dry deciduous forest declined. The decline of forest taxa (*Euphorbia* and *Ephedra*) was accompanied by a relative increase in fire-resistant vegetation (*Prosopis* and Ericaceae), along with plants that thrive in disturbed soils (Amaranthaceae and *Ambrosia*) (**Supplementary Material 3**). The last ∼60 years were characterized by continued degradation of regional dry forests.

Alterations to the aquatic environment are reflected by changes in the diatom assemblage. Between ∼270 and 70 cal yr BP, HP species were replaced by MP taxa, and *C. meneghiniana* became more abundant. This turnover in the composition of the diatom community suggests an increase in disturbance, likely associated with increasing water turbidity resulting from greater influx of soil particles from the watershed, increased

TABLE 2 | Zones of Namonte pollen record. Zonation was based on the CONISS analysis.

Zone	Stratigraphic position	Age range (cal yr BP)	Dominant taxa	Microcharcoal influx	Macrocharcoal influx	Description
P-4	20 – 12 cm	~18 cal yr BP – present	Poaceae (64%). *Carex* (17%) and other Cyperaceae (73%). *Botryococcus* (1,317 cm^{-3}).	Woody = 429,310 particles cm^{-2} yr^{-1}, herbaceous = 14,848 particles cm^{-2} yr^{-1}	Not recovered	Grass pollen remains dominant. *Euphorbia* pollen declines in abundance. Sedges pollen remain relatively stable. *Nymphaea* pollen appears sporadically. *Pediastrum* (200 cm^{-3}) concentration increases. *Botryococcus* concentration remains low. Microcharcoal influx decreases.
P-3	63.5 – 24 cm	195 – 35 cal yr BP	Poaceae (60%). *Carex* (22%) and other Cyperaceae (27%).	Woody = 2,586,854 particles cm^{-2} yr^{-1}, herbaceous = 249,975 particles cm^{-2} yr^{-1}	Influx = 106 particles cm^{-2} yr^{-1}, area = 204 mm^2 cm^{-2} yr^{-1}	Poaceae pollen remains dominant, while *Euphorbia* pollen declines. Pollen from Arecaceae, *Ficus*, *Combretum*, *Pandanus*, and Solanaceae increase. *Ambrosia*, Amaranthaceae, and *Prosopis* pollen are common. Sedges pollen increase, while *Nymphaea* pollen decreases. *Botryococcus* concentration decrease relatively and fungal spores of *Cirrenalia* increase slightly. Large increase in microcharcoal influx. Macrocharcoal influx and area decline sharply.
P-2b	103.5 – 63.5 cm	~545 – 195 cal yr BP	Poaceae (58%) and *Euphorbia* (9%). *Carex* (14%) and other Cyperaceae (30%). *Botryococcus* (28,623 cm^{-3})	Woody = 1,142,554 particles cm^{-2} yr^{-1}, herbaceous = 106,019 particles cm^{-2} yr^{-1}	Influx = 776 particles cm^{-2} yr^{-1}, area = 736 mm^2 cm^{-2} yr^{-1}	*Ephedra* pollen declines toward the end of the pollen zone. Several pollen taxa (Anacardiaceae, *Cassia*, and *Pandanus*) exhibit peaks in abundance, while Solanaceae pollen remains relatively constant (2.3%). Pollen of plant indicators of disturbance (*Ambrosia*, Amaranthaceae and *Prosopis*) are commonly found at low abundances (< 1%). *Botryococcus* concentration decreases and *Pediastrum* concentration becomes rare. Microcharcoal influx increases sharply. Macrocharcoal influx and area decrease significantly.
P-2a	118.5 – 103.5 cm	~915 – 545 cal yr BP	Poaceae (58%), *Euphorbia* (14%), and *Ephedra* (7%). *Carex* (19%) and other Cyperaceae (27%). *Botryococcus* (55,638 cm-3)	Woody = 162,311 particles cm^{-2} yr^{-1}, herbaceous = 26,410 particles cm^{-2} yr^{-1}	Influx = 1891 particles cm^{-2} yr^{-1}, area = 702 mm^2 cm^{-2} yr^{-1}	Pollen of other dry forest taxa (Arecaceae, *Combretum*, *Cassia*, *Pandanus,* and *Uapaca*) remains low. *Botryococcus* concentration increases, but *Pediastrum* concentration decreases. Microcharcoal influx increases. Macrocharcoal influx and area decrease slightly.
P-1	128 – 118.5 cm	~1,116 – 915 cal yr BP	Poaceae (41%), *Uapaca* (5%), *Euphorbia* (6%) and *Ephedra* (5%). Sedge pollen (*Carex*, *Uncinia*, and other Cyperaceae) (95%). *Botryococcus* and *Pediastrum* (33,574 and 891 cm^{-3}, respectively)	Woody = 309,774 particles cm^{-2} yr^{-1}, herbaceous = 18,966 particles cm^{-2} yr^{-1}	Influx = 1937 particles cm^{-2} yr^{-1}, area = 1261 mm^2 cm^{-2} yr^{-1}	Relative high percentages of pollen of Poaceae, *Uapaca*, *Euphorbia* and *Ephedra*. Microcharcoal influx is relatively high. Macrocharcoal influx and area are abundant.

organic input from cattle excreta, and/or from people, cattle, and other domestic animals resuspending sediments along the littoral zone of the lake.

Dynamics of Vegetation and Aquatic Ecosystems

The fossil pollen record shows that grasslands and dry forest were the dominant vegetation components between ~1,145 and 545 cal yr BP (Zones P-1 and P-2a), when arid climate conditions prevailed in southwest Madagascar. The pollen assemblage was characterized by the presence of Poaceae, *Euphorbia*, *Ephedra* and other native taxa such as *Cassia*, *Pandanus*, *Uapaca,* and *Syzygium*. Regional speleothem records indicate that much of this period, from ~900 to 400 cal yr BP, was characterized by successive megadrought episodes, attributed to northward shifts in the position of the Intertropical Convergence Zone (ITCZ) and changing phases of the Indian Ocean Dipole (IOD) (**Figure 8**,

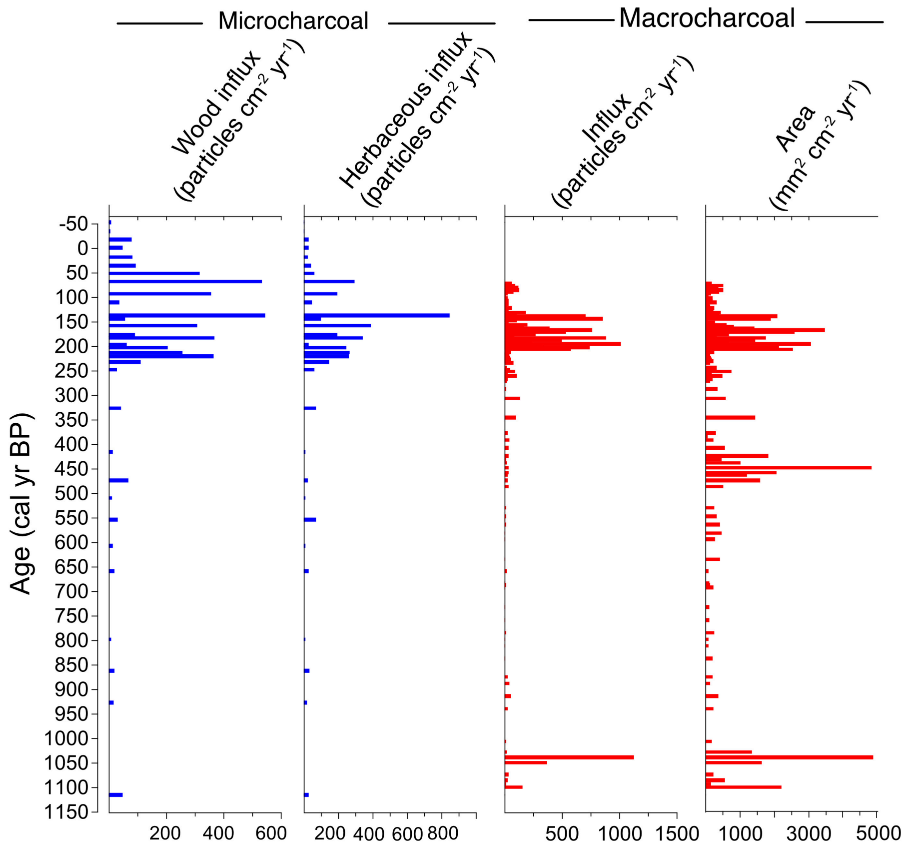

FIGURE 5 | Microcharcoal influx (particles cm^{-2} yr^{-1}), macrocharcoal influx (particles cm^{-2} yr^{-1}), and macrocharcoal area (mm^{2} cm^{-2} yr^{-1}) from the Namonte sediment core, southwest Madagascar.

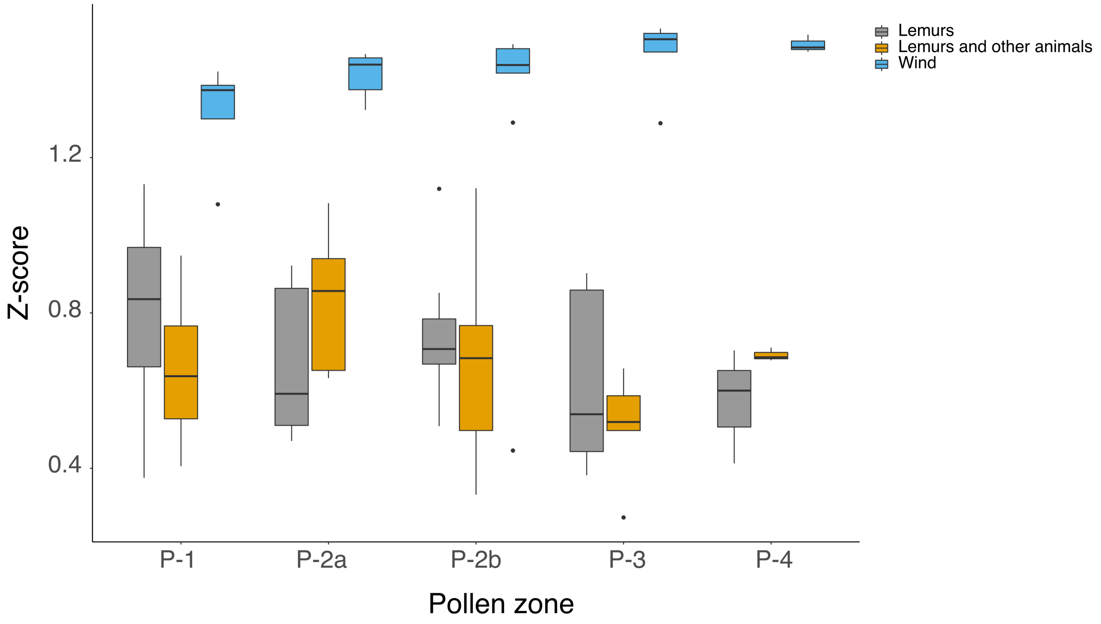

FIGURE 6 | Box-and-whisker plots of the normalized abundances (z-score) for pollen types, distinguished by seed dispersal mechanism, in the sediment core from Namonte, southwest Madagascar.

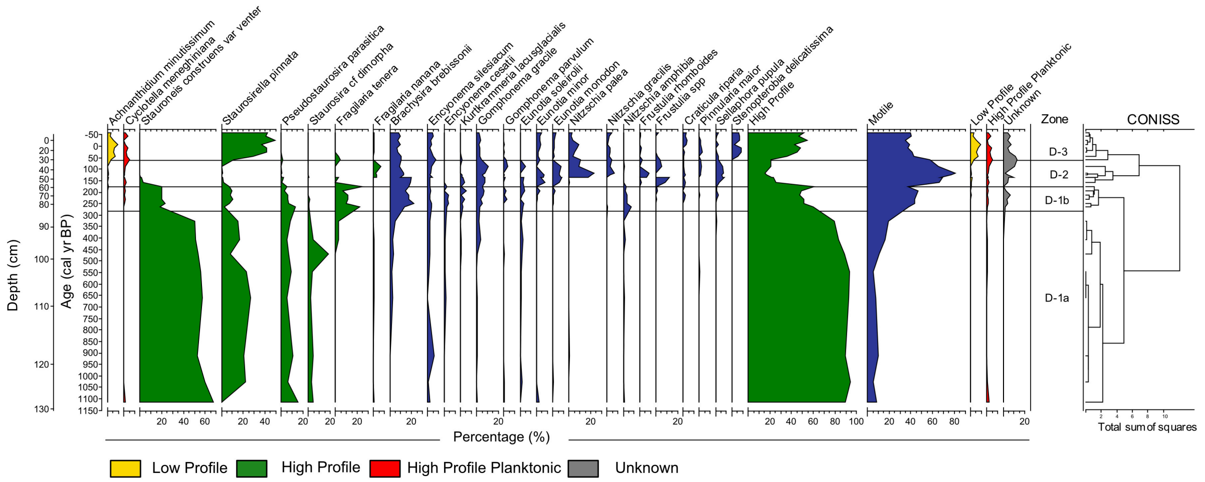

FIGURE 7 | Diatom relative abundance and functional group sums versus depth and calibrated radiocarbon age in the sediment core from Namonte, southwest Madagascar. CONISS analysis on the right side of the diagram shows the three major diatom zones, with zone D-1 divided into two subzones.

TABLE 3 | Zones of Namonte diatom record. Zonation was based on the CONISS analysis.

Zone	Stratigraphic position	Age range (cal yr BP)	Dominant taxa	Description
D-3	32–0	70 – present	*S. pinnata* increases again (30%), species from D-2 are still present but in low percentages. *Achnanthidium minutissimum* and *Cyclotella meneghiniana* increase although with small abundances.	High Profile and Motile Profile diatoms are dominant. There is an increase in Low Profile and Planktonic diatoms.
D-2	60–32	180–70	*Brachysira brebissonii* (5%); other species increase (2.5%) such as *Nitzschia palea, Sellaphora pupula, Eunotia monodon, Fragilaria nanana*	Motile species dominate over High Profile diatoms.
D-1b	85–60	~270–180	*S. construens* var *venter* (10%), *Brachysira brebissonii* (10%), *S. pinnata* (5%), *Fragilaria tenera* (<5%),	High Profile diatoms are still abundant, and Motile Profile diatoms increase.
D-1a	128–85	~1,116–270	*Staurosira construens* var *venter* (> 50%) *Staurosirella pinnata (20%), Pseudostaurosira parasitica (10%)*	Dominance of High Profile diatoms.

Virah-Sawmy et al., 2016; Li et al., 2020). Vegetation turnover was also documented during this period at other sites on the island, and it has typically been attributed to the displacement of the ITCZ. For example, near Lakes Mitsinjo and Anjohibe, grasslands expanded ~1,000 cal yr BP (Matsumoto and Burney, 1994; Crowley and Samonds, 2013), and, near Andolonomby, xerophytic bush intermixed with palm trees expanded between ~1,000 and 500 cal yr BP (Virah-Sawmy et al., 2016).

The XRF analysis of the core identified relatively high Ca/Zr values during the period between ~1,145 and 400 cal yr BP, which likely was a consequence of drier conditions that resulted in $CaCO_3$ precipitation (Haberzettl et al., 2007; Kylander et al., 2011). Aridity during the start of this interval is consistent with records from East Africa that document relatively dry conditions during the Medieval Warm Period (1000-700 cal yr BP), followed by a wetter interval coincident with the latter part of the Little Ice Age (~300 cal yr BP) (Newton et al., 2006; Tierney et al., 2013).

The diatom assemblage also indicates relatively stable shallow lacustrine conditions between ~1,145 and 270 cal yr BP (**Figure 8**, Sub-zones D-1a and D1b). Dominance of HP diatoms, especially *S. construens,* during that time suggests relatively little disturbance (Passy, 2007). Similar patterns have been observed in other records, including the one from Lake Tritrivakely, Madagascar (Gasse and Van Campo, 2001). Presence of *S. construens* var. *venter, S. pinnata, P. parasitica,* high abundance of pollen of sedges (*Carex* and other Cyperaceae) and high concentrations of the green alga *Botryococcus*, also suggest shallow and mesotrophic to eutrophic waters (**Supplementary Material 4**) (Wünnemann et al., 2010). An increase in *Nymphaea* (water lily) implies a slight increase in water levels between ~400 and 200 cal yr BP. The persistence of taxa in the paleoecological record throughout this period suggests that both terrestrial and aquatic ecosystems were resistant in the face of a relative decrease in precipitation that impacted southern Madagascar.

A major change in terrestrial plant composition took place between ~405 and 50 cal yr BP (P-2b and P-3). During that period, grasslands expanded and fire-resistant taxa (Ericaceae and *Prosopis*) and disturbance taxa (Amaranthaceae and *Ambrosia*) became more abundant. Vegetation turnover was associated with an increase in fire activity at both local and regional scales, as expressed by increases in both macro- and microcharcoal influx. This shift in vegetation and fire activity coincided with two dry periods recorded in speleothem $\delta^{18}O$ and in *Adansonia* tree-ring $\delta^{13}C$ values from ~320 to 260 cal yr BP and ~100 to 0 cal yr BP in northwest and southwest Madagascar, respectively (Scroxton et al., 2017; Razanatsoa, 2019). A similar

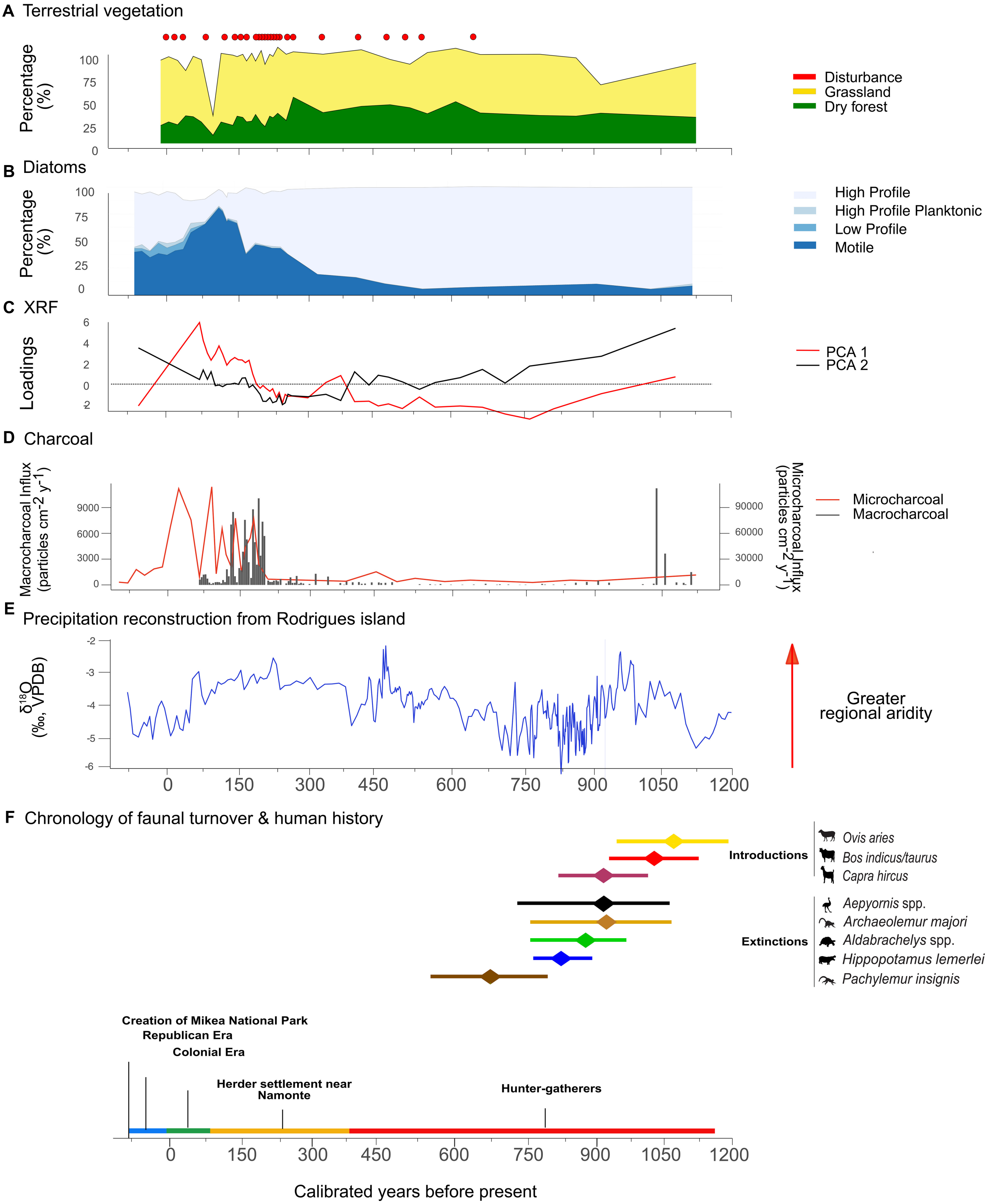

FIGURE 8 | Abbreviated paleoecological diagram for the last ~1,145 years, inferred from the Namonte core, southwest Madagascar. **(A)** Pollen percentages of disturbance taxa, grasslands, and dry forest, **(B)** percentages of diatom guilds, **(C)** PCA1 and PCA2 of XRF analysis, **(D)** Influx of macrocharcoal and microcharcoal particles, **(E)** Precipitation reconstruction from the Rodrigues Island, Indian Ocean, speleothem δ^{18}O record (Li et al., 2020), and **(F)** chronology of faunal turnover (based on classical confidence intervals from Hixon et al., 2021a) and approximate human history based on archaeological, written and oral records (Douglass et al., 2019b).

vegetation trend was recorded at Lake Longiza, where grasslands expanded in association with an abrupt increase in charcoal particles and coprophilous fungi between 580 and 30 cal yr BP (Razanatsoa et al., 2021b). These results likely indicate that vegetation turnover was a consequence of changing climate conditions that favored ignition of vegetation and spread of fires, but changes in human activities may have also driven vegetation change and a decline in dry forest extent.

Changes in terrestrial ecosystems between ∼180 and 70 cal yr BP coincided with a dramatic turnover in the freshwater diatom community of the lake (D-2). MP diatoms increased in abundance during that period, which likely indicates increased physical disturbance of the aquatic environment, possibly by higher soil erosion in the watershed and increased detrital input to the lake (Jones et al., 2014). Motile diatoms fare relatively well during physical disturbance, because they possess the ability to move away from disturbed areas (Jones et al., 2014) and compete well for nutrients in eutrophic environments (Passy, 2007). Higher sediment input, most likely from soil erosion, is supported by relatively rapid sedimentation rates (0.54 cm yr^{-1}) and high K/Zr and Fe/Zr values (Piva et al., 2008; Kylander et al., 2011; Aufgebauer et al., 2012).

The diatom assemblage also suggests increased variation in lake levels and water quality. *C. meneghiniana* increases in abundance ∼90 cal yr BP, likely associated with an increase in water turbidity (Hassan, 2013). Species of *Eunotia* and *Pinnularia* also become more common during that time, which could indicate periods of low water level (Gasse and Van Campo, 2001). The turnover in the diatom community suggests significant changes in the physical and chemical characteristics of the lake around ∼180 cal yr BP, which persisted until ∼70 cal yr BP. Relatively low Si/Zr values in sediment since ∼180 cal yr BP reflect relatively low deposition of biogenic silica, which may have resulted from a combination of declines in diatom production and increased detrital input (Agnihotri et al., 2008; Dickson et al., 2010). Further geochemical studies on the lake sediment will provide additional information regarding the factors that influence biogenic silica variation through time.

During the last ∼70 years, the dry deciduous forest declined, while grasslands expanded, and extra-local taxa increased. The presence of Amaranthaceae, *Ambrosia,* and *Prosopis* suggests degradation of dry forests associated with the establishment of species that are resistant to fire, trampling, and browsing pressures. The aquatic community of Namonte also displays evidence of considerable change during this time. Increases in abundance of colonizers *S. pinnata*, and *A. minutissimum* (Berthon et al., 2011) and LP and MP species, indicate intermittent physical disturbance, possibly associated with habitat degradation, highly variable lake levels, and environmental changes in the watershed (Passy, 2007; Berthon et al., 2011; Velez et al., 2021). High variation in the abundance of sedges and a relative increase in the abundance of *Typha* also support an inference for changes in lake level and periodic swampy conditions. These changes were previously linked to overgrazing and social conflict in the region, which forced local people into sedentism (Irwin et al., 2010). Ecosystem degradation today is likely exacerbated by aridification associated with climate change and abandonment of traditional land-management practices (Tucker et al., 2010; Virah-Sawmy et al., 2016; Razanatsoa et al., 2021a).

Fire Activity

Charcoal particles are useful proxies for past fire activity. Macrocharcoal is usually considered evidence of local fires, and microcharcoal as evidence of more distant fires (Clark and Royall, 1996). The spatial scale reflected by charcoal particle size depends on the environmental characteristics of the site, such as topography and predominant wind direction (Whitlock and Larsen, 2002). In the case of Namonte, macrocharcoal particles could originate from burning within the small lake catchment or from fires on the coast, ∼11 km to the west. Fires that burn areas > 0.02 km^2 can produce convective columns that extend > 1 km into the air and are capable of transporting macrocharcoal as much as ∼10 km (Clark, 1988). Thus, macrocharcoal recovered from Namonte probably came from the lake basin proper and/or the coast. In contrast, microcharcoal can travel several to > 100 km from its source, so microcharcoal in Namonte may have traveled from fires at considerable distances from the waterbody (Clark, 1988).

High values of charcoal particles suggest that fire activity was widespread around Namonte and in nearby areas during the last ∼1,145 years (average microcharcoal influx: 1,435,304 particles cm^{-2} yr^{-1}). Macrocharcoal particles were common between 1,145 and 1,000 cal yr BP, at a time when hunter-gatherers and possibly early pastoralists were present in the region (Douglass et al., 2019a; Hixon et al., 2021a). Large concentrations of macrocharcoal (> 200 particles cm^{-3}) during that early period indicate the occurrence of large fires near Namonte. Although it is possible that people used fire for hunting and possibly land clearing for livestock grazing, arid conditions likely favored the ignition and spread of natural fires in the fire-prone grasslands (Virah-Sawmy et al., 2009). The relatively great abundance of charcoal of all size classes suggests both high fire activity within the lake catchment and long-distance transport, perhaps from the coast, associated with foraging (Douglass et al., 2018).

Between ∼1,000 and 70 cal yr BP, macrocharcoal values increased dramatically, with a peak between ∼205 and 130 cal yr BP (macrocharcoal influx = 4,303 particles cm^{-2} yr^{-1}, macrocharcoal area = 1,392 mm^2 cm^{-2} yr^{-1}), suggesting continued large-scale landscape transformation near Namonte. High charcoal influx overlaps with a decline in tree taxa, suggesting that forests were intentionally burned to expand grasslands for zebu and ovicaprids (Douglass et al., 2018; Hixon et al., 2021a,b). A peak in macrocharcoal area (average 1,896 mm^2 cm^{-2} yr^{-1}) between ∼460 and 425 cal yr BP could also indicate intense fire activity associated with vegetation clearing by local pastoralists and management of grasslands. The abundance of macrocharcoal particles (2,600 ± 4,207 particles cm^{-3}) is similar to that found in sediments associated with large-scale landscape clearance (> 200 particles cm^{-3}) in Mauritius (Gosling et al., 2017). Moreover, a similar increase in fire activity was observed ∼589 cal yr BP at Lake Longiza and ∼450 cal yr BP in southeast Madagascar, during a period of cultural transformation, when the size of settlements increased and cattle herding activity intensified (Razanatsoa et al., 2021b).

A large peak in woody and herbaceous microcharcoal influx (average 2,395,921 and 227,006 particles cm^{-2} yr^{-1}, respectively) is observed between ∼230 and 35 cal yr BP. Intense fire activity during that period may have been the product of maintenance of grazing areas for herds of zebu. Microcharcoal influx decreased over time but remained relatively high through the period of French colonization (1897–1958 CE) and following the establishment of the Malagasy Republic (1958 to present). Despite colonial and post-Independence state-imposed sanctions designed to discourage burning and reduce deforestation and soil erosion (Kull and Laris, 2009), paleoecological and historic records show that fires remained common in the region. The period of French colonization was characterized by rapid and widespread resource exploitation, such as maize production, that involved changes in the local economy and impacted the livelihoods of native people (Wietzke, 2015). During the last 40 years, fire activity has decreased near Namonte. This could be the consequence of changes in pastoral practices and intensification of cash-cropping (Scales, 2011). Persistence of charcoal in the record, however, reflects continued use of fire to prepare fields for agriculture, produce fuel charcoal, control pests, mitigate the impacts of wildfires, and protest political and economic regimes (Kull, 2002; Kull and Laris, 2009).

Results from this study suggest that the landscape transformation was the product of fire intensification, likely associated with the management of grasslands for introduced cattle (Bloesch, 1999; Kull, 2002; Davis and Douglass, 2021). High concentrations of charcoal particles are associated with the concomitant increase of Poaceae (∼65%) over time in the region. A similar pattern was detected in sediment deposited between 1,250 and 850 cal yr BP in several water bodies across Madagascar, including Lakes Amparihibe, Kavitaha, Longiza, Mitsinjo, Ranobe, and Tritrivakely (Burney, 1987a; Matsumoto and Burney, 1994; Gasse and Van Campo, 1998; Burney et al., 2004; Hixon et al., 2021b; Razanatsoa et al., 2021b). This evidence indicates a close relationship between forest burning and grassland expansion and the important role that herders played in the transformation of the landscape during the last millennium.

Legacy of Megafauna Extinction

Several megafauna (> 45 kg) species inhabited southwest Madagascar during the Late Holocene, including giant lemurs (*e.g., Megaladapis edwardsi* and *Hadropithecus stenognathus*), elephant birds (*e.g., Mullerornis modestus* and *Aepyornis* spp.), pygmy hippos (*Hippopotamus* spp.), and giant tortoises (*Aldabrachelys* spp.) (Crowley, 2010; Goodman and Jungers, 2014). These species played key ecological roles, including seed dispersal of native plants, maintenance of grasslands through grazing, and nutrient cycling in aquatic and terrestrial ecosystems (Godfrey et al., 2008; Godfrey and Crowley, 2016). Directly ^{14}C-dated assemblages of megafauna bones from southwest Madagascar suggest that populations of large animals started to decline by ∼2,500 cal yr BP and disappeared from the record by ∼1000 cal yr BP (Crowley, 2010; Hansford et al., 2021; Hixon et al., 2021a). The long-term ecological consequences of these extinctions provide critical context for current conservation and reintroduction/rewilding efforts, yet they remain poorly understood (Pedrono et al., 2013; Godfrey et al., 2019).

Southwest Madagascar is inhabited by several tree species that rely on large-bodied animals for seed dispersal (*e.g.*, species of *Adansonia*, Didiereaceae, Arecaceae) (Albert-Daviaud et al., 2020). Remnant lemur species, introduced bushpigs, and people may continue to disperse endemic seeds, yet multiple plant taxa are considered to have been "orphaned" by the extinction of their seed dispersers (Federman et al., 2016). In Namonte, the pollen record reveals the legacy of megafauna extinction on terrestrial ecosystem composition. The abundance of plant taxa dispersed exclusively by animals, particularly lemurs, decreased from ∼1,145 cal yr BP to present. In contrast, plants with wind-dispersed seeds became more abundant over time. Reduced coverage of dry forests may have been, in part, a consequence of megafauna extinctions, because: (1) several plant species lost their seed dispersers, which negatively impacted their life cycles by creating a bottleneck for seed germination and seedling recruitment; (2) the seed shadow pattern was altered, resulting in limited dispersal in both space and time; and (3) the population genetic structure of plant species was negatively affected because gene flow via seed movement was restricted (Guimarães et al., 2008; Pires et al., 2018). Plants that lost dispersers prior to 1,100 cal yr BP may today be more vulnerable to extinction in the face of climate change and land use intensification because they are unable to increase their geographic distribution.

Burney et al. (2003) suggested that a decline in megafauna probably led to proliferation of fires in the dry forest, but results from our study do not show a clear connection between fire prevalence and loss of large animals. Both the microcharcoal and macrocharcoal records from Namonte show that fires were widespread in the region during the last ∼1,145 years. The high incidence of fire over the last millennium was likely a consequence of arid climate conditions, combined with the settlement of agro-pastoralists, decline of megafauna, and expansion of grasslands in the region.

CONCLUSIONS

The paleoecological record in southwest Madagascar suggests that environmental impacts of anthropogenic activities were significant over the last ∼1,145 years. People have managed and modified this landscape over the last millennium, particularly following settlement of agro-pastoralists and the introduction of zebu and ovicaprids. Extensive cattle pastoralism evidently involved the use of fire to promote regrowth of palatable grasses at the expense of dry forest taxa. Pastoralism also impacted aquatic diatom communities, which probably responded to the effects of deforestation, soil erosion, and organic input to the lake. Interactions among humans, an increasingly arid climate, and disappearance of endemic megafauna, likely favored the establishment of fire-resistant vegetation and the reconfiguration of vegetation communities in the Malagasy drylands. This study highlights the advantages of integrating multiple paleoecological, archaeological and historical records to make inferences about long-term legacies of climate change and anthropogenic activities on terrestrial and aquatic ecosystems. It also highlights the vulnerability of insular ecosystems to intensifying anthropogenic impacts today.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

SH, MB, JC, and DK designed the research and collected the samples. KD organized and managed fieldwork. AD, SH, MV, and BC analyzed the samples. AD, SH, and MV wrote the draft of the manuscript. SI and KD assisted with the analysis. All authors commented, provided input to the manuscript, and approved the submitted version.

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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.2021.688512/full#supplementary-material

Supplementary Material 1 | Principal component analysis of XRF data from the Namonte sediment core, southwest Madagascar, with loadings illustrated by vectors. The lower core section (129-60 cm depth), corresponds to diatom zone D-1 and pollen zones P-1 and P-2, has a geochemical composition that is distinct from the upper core section (60-33 cm depth), which corresponds to diatom zone D-2 and pollen zone Z-3.

Supplementary Material 2 | XRF data from the Namonte sediment core, southwest Madagascar.

Supplementary Material 3 | Ecology of the main plant taxa found in the Namonte sediment record, southwest Madagascar (Vincens et al., 2007).

Supplementary Material 4 | Ecology of the main diatoms found in the Namonte sediment record, southwest Madagascar.

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Early Human Colonization, Climate Change and Megafaunal Extinction in Madagascar: The Contribution of Genetics in a Framework of Reciprocal Causations

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INTRODUCTION

The extinction of the megafauna in Madagascar and surrounding archipelagos (Seychelles, Comoro, and Mascarene islands) has been associated with evidence of ecological transformations, explained either by the increase of human activities (Hixon et al., 2018, 2021; Douglass et al., 2019; Godfrey et al., 2019; Railsback et al., 2020) or hydroclimatic shifts (Virah-Sawmy et al., 2009; Quéméré et al., 2012) or a combination of both (Salmona et al., 2017; Li et al., 2020; Teixeira et al., 2021). Whereas the Mascarenes lost their large-bodied endemic species within two centuries, in close association with human arrival (1638–1691 CE), in Madagascar the process has been estimated to be far slower, over a period of two millennia from 2,400 to 500 cal yBP (Godfrey et al., 2019). The temporal overlap of climate- and human-induced impact makes it challenging to discern primary from secondary causes (Burney et al., 2004; Crowley, 2010). Thus, any ultimate assessment would need an understanding of the phases of human occupation coupled with a finer temporal resolution of regional climate and ecological variability.

Over the last few years, the question has been addressed by contributions from a wide spectrum of disciplines, of which genetics and genomics are among the most promising (e.g., Quéméré et al., 2012; Williams et al., 2020). The results show a complex web of relationships between possible causal factors. These findings offer the opportunity to reconsider both human and climatic factors as agents that can trigger ecological outcomes through processes of direct and indirect causal chains.

THE DIALECTIC HUMAN/CLIMATIC FACTORS

The earliest dates for human activities in Madagascar span from >10,500 to 1,350 cal yBP (radiocarbon calibrated years before present) (Burney et al., 2004; Muldoon, 2010; Dewar and Richard, 2012; Anderson et al., 2018; Hansford et al., 2018; Douglass et al., 2019). There is uncertainty about the oldest evidence (bone remains of elephant birds and pygmy hippos), variously interpreted as either butchery cutmarks or post-mortem artifacts (see Mitchell, 2019). Nonetheless, early sporadic presence of hunter/foragers in north-western and southern Madagascar cannot be definitively excluded. Artifacts more clearly associated with human activities appeared about 2,000 cal yBP (Burney et al., 2003, but see also Douglass et al., 2019; Mitchell, 2019), pointing to a more stable presence. However, the scarcity of extensive human-faunal interplay (hunting sites, butchery tools, and abundant cutmarks) and the limited number of non-native species introduced suggest a negligible ecological impact of these earlier incomers (Gommery et al., 2011).

Unambiguous evidence of a human demographic transition, driven by a massive immigration of Austronesian-speaking people from island Southeast Asia (Adelaar, 2009; Tofanelli et al., 2009; Tofanelli and Bertoncini, 2010; Cox et al., 2012; Crowther et al., 2016; Pierron et al., 2017; Anderson et al., 2018), can be reconstructed from post-1,300 cal yBP archeological remains, distributed in all the Malagasy ecoregions and the Comoros (Cox et al., 2012; Crowther et al., 2016; Anderson et al., 2018; Godfrey et al., 2019). The transition likely represented a cut-off between a regime of minimal ecological impact and a phase of intensive exploitation of natural resources due to the inclusion of Madagascar and the surrounding islands in the maritime trade network around the Indian Ocean rim.

Reconstructions of climate shifts based on speleothem and sediment analyses are consistent with these dates. The time when δ^{13}C and δ^{18}O isotope trends decoupled is used as a proxy to disentangle anthropogenic and climate effects. Investigations of stalagmites at Anjohibe Cave in northwestern Madagascar are eloquent (Burns et al., 2016; Wang et al., 2019; Railsback et al., 2020). They suggest a rapid increase in δ^{13}C values not correlated to a simultaneous growth in δ^{18}O values from by 1,300 cal yBP. This is interpreted as a replacement of C3 forests with C4 grasslands and soil erosion possibly related to the practice of "burning horticulture," under steady humidity conditions. In certain regional contexts, reductions in forest coverage correlate temporally with mutually related variables, such as the pace of megafauna demographic decline (Godfrey et al., 2019; Hixon et al., 2021), human population growth and the introduction of domesticated species (Joseph and Seymour, 2020).

More questionable are the possible anthropogenic causes of the faunal decline (involving among others *Palaeopropithecus, Archaeolemur, Megadalapis, Hadropithecus, Mesopropithecus, Pachylemur,* and *Hippopotamus* sp.) that occurred in different ecoregions a 1,000 years (2,400–1,300 yBP) before the first evidence of a stable colonization (Crowley, 2010; Anderson et al., 2018; Hansford et al., 2018; Godfrey et al., 2019; Faina et al., 2021; Hixon et al., 2021).

During the Early/Middle Holocene the Malagasy megafauna showed resilience to prolonged drought events, which changed habitats in terms of vegetation coverage and water regime (Burney et al., 2004; Quéméré et al., 2012; Wang et al., 2019). In particular, the 5,200 and 4,200 cal yBP aridity peaks are well defined in northwestern Madagascar (Wang et al., 2019). However, at no time was the entire island affected by massive natural drought, due to the antiphase between the north-west and the central and south (Wang et al., 2019). In contrast, the Late Holocene shows the culmination of a millennial-scale drying trend with major aridity peaks between 2,000 and 500 cal yBP in different regions (Virah-Sawmy et al., 2010; Li et al., 2020). At Asafora Cave in the southwest stable carbon and oxygen isotope trends are coupled and suggest increasing CAM/C4 plant coverage and aridification between 3,320 and 880 yBP (Faina et al., 2021). Other lines of evidence support a scenario of a highly fluctuating landscape with a mosaic of grassy biomes and forested habitats at different altitudes and a diversity of endemic grass species spanning millennia (Bond et al., 2008; Vorontsova et al., 2016; Yoder et al., 2016; Samonds et al., 2019; Solofondranohatra et al., 2020; Crowley et al., 2021). This questions the dichotomy between natural and anthropogenic transformation of modern grasslands and the extent of the indirect role of humans (use of fire, introduction of domesticated species) in triggering mega-herbivore decline.

A reliable scenario should not disregard the long-standing relationships among droughts, plant communities, natural fires, and mega-herbivores (elephant birds, giant lemurs, giant tortoises, and hippopotami) that pre-dated human arrival (Samonds et al., 2019).

DISCUSSION

Speleothems and sediments are not the only source of past environmental transformations. Biological systems are intimately related to their habitats and, when investigated in appropriate contexts, they become archives of the major changes that have occurred. From this perspective, the genomes of living and subfossil animals retain signs of demographic fluctuations that may be interpreted under model-free and model-based parameters to infer either the human impact on wild fauna (Frantz et al., 2016; Pujolar et al., 2017) or the effect of climate changes on population size and structure (Kozma et al., 2018; Miller et al., 2021; Song et al., 2021).

The effective population size N_e is a key parameter in ecology and conservation biology. In one of its most widely used forms, it infers the size of an idealized population (Wright–Fisher) which, through inbreeding and/or genetic drift, underwent the same loss of genetic diversity observed in the population under study. There are many ways to genetically estimate N_e and important theoretical advances have recently been made in this field (e.g., Husemann et al., 2016; Hill and Baele, 2019). Widely used approaches test effective size declines under the statistical framework of the Coalescent Theory or the coalescent (Kingman, 1982; Wakeley, 2008). In this, the pairs of lineages of a sampled genealogy merging into an ancestral one while going backward in time (coalescence events) are compared with the expected rate of a modeled steady population: the more coalescence events, the smaller or more structured the population. Cross-disciplinary research teams have attempted to merge genetically based reconstructions of historic demography for Malagasy fauna with ecological and ethological evidence. For example, although the population size and range distribution of the extant large lemur *Propithecus tattersalli* is decreasing today, Quéméré et al. (2012) revealed, *via* bottleneck modeling, a population collapse much older than the likely arrival of humans in their current range (northern Madagascar). Similarly, Bertoncini et al. (2017) inferred habitat shifts from the genetic diversity of a medium-sized lemur (*Eulemur collaris*) living in south-eastern Madagascar (Rakotoarisoa, 1997; Virah-Sawmy et al., 2010). Genetic estimates of N_e and mitochondrial coalescence times depict a scenario of strong demographic contraction for *Eulemur* groups now separated by extended strips of grasslands and swamps. This is in line with an original condition of mixed woodland forest and a rapid transition to an open habitat dominated by ericoid grassland driven by marine surges before 700–1,500 cal yBP (Virah-Sawmy et al., 2009, 2010). Other studies detected recent bottlenecks in species from different regions over the island with a population decrease of approximately two orders of magnitude that occurred in the last millenium both in small nocturnal lemurs (*Lepilemur edwardsi*: Craul et al., 2008; *Microcebus ravelobensis*: Olivieri et al., 2007; *Microcebus murinus* and *Microcebus ravelobensis*: Teixeira et al., 2021) and larger diurnal lemurs (*Lemur catta*: Parga et al., 2012; *Propithecus verreauxi*: Lawler, 2008; *Propithecus perrieri* and *Propithecus tattersalli*, Salmona et al., 2017). Taken together, such studies depict more complex relationships between the candidate factors of faunal demise.

Given the endangered status of the Malagasy living fauna (Schwitzer et al., 2014), which makes non-invasive sampling a common practice, and the low quality of DNA from fossil remains (e.g., Dabney et al., 2013), approaches that maximize the reconstruction of demographic profiles from few low-coverage genomes are a priority. Methods combining hidden Markovian chains and the coalescent (PSMC, Pairwise Sequentially Li and Durbin, 2011; MSMC, Multiple Sequentially Markovian Coalescent, Schiffels and Durbin, 2014) allow millennial time-series of population size/structure fluctuations to be obtained to support evidence of past ecological shifts even from a single specimen (Stoneking, 2017). Ideally, the graphs based on the Markovian coalescent approaches represent more exhaustive indicators of extinction dynamics than the extent of the skeletal record.

To date PSMC has been applied to whole genomic data from hibernating dwarf lemurs (*Cheirogaleus medius*, *C. major*, *C. crossleyi*, and *C. sibreei,* Williams et al., 2020) and mouse lemurs (*Microcebus murinus*, *M. ravelobensis*, Teixeira et al., 2021). In the former study, evidence for a slow decline in the last 50,000 years, long before the arrival of any human beings on the island, was found. Long-term reductions in N_e and low heterozygosity may have heavily affected the survival of dwarf lemurs due to inbreeding depression, namely the expression of detrimental genes or the scanty diversity across immune genes (Morris et al., 2015; Rogers and Slatkin, 2017). Interestingly, a less fluctuating N_e was estimated in the genome of *C. sibreei*, the only species adapted to high-altitude habitats, consistent with the paleoecological evidence of more stable habitats in the Central Highlands (Wilmé et al., 2006; Samonds et al., 2019). It can be argued that climatic pulsing exerted more extreme demographic consequences on low-altitude species, which likely experienced greater levels of habitat fragmentation, vegetation shifts, cyclones, and marine transgressions/tsunami. These climatic shifts have been hypothesized to be frequent during the Quaternary and used to explain the remarkable process of speciation on the island (Wilmé et al., 2006).

CONCLUSION

Whether humans or climatic shifts are the primary source that triggered the megafaunal extinction in Madagascar is still highly questioned. There is general convergence upon the fundamental role that the demographic growth of Austronesian colonizers and their introduction of subsistence agriculture had played in the over-exploitation of natural resources by around 1,300 yBP (e.g., Crowther et al., 2016; Anderson et al., 2018; Godfrey et al., 2019). There is also growing evidence of complex climate-driven shifts in geological and biological archives that suggests a move away from the narrative of human/climate duality and toward a paradigm of mutual rather than distinct causality (Salmona et al., 2017; Li et al., 2020). To further complicate the picture, the relative contribution of multiple drivers of change appears to vary among the regions of the island depending on the local climate, the faunal/vegetational assemblages and the pattern of human settlement (e.g., Virah-Sawmy et al., 2010; Yoder et al., 2016; Wang et al., 2019; Railsback et al., 2020; Teixeira et al., 2021). We hope that an increase in cross-disciplinary research will help to clarify whether historical human colonization of Madagascar and neighboring archipelagos were facilitated by a long-term biotic stress experienced by endemic megafauna. From this perspective, genomes of both living and extinct taxa, at either individual or population level, need to be explored more extensively as repositories of past demographic trends closely associated with changing ecosystems.

AUTHOR CONTRIBUTIONS

ST wrote the manuscript. SB and GD contributed to the interpretation and the revision of the work. All authors contributed to the article and approved the submitted version.

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Genetic Insights Into the Introduction History of Black Rats Into the Eastern Indian Ocean

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Islands can be powerful demonstrations of how destructive invasive species can be on endemic faunas and insular ecologies. Oceanic islands in the eastern Indian Ocean have suffered dramatically from the impact of one of the world's most destructive invasive species, the black rat, causing the loss of endemic terrestrial mammals and ongoing threats to ground-nesting birds. We use molecular genetic methods on both ancient and modern samples to establish the origins and minimum invasion frequencies of black rats on Christmas Island and the Cocos-Keeling Islands. We find that each island group had multiple incursions of black rats from diverse geographic and phylogenetic sources. Furthermore, contemporary black rat populations on these islands are highly admixed to the point of potentially obscuring their geographic sources. These hybridisation events between black rat taxa also pose potential dangers to human populations on the islands from novel disease risks. Threats of ongoing introductions from yet additional geographic sources is highlighted by genetic identifications of black rats found on ships, which provides insight into how recent ship-borne human smuggling activity to Christmas Island can negatively impact its endemic species.

Keywords: *Rattus rattus*, Christmas Island (Indian Ocean), Cocos (Keeling Islands), colonization and extinction, *cytochrome b*, RAD-seq, hybridisation

INTRODUCTION

The invasive black rat (*Rattus rattus*) has a well-documented history of negative impacts on indigenous island fauna at a global scale (Towns et al., 2006), e.g., Indian Ocean – (Cheke and Jones, 1987), Mediterranean – (Martin et al., 2000; Ruffino et al., 2009), Atlantic – (Angel and Cooper, 2006), Pacific – (Atkinson, 1977; Spennemann, 1997). In the Indian Ocean basin, transport of black rats has occurred over a long time frame (>4,000 years in north Africa, de Graaf and Black, 1981), in particular facilitated by a long history of human maritime movement around the western Indian Ocean and its major island groups (Tollenaere et al., 2010). Black rats have been implicated in extinction events in this region e.g., the Mascarene and Seychelles groups (Towns et al., 2006), as well as major impacts on human health through disease transmission, e.g., plague on Madagascar (Rahelinirina et al., 2018).

What makes the black rat a particularly dangerous disease threat is that it can both transmit diseases to other mammals and acquire disease it has never been exposed to previously. Together with the propensity for the black rat to both live with human populations (commensalism) and disperse through the agency of human trade and transport, the black rat represents a disease risk factor that should not be ignored. A further factor yet to be explored is the possibility that black rat populations, having expanded their ranges with the intensification of agriculture and worldwide shipping networks, now meet with the possibility for the suite of zoonotic diseases they carry to cross rat-host species boundaries and/or produce novel recombinant genotypes that neither rat-host has been exposed to. Common diseases known to infect black rats include *Yersinia pestis* (plague), *Bartonella*, *Leptospirosis*, *Orientia tsutsugamushi* (scrub typhus), *Salmonella,* and *Hepatitis E* (Kosoy et al., 2014). Novel recombinants of these or other diseases may pose risks to human populations if multiple black rat taxa come into contact outside of their native ranges (i.e., both on islands in the Indian Ocean as well as around the world).

Islands in the eastern Indian Ocean have been impacted by black rats for almost 200 years. Black rats colonized Direction Island (Pulu Tikus = Rat Island) in the Cocos-Keeling Islands (CCK) at some point between European discovery of the islands in 1643 (Gibson-Hill, 1949) and permanent human settlement in 1827 (Wood-Jones, 1909). This island group comprises 26 islands (total area ∼14 km^2) in a southern (main) atoll and a single island (Pulu Keeling or North Keeling Island, 1.2 km^2) situated 24 km north of the main atoll (see **Supplementary Figure 1**). Rats were identified as one of the major threats for the endemic CCK buff-banded rail, *Gallirallus philippensis andrewsi* (Stokes et al., 1984), which until recently survived only on the rat-free Pulu Keeling. In 2013, rails were successfully reintroduced to Horsburgh Island, the only rat-free island in the main atoll (Woinarski et al., 2016). Analysis of the extinction of native *Rattus* on Christmas Island (CXR) points to disease introduced by flea-carrying black rats as a contributing factor (Wyatt et al., 2008). These threats by black rats are also ongoing *via* people smuggling on small boats, with the landing of a vessel carrying asylum seekers on Pulu Keeling in 2012 sparking major concerns that rats could establish on this important seabird island.

Threats to wildlife from black rats are particularly severe on remote islands but are also a problem on offshore islands where introductions from mainland sources can occur more frequently. On the west coast of Australia, black rats have invaded at least 40 offshore islands impacting the native avian, mammalian, and reptilian fauna (Burbidge and Morris, 2002; Morris, 2002). With increased development of this coastal region by the mineral and energy sector, and an increase in ownership of private vessels for recreation, the opportunities for black rat movement are on-going (Burbidge and Morris, 2002) and present a constant threat of re-invasion at sites after successful eradication programs (Morris, 2002; Greenslade et al., 2013; Burbidge and Abbott, 2017). Thus, identification of potential re-invasion sources is an important step during the planning of eradication events (Abdelkrim et al., 2005). Or in the case of CCK, knowledge of dispersal patterns of rats between the islands in the main atoll may be critical in planning the eradication of this pest.

Earlier accounts of the identity of eastern Indian Ocean *Rattus* species were hamstrung by the lack of an adequate regional framework within which to assess island forms. Traditionally, differences in coloration were used to differentiate new species when this trait is now known to simply reflect natural variation within a species/subspecies (Tate, 1950; Musser and Califia, 1982; Pickering and Norris, 1996). For example, Wood-Jones (1909) suggested there were three races of rats present in the CCK. The "original" Direction Island rat from a ship in 1825, plus, a more destructive taxa, believed to be *Mus decumanus* (*R. norvegicus*) that was reportedly introduced, through shipwreck, in 1878, and the black rat (*R. rattus*), which was supposedly a later addition *via* trade or shipwrecks. The Direction Island form was subsequently described by Tate (1950) as a new subspecies, *R. rattus keelingensis*. Musser and Califia (1982) originally listed *Rattus rattus keelingensis* (found on Pulau Tikus in the Cocos-Keeling Islands) as a synonym of *Rattus rattus diardii*, which is included in *R. tanezumi*; Musser re-examined the holotype (collected in 1940) and part of the type series and now considers them introduced *R. rattus* (Wilson and Reeder, 2005). Recent genetic work supports Musser's assertion, where early samples of rodents collected from CXR (in 1900 and 1903) were in fact found to belong to *R. rattus* (Wyatt et al., 2008). The situation is further complicated by the recent recognition that black rats comprise multiple evolutionary taxa in a putative species complex, *R. rattus* species complex: RrC (Pages et al., 2010; Aplin et al., 2011). Although based on mitochondrial DNA (mtDNA) only at present, the global survey of black rat diversity by Aplin et al. (2011) with more detailed regional information from Indo-China (Pages et al., 2010) and the western Indian Ocean and periphery (Pages et al., 2010; Tollenaere et al., 2010), provide a genetic framework to investigate the genetic diversity, origins of the source populations, and minimum number of dispersal or introduction events.

An assessment of black rat diversity in the eastern Indian Ocean is timely, as at least three black rat mtDNA groups (RrC I, II, IV) occur in the periphery of this region and the RrCI "ship-rat" group (sub-group within RrC I) has accessed the region from further afield *via* global shipping (Aplin et al., 2011). Here, we use phylogeographic analyses of mtDNA *cytochrome b* (*cytb*) nucleotide gene sequences and nuclear DNA data (Single Nucleotide Polymorphisms, SNPs) of contemporary material in a regional context to investigate the diversity and dispersal history of black rats in the eastern Indian Ocean focusing on CXR and CCK. We have enhanced the existing reference framework with additional sampling from around the world, especially from Indonesia and Australia, so that we can assess the diversity and history of black rats in this region. We also wanted to examine interactions between the mtDNA and nuclear genetic signals of these black rats to examine potential for hybridisation between RrC taxa in the novel environments of CXR and CCK. Lastly, we also attempted to date the arrival and potential population turnover of RrC on CXR by incorporating ancient DNA samples and comparing to both modern and historic samples (Wyatt et al., 2008).

MATERIALS AND METHODS

Samples

We compiled a dataset of 553 modern black rats where we either generated mitochondrial DNA from tissue samples (*n* = 387), downloaded existing sequence from Genbank (*n* = 147), or requested from authors of other papers (*n* = 19), including from South-east Asia (*n* = 256), South Asia (*n* = 27), Africa (*n* = 43), the Americas (*n* = 31), Europe (*n* = 11), the Middle East (*n* = 20), Australia (*n* = 70), CCK (*n* = 45) and CXR (*n* = 50) (Tollenaere et al., 2010; Aplin et al., 2011) (see map in **Figure 1**). Details of all modern specimens analyzed along with GenBank accession numbers are presented in **Supplementary Table 1**. We also obtained mtDNA sequences from rat teeth and bones found in cave deposits on Christmas Island. Rat teeth (incisors or molars) and long bone samples (*n* = 48) were excavated from CXR from two caves, Sinkhole 1 (*n* = 15) and Runaway Cave (*n* = 33) – see **Supplementary Figure 2**. Radiocarbon dates were also generated from a range of rodent bone remains from Runaway Cave only, as no DNA could be obtained from the Sinkhole remains (see "Results" and **Supplementary Table 2**).

Mitochondrial DNA (mtDNA) Sequencing and Analysis (Modern Samples)

For modern tissue samples, DNA was extracted from alcohol or RNALater® preserved liver, tail or ear with the Gentra Puregene DNA extraction protocol (QIAGEN) following the manufacturer's instructions. Part of the mtDNA *cytochrome b* (*cytb*) gene was PCR amplified and directly sequenced from the modern samples following the methods in Aplin et al. (2011) with the primers LM1268 and HM1269 (see **Supplementary Table 3**). Chromatograms were edited, and sequences were aligned and trimmed to a common 945 bp in length in Geneious 7.1.2[1]. Any samples that could be sequenced for at least 600 bp of the 945 bp were also included in the *cytb* network analysis where they represented a unique location. Initially, sequences were assigned to RrC groups within a framework of representative *cytb* sequences from Aplin et al. (2011). For each RrC mtDNA group identified from Aplin et al. (2011) as "RrC I," "RrC II," "RrC IV" (hereafter designated by "mtClade I," "mtClade II," and "mtClade IV"), we then generated median joining networks using PopART (Population Analysis with Reticulate Trees; Bandelt et al., 1999; Leigh and Bryant, 2015) to show the relationships among haplotypes (**Supplementary Figures 3–5**).

Mitochondrial DNA (mtDNA) Sequencing and Analysis (Ancient Samples)

For ancient samples, DNA was extracted from the Christmas Island black rat dentaries/bones using the DNeasy Kit (Qiagen) with modification following procedure described in Thomson et al. (2014) in the ancient DNA lab at the Australian Centre for Ancient DNA (ACAD) at the University of Adelaide. Extraneous dirt was removed from the bones/teeth prior to entry into the ancient DNA lab but due to the small size of the bones/teeth, bleach was not used to decontaminate the samples. DNA was extracted from 48 samples and attempts were made to PCR amplify and sequence four small fragments of *cytb* using the primers listed in **Supplementary Table 3** and PCR reaction conditions described in Louys et al. (2020). Re-amplification and re-sequencing were performed for each PCR for each specimen. PCR clean-up and Sanger sequencing were conducted at the Australian Genome Research Facility Ltd (Australia).

SNP Analyses (Modern Samples)

Nuclear SNPs were generated using a RAD-seq protocol modified from Poland et al. (2012) for a subset of the modern samples from the *cytb* dataset (*n* = 190). A two-enzyme restriction digest protocol (*EcoRI* and *SphI*) was used to generate a library consisting of DNA fragments with a forward primer and reverse primer on either end following the protocol of White et al. (2018). The raw Illumina NextSeq fastq.gz files were demultiplexed using GBSX v1.3 using the GBS option and allowing one mismatch in the barcode or enzyme cut site (Herten et al., 2015). Bbduk v36.32 and bbduk2 v36.32 were used to filter the data using the following parameters: chastity filtering, adapter trimming from the 3′ end of the reads, trimming of the restriction enzyme recognition cut site at the 5′ end of the reads, quality trimming to Q10 using the Phred algorithm, and then length filtering of all reads to 58 bp in length. The Stacks v1.40 "ustacks" program was run on each demultiplexed sample to form exactly matching stacks with a minimum depth of coverage of three required to form a stack (*m* = 3), a maximum of two mismatches between stacks to form homologous loci (M = 2), and a maximum of four mismatches between stacks when adding secondary reads (Catchen et al., 2013). The maximum number of stacks allowed at a single de novo locus was set at 3 (max_locus_stacks = 3) while the removal algorithm was used to drop highly repetitive stacks (and nearby errors) and the deleveraging algorithm was used to resolve over merged tags. The model type used to call homozygotes and heterozygotes was set to "bounded" with a lower bound of epsilon (error rate) of 0.0001 and an upper bound of 0.1.

A catalog (consensus set of loci) for each species was generated using the Stacks v1.40 "cstacks" program allowing five mismatches (*n* = 5) between different sample's stacks when generating the catalog. The Stacks v1.40 "sstacks" program was used to map each sample's stacks back against this catalog to assign consistent labeling on the homologous loci in all samples. The Stacks v1.40 "populations" program was then run on all samples, with only the first SNP in a marker being called, allowing a minimum minor allele frequency of 0.05, a maximum observed heterozygosity of 0.80 required to process a nucleotide site at that locus, and requiring at least 50% of samples to be called at a locus to retain a marker. The markers were output as a genepop file and the "Adegenet" package v2.1.5 in R (Jombart, 2008) was used to conduct prinicipal component analyses to examine the nuclear genetic relationships between the RrC mtDNA groups.

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[1] https://www.geneious.com

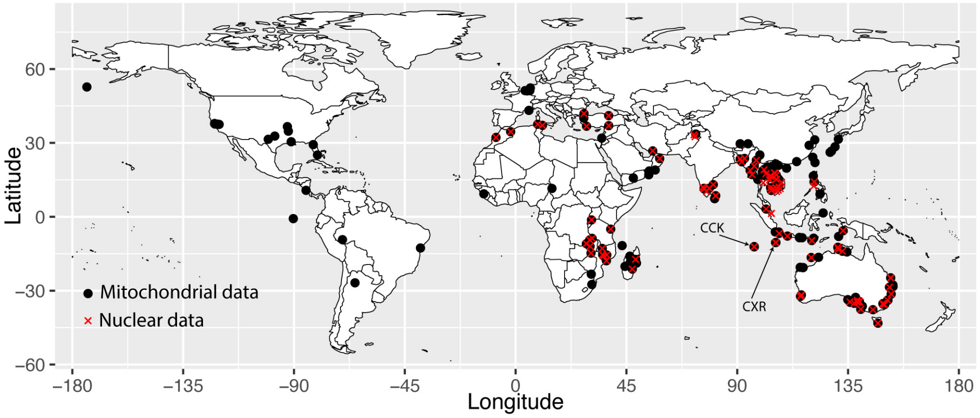

FIGURE 1 | Map showing sample locations from this paper. Black circles represent samples sequenced for the *cytb* mtDNA gene, and red crosses represent samples sequenced for nuclear SNP markers.

Structure v2.3 (Pritchard et al., 2000), a model-based clustering methods, was used to investigate the species/population structure of each of the RrC mtDNA groups, using the admixture model and running for 100,000 generations with 20,000 generations removed as burnin, for k = 1–8 for five replicates each, with Clumpak used to process the file (Kopelman et al., 2015). Both the Pritchard method (likelihood of K; Pritchard et al., 2000) and Evanno method (delta K; Evanno et al., 2005) of evaluating optimal values of K were plotted in R. However, Evanno et al. (2005) finds that delta K is the better method for evaluating the most likely K when strong population structure is present and when sample and marker sizes are large; Pritchard et al. (2000) also recommend aiming for the smallest value of K that captures the major structure of the data, so we felt that the delta K method was the more appropriate *post hoc* method for selecting K for this dataset. The R package "PopGenome" v2.7.5 (Pfeifer et al., 2014) was used to generate diversity statistics for the modern *cytb* sequences.

The R package parallelnewhybrid (Wringe et al., 2016; based on the NewHybrids software of Anderson and Thompson, 2002) was used to examine the hybridisation history for the CXR and CCK Lineage IV samples (based on nuclear genetic signatures from PCA above) and infer an ancestral population from the other RrC Lineage IV samples in our dataset using 200 loci with the highest information content calculated with the R package snpReady v0.9.6 (Granato, 2021). Three replicates were run with these 200 loci for 1,000,000 sweeps and 300,000 burnin, with the posterior probabilities for each sample averaged across the replicates and the standard deviation calculated to confirm convergence of the replicate runs.

RESULTS

Christmas Island (CXR)

Mitochondrial *Cytochrome b* (*cytb*) Diversity

We found three of the RrC mtDNA groups defined by Aplin et al. (2011) on CXR (mtClade I, mtClade II, mtClade IV: mtDNA haplotypes are numbered from **Supplementary Figures 3–5** and defined as "H, # of haplotype, -, MtClade," e.g., "H1-I"). MtClade I (n = 2, haplotypes = 1; H41-I) was found in both a forest location and a building on CXR (but not elsewhere in our sampling locations, although it is two base pairs different to H40-I found on CCK; **Supplementary Figure 3**), while mtClade II (n = 2, haplotypes = 2; H48-II and H77-II; **Supplementary Figure 4** and **Table 1**) was found in built up areas and on an asylum-seeker vessel on CXR, but also in Australia (H48-II) and Indonesia (H77-II). MtClade IV was by far the most numerous (n = 46, haplotypes = 2) and was found both in built up and forested areas (**Supplementary Figure 5** and **Table 1**). The most common mtClade IV haplotype found on CXR (n = 43; H66-IV) is also found in Indonesia (Java and Sumba), and Vietnam, while the rarer mtDNA haplotype (n = 3; H1-IV) is also found in Indonesia, Singapore, and the Philippines (**Supplementary Figure 5**). Not surprisingly, the diversity of each of these mtClades on CXR were considerably lower than in our reference dataset, as well as those found on CCK (**Table 1**). There was also no evidence of significant demographic population expansions for either each CXR mtClade separately, nor for all the CXR samples taken together (non-significant Tajima's D and Fu and Li's F*, **Table 1**).

Twenty-four of the 48 ancient teeth/bone samples yielded sequence from one or more of the *cytb* fragments, however, only four samples provided clean DNA sequence of the RrC without contamination (**Supplementary Table 4**). These four samples were only from the upper layers of Runaway Cave (TP1 20–30 cm below the surface), which dates to between 0–290 years ago and so are considered modern (**Supplementary Table 2**). Three of the four confirmed RrC samples were mtClade IV and the fourth sample was mtClade I (**Supplementary Table 4**). Additional rodent incisors were isolated from lower layers of Runaway Cave with older dates (TP1 70–80 cm deep, dated to 1564–1709 cal BP), however, no samples yielded DNA from this deep in the site. Three rodent teeth from Runaway Cave yielded *R. macleari* sequence (described elsewhere; from TP1 20–30 cm, TP1 40–50 cm, and TP2 20–40 cm layers). So, we cannot rule-out that the

TABLE 1 | Diversity statistics for the modern *cytb* dataset (945 bp).

	# individuals	# biallelic sites	# polyallelic sites	Haplotype diversity	Nucleotide diversity	Tajima's D	Fu and Li's F*	Transition/ Transversion ratio
CCK All mtClades	46	59	0	0.350	0.01161	−0.644	0.805	13.75
CCK mtClade I	41	8	0	0.187	0.00065	−1.898	−1.792	7.00
CCK mtClade IV	5	3	0	0.400	0.00127	−1.048	−0.631	–
CXR All mtClade	52	82	0	0.250	0.00991	−1.701	0.061	15.40
CXR mtClade I	2	0	0	0.000	0.00000	–	–	–
CXR mtClade II	2	12	0	1.000	0.01270	–	–	11
CXR mtClade IV	48	10	0	0.120	0.00127	−1.351	0.589	–
Reference All mtClades	274	160	22	0.977	0.02981	0.277	−0.464	10.42
Reference mtClade I	90	35	0	0.903	0.00380	−1.499	−2.298	4.00
Reference mtClade II	78	57	7	0.938	0.00753	−1.268	−1.931	27.50
Reference mtClade IV	106	100	6	0.988	0.00922	−1.780	−2.511	5.67

rodent incisors from the lowest layer (which did not yield DNA) were actually *R. macleari*.

Nuclear Genome Diversity

When we compared the 30 samples from the CXR to those of mtClade I and mtClade IV groups from around the world (n = 153) using principal component analysis (PCA) and structure analysis for 32,568 loci, and hybridisation analysis using 78 samples (n = 29 from CXR; n = 47 from SE Asia) for the most informative 200 loci, we were able to identify the divergent nature of the CXR RrC samples.

Principal Component Analysis

In the PCA (**Figure 2**), the first principal component (PC1) generally separates RrC mtClade I samples from mtClade II and mtClade IV samples (Group 1 vs. Group 2), while PC2 separates CXR mtClade IV samples from mtClade II and mtClade IV samples from elsewhere. When we examine PC2 vs. PC3 (**Figure 3**), we see the separate ancestry of mtClade II vs. mtClade IV (native range for each mtClade is at maximum positive and maximum negative values of PC3, respectively). The major patterns (mtClade I: negative PC1; mtClade II: positive PC1 and negative PC2; mtClade IV: positive PC1 and both positive and negative PC2) appear to reflect the true nuclear backgrounds of these RrC taxa (hereafter designated by "Lineage") previously only known from mtDNA heritage, based on knowledge of their home ranges (i.e., native range of mtClade I: India; native range of mtClade II: China/NW Laos/NW Thailand/NW Vietnam/Myanmar; native range of mtClade IV: Cambodia/SE Laos/SE Thailand/SE Vietnam; see **Figure 4**). All native range locations refer to those locations first established in Aplin et al. (2011) through mtDNA sequencing or by correlating these mtClades with known taxa (i.e., RrC LI = *Rattus rattus* = Oceanic *R. rattus* 2n = 38; RrC LII = *Rattus tanezumi* northern = Asian *R. rattus* 2n = 42; RrC LIV = *Rattus tanezumi* southern = Asian *R. rattus* 2n = 40) (Yosida, 1980; Aplin et al., 2003). When we compare the "mtClade" and nuclear "Lineages" of samples we observe both concordant mito-nuclear patterns, which we suggest represents traditional RrC taxa, and discordant mito-nuclear patterns, representing mtDNA capture/hybridisation.

Looking closely at the 30 CXR samples where we generated nuclear SNP data (n = 28 with mtClade IV and n = 2 with mtClade I), we see that all of the mtClade IV and one of the mtClade I samples form their own divergent sub-group (positive PC1 and positive PC2 values in PCA in **Figure 2**). When we removed this divergent CXR Lineage IV group and re-ran the PCA (**Supplementary Figure 6**), we see the same separation of mostly concordant mtClade I/Lineage I (Group 1) vs. mostly concordant mtClade II/Lineage II and mtClade IV/Lineage IV (Group 2) in PC1. In PC2 we also see a separation of mostly concordant mtClade II/Lineage II vs. mostly concordant mtClade IV/Lineage IV, suggesting that the mtClade IV/Lineage IV (non-CXR) is a real lineage and not purely an artifact of the divergent CXR mtClade IV/Lineage IV being present in the PCA analysis (**Figure 2**). When we examine the mtClade I samples from CXR, we see that similar to the divergent nature of the Lineage IV CXR samples, the one mtClade I/Lineage I CXR sample has a much higher PC2 value than all other Lineage I samples, suggesting that it also might have been subject to isolation and genetic drift on CXR since colonization of the island. When we examine the discordant mtClade I/Lineage IV CXR sample (ABTC136477 from Pink House that falls with the concordant mtClade IV/Lineage IV samples from CXR in the PCA in **Figure 2**), we note that it shares a rare mtClade haplotype (HAP 41-I) with the concordant mtClade I/Lineage I CXR sample, suggesting mtDNA capture of this rare mtClade I haplotype likely occurred on CXR.

Structure Analysis

The structure analysis of all the RAD-seq samples (**Figure 5A**) showed the most likely clustering as K = 2 (see **Supplementary Figure 7** for delta K plot, although see **Supplementary Figure 8** for the contrasting probability of K plot), which supports the main split in PC1 from the PCA, with mtClade I (Group 1) showing a separate ancestry from mtClade II/IV (Group 2). When we removed Group 1 and re-ran the structure analysis [recommended by Evanno et al. (2005) to identify lower hierarchical levels of population structure], we found the most likely clustering as K = 3 or 5 (depending on whether delta K or probability of K was used; see structure plots in **Figures 5B,C**;

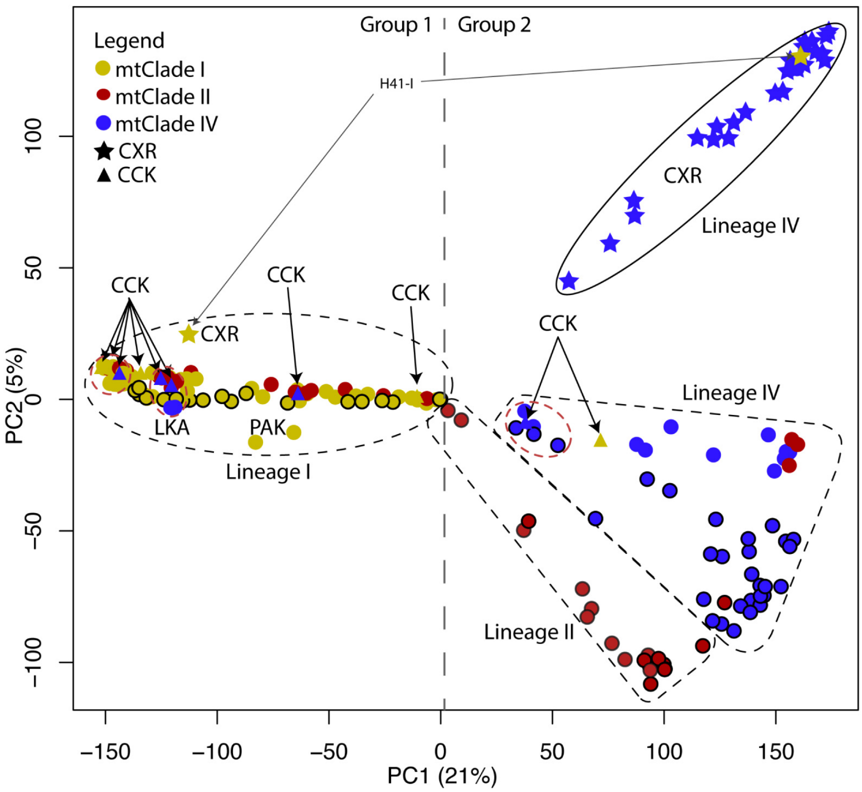

FIGURE 2 | PCA of nuclear SNP marker dataset (showing PC1 vs. PC2). PC1 explains 21% of the variance and PC2 explains 5% of the variance. Colored circles represent the mtClades, with black outlines around circles indicating samples from the native range (i.e., has concordant mtClade/Lineage signatures). The position (and dashed shapes) in PC1 and PC2 represent the nuclear background—LIV samples from their native range are more likely to represent concordant mtClade IV/Lineage IV samples, LII samples from their native range more likely represent concordant mtClade II/Lineage II samples, LI samples from their native range are more likely to represent mtClade I/Lineage I samples. The divergent Christmas Island LIV samples are outlined in an oval in the upper right-hand side of the figure. The dashed gray vertical line shows where the divide between Group 1 and Group 2 samples identified in the Structure analysis (**Figure 5**). The dashed red outline represents mostly introduced range Lineage IV samples that may include the source population of at least one of the CCK Lineage IV samples.

Supplementary Figure 9 for delta K plot and **Supplementary Figure 10** for probability of K plot). In the K = 3 structure plot (**Figure 5B**), the divergent nature of the CXR Lineage IV samples is clear, as they form a separate sub-group compared to Lineage II and the rest of Lineage IV. However, we can also gain some insights as to source populations of the CXR Lineage IV samples from the K = 5 structure analysis of Group 2: the main other ancestry (green portion of the CXR samples in **Figure 5C**) reflected ancestry from introduced range locations of Lineage IV. This suggests that gene flow between Indonesia, Malaysia, the Philippines, or Singapore to CXR may have occurred.

Hybridisation Analysis

We wanted to investigate gene flow between the Lineage IV populations identified in our PCA and structure analyses, so we conducted hybridisation analyses (**Figures 6A,B**). Samples with pure population 1 ancestry identified in our hybridisation analysis (labeled "Pure 1" in **Supplementary Table 5**, **Figure 6B**) are from Cambodia, Laos, and Vietnam (all native range for the RrC LIV taxon). All the samples with pure population 2 ancestry were from Christmas Island, which suggests that either we have not sampled the core range of this taxa or it represents the sole remaining location of this lost taxa. No first generation "F1" hybrids were identified in our samples, nor were any backcrosses with "Pure 2" hybrids (labeled "Backcross 2" in **Figure 6B**).

Cocos-Keeling Islands (CCK)

Mitochondrial *Cytochrome b* (*cytb*) Diversity

We identified 40 mtClade I sequences on four islands of CCK, belonging to four haplotypes: H1-I, H15-I, H35-I, and H40-I. They were found on Direction Island ($n = 1$; H1-I), Home Island ($n = 22$; H1-I), South Island ($n = 5$; H1-I), and West Island ($n = 12$; H1-I, $n = 8$; H15-I, $n = 1$; H35-I, $n = 1$; H40-I, $n = 2$; **Supplementary Figure 1**). These mtClade I haplotypes were also found in Australia (H1-I, H15-I), Guinea (H1-I), Tunisia (H1-I), Morocco (H1-I), the Netherlands (H1-I, H35-I), Sri Lanka (H35-I), Turkey (H1-I), and the United States (H1-I; **Supplementary Figure 3**). In fact, the most common haplotype (H1-I) is the basal haplotype of the original "ship rat" sub-group, first identified in Aplin et al. (2011) as the likely RrC group brought to Europe and many European colonies along shipping routes. We expanded the geographic sampling and found this "ship rat" sub-group worldwide (in Australia, Argentina, Brazil, Costa Rica, Ecuador,

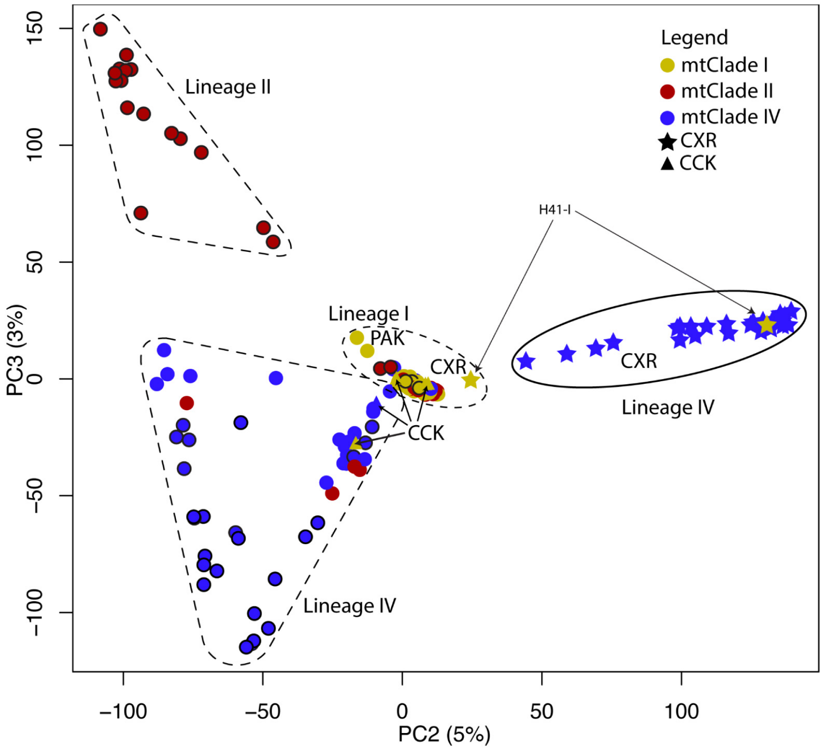

FIGURE 3 | PCA of nuclear SNP marker dataset (showing PC2 vs. PC3). PC2 explains 5% of the variance and PC3 explains 3% of the variance. Colored circles represent the mtClades, with black outlines around circles indicating samples from the native range (i.e., has concordant mtClade/Lineage signatures). The position (and dashed shapes) in PC2 and PC3 represent the nuclear background—LIV samples from their native range are more likely to represent concordant mtClade IV/Lineage IV samples, LII samples from their native range more likely represent concordant mtClade II/Lineage II samples, LI samples from their native range are more likely to represent mtClade I/Lineage I samples. The divergent Christmas Island LIV samples are outlined in an oval in the middle right-hand side of the figure.

France, Guinea, Iran, Israel, Morocco, Netherlands, Tunizia, Turkey, and United States; see **Supplementary Figure 3**). The geographic sampling that we added to the mtClade I dataset also identified a second "ship rat" sub-group that was found in a more limited set of worldwide locations (Australia, Comoros, India, Indonesia, Malawi, Mozambique, Oman, Tanzania, United States, and Yemen; see **Supplementary Figure 3**). Not surprisingly, the more basal and central haplotype nodes of this "ship-rat 2" sub-group were found in India (home range of mtClade I).

Five mtClade IV sequences (haplotypes = 2) were found across two islands: Direction Island ($n = 1$) and West Island ($n = 4$) (**Supplementary Figure 5**). The most common mtClade IV haplotype ($n = 3$, H6-IV) is also found in Sri Lanka, while the rarer mtDNA haplotype ($n = 1$; H4-IV) is not found elsewhere amongst our sampling locations (**Supplementary Figure 5**). Not surprisingly, the diversity of each of these mtClades were also considerably lower than in our reference dataset but higher than those found on CXR (**Table 1**). There was also no evidence of significant demographic population expansions for either each CCK mtClade separately, nor for all the CCK samples taken together (non-significant Tajima's D and Fu and Li's F*, **Table 1**).

Nuclear Genome Diversity

When we compared the nuclear dataset for the 11 CCK samples to those of mtClade I and mtClade IV groups from around the world ($n = 153$) using principal component analysis (PCA) and structure analysis for 32,568 loci, we were able to see distinct patterns that help identify the likely source location from where the CCK RrC originated.

Principal Component Analysis

There are approximately even numbers of concordant and discordant mito-nuclear RrC samples found on CCK. From the 11 samples, five were found to be concordant mtClade I/Lineage I with one concordant mtClade IV/Lineage IV sample, and five samples had discordant mito-nuclear patterns (one mtClade I/Lineage IV and four mtClade IV/Lineage I). The only discordant mito-nuclear sample without nearby samples on the PCA (**Figure 2**) is the mtClade I/Lineage IV CCK sample (ABTC118517 from Direction Island), which has a PC1 value half-way in between the cluster that includes the mtClade IV/Lineage IV sample from CCK (ABTC118515 from Direction Island)/Philippines/Cambodia/Malaysia (i.e., mostly introduced range for the RrC LIV taxon) vs. the other mtClade IV/Lineage IV samples from Vietnam, Thailand, Laos, Philippines, Malaysia, and Singapore (i.e., mostly native range for the RrC LIV taxon). When we examine the other discordant mito-nuclear samples, we find the four mtClade IV samples that cluster with what is otherwise considered a Lineage I background (ABTC123583, ABTC127862, ABTC130621, and ABTC137789) are all from

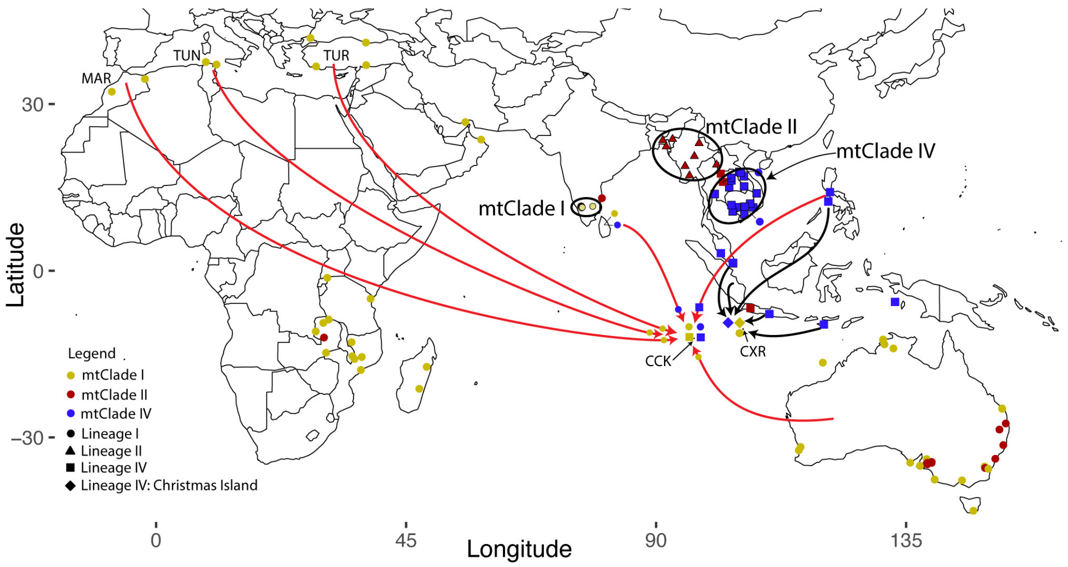

FIGURE 4 | Map showing samples sequenced for both the *cytochrome b* mtDNA gene and the nuclear SNP markers. Colors represent the mtDNA signals (mtClades) and shapes represent the nuclear signals (Lineages). The black ovals outlining the shapes represent concordant mtClade/Lineage samples (and so represent the native ranges of these RrC taxa). Arrows indicate possible sources of rodents on CCK and CXR based on similarities in either mtClade haplotypes and/or nuclear Lineages (as discussed in the text). The black arrows represent evidence from purely "mtClade" information, the red arrows represent evidence from both "mtClade" and nuclear "Lineage" information. The red arrows have a symbol near their head that represents the "mtClade" (color) and "Lineage" (shape) of the link between the source and sink population.

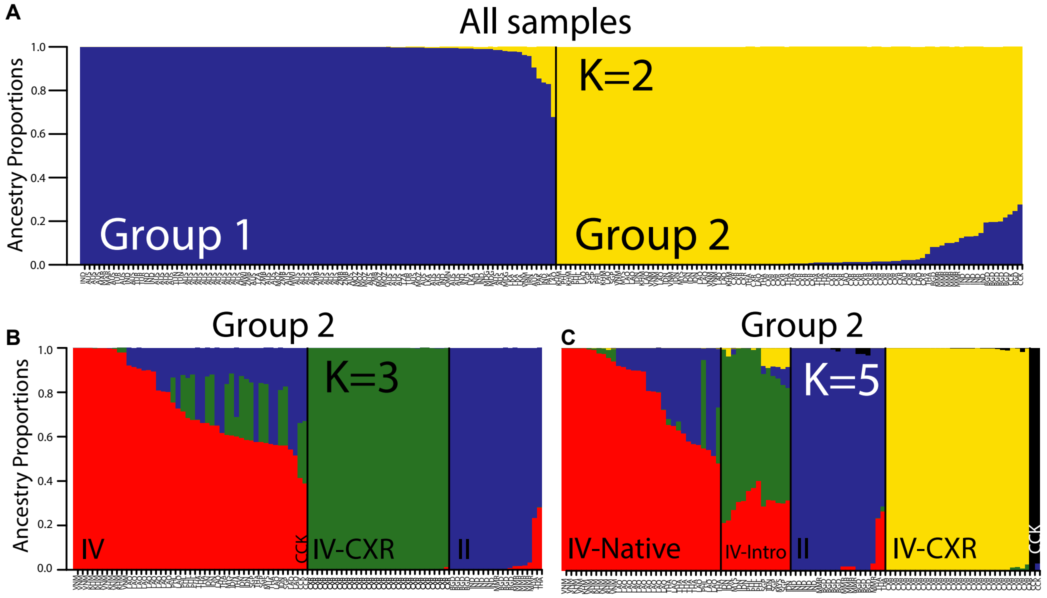

FIGURE 5 | Structure analysis for the nuclear SNP marker (RAD-seq) dataset for **(A)** all samples; **(B)** $K = 3$ using the nuclear SNP marker dataset for Group 2 identified in **(A)**; and **(C)** $K = 5$ using the nuclear SNP marker dataset for Group 2 identified in **(A)**. Each bar represents a sample, and each color represents an ancestral group. The main split in **(B)** represents Lineage IV from CXR vs. Lineage II (mito-LII/nuc-LII from native ranges, i.e., Bangladesh [*n* = 7], India [*n* = 5], Myanmar [*n* = 5], Thailand [*n* = 2]) vs. Lineage IV from both native and introduced range (Lineage IV from Cambodia [*n* = 5], Laos [*n* = 14], Thailand [*n* = 6], Vietnam [*n* = 6] and the Philippines [*n* = 1], CCK [*n* = 2], Indonesia [*n* = 6], Malaysia [*n* = 2], the Philippines [*n* = 3], Singapore [*n* = 3]). The two CCK samples are labeled. The main split in **(C)** represents Lineage IV from Christmas Island vs. Lineage IV from CCK vs. Lineage II (mtClade II/Lineage II from native ranges, i.e., Bangladesh [*n* = 7], India [*n* = 5], Myanmar [*n* = 5], Thailand [*n* = 2]) vs. native range Lineage IV (Lineage IV from mainly native range locations, i.e., Cambodia [*n* = 5], Laos [*n* = 14], Thailand [*n* = 6], Vietnam [*n* = 6] and the Philippines [*n* = 1]) vs. Lineage IV from introduced range locations (i.e., Indonesia [*n* = 6], Malaysia [*n* = 2], the Philippines [*n* = 3], Singapore [*n* = 3]).

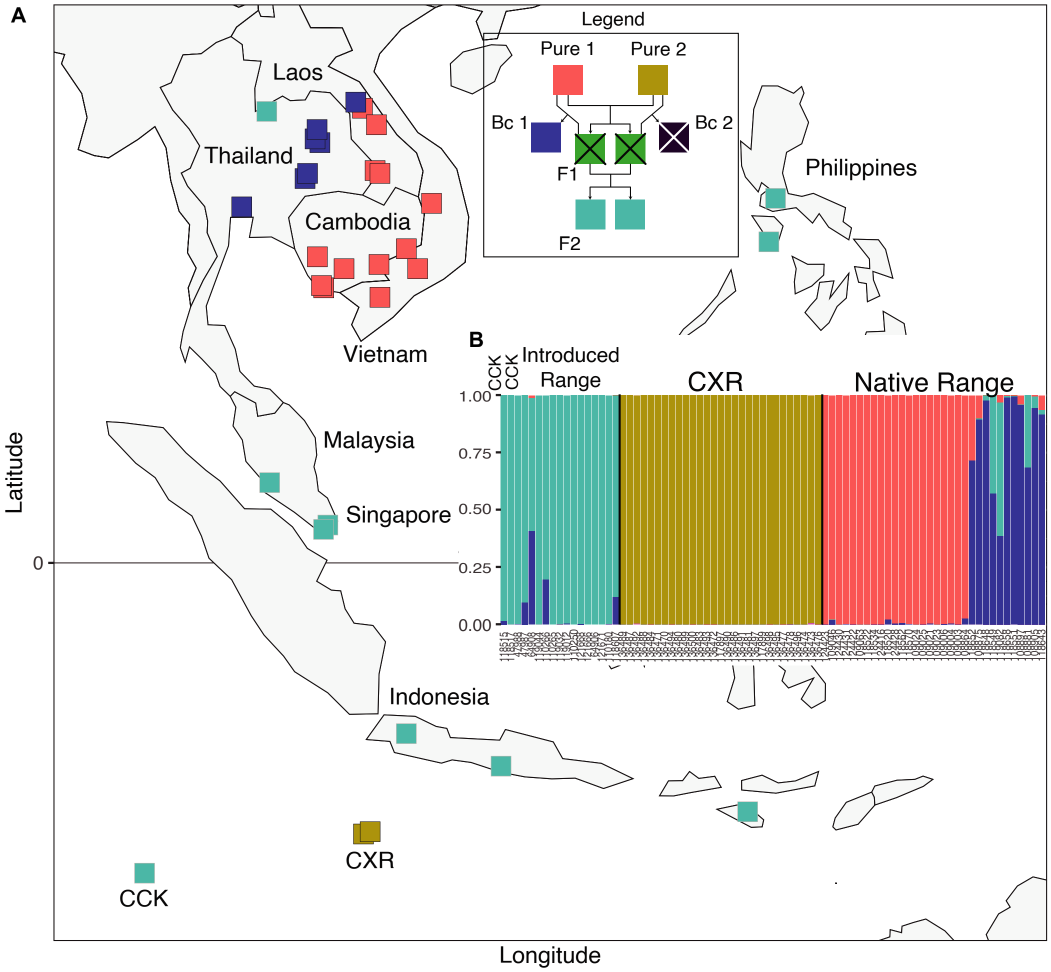

FIGURE 6 | Hybridisation analysis with **(A)** map showing the sample locations with pure 1 ancestry, pure 2 ancestry, backcross 1 ancestry, and F2 ancestry (legend shows how each of these types of hybrids are related); and **(B)** plot showing hybridisation ancestry for nuclear SNP marker dataset for those samples with Lineage IV nuclear signatures (Group 2 identified in **Figure 5** but excluding Lineage II). Each bar in **(B)** represents a sample, and each color represents a hybridisation type (crossed out hybridisation types in the legend represents those absent from the dataset).

West Island and they fall with samples from other locations on the PCA (Australia, multiple countries in Africa, the Middle East, and South Asia; summarized in **Table 2**), suggesting these locations might be the source of these mismatched samples (i.e., the rats arrived with the discordant mito-nuclear genome from an introduced range location). These results highlight how mtDNA capture of both mtClade I and mtClade IV by the other nuclear background is quite common (5/11 = 46% of the CCK samples are discordant mito-nuclear RrC samples).

In the Group 2 PCA analysis (**Figure 7**), we see the two Lineage IV CCK samples fall in the center of the PCA close to two of the concordant mtClade II/Lineage II samples. These two mtClade II/Lineage II samples also appear in the center of the first PCA analysis (**Figure 2**) suggesting they might actually have Lineage I nuclear backgrounds. However, these two samples still fall within Group 2 of the main structure analysis (the other Lineage II samples are in Group 2; **Figure 5A**) and Lineage II of the K = 3 and K = 5 Group 2 structure analyses (**Figures 5B,C**).

Structure Analysis

In the K = 5 structure plot (**Figure 5C**), the only sub-group that is further split apart from the K = 3 analysis is the non-CXR Lineage IV samples, where a group of mostly native range Lineage IV samples (i.e., Cambodia [*n* = 5], Laos [*n* = 14], Thailand [*n* = 6], Vietnam [*n* = 6], and the Philippines [*n* = 1]) split from the rest of the introduced range Lineage IV samples (i.e., Indonesia [*n* = 6], Malaysia [*n* = 2], the Philippines [*n* = 3], Singapore [*n* = 3]), and the few CCK Lineage IV samples form a third new group.

Contrasting Mitochondrial vs. Nuclear Signals to Identify Source Populations

When we search for a source population by comparing locations with similar mtDNA (same or similar mito-haplotypes) and nuclear backgrounds (within ± 10 PC1/PC2 values), we see that four concordant mtClade I/Lineage I samples have the exact same mito-haplotype (H1-I) and similar nuclear backgrounds

TABLE 2 | Summary table of sample numbers for overlapping mtDNA and nuclear datasets to examine source locations for Christmas Island and Cocos-Keeling Island RrC rodents.

Population	# of samples	mtClade haplotype	Source pops (mtDNA only)	Nuclear Lineage	Source pops (nuclear only)	Common source pops (mtDNA and nuclear)
Christmas Is.	1	HAP 41-I	–	LI	–	–
Christmas Is.	1	HAP 41-I	–	LIV	–	–
Christmas Is.	3	HAP 1-IV	Philippines (2), Singapore (1), Indonesia (1)	LIV	–	–
Christmas Is.	25	HAP 66-IV	Indonesia (Java and Sumba; 2)	LIV	–	–
Cocos-Keeling Is.	4	HAP 1-I	Australia (8), Turkey (2), Tunisia (1), Morocco (2)	LI	Australia (28), Mozambique (7), Turkey (3), Zimbabwe (6), Malawi (1), Tunisia (2), South Africa (1), Oman (1), Sri Lanka (3), Madagascar (2), India (2), Iran (1), Morocco (1)	Australia (7), Turkey (2), Tunisia (1), Morocco (1)
Cocos-Keeling Is.	1	HAP 40-I	–	LI		–
Cocos-Keeling Is.	4	HAP 6-IV	Sri Lanka (3)	LI	Sri Lanka (3)	Sri Lanka (3)
Cocos-Keeling Is.	1	HAP 35-IV	Lao (1)	LI		–
Cocos-Keeling Is.	1	HAP 65-IV	Vietnam (1)	LI		–
Cocos-Keeling Is.	1	HAP 1-IV	Philippines (2), Singapore (1), Indonesia (1)	LIV	Cambodia (2), Philippines (1), Malaysia (1)	Philippines (1)
Cocos-Keeling Is.	1	HAP 4-IV	–	LIV		–

as seven samples from mainland Australia, two from Turkey, and one each from Tunisia and Morocco. Only one of the four discordant CCK mtClade IV/Lineage I samples had PC values close to other locations, namely three mtClade IV/Lineage I samples from Sri Lanka, although all four do also share the same mito-haplotype (HAP 6-IV) as the three Sri Lankan samples. Three of these four CCK mtClade IV/Lineage I samples form a cline away from the closest Sri Lankan samples in the PCA, suggesting genetic drift away from this potential source population (although to a much weaker degree than the genetic drift occurring on CXR). However, the fourth CCK mtClade IV/Lineage I sample did not have any close mito-nuclear matches. The mtClade I/Lineage I sample (ABTC123580) closest to the middle of the main PCA plot (**Figure 2**) does have a similar nuclear background to a range of potential source locations (Australia, India, Madagascar, and Morocco), however, none with the same or similar mito-haplotype (4 bp different to a sample from Madagascar: HAP 40-I vs. HAP 27-I). The closest source location for the concordant mtClade IV/Lineage IV sample from CCK (ABTC118515) was a mtDNA sample from Malaysia but the mito-haplotype differed by 3 bp (HAP 4-IV vs. HAP 9-IV).

DISCUSSION

Source Population of RrC on CXR

By incorporating both mtDNA and nuclear datasets, we can see how each of these Indian Ocean island groups have quite distinct colonization histories and degree of gene flow for the RrC samples (see **Figure 4**). Although there are no shared mitochondrial or nuclear haplotypes between CXR and CCK the fact that the sole CXR mtClade I haplotype (found in two individuals) is only two mutations different from a CCK mtClade I haplotype suggests some level of gene flow between the two island groups may have occurred. One of these CXR mtClade I haplotype samples has also had it's mitochondrial genome captured by a RrC individual with the divergent CXR Lineage IV nuclear background, suggesting that hybridisation event occurred on CXR. We can also see suggestions of at least one source of the other mtClade groups introduced to CXR, Indonesia: HAP 1-IV (found on Flores and Kei Besar islands), HAP 66-IV (Java and Sumba islands), and HAP 77-II (Java) are all present on different Indonesian islands.

The highly divergent nature of the CXR samples also makes identifying a source population difficult in that all the CXR RrC appear to have undergone isolation and possible drift since introduction, although it is nearly impossible to predict whether the divergent Lineage IV sub-group represents huge levels of genetic drift or simply a lack of sampling of the source population. There is no evidence of a post-bottleneck population expansion from the *cytb* dataset which is unusual for a population colonizing an island, suggesting that either a large initial RrC population colonized the island or there was a sustained influx of subsequent gene flow. When we search for a source population for the CXR samples by comparing locations with similar mtDNA and nuclear backgrounds, we see that none of the CXR samples had any similar nuclear signal to our set of reference samples (based on the PCA in

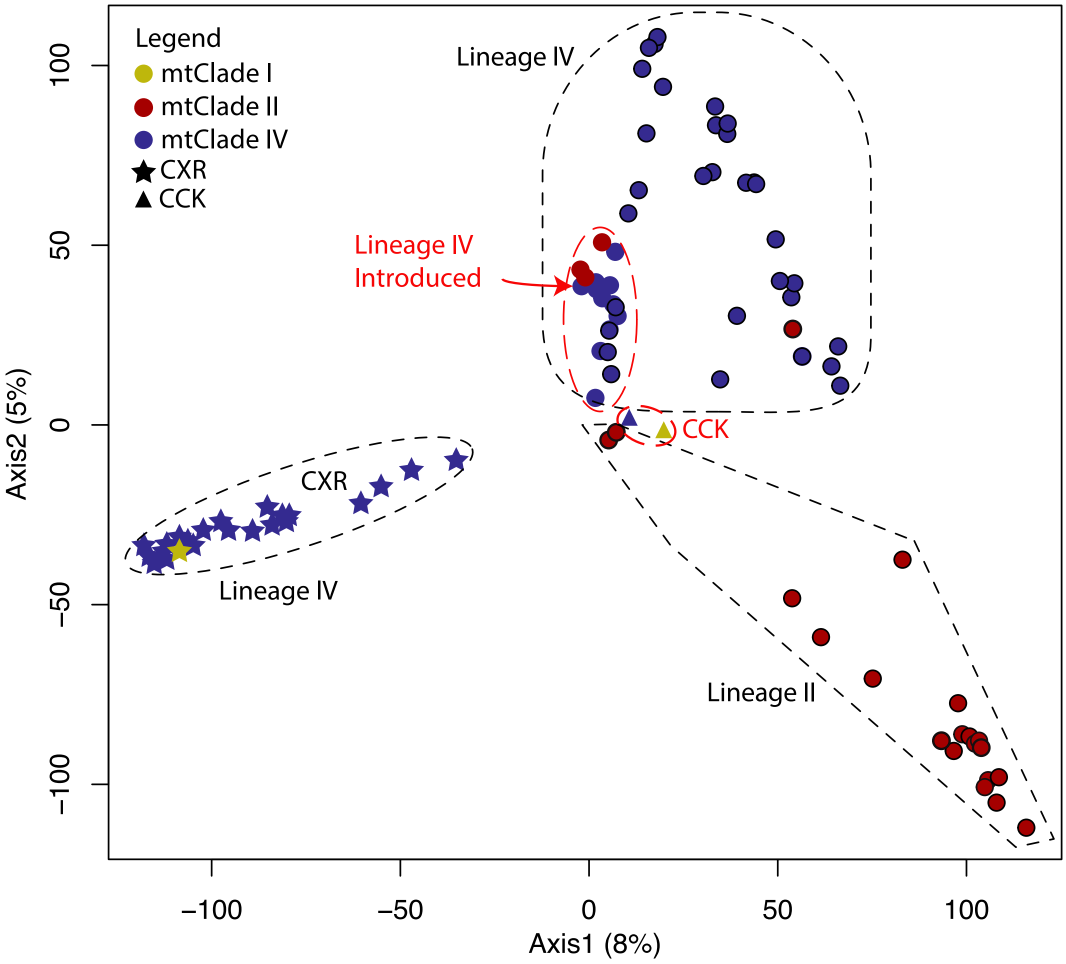

FIGURE 7 | PCA of nuclear SNP marker dataset for Group 2 identified in **Figure 5**. PC1 explains 8% of the variance and PC2 explains 5% of the variance. Colored circles represent the mtClades, with black outlines around circles indicating sample was found within the native range. The dashed shapes in PC1 and PC2 represent the populations identified in the structure analysis of Group 2—K = 3 sub-groups indicated by black dashed outlines and the two extra sub-group identified in K = 5 are indicated in red dashed outlines. The native range Lineage IV samples that fall within the red dashed "Lineage IV Introduced" outline actually fall with the other Lineage IV native range samples in the K = 5 structure analysis (i.e., the ancestry patterns identified in the structure analysis do not correspond to the clustering analysis found in this principal component analysis).

Figure 2). Hybridisation analysis suggests that the ancestral event that created the divergent CXR Lineage IV sub-group is either not recent or did not occur on Christmas Island. When we examine the hybridisation history of the Lineage IV samples from CXR compared to the rest of the Lineage IV samples, we see clear evidence of the CXR Lineage IV samples having pure ancestry from a core mainland population not present in our samples ("Pure 2" in **Supplementary Table 5**). In addition, the fact that the "F2" hybrids (two generations away from "Pure 2" samples) were found in Indonesia, Malaysia, Philippines, Singapore, and Thailand (RrC LIV taxon's introduced range; **Figure 6**), and the "Backcross 1" (backcrosses with "Pure 1" that are also two generations away from "Pure 2" samples) were found in Laos and Thailand (RrC LIV taxon's native range), suggests that there is some sort of continuous gene flow from the core range of the ancestral "Pure 2" population (if not from CXR, then from wherever that is located). The link between CXR and introduced range locations is further supported by the structure analysis, which shows that concordant mtClade IV/Lineage IV samples from CXR contain minor levels of ancestry from Lineage IV's introduced range locations. Sampling more widely across the introduced range locations (especially islands of Indonesia) may identify a single source population that contains all of the currently sampled mtClade haplotypes, the third mtClade haplotype (the rare HAP 41-I currently unsampled outside of CXR), and nuclear signals that either match the CXR samples or are similar enough to have given rise to them followed by genetic drift.

Dating the Arrival of RrC on CXR

By examining the ancient DNA samples from CXR we were hoping to be able to date the arrival of RrC on the island. The lack of amplifiable DNA from the lower layers of CXR deposits meant that this was not possible. In addition, the presence of other *Rattus* species on the island (although *R. macleari* and *R. nativitatis* are both now extinct) means that we cannot necessarily assume rodent bones/teeth from the lower layers belong to RrC. Therefore, we are still unsure of when RrC originally arrived on CXR. We do know that between 1900 and 1903 there were only mtClade I detected on CXR (7 out of 7 samples sequenced for *cytb;* Wyatt et al., 2008), however, this doesn't appear to be the case any longer, both from the modern and ancient/historic sample perspective. Not only are 3 of the 4 (75%) of the ancient DNA samples mtClade IV vs. mtClade I, but the majority of modern CXR tissue samples from this study were found to be mtClade IV (92%; 46 out of 50 samples) and of the 30 samples that were sequenced for nuclear SNPs almost all (97%; 29 out of 30 samples) showed a unique and divergent nuclear Lineage IV background. This highly divergent population of Lineage IV may represent the original RrC to colonize the island, which may have been isolated from subsequent gene flow to the island since: (1) its original colonization (if we assume Lineage IV was simply missed in the early 1900's collections, Wyatt et al., 2008); or (2) the early 1900's (if we assume replacement of mtClade I with mtClade IV has occured in the intervening 120 years, Wyatt et al., 2008), with either the source population of this divergent Lineage IV unsampled in our study or now absent from its original location.

Mitochondrial (mtDNA) Capture on CXR

In addition to these signatures of isolation of the CXR nuclear gene pool, the fact that there is a "rare" mtClade haplotype shared between a mtClade I/Lineage I and a mtClade I/Lineage IV sample from CXR suggests that at least one instance of mtDNA capture of mtClade I by RrC with a nuclear Lineage IV background occurred on CXR. It appears from our reference dataset that mtDNA capture is widespread in the RrC, with almost every combination found: mtClade I/Lineage II, mtClade I/Lineage IV, mtClade II/Lineage I, mtClade II/Lineage IV, and also mtClade IV/Lineage I (**Figure 2**). These mitochondrial captures are obvious signs of hybridisation events between RrC taxa that may never have previously had contact in the wild.

Cocos-Keeling Islands (CCK)

Source Locations for RrC on CCK

When examining the mtDNA patterns for evidence of source populations for RrC on CCK, we see plenty of possible locations, but only a couple have multiple lines of evidence for Lineage I sources (i.e., both mtDNA and nuclear links): Australia, North Africa/Middle East, South Asia (**Table 2**). The link between CCK and Australia is not unexpected given that the administrative responsibility for CCK was transferred to Australia in 1955. Links to these other possible source locations are also backed up by historical records. Operation Pharos during World War II, which involved the construction of a secret airfield and base on West Island during 1944–1945 (Rosum, 2000), may explain the link between these sites in North Africa and the CCK (**Figure 4**). Furthermore, troops from Sri Lanka were also stationed in CCK during World War II (Crusz, 2001), potentially explaining the Sri Lankan link.

The most parsimonious explanation for the two similar CCK Lineage IV samples is that they stem from one introduction to CCK, therefore we may be looking for one source population containing both concordant mtClade IV/Lineage IV and discordant mtClade I/Lineage IV RrC. If we only consider the more nuanced nuclear data to identify this source population (given their higher information content compared to the mtDNA *cytb* 945 bp sequenced here) and assume that capture of the mtClade I genome actually occurred in the source population rather than on CCK then we see that there are a limited number of possible sources. Based on the shipping history of CCK we propose that Island Southeast Asia, specifically the Philippines, is the most likely source population. It is possible that both the concordant mtClade IV/Lineage IV and the discordant mtClade I/Lineage IV CCK RrC originated there, so focused sampling effort may locate the source of the CCK RrC. The high degree of mitochondrial capture that we find on CCK between the RrC taxa does not support historical claims by Wood-Jones (1909) that the "original" rat, *R. rattus keelingensis* (now suspected to be RrC mtClade I), on Direction Island remained separated from other races of rats found in the main CCK atoll. Rather, the speculative accounts provided in the Colonial Reports (Straits Settlement, 1897) of multiple rat introductions from various shipwrecks, trade and local transport between the islands appears to more accurately represent the complex history of RrC in the eastern Indian Ocean.

Comparing CXR and CCK

Although there are no shared mitochondrial or nuclear haplotypes between CXR and CCK the fact that the sole CXR mtClade I haplotype is only two mutations different from a CCK mtClade I haplotype suggests some level of gene flow may have occurred. The F2 hybrids detected in the CCK Lineage IV samples (i.e., two generations away from the "Pure 2" samples from CXR) might also suggest some level of gene flow between the two island groups. However, this line of evidence suggests the same level of gene flow between CXR and many Indonesian islands (*via* the presence of F2 hybrids), which is unlikely given there is no evidence of the CXR divergent nuclear signature present in Indonesia.

In fact, the most parsimonious explanation for the observed mitochondrial and nuclear DNA patterns is a direct link between introduced range Lineage IV locations and CCK but an indirect or older link between introduced range Lineage IV locations and CXR. The RrC gene flow to these eastern Indian Ocean islands may be historic and stem from trade in the late 1600's between these two island groups (e.g., ships called in at CXR from CCK and Jakarta as resupply to the Clunies Ross family and workers living there, Gibson-Hill, 1949).

Disease Implications

The mitochondrial capture documented here has implications for the zoonotic diseases that each RrC taxa may carry, with novel interactions potentially creating completely new infectious agents. As many of the modern RrC samples from CXR and CCK were found in association with built up areas (houses, offices, sheds, etc.), any novel zoonotic diseases created by these hybridisation events has the potential to cross over to the humans. Given much of the disease work done linking zoonotic diseases to their rat-hosts is likely to have been conducted prior to our understanding of the complexities of the RrC, little knowledge exists about which RrC taxa actually act as hosts for these black rat zoonotic diseases. This makes it difficult to predict how new interactions between these RrC taxa outside of their native ranges might influence any recombinant or novel zoonotic diseases capable of crossing the species barrier to humans.

CONCLUSION

We conclude that there were multiple introductions of RrC black rats to the Christmas Islands (CXR) and the Cocos-Keeling Island (CCK) groups in the eastern Indian Ocean. This is not surprising given the islands offer a land refuge between Indonesia and Australia, evidenced by the common arrival of asylum seeker vessels to the islands. While we know less about the genetic history of RrC on CCK (no previous genetic work and no ancient samples), we were able to identify that there were at least two (and possibly three) separate introductions of RrC to CCK: an introduction from Australia, Morocco, Tunisia or Turkey, an introduction from Sri Lanka, and possibly a mixed introduction from the Philippines containing both concordant mtClade IV/Lineage IV and discordant mtClade I/Lineage IV, based on common locations for the mtDNA and nuclear signatures. We find evidence from the mtDNA data that Indonesia is the most parsimonious source for the rodents on CXR although no sign of that introduction pathway is evident in our nuclear analysis. Sampling from the islands of Indonesia and the Philippines (for more recent source populations) and mainland Southeast Asia (for ancestral native range source populations of Lineage IV) may help further elucidate the colonization history of the RrC on CXR and CCK.

Genetic drift also appears to have impacted the RrC on CXR to a large degree but not as strongly on CCK, possibly due to the mixing between RrC on the different islands within the CCK group. These different genetic patterns allow us to establish that little recent gene flow has occurred between CXR and CCK. However, the evidence presented here does show how these multiple introductions of such an invasive pest species to a remote island has important implications for the biosecurity of neighboring countries, including Australia with its many unique and endemic taxa. Without more information about the timing of these introductions from the different locations (either through regular trapping and sampling of RrC and/or carbon dating of individual bones/teeth that also produce DNA) we can only speculate about how often and in what sort of numbers RrC are still making their way to CXR and CCK.

We also find extensive evidence of bi-directional mtDNA capture between RrC Lineage I/RrC Lineage IV and RrC Lineage I/RrC Lineage II, but also uni-directionally of mtClade II by Lineage IV. These mtDNA capture events appear to have occurred in both source populations and on CXR. These signals of mito-nuclear discordance represent hybridisation events that have important zoonotic disease implications, a particularly timely reminder that commensal pest species can act as both reservoirs and vectors of dangerous and potentially novel diseases.

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The *cytochrome b* data presented in the study are deposited in the NCBI Genbank repository, accession numbers OL865449-OL865582. The RAD-seq raw data presented in the study are deposited in the NCBI SRA repository, under BioProject PRJNA788573 and accession numbers SAMN24011995-SAMN24012184.

ETHICS STATEMENT

Ethical review and approval was not required for the animal study because all samples were sourced from existing tissue collections associated with museum collections.

AUTHOR CONTRIBUTIONS

KA, AW, and SD contributed to the conceptualization, investigation and design of the study. AW, MH, SM, TB, and VT performed the statistics, analysis and were responsible for data validation. HS, RP, NH, DA, CP, HM, GC, PP, and AA provided resources to carry out the work. SD and KA were responsible for the administration and supervision of the research project. VT, KA, and AW wrote the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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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.2021.786510/full#supplementary-material

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Rain Forest Fragmentation and Environmental Dynamics on Nosy Be Island (NW Madagascar) at 1300 cal BP Is Attributable to Intensified Human Impact

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Madagascar houses one of the Earth's biologically richest, but also one of most endangered, terrestrial ecoregions. Although it is obvious that humans substantially altered the natural ecosystems during the past decades, the timing of arrival of early inhabitants on Madagascar as well as their environmental impact is still intensively debated. This research aims to study the beginning of early human impact on Malagasy natural ecosystems, specifically on Nosy Be island (NW Madagascar) by targeting the sedimentary archive of Lake Amparihibe, an ancient volcanic crater. Based on pollen, fungal spore, other non-pollen palynomorph, charcoal particle and diatom analyses combined with high-resolution sediment-physical and (in)organic geochemical data, paleoenvironmental dynamics during the past three millennia were reconstructed. Results indicate a major environmental change at ca. 1300 cal BP characterized by an abrupt development of grass (C_4) dominated and fire disturbed landscape showing the alteration of natural rain forest. Further, increased soil erodibility is suggested by distinct increase in sediment accumulation rates, a strong pulse of nutrient input, higher water turbidity and contemporaneous increase in spores of mycorrhizal fungi. These parameters are interpreted to show a strong early anthropogenic transformation of the landscape from rain forest to open grassland. After ca. 1000 cal BP, fires remain frequent and vegetation is dominated by forest/grassland mosaic. While natural vegetation should be dominated by rain forest on Nosy Be, these last results indicate that human continuously impacted the landscapes surrounding the lake. At a local scale, our data support the "subsistence shift hypothesis" which proposed that population expansion with development of herding/farming altered the natural ecosystems. However, a precise regional synthesis is challenging, since high-resolution multi-proxy records from continuous sedimentary archives as well as records located further north and in the hinterland are still scarce in Madagascar. The lack of such regional synthesis also prevents precise comparison between different regions in Madagascar to detect potential (dis)similarities in climate dynamics, ecosystem responses and anthropogenic influences at the island's scale during the (late) Holocene.

Keywords: maar lake, soil erosion, palynology, charcoal, diatom, sedimentology, leaf-wax *n*-alkanes, paleoenvironment

INTRODUCTION

Environmental change is a consequence of various kinds of causes. For one thing, natural factors are driving climate and environmental dynamics, however mostly on longer (millennial/orbital) time-scales. These natural, long-term dynamics are recently challenged by a global overprint of direct human impact on all compartments of nature, most obviously seen in increasing rates of loss in biodiversity. Also during past millennia, human impact has triggered environmental change and biodiversity loss, however only on local or regional scale. In this context the conservation of natural ecosystems and biodiversity is one of the greatest challenges of the 21st century (IPCC, 2021). The key to estimate future developments of ecosystems and to improve conservation strategies is, to study and disentangle past human impact and natural factors of climate and environmental dynamics. This is especially important in "closed" and "isolated" environments such as islands which generally harbor endemic and vulnerable biodiversity (Nogué et al., 2017, 2021; Whittaker et al., 2017; Wood et al., 2017). In tropical to subtropical regions, islands and their ecosystems were frequently impacted by human colonization (Burney, 1997; Kahn et al., 2015; Gosling et al., 2017; Castilla-Beltrán et al., 2019; de Nascimento et al., 2020). Without written archives, paleorecords (e.g., from lake sediments, speleothems, peatbogs) are one of the best tools to assess human impact in the past (Battarbee and Bennion, 2011; Garcin et al., 2018a; Wang et al., 2019). However, the distinction between natural and human induced ecosystem shifts within these archives can be challenging. Human activities, such as deforestation or artificial fire, which lead to a loss of trees can easily be mixed up with natural effects like very dry climatic conditions (e.g., Clist et al., 2018; Garcin et al., 2018b; Maley et al., 2018; Bayon et al., 2019). Madagascar, characterized by one of the world's biologically richest ecosystems, does not deviate from this rule. Early human colonization and its impact on natural environmental changes of this island has been intensively debated for decades (Burney et al., 2003; Virah-Sawmy et al., 2010; Dewar et al., 2013; Anderson et al., 2018; Anderson, 2019; Godfrey et al., 2019; Crowley et al., 2021). Whereas initial settlement of Madagascar prior to 2000 cal BP still remains poorly resolved (Dewar et al., 2013; Anderson et al., 2018; Hansford et al., 2018; Douglass et al., 2019), recent studies on speleothems from northwestern Madagascar suggested that a major ecosystem shift, recorded at ca. 1250-1200 cal BP, was the result of an abrupt transition in human subsistence strategy (Burns et al., 2016; Voarintsoa et al., 2017; Railsback et al., 2020). The "subsistence shift hypothesis," that consists to the transition from hunting/foraging to herding/farming, has been proposed by Godfrey et al. (2019) to explain the observed changes. Specifically, this transition would have affected habitats by strongly increasing fire frequency which triggered a rapid expansion of grassland at the expense of forest. In addition, population expansion and hence increased anthropogenic impacts, as well as introduction of livestock (Dewar and Wright, 1993) is assumed to have led to destruction of natural wildlife habitats and finally may have caused the extinction of Madagascar's megafauna (Crowley, 2010). Recent studies on the herbivore's diet support various competition factors between endemic and introduced fauna superimposed by environmental change as the main reasons for endemic extinctions (Hixon et al., 2021b,a). Despite these significant advances, disagreements still remain between studies from different regions, regarding the timing and intensity of changes, and the respective interrelation between humans and climate (e.g., Burney, 1987; Matsumoto and Burney, 1994; Virah-Sawmy et al., 2010; Anderson et al., 2018; Godfrey et al., 2019). In order to improve our understanding of this critical and complex transition, it is a necessity to increase spatial resolution of paleoenvironmental study sites to provide new data. Furthermore, the reanalyzes of previously studied sites with more detailed analyses are important as they can improve chronologies, add new proxies or increase the spatial or temporal data-resolution.

In this context, the present study focuses on Lake Amparihibe from Nosy Be island first studied by Burney (1999) and Burney et al. (2003). Previous results showed an increase in fire activity with a rise of *Sporormiella* at 1130 ± 50 ^{14}C BP which corresponds to a calibrated age [Calib 8.20 (Stuiver and Reimer, 1993) using the SHCal20 curve (Hogg et al., 2020)] of 1000 $^{+180}/_{-90}$ cal BP. This was interpreted as human transformation of the local landscape with the development of agriculture (e.g., rice) and first introduction of livestock (cattle, goats and sheep) on Nosy Be by Islamized Indian Ocean traders (Burney et al., 2003; Wright and Radimilahy, 2005). This site therefore represents a key record to illustrate human induced environmental change for the northwestern region of Madagascar and is frequently used as a benchmark for regional comparisons (e.g., Railsback et al., 2020). However, chronological control of this study is quite poor (two radiocarbon dates), and detailed study of sedimentological changes and past vegetation dynamics have not been published. To refine previous analyses and close these obvious gaps, Lake Amparihibe was once more targeted, especially as this site also exhibits excellent conditions to provide a high-resolution record of paleoenvironmental change. Lake Amparihibe represents a deep crater lake (ca. 50 m water depth) making it impervious against desiccation. Thus, it is anticipated that sediments within the lake have continuously recorded past environmental changes in a region where deep lakes are rare, particularly at low elevation. The location of the lake in the northwestern region, close to the coast, makes it also ideal to study initial human impact, since occupation and the establishment of settlements are anticipated to have occurred quite early in this region (Radimilahy, 1997; Dewar et al., 2013; Douglass et al., 2019).

Thus, pollen, fungal spores, other non-pollen palynomorphs (NPPs), macro-charcoal particles and diatom analyses combined with high-resolution sediment-physical and (in)organic geochemical data from Lake Amparihibe will provide an excellent base for comparisons with high-resolution paleoclimate records obtained from speleothems in northwestern Madagascar (Burns et al., 2016; Scroxton et al., 2017; Voarintsoa et al., 2017; Wang et al., 2019; Li et al., 2020; Railsback et al., 2020). Such multiproxy comparisons of different geoarchives are essential for better distinguishing natural from human induced ecosystem shifts in the past.

ENVIRONMENTAL SETTING

The small island of Nosy Be (320 km^2) is located approximately 10 km off the northwestern Madagascar coast (**Figure 1A**). Nosy Be island is formed by a sedimentary bedrock pierced by volcanic vents and plutonic intrusions during the late Cenozoic and Quaternary (14-0.5 Ma; Cucciniello et al., 2016). This activity resulted in an important volcanic complex surrounding the peak of Mt. Passot (329 m a.s.l., western Nosy Be) with lava flows and tuff rings filled by nine freshwater lakes. The largest of these maar lakes, Lake Amparihibe (-13.32°N, 48.21°E, 71 m a.s.l., 163 ha, **Figure 1B**), a sub-circular crater of 1.5 km diameter with steep slopes at the lake shore and ca. 50 m water depth (**Figures 1B,C**), is the target of this study. Its catchment with a size of 713 ha is drained by three major channels, two of them passing the two maar lakes east of the lake (Antsidihy and Maintimaso) and one originating from a third maar lake (Bemapaza). Located on altitudes of 236 m a.s.l. (Bemapaza), 94 m a.s.l. (Antsidihy) and 89 m a.s.l. (Maintimaso) all the lakes are connected hydraulically to Lake Amparihibe forming a lake-cascade and serve as primary sediment traps for a big portion of the catchment (**Figure 1B**).

Climate is tropical sub-humid in northwestern Madagascar, the region surrounding Nosy Be and Ampasindava bay and it corresponds to the most humid area of the west coast of Madagascar. Mean annual temperature is around 25°C without major seasonal variability. Due to its location, precipitation at Nosy Be is affected by the proximity to the ocean (Mozambique Channel, Indian Ocean) with mean annual precipitation ranging around 2000 mm (Hijmans et al., 2005). Precipitation rates show a strong seasonality, with a maximum during austral summer (November to April) including strong summer monsoon rainfalls accompanied by frequent tropical storms or cyclones, related to the southern position of the Inter Tropical Convergence Zone. During austral winter, rainfalls are less and generally related to trade winds.

With a dry season almost absent, the natural vegetation is a subhumid rain forest called Sambirano rain forest (Koechlin et al., 1974). This forest is part of the East-West rain forest corridor distributed between northwestern and northeastern Madagascar (**Figure 1A**). Despite some differences in species composition compared to the forest developed in eastern Madagascar, the main plant families are similar (Koechlin et al., 1974). Among the main tree families are Euphorbiaceae, Rubiaceae, Araliaceae, Ebenaceae, Sapindaceae, Anacardiaceae, Elaeocarpaceae, Lauraceae, Myrtaceae and among the most represented shrub are Ochnaceae, Erythroxylaceae, Myrsinaceae and Celastraceae. Liana and epithetic plants are also well represented by Apocynaceae, Fabaceae, Acanthaceae and Combretaceae. Some families are highly diversified and include many different genera and species, among them are Urticaceae and Melastomataceae. However, due to human impact, natural vegetation on Nosy Be island is now characterized by a secondary complex vegetation including about 14% of rain forest, 41% of wooded savanna, 12% of grasslands and 33% of crops mosaics (Mayaux et al., 2000). Typical trees of secondary forest, such as *Trema orientalis* are now common in the remaining Sambirano rain forest (Rasoanaivo et al., 2015). Close to the study site, west of Lake Amparihibe, the vegetation is dominated by a wooded grassland-bushland mosaic. To the east, vegetation assemblage shows a succession following an altitude gradient up to the peak of Mt. Passot, with a wide spectrum of species from shrub bushland to rain forest (Koechlin et al., 1974; Moat, 2007).

MATERIALS AND METHODS

Pre-site Survey/Hydro-Acoustics

Prior to sediment sampling a shallow seismic survey was conducted to map basin morphology, sediment thickness and structures. A parametric sediment echosounder (SES 2000light, Innomar Technologie) with a primary frequency of 100 kHz and a secondary frequency range of 4 – 15 kHz, depending on the desired resolution and penetration depth was applied. Positioning was provided by GPS (Navilock NEO M8U Multi GNSS UDR Receiver). The echosounder was calibrated to a sound velocity of 1460 ms^{-1} for depth measurements. With these settings, a dense grid of altogether 25 km of profiles were acquired. Final processing of the data was done with the software ISE 2.95 (Innomar Technologie).

Sampling, Water Data, and Chronology

Fieldwork was carried out in November 2016 and based on the shallow seismic survey, two positions within the lake were identified as the most suitable for coring using a gravity coring system (06/2021[1]). AMP16-1 (-13.323917°; 48.209889°) with a total length of 164.5 cm was taken at a water depth of 45 m, ∼300 m apart from AMP16-2 which is 168 cm long and obtained at the deepest part of the lake (-13.322106°; 48.211828°, 50 m water depth) (**Figure 1B**). Concurrently, vertical *in situ*

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[1] http://www.uwitec.at

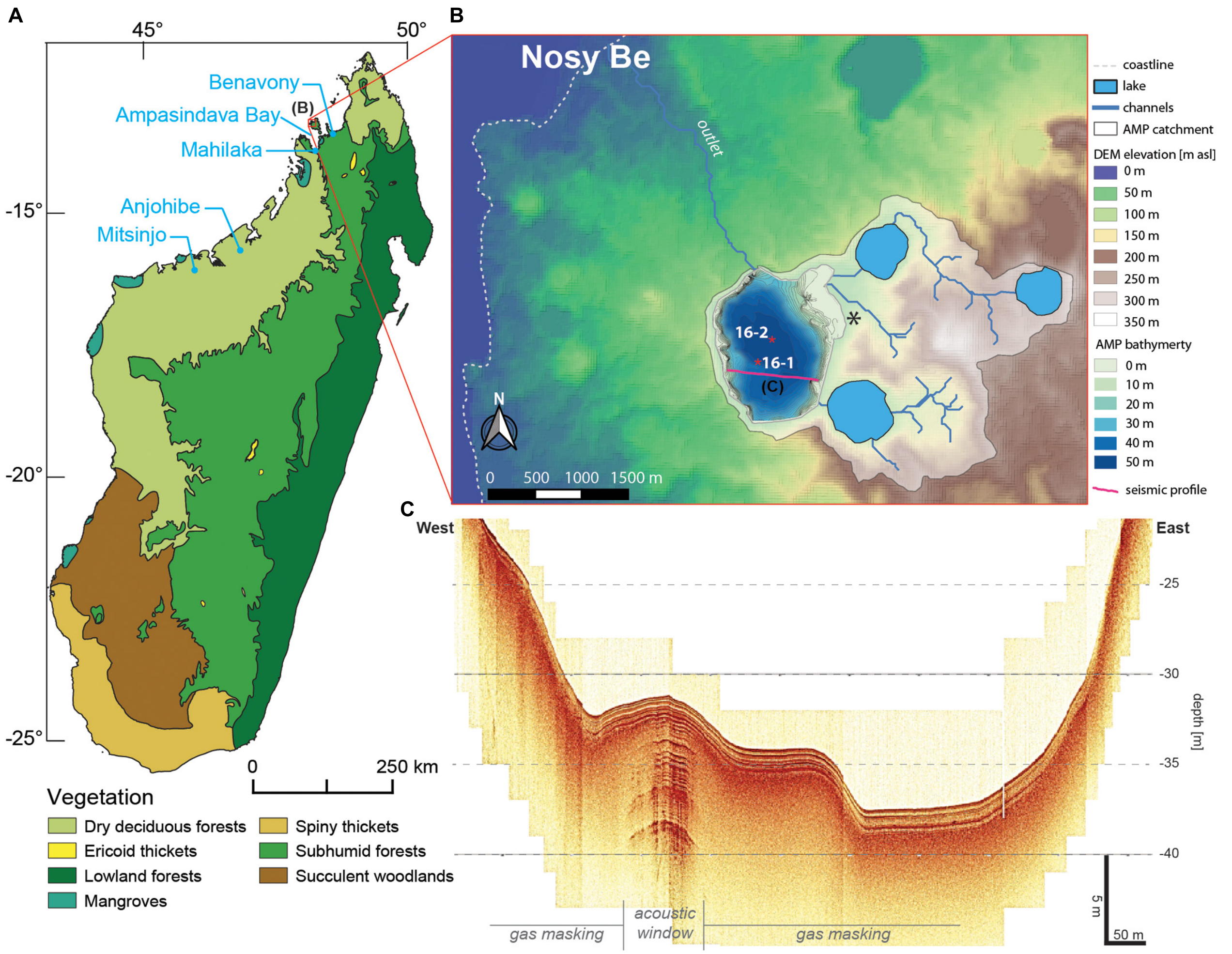

FIGURE 1 | (A) Distribution map of natural biomes in Madagascar (Olson et al., 2001). **(B)** Close up topography of western Nosy Be including the catchment of Lake Amparihibe (AMP), lake bathymetry, coring positions (red stars) and the location of the seismic profile in the lake (purple line) shown in panel **(C)**, as well as an archeological site (black asterisk; Wright and Radimilahy, 2005) (data source: DEM data derived from SRTM 1 arc-second (06/2021 – https://earthdata.nasa.gov/); bathymetric data based on interpolation of seismic profile lines; map creation with QGIS 3.1). **(C)** Typical seismic image of Lake Amparihibe. The uppermost ca. 1.5 m of the deposits show clearly layered sediments, further penetration is only possible within acoustic windows, which show well-layered sediments down to at least 10 m sediment depth. The limited penetration results from widely distributed gas in the sediment most likely due to decomposition of organic matter. A clear basement reflector was not detected.

water parameter measurements were conducted using a WTW MPP 3430 multi parameter probe for pH, dissolved oxygen, conductivity and temperature next to AMP 16-1 (**Figure 1B**). Water transparency was assessed with a Secchi disk. Cores were stored under cool (4°C) and dark conditions at the laboratory facilities (Physical Geography department, Friedrich-Schiller-University Jena, Germany) until further processing. Cores were split, photographed and described following standard protocols. Magnetic susceptibility was scanned in 2 mm steps with three replicate measurements using a MS2E surface scanning sensor (Bartington Instruments). Based on the initial description, both cores showed different sediment accumulation rates with AMP 16-1 obviously reaching farther back in time. However, since previous analyses of AMP 16-1 found hints for a reworked upper part of the core (at least uppermost 20 cm; Haberzettl et al., 2021; **Supplementary Figure 1**), the two cores were aligned and combined to a composite master sequence ("AMP-16") using lithological description, patterns of magnetic susceptibility, and specific marker layers (**Figure 2** and **Supplementary Figure 1**). The most outstanding marker layer, expressed as a 6 mm thick orange-brown fine-grained layer, exhibiting the maximum value in magnetic susceptibility at 99.4 cm core depth in core AMP 16-1, as well as its equivalent layer at 156 cm depth in core AMP 16-2 (**Supplementary Figure 1**) was used as transition depth from AMP 16-2 (=upper part of the composite) to AMP 16-1 (=lower part of the composite).

Due to the lack of plant macro-remains, the age model relies on AMS radiocarbon dating of three bulk sediment samples from each core, performed at either Beta Analytic Inc. (Miami, FL, United States) or the Poznań Radiocarbon Laboratory (Poznan, Poland) (**Table 1**). The age of the sediment surface is anticipated to be modern, and was thus set to the year of coring (AD 2016 = −66 cal BP). The age model was performed as a function the composite depth with the *R*Studio software with the *R*-package "Bacon" (V. 2.5.6) (Blaauw and Christen, 2011) using SHCal20 calibration curve (Hogg et al., 2020).

Sedimentological and Geochemical Analyses

A total of 46 samples were taken at intervals of 2 to 18 cm depending on sediment layering for grain size analyses. Sample aliquots of ~1 g were treated with H_2O_2 (10%, 30%, heated to 80°C for 2 h) to remove organic matter. Subsequently samples were repeatedly washed with deionized water and centrifuged until pH-neutrality. Measurements were carried out using a laser diffraction particle size analyzer (Beckman Coulter LS 13320) applying the Fraunhofer optical model for equivalent particle size diameter calculation. Each sample was measured in seven runs until signal reproducibility. Statistical indices (median size, sorting, particle size fractions) were calculated using a modified version of the MS Excel® Macro Gradistat V4.5s (Blott and Pye, 2001).

A total of 28 samples (ground to particle size $< 40\ \mu m$) were analyzed at a coarser resolution for Total Carbon (TC), which equals total organic carbon (TOC) since all samples were carbonate free (no reaction with HCl), as well as Total Nitrogen (TN), bulk $\delta^{13}C$ and $\delta^{15}N$ and biogenic silica (BiSi). For carbon and nitrogen analyses, as well as their stable isotopic signature aliquots of 15 mg were packed into tin-boats and analyzed by an element analyzer (Vario EL Cube, Elementar) coupled to an IRMS (Isoprime Vision, Elementar). Based on triplicate measurements precision is 0.21% for TC and 0.01% for TN. T(O)C and TN were used to calculate the molar C/N. Bulk organic $\delta^{13}C$ and $\delta^{15}N$ were measured against certified standards (L-Prolin, EDTA and USG65) and reported in standard δ notation (‰) against Vienna Pee Dee Belemnite (VPDB) and Air, respectively. Relative errors based on triplicate measurements are 0.05 ‰ for $\delta^{13}C$ and 0.31‰ for $\delta^{15}N$.

The same set of ground samples was analyzed for biogenic silica following a modified protocol of Ohlendorf and Sturm (2008). Sample aliquots of 40 mg were dissolved using 10 ml NaOH (1 mol l^{-1}) supported by 3 min ultrasonic application and subsequent heating at 100°C for 2 h. Si was measured at sample aliquots (pH set between 1 and 3) using an inductively coupled plasma-optical emission spectrometer (ICP-OES 725-ES, Varian). To account for non-biogenic Si, Al was measured as well, and minerogenic Si was subtracted assuming a Si/Al ratio of 1/1 for dissolved clay minerals.

A total of 21 samples were taken for leaf-wax *n*-alkanes analyses at sampling intervals between 2 and 18 cm. 10 ml dichloromethane (DCM): methanol (MeOH) (9:1) was added to sample aliquots of 1 to 3.4 g dry ground sediments and extraction was carried out using an ultrasonic bath in three 15 min-cycles. The resulting total lipid extract was separated over aminopropyl pipette columns. The *n*-alkanes were eluted with 4 ml hexane. Measurement was carried out using gas chromatography with flame ionization detection (GC-FID) (7890B-GC System, Agilent Technologies) equipped with a HP5MS column (30 m, 320 μm, 0.25 μm film thickness). For identification and quantification an external *n*-alkane standard (*n*-alkane mix nC_{21} - nC_{40}, Supelco) was used. *n*-Alkane concentration was calculated as sum of nC_{21} to nC_{35}. Contributions from aquatic plants can be estimated with the Paq index (C23 + C25)/(C23 + C25 + C29 + C31) following Ficken et al. (2000). The average chain length (ACL), for example based on C_{27}, C_{29}, C_{31} and C_{33}, can be used to characterize the input from the terrestrial higher plants, with longer chains indicating more input from grasses compared to deciduous trees (Poynter et al., 1989; Zech et al., 2010, 2013a,b; Schäfer et al., 2016). We here also adopt an ACL' based on C_{29}, C_{31} and C_{33}, as well as an ACL″ based only on C_{31} and C_{33}.

Paleoecological Analyses

Paleoecological analyses include palynological analyses [counting of pollen grains, fern spores and non-pollen palynomorphs (NPPs)], counting of sedimentary macro-charcoal particles ($>125\ \mu m$) and counting of diatoms. All analyses were performed on the composite master sequence AMP-16 except for diatoms performed solely on core AMP 16-2.

Palynological Analyses

For pollen and spore extraction, 22 samples of 0.5 cm^3 samples at intervals between 5 and 10 cm were prepared following a standard chemical protocol (Faegri and Iversen, 1975; Daniau et al., 2019). Pollen grains and fern spores were counted using a light microscope (Zeiss) at ×400 magnification, and a minimum sum of 300 terrestrial pollen grains were counted for each sample. The references consulted for identification of pollen and spores included several atlases (Straka and Freidrich, 1989; Gosling et al., 2013; Schüler and Hemp, 2016; Rasoloarijao et al., 2019), the online African Pollen Database (06/2021[2]) and the reference collections of University of Göttingen (06/2021[3]) and ISEM (06/2021[4]). Percentages of pollen and fern spores were computed on the terrestrial pollen sum and the pollen record was subdivided into significant zones by applying a constrained cluster analysis by sum of squares performed with terrestrial pollen (CONISS, Grimm, 1987). Fungal spores were counted on pollen slides at an interval varying between 10 and 30 cm. A minimum fungal spore sum of 100-300 was counted for each sample, except for the depth 96 cm where only 73 spores were found. Fungal spore and other NPP identification are based on NPP Image Database (Shumilovskikh L. S. et al., 2021). Statistical analyses were performed using the *R*Studio software (Version 1.2.1335) with the package "Rioja" (Version 0.9-21) (Juggins, 2015).

Sedimentary Macro-Charcoal Particles

For macro-charcoal counting a total of 220 contiguous sediment samples of 0.5 cm^3 were retrieved. The extraction of sedimentary

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[2] http://apd.sedoo.fr/accueil.htm

[3] https://www.uni-goettingen.de/en/databases+and+collections/97306.html

[4] https://data.oreme.org/palyno/palyno_gallery

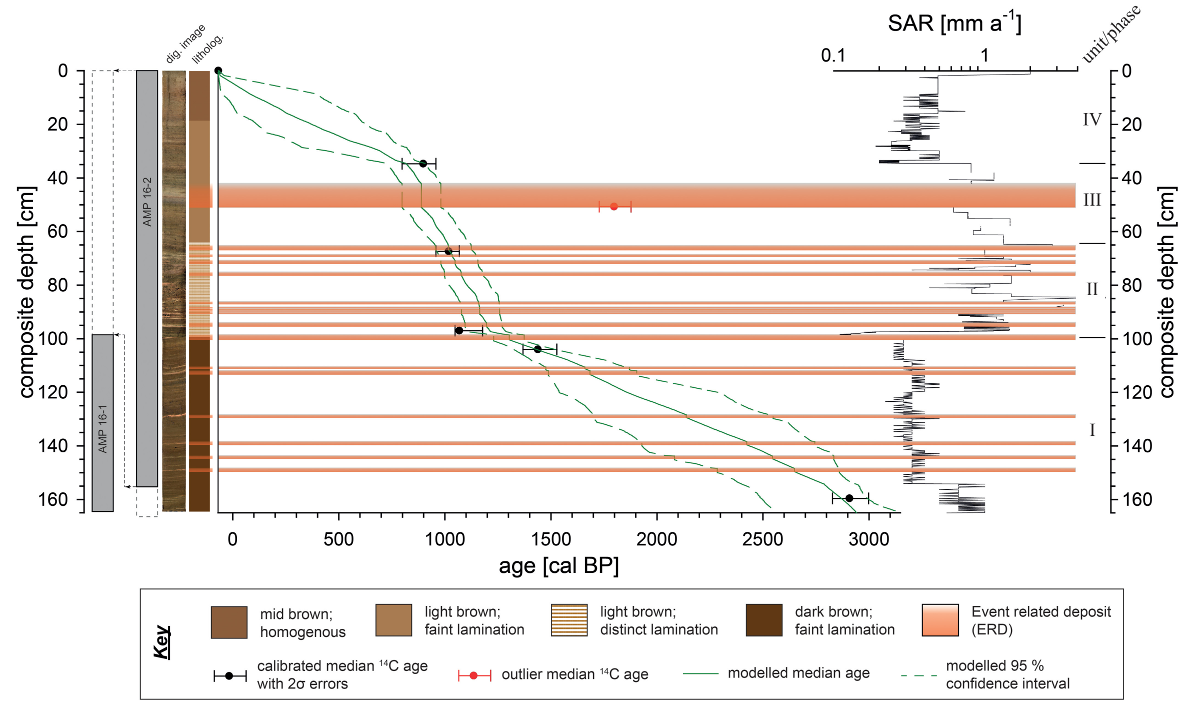

FIGURE 2 | Transition between the sediment cores AMP 16 1 and 16-2, digital image, lithological sketch, age-depth model and sediment accumulation rate (SAR) of composite sequence AMP-16. The composite was established based on parallelization of visual marker layers as well as magnetic susceptibility patterns of the two sediment gravity cores AMP 16-1 and AMP 16-2 (**Supplementary Figure 1**). Age-depth relation is based on a Bayesian model (Blaauw and Christen, 2011) with medians and the 2σ error ranges of five AMS calibrated ^{14}C ages using the SHCal20 dataset (Hogg et al., 2020). Centimeter-scale SAR variability are an artifact that does not provide a centimeter-scale prediction of SAR but merely a range of possible SAR in different core sections.

TABLE 1 | Accelerator Mass Spectrometry (AMS) radiocarbon ages of sediment core AMP16-1 and AMP16-2.

core ID	Lab code	core depth [cm]	composite depth [cm]	material	δ^{13}C [‰]	conv. ^{14}C age [BP]	age error [±]	median age [cal BP]	2 σ Error	
									error-	error+
surface *[1]	–	0	0	–	–	–	–	−66	0	0
AMP16-2	Beta-457952	50.6	34.7	bulk organic sediment	−25	1040	30	900	100	60
AMP16-1 *[2]	Poz-98911	51	50.7		–	1915	30	1800	70	80
AMP16-2	Beta-457953	110.6	67.4		−26	1170	30	1020	60	50
AMP16-1	Poz-98912	96.5	97		–	1215	30	1070	20	110
AMP16-2	Beta-457954	165.5	104		−29.5	1590	30	1440	70	90
AMP16-1	Poz-98913	159.5	159.6		–	2850	30	2910	80	90

*[1] *year of sampling;*

*[2] *inverse age/outlier, rejected from age modeling;*

Radiocarbon dates were measured on total organic matter of bulk sediment. Age calibration is computed by running the R-package "Bacon" (V. 2.5.6) with RStudio software with the (Blaauw and Christen, 2011) and by using SHCal20 calibration curve (Hogg et al., 2020).

macro-charcoal particles followed the standard protocol from Stevenson and Haberle (2005). Macro-charcoal particles were counted using a digital microscope at 5.0 magnification (Zeiss) and wooden and grass-based charcoal were distinguished following morphological description from Enache and Cumming (2006). Macro-charcoal concentration (particles cm^{-3}) and macro-charcoal influx (particles cm^{-2} year^{-1}) were computed for each sample.

High Resolution Pollen and Macro-Charcoal Particles Counting From Core AMP16-1

To reconstruct the ecological shift occurring at the transition between the two sediment cores with high precision, Poaceae pollen and macro-charcoal particle were counted on 15 contiguous additional samples from core AMP16-1 that encompasses this transition between the depth 110 and 96 cm. These detailed analyses performed every centimeter (for pollen and macro-charcoals) allow to trace environmental changes with high precision, without any potential disturbance from the switch between the two sediment cores in the composite master sequence AMP16 (**Figure 2** and **Supplementary Figure 1**). For these contiguous samples, the same previously mentioned chemical treatment for pollen and macro-charcoal particle extraction were used. To obtain Poaceae percentages, a minimum of 100 terrestrial pollen grains were counted among which only Poaceae was identified.

Diatom Analyses

Diatom analyses were performed every 6-10 cm. Sample preparation and concentration assessment were conducted following standard procedures (Kalbe and Werner, 1974; Battarbee and Bennion, 2011). If possible, a minimum of 400 valves was identified in each sample. In samples with very low diatom concentration, analyses were stopped when 1000 microspheres had been counted. A simple preservation index was tested by counting at least 100 specimens of *Aulacoseira granulata* and differentiate between intact and broken valves (ratio I/B). Permanent slides for light microscopy were prepared using Naphrax® as a mounting medium. Slides analyses was performed using a Leica DM 5000 B light microscope with differential interference contrast, equipped with a ProgRes® CT5 camera, under oil immersion at ×1000 magnification. Identification is mainly based on (Krammer and Lange-Bertalot, 1986, 1988, 1991a,b), Houk and Klee (2007); Houk et al. (2010), Lange-Bertalot et al. (2017) and other relevant taxonomic publications (e.g., Klee et al., 2000). Stratigraphic diatom zones (DZ) were defined by hierarchical cluster analysis of taxa occurring with > 1% using PAST ver. 4.04 (Hammer et al., 2001). Down-core changes in diatom results were visualized using C2 software version 1.7.7. (Juggins, 2007).

RESULTS

Bathymetry and Seismic Survey

The basin morphology (**Figure 1B**) is characterized by steep slopes, both on shore and under water. An asymmetric shape in W-E direction might result from a former mass movement at the western side of Lake Amparihibe. A rather shallow-water area is notable in the NE. It may, alternatively, represent an alluvial fan due to river inflow and deposition of sediments from the catchment or result from a fossil mass movement deposit, probably due to a slope failure from a crater wall of the lake located to north/east of Lake Amparihibe.

Seismic survey of sedimentary structures shows typically well layered and undisturbed deposits within the upper ca. 1.5 m followed by a reflector that does not allow further penetration (**Figure 1C**). This behavior can be explained by natural gas within the sediment that prevents the acoustic waves from further penetration. Only rare acoustic windows containing less gas give further insight into the sedimentary structure and show that the deeper infill consists of well layered sediments as well, at least down to ca. 8 m sediment depth. This represents a minimum thickness of the sedimentary infill, as gas occurrence prevents further penetration here as well. Thus, a hard-rock basement has not been detected so far.

Lake Water Characteristics

Lake Amparihibe is alkaline (pH ∼8.7) and dissolved oxygen values of surface waters are about 7.9 mg L^{-1} (∼103%), while vertical water parameter measurements confirm anoxic bottom waters (**Supplementary Figure 2**). Water temperature is high and decreases with depth from 29.3°C to 27.2°C. Temperature depth profile shows that the lake was thermally stratified in November 2016. Electrical conductivity is around 245 $\mu S\ cm^{-1}$ and Secchi depth about 2.5 m.

Sedimentology and Chronology

Sediment core parallelization using magnetic susceptibility patterns of both cores resulted in an almost perfect fit with a correlation coefficient of r = 0.83 (**Supplementary Figure 1**). According to this fit, the composite record has a total length of 164.5 cm. The lower part of the composite is represented by the lower section of AMP 16-1 from 164.5 to 99.4 cm, whereas the upper 99.4 cm are represented by the compressed core AMP 16-2 from 156.2 to 0 cm (**Figure 2** and **Supplementary Figure 1**).

The composite record generally exhibits dark to light brownish sediments with various light grayish to reddish intercalated 1 mm- to 15 mm-thick layers. Sediments are mainly composed of clayey silts with only little portions of sand (max. 5.6%, see **Supplementary Figure 3**). From 164.5 to 99.5 cm the record shows general dark brownish colors and only few intercalated grayish and reddish faint layers. Six of the intercalated layers are outstanding since they are quite distinct, exhibit reddish color and show higher proportions of sand. Between 99.5 and 64 cm lamination is much more distinct, layer thickness varies between 1 and 5 mm, and the overall sediment color is brighter. Between 64 and 21.5 cm sediment color and texture differ from the lower parts. Color changes to light brown and particles are distinctively finer with higher proportions of clay. Aside of an indistinct lamination, an 8.7 cm thick grayish layer with a dark, coarse base a reddish center and a fining upward trend is outstanding from 50.8 to 42.1 cm composite depth. In the uppermost unit, the color changes to homogenous slightly darker brown.

The outstanding layers with a minimum thickness > 4 mm, showing both a particle size fining upward trend and peaks in magnetic susceptibility, were interpreted as Event Related Deposits (ERDs) (**Figure 2**). Assuming a quick (hours to days) sedimentation as turbidity currents, these ERD layers were omitted for age modeling. One of the dated samples shows an inverse age, since it was taken from the base of an ERD, and was thus rejected from age-modeling (**Figure 2** and **Table 1**). The model is thus based on five radiocarbon ages in stratigraphic order and reveals a basal age of 2940 cal BP. This chronology refines a paleomagnetic-supported age model previously published for AMP 16-1 (Haberzettl et al., 2021).

Sediment Accumulation Rate (SAR) is variable ranging between 0.1 and 4 mm a^{-1}. At the lowermost part of the record (164.5 to 97 cm) SAR is low ranging between 0.1 and 0.6 mm a^{-1}. At 97 cm composite depth, SAR dramatically increases to values ranging around 1.3 mm a^{-1} and remains on this high level until 61.2 cm, showing some major peaks of up to 4 mm a^{-1}. Between 61.2 and 34.5 cm, a slight declining trend to 0.8 mm a^{-1} on average is notable. At 34.5 cm a distinct shift to low values ranging around 0.4 mm a^{-1} occurs. A very slight increment tendency is visible toward the top of the record with SARs up to 0.5 mm a^{-1}, while within the uppermost 0.5 cm of the record the value increases to 2 mm a^{-1}, which is likely an artifact of age modeling.

Based on lithological properties, the age-depth model, as well as the SAR, four sedimentary units (phases) were assigned, i.e., unit I from the base of the record to 99.5 cm (2940 – 1300 cal BP), unit II from 99.5 to 64 cm (1300 to 1000 cal BP), unit III from 64 to 35 cm (1000 – 820 cal BP), and unit IV from 35 cm to the top of the record (820 cal BP - today).

Physical Sediment Properties

Magnetic Susceptibility

The composite magnetic susceptibility pattern shows values between 86 and 7035 $\times 10^{-6}$ SI (**Figure 3**) with noticeable distinct narrow peaks matching the light grayish and reddish ERDs (**Supplementary Figure 1**). These peaks also represent the maximum values in the record. In unit I (2940 to 1300 cal BP) values are generally on a low level of around 600 $\times 10^{-6}$ SI. Values drop down from around 1800 $\times 10^{-6}$ SI in unit II (1300 to 1000 cal BP) to ca. 1000 $\times 10^{-6}$ SI at 1000 cal BP in unit III (1000 to 820 cal BP). They distinctly increase at 890 cal BP to 3400 $\times 10^{-6}$ SI and decline steadily thereafter until the top of unit III (820 cal BP) reflecting the uppermost ERD. Unit IV (820 cal BP - today) shows further declining magnetic susceptibility values with some internal variation to 800 $\times 10^{-6}$ SI at 500 cal BP. After another broad peak centered at ca. 430 cal BP showing values of ca. 1600 $\times 10^{-6}$ SI, the remaining record reveals fairly stable values ranging around 1100 $\times 10^{-6}$ SI. However, the distinct minimum during the youngest part of the record (after 10 cal BP) is likely attributed to measurement edge effects.

Particle Size Characteristics

Grain size distributions in all samples are characterized as bi- to polymodal and poorly sorted (**Figure 3** and **Supplementary Figure 3**). Median grain size ranges between 4.9 and 16.4 μm. Unit I (2940 to 1300 cal BP) displays the occurrence of coarser particles between 6.6 and 16.4 μm, with a general fining trend. Particle size median (D50) is distinctively smaller 4.9 and 9.4 μm after 1300 cal BP and shows no grading trend and only minor variability. Particle sorting (σ), however generally described as poor, is quite variable over the entire covered time span. In unit I, deposits are very poorly sorted. From 1300 to 820 cal BP (unit II and III) sorting tends to be better, but highly variable and remains quite stable afterward in unit IV (820 cal BP - today). Skewness (S_k) in the distribution of all samples is positive, but comparable to the sorting showing internal variability. In the older deposits (unit I, 2940 to 1300 cal BP) S_k reveals lower values with some variability and an increasing trend. In unit II and III, from 1300 to 820 cal BP, S_k is on an intermediate level with high internal variability and remains on a high positive level toward the top of the record (unit IV).

Geochemical Characterization

T(O)C, TN as well as the C/N ratio follow the units of the AMP-16 record, but unit II and III (1300 to 820 cal BP) are merged (**Figure 3**). In general, TC varies between 2.1 and 13.4%, and TN shows contents from 0.2 to 1%. Stable, high amounts of TC and TN are observed within unit I (2940 to 1300 cal BP). In unit II (1300 to 1100 cal BP), TC and TN drop distinctly and remain low and relatively stable, particularly during unit IV (after 820 cal BP). The C/N ratio drops from relatively high values, partly exceeding 16 in unit II (at 1200 cal BP), to values below 14 in the units above. $\delta^{13}C$ reveals the most negative values of around -30.3 ‰ in unit I (2940-1300 cal BP), a shift to more positive values (>-27 ‰) in unit II and III (until 820 cal BP), and values stabilize around -28 ‰ in unit IV (after 820 cal BP) (**Figure 3**). Stable values for $\delta^{15}N$ of around 1.8 ‰ occur in unit I (2940 to 1300 cal BP) as well as in untis II and IV (after 1000 cal BP), but reveals a distinct enrichment of up to 4.3 ‰ in unit II (**Figure 3**).

Biogenic silica (BiSi) contents range between 2.6 and 23.7% (**Figure 3**). The amount shows a decreasing trend during unit I and unit II until 1100 cal BP, when it reaches its minimum. Contents are dramatically increasing to the maximum thereafter and are again decreasing at ca. 700 cal BP, however remaining on a constant intermediate level of ca. 12% toward the top.

n-Alkanes occur in all investigated samples, and the chromatograms show the odd over even predominance typical for plant-derived leaf-waxes (e.g., Schäfer et al., 2016). Because of the low concentrations of the even *n*-alkanes and insufficient peak separation from other aliphatic compounds, we quantified only the more abundant odd *n*-alkanes. The sum of the odd *n*-alkanes (nC_{21} to nC_{35}) reaches 20 μg g^{-1} dry sediment in unit I (2940 to 1300 cal BP), drops below 10 μg g^{-1} in unit II and III (1300 to 820 cal BP), and increases again over the last few centuries (**Figure 4**). The Paq is low at ca. 0.1 in unit I, increases to values > 0.2 in unit II and III, and exceeds values > 0.4 in unit IV. The ACL mirrors this trend, starting with values around 30.5, dropping in unit II and III, and reaching values < 29.5 in unit IV. Excluding C_{27}, or even C_{27} and C_{29}, for the calculation of the ACL′ and ACL″, respectively, of course increases the values, but it also reduces and even removes the trend toward shorter chain length. The remaining feature of the ACL″ is a pronounced maximum in unit II.

Paleoecological Analyses

Palynological Analyses

A total of 93 different pollen and spore taxa and 89 NPP types have been identified. Based on the cluster analysis (CONISS) the pollen diagram is subdivided into three significant pollen zones (PZ, **Figure 5**).

PZ-1 (165-100 cm/2940-1300 cal BP/unit I): Pollen assemblages mainly consist of arboreal pollen (AP 80-90%) and show a high tree diversity. The most abundant AP correspond to Moraceae/Urticaceae (20-30%), *Celtis* (ca.

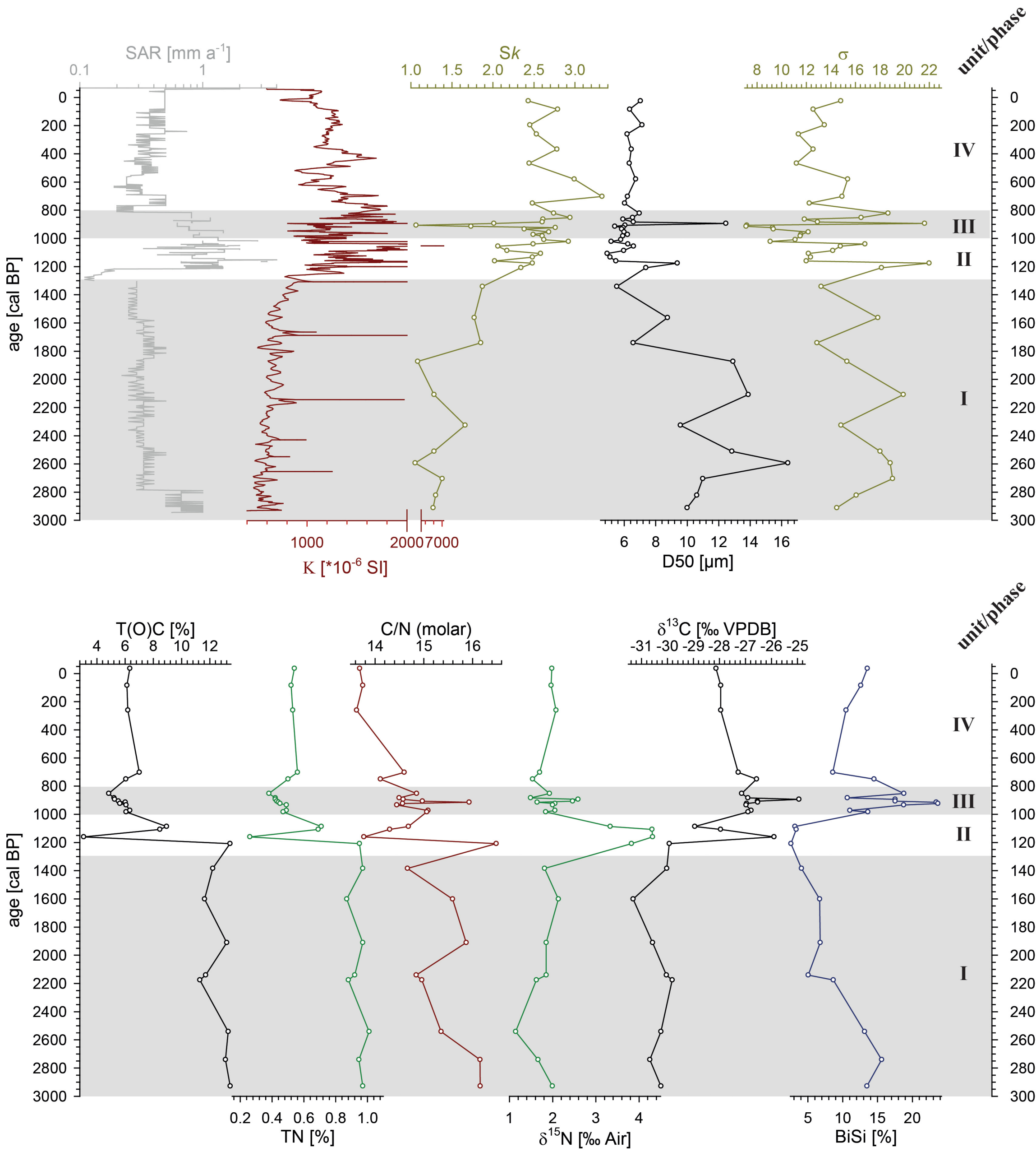

FIGURE 3 | Sedimentological parameters of composite record AMP-16. Upper panel: sediment accumulation rate (SAR), magnetic susceptibility (K), particle size distribution skewness (S*k*), particle size median (D50) and particle sorting (σ). Lower panel: total (organic) carbon (T(O)C), total nitrogen (TN), molar C/N-ratio, δ^{15}N and δ^{13}C measured on the bulk organic faction, and biogenic silica content (BiSi). Gray shaded areas demarcate sedimentological units (I to IV).

20%), *Macaranga/Mallotus* (ca. 10%) and Elaeocarpaceae (ca. 10%). Other AP with low values (< 5%) are also characteristic for this zone such as *Podocarpus, Weinmannia, Ilex*, Meliaceae/Sapotaceae, Anacardiaceae, *Noronhia*, Proteaceae and *Ilex*. Non-Arboreal Pollen (NAP) corresponding to herbs and shrubs show low values (5-15%) and are mainly characterized by a steady occurrence of Poaceae (5-10%), *Acalypha* (ca. 2%) and Begoniaceae (ca. 2%). Aquatic pollen taxa do not exceed 10% and fern spores are absent. Lignicolous fungal spore assemblage is diverse and presented by Xylariaceae, *Potamomyces*, *Brachysporium*, *Dictyosporium*, *Canalisporium pallidum*. Plant pathogens are presented by *Ustulina deusta* and *Lasioplodia*. Saprotrophs/coprophilous spore assemblage is poor. Among unknown NPPs, HdV-1033 and HdV-1036 are dominant.

PZ-2 (100-27 cm/1300-600 cal BP/units II, III and IV): AP diversity decreases as well as AP percentages that drop abruptly to 30%, then increase progressively up to 40% at the end of the PZ. Among AP, only percentages of *Trema*

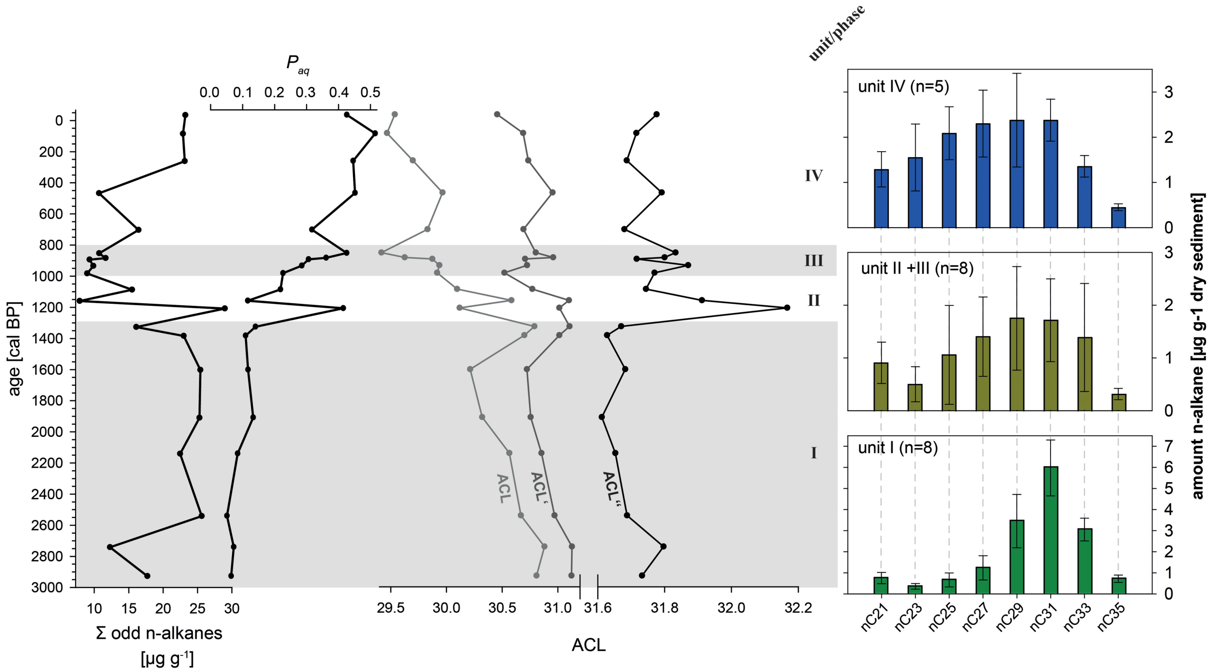

FIGURE 4 | Left plane: Leaf-wax n-alkane indices of composite record AMP-16. Sum of odd n-alkanes (nC21 to nC35), Paq, and average chain length ACL, ACL′(nC39-33), and ACL″(nC31,33). **Right plane:** mean n-alkane distribution patterns in respect to the sedimentological units (note that unit II and III were merged due to very similar distribution patterns).

increase slightly (up to 5-10%). Moraceae/Urticaceae (ca. 15-30%) and *Macaranga/Mallotus* (ca. 5%) still remain among the dominant AP. Poaceae pollen increase abruptly up to 60% then decrease progressively and reach 50% at the end of the PZ showing an opposite trend to AP. Other NAPs remain with low values. Ericaceae percentages show a slight increase (up to ca. 5%) and slight percentage decreases are recorded for *Acalypha* (<2%) and Begoniaceae (<2%). Percentages of aquatic pollen are characterized by an important increase in *Potamogeton*, a slight increase in Cyperaceae and *Lemna* is not recorded anymore. A steady occurrence of fern spores is recorded but with low values (< 3%) and the algae *Botryococcus* shows an increase at ca. 20% from ca. 1000 cal BP. Considerable changes in fungal spores are indicated by a sharp increase in *Coniochaeta ligniaria* associated with *Delitschia*, *Cercophora* and *Sordaria*. Spores of pyrophilous fungi *Gelasinospora* and *Neurospora* occur, while diversity of lignicolous assemblage decreases. Plant pathogens are presented by *Lasioplodia*, *Tetraploa aristata*, *Dictyoarthrinium* cf. *sacchari* and rusts uredospores.

PZ-3 (27-0 cm/from 600 cal BP/unit IV): The progressive increase in AP which started in PZ-2, continues in this zone with AP reaching 70%. AP are mainly dominated by Moraceae-Urticaceae (20-30%), *Macaranga/Mallotus* (5-10%) and *Trema* (20%). This zone is also characterized by the occurrence of new AP taxa such as *Mimosa* (up to 5%) or Myrtaceae (up to 3%) while several taxa characteristic of the first zone such as *Podocarpus*, *Weinmannia*, *Ilex* or Meliaceae/Sapotaceae are almost not recorded anymore. Among the NAP, only Poaceae pollen indicate significant changes characterized by a progressive decreasing trend from 45% to 25%. At ca. 10 cm depth an increase in the aquatic pollen Cyperaceae (up to 8%) is recorded. The other aquatic pollen, fern spores and *Botryococcus* do not show marked changes. PZ-3 is characterized by a further increase in diversity of coprophilous assemblages by *Arnium*, *Apiosordaria* and *Podospora anserina*-type. Chlamydospores *Glomus*-type occur constantly. Assemblage of lignicolous fungi change to *Curvularia*, *Podospora curvispora*, *Canalisporium pulchrum*, *Megalohypha aqua-dulces*, *Caryospora*, *Zopfiella lundquistii*. Plant pathogens diversity increase by several *Spegazzinia* species. Diversity of other spores decreases.

Sedimentary Macro-Charcoal Particles

Prior to 1300 cal BP, macro-charcoal particles occur in every sample, but concentrations and influx remain very low (**Figures 6A,B**). Following morphological descriptions from Enache and Cumming (2006), most macro-charcoal particles are wood-based. At ca. 1300 cal BP (unit II, 1300 to 1000 cal BP), a marked increase of concentration and influx is recorded with peaks exceeding 300 particles cm^{-3} and 40 particles cm^{-2} year^{-1}, respectively. Grass-based charcoal particles increase at the same time with percentages varying around 30% and peaks exceeding 40%. Subsequently, percentages decrease after 1000 cal BP and remain generally below 30%. From 1000 cal BP (unit III and IV, 1000 cal BP to today), macro-charcoal concentration and influx also tend to decrease. After a last peak above 300 particle cm^{-3}, between 820 and 750 cal BP, concentrations fluctuate around 100 particles cm^{-3}. Macro-charcoal influx indicates a progressive decreasing trend from

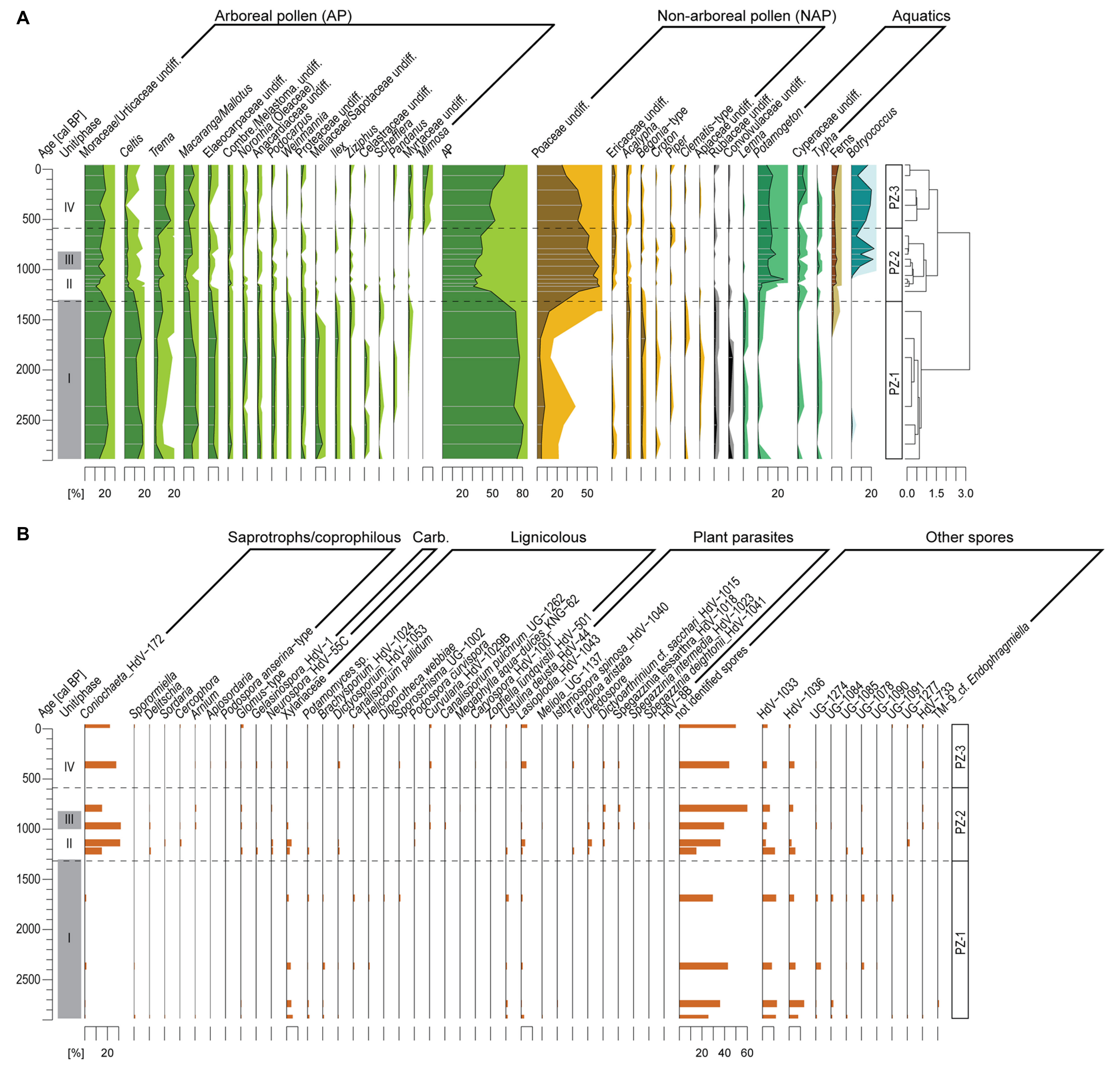

FIGURE 5 | (A) Pollen and fern spore records of composite record AMP16 retrieved from Lake Amparihibe (Nosy Be, Madagascar) plotted on an age scale. Percentages of pollen and fern spores were calculated on the terrestrial pollen sum. Pollen zone (PZ) indicated by dashed lines were identified by a cluster analysis (CONISS, Grimm, 1987). The light-colored pollen curves correspond to exaggerated curves by a factor 5. **(B)** Fungal spore record plotted on an age scale of composite record AMP-16. Percentages are calculated based on total count of fungal spores. Gray shaded areas demarcate sedimentological units.

1000 cal BP and values stabilize from ca. 750 cal BP varying around 5 particles cm^{-2} year^{-1}. This decrease in influx is partly the result of the decrease in SAR (**Figure 2**).

High Resolution Data From Core AMP16-1 (110-96 Cm Depth; Ca. 1640 to 1200 Cal BP)

Between 110 and 100 cm (ca. 1640-1300 cal BP) low percentages of Poaceae (<10%) and macro-charcoal (max. 16 particles cm^{-3}) are recorded (**Figure 6C**). Above 100 cm (<1300 cal BP), Poaceae show a continuous increase and reach 40% at 97 cm (ca. 1200 cal BP). Macro-charcoal particles show two important increases above 100 cm depth. The first increase corresponds to a peak at 99 cm and maximum concentration (368 particles cm^{-3}, ca.1300 cal BP) is reached in the sample where Poaceae percentage shows the first marked increase. This macro-charcoal peak at 99 cm occurs contemporaneously to a peak in magnetic susceptibility. The second increase starts at 97 cm (ca. 1200 cal BP) and macro-charcoal concentration reaches ca. 580 particles cm^{-3} at 96 cm.

Diatom Analyses

A total of 30 diatom species have been identified in the sequence. Overall, two planktonic taxa, *Discostella* cf. *mascarenica* (Klee, Houk and Bielsa) Houk & Klee and *Aulacoseira granulata*

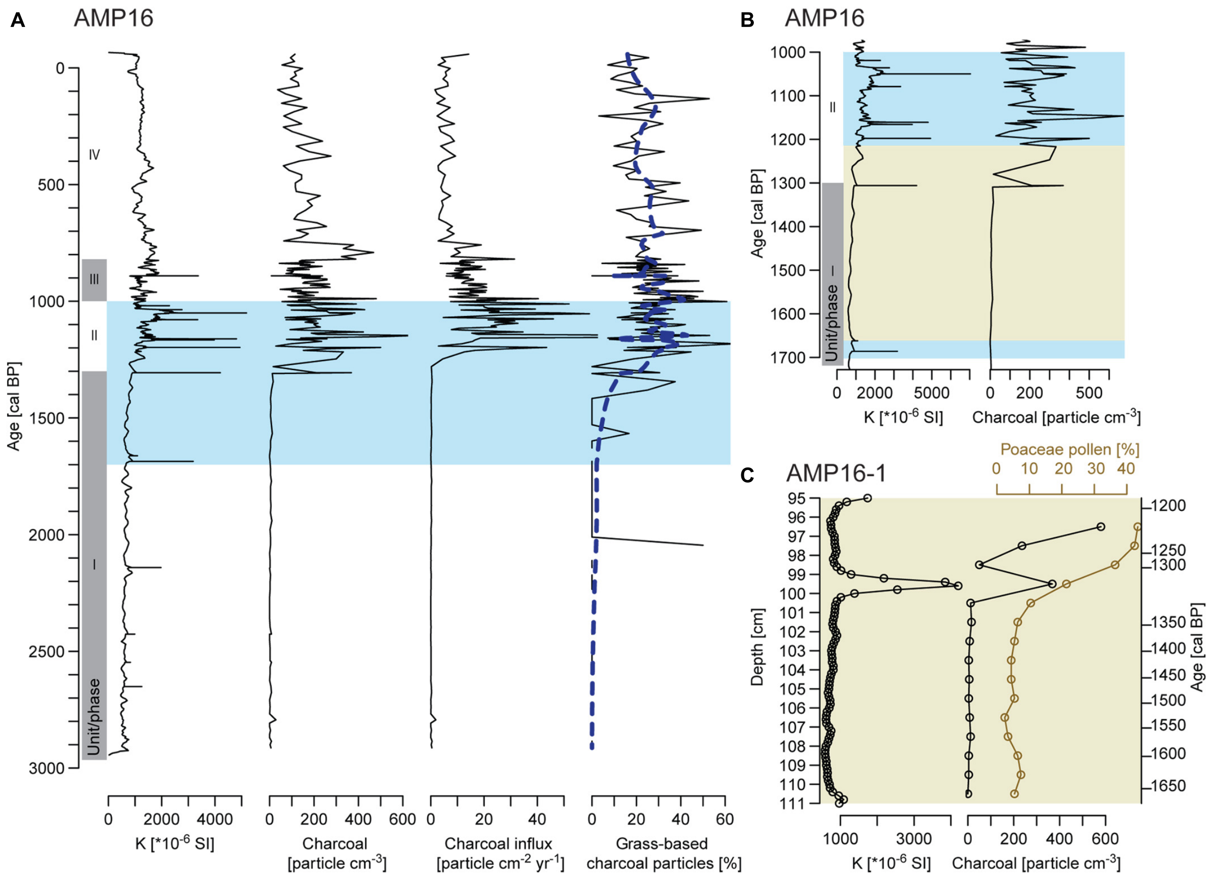

FIGURE 6 | (A) Comparison between records of magnetic susceptibility (K), macro-charcoal concentration, macro-charcoal influx and percentage of grass-based charcoal particles of composite record AMP-16. Blue dashed line represents the evolution of the proportion of grass-based macro-charcoal along depth estimated by applying a binomial generalized additive model smoother with a 25-degree-of-freedom thin plate regression spline basis (gam function in mgcv R package) to the dataset composed of each macro-charcoal depth and a value 0 for a wooden-based charcoal or 1 for a grass-based one. The blue area indicates the period selected in panel **(B)** showing precise comparison between magnetic susceptibility and macro-charcoal concentration of composite record AMP-16. The light green area indicates the period selected in panel **(C)** showing the transition zone recorded from core AMP16-1 and comparing magnetic susceptibility, macro-charcoal concentration and pollen percentages of Poaceae. Gray shaded areas on panels **(A,B)** demarcate sedimentological units.

(Ehrenberg) Simonsen agg., clearly dominate the low diversity assemblages (**Figure 7**). Most samples yield high diatom concentrations [up to 60 × 10^8 valves g^{-1} dry weight (DW)]. However, between 1310-1040 cal BP, diatom concentration was low and valve preservation poor (ratio I/B: 0.6-0.7). Hierarchical cluster analysis identified three major diatom zones (DZ-1 - DZ-3) and three subzones (DZ3a-c).

In the oldest part of the core (DZ-1, 1630-1310 cal BP), diatom concentrations are high with values between 11 × 10^8 to 60 × 10^8 valves g^{-1} DW. Planktonic species *Discostella* cf. *mascarenica* is by far the most abundant species (> 96%) and almost no benthic taxa are observed. The following zone (DZ-2, 1310-1130 cal BP) is distinguished by almost sterile samples with < 0.025 × 10^8 valves g^{-1} DW. First and frequent occurrences of *Aulacoseira granulata* together with a minor proportion (6.8%) of benthic and epiphytic taxa such as *Navicula* Bory de Saint-Vincent s.l., *Nitzschia* Hassall spp. and *Gomphonema* Ehrenberg spp. characterize DZ-3a (1130-1080 cal BP). *Discostella* cf. *mascarenica* is barely present anymore. Although diatom concentration is still low in the lowermost part of zone DZ-3b (1080-570 cal BP), numbers quickly increase up to 49 × 10^8 valves g^{-1} DW. Assemblages almost exclusively consist of *Aulacoseira granulata* agg. (>96%). The uppermost part of the sequence (DZ-3c, from 570 cal BP) is still overall dominated by *Aulacoseira granulata* agg. (91-96%) but benthic and tychoplanktonic taxa slightly increase in abundances (up to 7.3%) compared to the previous subzone DZ-3b.

DISCUSSION

Local Environmental Changes

Initial Environmental Conditions Prior 1300 cal BP

Between 2940 and 1300 cal BP, sedimentological and vegetation data do not show major changes (**Figures 3**, **5A**). The high dominance of tree taxa suggests a large area of forest. Most tree taxa that are described as typical of rain forest in modern and fossil pollen samples from Madagascar are well

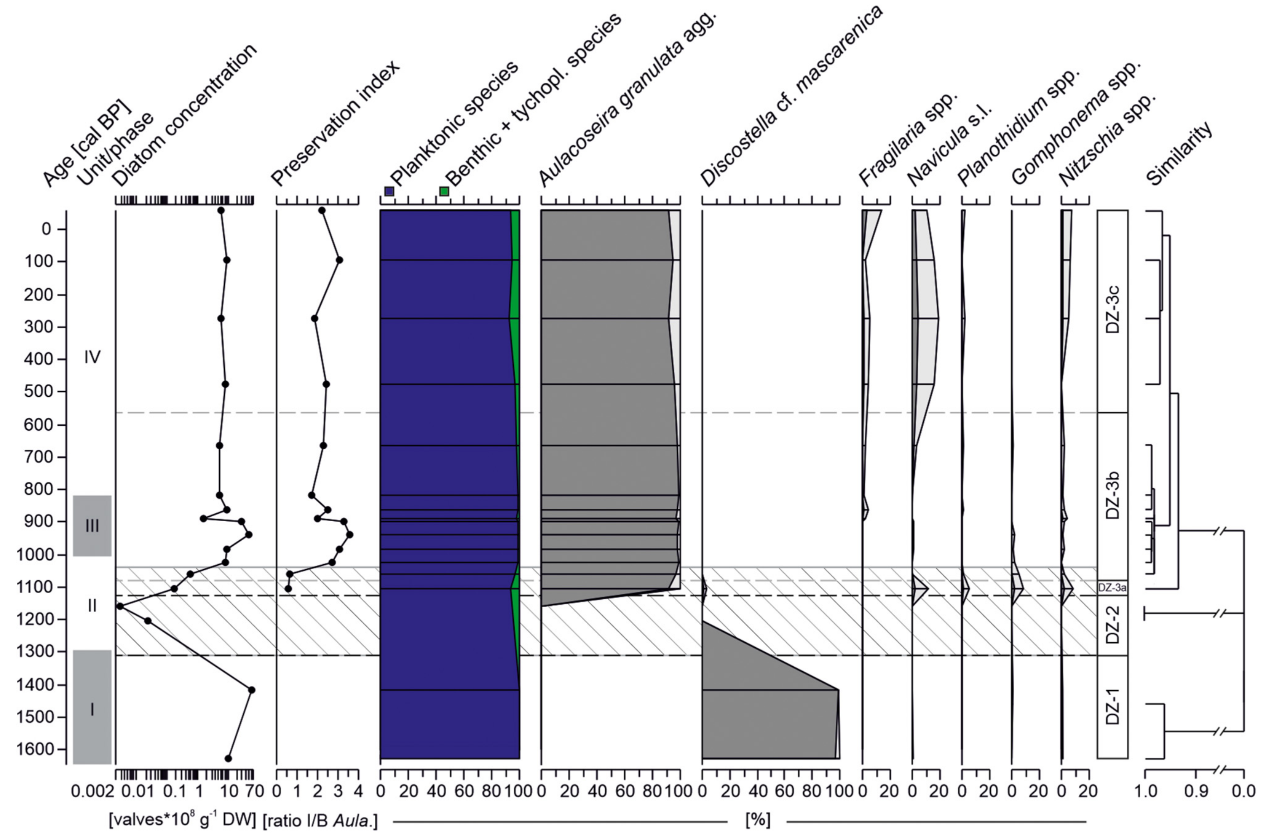

FIGURE 7 | Diatom record from core AMP 16-2 retrieved from Lake Amparihibe plotted on an age scale with relative abundances taxa (>1%), diatom concentration (DW: dry weight), preservation index (ratio intact to broken valves of *Aulacoseira granulata*) and abundances of benthic + tychoplanktonic and planktonic taxa. Samples with less than 15 valves counted were excluded from abundance plots. Diatom zone (DZ) indicated by dashed lines were identified by a hierarchical cluster analysis. The lighter colored diatom curves correspond to exaggerated curves by a factor 5. Hatched area indicates zone of lowest diatom concentration and poorer valve preservation. Gray shaded areas on the left demarcate sedimentological units (I to IV).

represented in this period (e.g., Moraceae/Urticaceae, *Celtis*, Elaeocarpaceae, *Macaranga/Mallotus* and *Podocarpus*; Burney, 1988; Gasse and Van Campo, 2001). This suggests that the dense and humid rain forest was the dominant vegetation prior to 1300 cal BP on Nosy Be. The low fire activity during the same time confirms the occurrence of rain forest developed under humid environmental conditions and low disturbance regime (**Figure 6A**). Furthermore, the presence of a wide variety of lignicolous fungi indicate the availability of dead wood substrate in the lake catchment as well (**Figure 5B**).

Sedimentological and geochemical results are consistent with the dominance of rain forest prior 1300 cal BP. Relatively low SAR supports the assumption of dense vegetation stabilizing the topsoils in the catchment (**Figure 2**). The comparably coarse particle median (**Figure 3**) might either be indicative for lacking grasses and thus a missing "filter" for larger minerogenic particles flushing into the lake by inflowing water, or coarser particles might point to comparably moist conditions with higher amounts of precipitation and thus higher transport energy of the inflows (Conroy et al., 2008). High organic carbon contents, high C/N-ratios, and high amounts of leaf-wax *n*-alkanes during this phase further suggest high productivity within the catchment and input of terrestrial organic matter (Meyers and Ishiwatari, 1993; **Figures 3**, **4**). The depleted δ^{13}C values of the bulk organic matter point to predominantly C_3 vegetation (**Figure 3**; Farquhar et al., 1989; Meyers, 1994; Diefendorf et al., 2010).

The *n*-alkane patterns show a dominance of $n\mathrm{C}_{29}$, $n\mathrm{C}_{31}$, and $n\mathrm{C}_{33}$, and the Paq is accordingly very low. This indicates a dominant input from higher terrestrial plants over input from aquatic sources (Eglinton and Hamilton, 1967; Zech et al., 2010). Distinguishing between input from grasses and herbs versus deciduous trees, as has been done in other studies (e.g., Zech et al., 2013b; Schäfer et al., 2016), needs to take into account that common plants of rain forests synthesize high amounts of $n\mathrm{C}_{31}$ and $n\mathrm{C}_{33}$ (Gnecco et al., 1989; Abas and Simoneit, 1998; Li et al., 2016; Teunissen van Manen et al., 2019). The high ACL values in comparison to northern mid-latitude locations (e.g., Europe) thus reflect the local rain forest signal, and should not be misinterpreted to indicate dominant input from grasses and herbs.

Ecosystem Shift From 1300 to 1000 Cal BP

From 1300 cal BP, most tree taxa decrease and some of them almost entirely disappear (e.g., *Podocarpus*, *Weinmannia*, *Ilex*, Meliaceae/Sapotaceae, **Figure 5A**). Inversely, an increase of herbs (mainly Poaceae) is observed. Together with an enrichment in $\delta^{13}C$ of the bulk organic fraction further suggesting a shift from C_3 to more C_4 vegetation (Farquhar et al., 1989; Meyers, 1994; Diefendorf et al., 2010), this points to the development of a mosaic of grassland and forest (**Figure 3**). Combined with the increase in macro-charcoal mainly associated with increased grass-based charcoal particles (**Figure 6A**), our results suggest an abrupt development of grasses dominated and fire disturbed landscape and confirm the alteration of the rain forest. High-resolution paleoecological analyses during that critical transition (see **Figure 6C**) reveal that grassland developed within few decades and occurs simultaneously with increases of fires. The co-occurrence between the first peak of macro-charcoal particles and the peak of magnetic susceptibility indicate that fires were local to the catchment and led to the observed forest alteration and initiated the increase of soil erosion. Similar observations were made at Laguna Potrok Aike, Patagonia where increased frequency dependent magnetic susceptibility and increased charcoal accumulation rates indicated the destruction of the vegetation cover by fire leading to enhanced soil erosion (Haberzettl et al., 2006).

Vegetation changes are also evidenced by the considerable development of saprophilous/coprophilous fungal spores (**Figure 5B**), that generally develop on decaying plant remains (e.g., litter) and/or herbivore livestock dung (e.g., Krug et al., 2004; Shumilovskikh L. et al., 2021; van Asperen et al., 2021). Plant parasitic fungi such as *Tetraploa aristata*, *Spegazzinia* sp., *Dictyoarthrinium* cf. *sacchari* indicate wide spread of herbaceous monocots and dicots as well while lignicolous fungi such as Xylariaceae decrease after 1100 cal BP (Shumilovskikh L. et al., 2021). Therefore, this complete rearrangement of lignicolous and plant parasites fungal spores confirms an important forest dieback at the expense of grassland. In addition to vegetation changes, enhanced soil erosion is also indicated by *Glomus*-type (**Figure 5B**), representing chlamydospores of the arbuscular mycorrhizal fungi growing symbiotically on plant roots (van Geel et al., 1989).

Sediment physical and organic characteristics are altered at this transition and SAR is increasing by almost one order of magnitude, supporting the pronounced decrease in tree cover associated with increased vulnerability of the soils to erosion. This is also visible in the higher frequency of ERDs occurring within the deposits (**Figure 2**). Following a short-term coarsening of the particles between 1300 and 1200 cal BP, the fining of the minerogenic particles accompanied by slightly better sorting and a more positive skewness of the distributions is observed at ca. 1150 cal BP (**Figure 3**). These changes suggest a selective deposition based on alteration of transport processes, i.e., lower amount of transport energy or shielding (McLaren, 1981; McLaren and Bowles, 1985). In this context, the development of *Potamogeton* from 1150 cal BP onward as an emergent aquatic plant, which likely covered the shallow (near shore/littoral) water areas, might have acted as sediment trap for larger particles. A lake level increase could have provided shallow water areas for macrophytes growth, since this would inundate the northwestern area of the catchment leading to the formation of a larger shallow water area, with emerging aquatic vegetation acting consequently as source of aquatic biomass and as sink for coarse minerogenic particles. A comparable process has been observed recently using aerial imagery (**Supplementary Figure 4**). The lake level increase might also be associated with enhanced nutrient supply, which, in combination, most likely explain the rise of aquatic vegetation and algae which is also supported by a distinct shift to rather low C/N-ratios (Meyers and Ishiwatari, 1993). The exceptional enrichment in $\delta^{15}N$ during this phase might support the enhanced nutrient supply through the input of isotopically enriched N with either topsoil (Ochiai et al., 2015), or distinctive input from anthropogenic/livestock sources (sewage) (Enters et al., 2010). Alternatively, denitrification of the system due to tenacious anoxic conditions at the lake floor might be an explanation for the high $\delta^{15}N$ (Enters et al., 2010).

This increase of soil erosion impacted lake ecosystem dynamics by increasing nutrient discharges which probably contributed to the development of the aquatic plant *Potamogeton* followed by the development of the green algae *Botryococcus*. A change in lake ecosystem dynamic is further supported by the diatom record characterized by minimum concentration values between 1300 and 1040 cal BP (concentration minimum peaking at 1160 cal BP) and minimum valve preservation at ca. 1100 cal BP (**Figure 7**). Low concentration values are likely caused by enhanced catchment erosion and input of minerogenic material into the lake with associated dilution of autochthonous material. Additionally, the low valve preservation is suggested to be linked to both, mechanical breakage in a high dynamic (energy) environment, and potentially to an increase in pH (Flower and Ryves, 2009). A distinct shift in the dominating planktonic diatom species from *Discostella* cf. *mascarenica* to *Aulacoseira granulata* agg. further proofs a change in the lake ecosystem following the transitional phase. *Discostella mascarenica* is a rare species and only little is known on its distribution and ecological preferences. It was described from a small, alkaline, eutrophic freshwater pond on Réunion island, situated 800 km to the east of Madagascar (Klee et al., 2000). *Aulacoseira granulata* occurs worldwide in a wide range of trophic conditions but is often associated with more eutrophic waters. Moreover, it is frequent under turbulent conditions, capable to survive in higher turbid waters, has high growth demands for silica and has also been connected to phases of increased erosion (Kilham et al., 1986; Costa-Böddeker et al., 2012; Bicudo et al., 2016; Nardelli et al., 2016). Shifts among *Discostella* and *Aulacoseira* have been associated with physical restructuring of the water column, whereby small cyclotelloid species like *Discostella* benefit from a strongly stratified water column and larger-celled *Aulacoseira* taxa are favored by strong vertical mixing (Rühland et al., 2015). Thus, the change from *Discotella* cf. *mascarenica* to *Aulacoseria granulata* agg. in Lake Amaprihibe supports the assumption of a catchment alteration leading to increased turbulence and turbidity.

The distinctive decrease in leaf-wax *n*-alkane amount, the shift to shorter chain *n*-alkane predominance and the marked increase in Paq further supports the emergence of aquatic vegetation (Ficken et al., 2000; Aichner et al., 2010; Castañeda and Schouten, 2011) as the result of a change in nutrient supply to the lake. Decreasing ACL values document the input of shorter homologs. In order to evaluate and reduce a potential bias of aquatic and emergent plants (likely also producing C_{27} and C_{29} to some degree), the modified ACL′ and ACL″ is applied. The increase at 1300 cal BP in these modified indices point to enhanced input of long-chain C_{33} likely originating from grasses. This would also support the increase in $\delta^{13}C$ of the bulk organic fraction, which suggest a shift to higher amounts of C4 vegetation.

Development Toward Modern Vegetation Conditions

After 1000-900 cal BP, a slow and progressive forest recovery is evidenced by slight decrease of Poaceae pollen percentages and slight reduction of fire activity, while pioneer tree taxa (e.g., *Macaranga/Mallotus*) tend to increase (**Figures 5A**, **6**). The coeval pronounced increase in biogenic silica (BiSi) until 820 cal BP (**Figure 3**), coinciding with high diatom concentrations, especially of the heavily silicified species *Aulacoseira granulata*, however indicates an enhanced nutrient input (Ferris and Lehman, 2007). The further lowering in C/N as well as the high Paq afterward also suggest a predominance of aquatic (macrophyte and algae) biomass production (Meyers, 1994, 2003; **Figures 3**, **4**). Forest recovery and the decrease in fire occurrences continues after 600 cal BP, evidenced by still decreasing Poaceae pollen percentages, moderate high charcoal concentration and a slight depletion trend in the $\delta^{13}C$ record toward C_3 vegetation endmember. However, pollen assemblages reveal a different tree composition than in rain forest prior to 1300 cal BP. Pioneer tree taxa characterized by fast recovery after disturbance (*Trema*, *Macaranga/Mallotus*) are more abundant, while several tree taxa do not recover (*Podocarpus*, *Weinmannia*, *Ilex*, Meliaceae/Sapotaceae or *Schefflera*) and new ones appear (Myrtaceae and *Mimosa*). This new tree assemblage points to the development toward modern vegetation conditions which are characterized by a secondary complex vegetation including rain forest, wooded savanna and grasslands with crops mosaics (Mayaux et al., 2000). The result of this substantial change of the landscape is also evidenced by a stable intermediate SAR and the deposition of constantly small minerogenic particles with a sorting and a distribution skewness on a stable but very different level, compared to the initial phase (unit I, **Figures 2**, **3**). Magnetic susceptibility on a quite stable intermediate level suggests a constant input of soil material, which is likely originating from farming activities in the catchment of the lake.

Regional Implications in Northwestern Madagascar

Several studies proposed that human arrival in Madagascar occurred during the early or mid-Holocene (Dewar et al., 2013; Hansford et al., 2018). However, timing and modality of these early occupations are still debated. Except for cut marks on bones, no direct human evidence (archeological artifacts) has been described for the early Holocene (Hansford et al., 2018), while for the mid-Holocene, radiocarbon dating are controversial (Anderson et al., 2018; Anderson, 2019). The recent synthesis of Douglass et al. (2019) suggests that hunters/foragers populations inhabited the island at least since 2000 cal BP. Such activities generally consisting of ephemeral occupations are challenging to record with paleoecological archives since environmental impact is assumed to have been relatively low. Indeed, the vegetation surrounding Lake Amparihibe was mainly dominated by rain forest without major vegetation/environmental changes between 2940 and 1300 cal BP (**Figure 8A**). Consequently, if humans were inhabiting Nosy Be prior to 1300 cal BP, human activity was not strong enough to alter the vegetation composition, or at least, not strong enough to be detected with the applied paleoenvironmental proxies.

Previous Paleoecological Study From Lake Amparihibe

The previous study conducted on Lake Amparihibe by Burney et al. (2003) sets the date for the first occurrence of livestock and initial human impact to 1000 $^{+180}/_{-90}$ cal BP (calibrated age from original publication), by moderating the occurrence of *Sporormiella* and an increase in sedimentary macro-charcoal particles. Our results suggest a major transformation of rain forest vegetation, to an open, fire disturbed, landscape, but starting somewhat earlier at 1306 ± 70 cal BP (**Figure 8A**). The rapid development of grasses (within several decades), coupled with peaks of macro-charcoal particles and saprotrophs/coprophilous fungal spores shows the first detectable human impact in northwestern Madagascar. These results illustrate the development of agriculture likely related to fire for pasture. Human impact has altered the environment and led to a major impact on the sediment accumulation increasing by one order of magnitude (0.13 to 1.3 mm a^{-1}) within less than 100 years. The lake system reacted with changes in the trophic status on this sudden release of nutrients transferred with the eroded soils.

Surprisingly, we were not able to confirm the predicted increase of *Sporormiella* in our record. After 1300 cal BP, a spore of *Sporormiella* has been counted only once on the top core while Burney et al. (2003) show that *Sporormiella* appear at the same time that macro-charcoal particles increase. Raper and Bush (2009) demonstrated that *Sporormiella* concentration declines from the shoreline across the first 100 m of a lake surface, highlighting the importance of the lake size and its changes in the interpretation of paleoecological records of *Sporormiella* abundance. Although both coring locations are in the central part of the lake, slight differences of distances from the shoreline might be an explanation since *Sporormiella* occur in low numbers (<2%) in Burney et al. (2003). However, evaluation of this effect in Nosy Be requires more research and other factors might also contribute to the different results (e.g., chemical treatments, spore identifications). Despite this difference, the entire assemblage of the saprotrophic/coprophilous fungi in our record strongly suggests presence of grazing around the lake (Shumilovskikh and van Geel, 2020; van Asperen et al., 2021), confirming previous results (Burney et al., 2003). By reaching the same conclusion, but with some difference in the results, we demonstrate that this is crucial to not only focus on one taxon, but to focus on the whole assemblages of fungal spores.

Local and Regional Comparison With Archeological Data

Comparison with archeological data reported by Douglass et al. (2019) reveals that this early human impact documented by our results on Nosy Be fits well with the major increase of radiocarbon dates in Madagascar and the maximum pace of

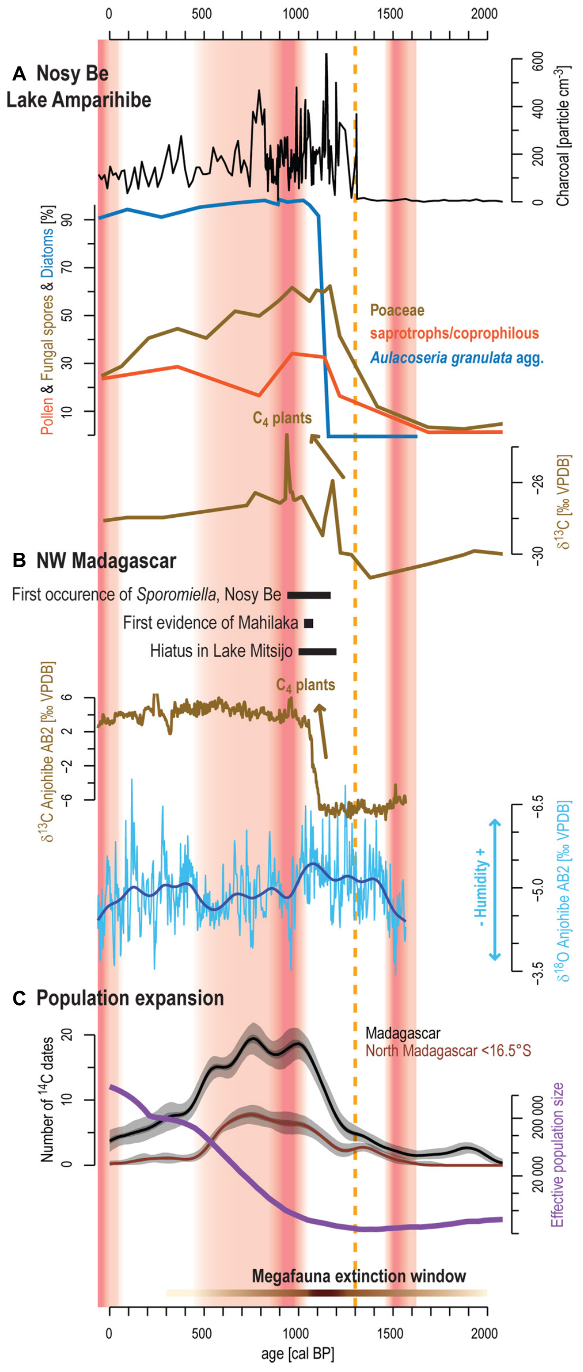

FIGURE 8 | Synthesis of environmental changes in northwestern Madagascar during the past 2000 years. **(A)** main results from sediment sequence AMP16 showing macro-charcoal concentration, percentages of Poaceae, saprotrophs/coprophilous fungal spores and diatom from *Aulacoseria granulata* agg. and the δ^{13}C signal. **(B)** Evidence of initial human occupation on Nosy Be (Burney et al., 2003) and Mahilaka (Crowther et al., 2016). Hiatus in Lake Mitsijo interpreted as a dry period (Matsumoto and Burney, 1994) and δ^{13}C and δ^{18}O speleothem profiles from Anjohibe cave showing C$_3$/C$_4$ vegetation and dynamic and precipitation changes (Scroxton et al., 2017). **(C)** Black curve and brown curve represent the number of ^{14}C dated archeological samples obtained from Douglass et al. (2019) for the whole

(Continued)

FIGURE 8 | island and north of 16.5°S. For each ^{14}C date, 1000 calibrated dates were drawn according to their probability distribution following calibration with the SHcal20 calibration curve (Hogg et al., 2020). Kernel density estimation with a bandwidth of 60 years was applied to each 1000 calibrated dataset and the median curve and the 5% and 95% percentiles computed. Purple curve shows the estimated changes in the effective population size after Pierron et al. (2017). The orange dashed line shows the main environmental change recorded on Nosy Be. The horizontal brown bar with varying saturation intensity shows timelines of pace megafaunal decline in Madagascar (Godfrey et al., 2019). The red shaded areas correspond to the dry periods defined by the δ^{18}O measured on the speleothem and varying saturation intensity to red marks high values within these periods.

megafauna extinction (**Figure 8C**). Demography history based on genomic data also revealed the same pattern with a major population expansion starting between 1250 and 750 cal BP (**Figure 8C**; Pierron et al., 2017). On Nosy Be, archeological surveys have shown first villages and hamlets on the western coast and overlooking Lake Amparihibe and Lake Anjavibe (Dewar and Wright, 1993; Wright and Radimilahy, 2005). Settlements from the coast had evidence of fishing activities while the interior settlements must have concerned solely with swidden cultivation of rice and the herding of cattle, goats and sheep (Wright and Radimilahy, 2005). Consequently, the establishment of such village or hamlet at 1300 cal BP, might be the best fit to explain our findings. Unfortunately, from these archeological surveys, no archeological remains (fish, turtle bones or mammal bones, carbonized coconut shells and local ceramics) have been dated on Nosy Be. However, ceramics are indistinguishable from those found during in Mahilaka, which corresponds to the oldest town described on Madagascar (Dewar and Wright, 1993; Radimilahy, 1997; **Figure 1A**). Mahilaka was an Islamic port located at 40 km south of Nosy Be in Ampasindava Bay and it formed, together with the Comoro islands, an important hub in the Indian Ocean trade network with several thousand inhabitants (Radimilahy, 1997; Crowther et al., 2016). Study of Crowther et al. (2016) dating rice remains in the area revealed that Comoro islands and Mahilaka were occupied at least from ca. 1250 cal BP (8th century) and from ca. 1000 cal BP (10th century), respectively. In this context, significant human impact at 1300 cal BP on Nosy Be island off the mouth off Ampasindava Bay certainly marks initial settlement of these populations in the region. After ca. 600 cal BP, human occupation declines and Mahilaka and surrounding villages in Ampasindava Bay including Nosy Be were abandoned (Dewar and Wright, 1993; Radimilahy, 1997). The reasons for this abandonment remain unclear (Wright and Radimilahy, 2005). Although recovery of forest and decrease of fires evidenced by our study may reflect this population decline, the continuous occurrences of macro-charcoal particles show that Nosy Be has certainly not been entirely deserted.

Climate Variability

To better understand the impact of these populations on natural ecosystems it is crucial to consider the potential contribution of natural factors such as climatic changes and provide robust comparisons with paleoclimate and paleoenvironmental records available in the region. Specifically, several speleothems from northwestern Madagascar help to address past variability of precipitation in this region (**Figures 1A**, **8B**). These records show that the mid- to late Holocene was characterized by a general drying trend punctuated by decadal-to-multidecadal megadroughts or prominent droughts (Wang et al., 2019; Li et al., 2020). A common feature revealed by these speleothems during the past 3000 years is an important megadrought centered around 900 cal BP (Scroxton et al., 2017; Voarintsoa et al., 2017; Wang et al., 2019; Li et al., 2020). Human impact and associated main environmental changes observed on Nosy Be at ca. 1300 cal BP occur earlier than this megadrought (**Figure 8**). Consequently, this drought cannot be considered as the main trigger of the ecosystem shift during the past millennium. A similar pattern is also recorded by $\delta^{13}C$ from the same speleothems showing the replacement of C_3 woodland habitat with C_4 grasslands preceding the megadrought. To explain this transition, Godfrey et al. (2019) proposed the "subsistence shift hypothesis" which suggests a shift from hunting/foraging to herding/farming between 1250 and 1050 cal BP. During this interval, settlement of new immigrant groups, concomitant expansion of human population on Madagascar combined with spread of pastoralism altered natural ecosystems and accelerated the pace of megafaunal decline on Madagascar (Godfrey et al., 2019; Li et al., 2020; Hixon et al., 2021b). Our data support this assumption on Nosy Be, that development of herding/farming activities from 1300 to 1000 cal BP fragmented the rain forest. At ca. 900 cal BP, our results indicate the largest ERD recorded during the past 3000 years and the maximum value of $\delta^{13}C$ of the bulk organic fraction (**Figure 2** and **Supplementary Figure 1**). This 8.7 cm thick layer might be related to a lake level decrease during the megadrought and it could explain the observed reworked material and the outlier radiocarbon date (**Table 1**). However, one must remain careful with the interpretation of this layer because humans were already settled in the vicinity of the lake and distinguishing the effect of human impact and climate change on ecosystems is challenging in this context. Additional study sites or precipitation-related proxy are therefore necessary to confirm this hypothesis. After ca. 500 cal BP, more humid conditions are evidenced by speleothems (Scroxton et al., 2017) and may have also contributed to the observed forest recovery on Nosy Be (**Figure 5**). However, except for the well constrained megadrought at 900 cal BP, speleothem records are partly showing contradicting precipitation trends, despite most of them originate from the same cave (Supplementary Figure 3 in Supplementary Material from Li et al., 2020), which makes them rather debatable.

In northwestern Madagascar, other study provided paleoecological data (**Figure 8B**). Lake Mitsinjo sediments (**Figure 1A**) recorded significant grassland development and an increase in charcoal particles occurred from ca. 1000-900 cal BP, that was preceded by a hiatus in sediment deposition (Matsumoto and Burney, 1994; Burney, 1999). In Benavony (**Figure 1A**), a marshy meadow, the first significant peak of macro-charcoal occurred even later at ca. 800 cal BP (Burney, 1999). Age uncertainties may be responsible for these discrepancies but small-scale spatial differences in the onset and intensity of human activities may also have played a role. Furthermore, influence of climatic changes cannot entirely be excluded, since vegetation changes in northwestern Madagascar occurred in the context of a multimillennial drying trend and several megadroughts occurred during the Holocene (Li et al., 2020). Resilience of every vegetation type in this region (dry deciduous forest, semi-deciduous forest, rain forest or montane vegetation) may have been altered differently to these climatic changes and to the increase of human activities. In this context, without additional and high-resolution paleoecological records it will further remain a matter of discussion to which extent megadroughts affected human impact on natural ecosystem alteration during the past millennium.

CONCLUSION

In this study, we investigated vegetation changes, fire regime, and various sedimentological proxies on the lake system of Lake Amparihibe on Nosy Be, an island located in northwestern Madagascar, which serves as a natural geoarchive. The lacustrine sediments provide insight into environmental dynamics of the past three millennia using multiple paleoenvironmental proxies. Paleoecological results indicate an ecosystem shift at 1300 cal BP characterized by a fragmentation of rain forest related to local fire intensification with development of herding and farming on Nosy Be island. This major ecological change also facilitated distinctively enhanced erosion of the local soils and thus strong sediment and nutrient input into the lacustrine system, resulting in significant aquatic community alterations. Our data confirm a first and strong human impact via agriculture and fire clearance starting at 1300 cal BP on Nosy Be. This supports the "subsistence shift hypothesis," at a local scale, which proposed that population expansion and intensification of human activities from 1250-1050 cal BP significantly altered the natural ecosystems (Godfrey et al., 2019). However, robust comparison to investigate if this significant and early human impact, after 1300 cal BP, altered ecosystems at a larger scale and not only on the coastal sites still requires high resolution multi-proxy records from continuous sedimentary geoarchives as well as records located further north and in the hinterland. Lack of such data also prevents precise comparison in Madagascar between different regions to discern different or common features of climatic changes, ecosystem responses and anthropogenic influences at the island's scale during the late Holocene. Provide paleoecological data beyond the late Holocene is also strongly recommended to document the influence of natural climate change on ecosystems dynamics and to understand the current state of Malagasy biodiversity (Teixeira et al., 2021). According to the shallow seismic survey and the age model Lake Amparihibe could fill this gap and contribute environmental data for at least the past 8000 years. Previous studies already recommended environmental and human history detailed investigations focusing on different regions of Madagascar (Dewar, 1997). This recommendation is still very relevant today and high-resolution paleoenvironmental data such as the ones provided here, or from new sites, are strongly needed to better understand current biodiversity and to help appropriate management and conservation of Madagascar's unique biomes.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

GD, VM, and TK designed the study. GD, J-JR, and KK organized and conducted the fieldwork. AR, ML, TK, MB, TH, LS, KK, and VM were responsible for laboratory analyses and data interpretation. AR and VM jointly wrote the first draft of the manuscript. ML, TK, RZ, CF, LS, LB, GD, and KK added sections to the manuscript. All authors discussed the manuscript and approved the submitted version.

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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.2021.783770/full#supplementary-material

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Colonization During Colonialism: Developing a Framework to Assess the Rapid Ecological Transformation of Mauritius's Pristine Ecosystem

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The colonization of Mauritius exemplifies the role played by humans in altering the ecosystems of remote oceanic islands. This paper focuses on how we study those islands first colonized under the global mantle of colonialism. Here we aim to provide a framework for historical ecological investigations to disentangle the processes, impacts, and outcomes of colonization during colonialism, considering local, regional, and global drivers. The paper provides a review of existing literature, outlines a proposed research program encompassing paleoecology, paleoclimatology, archeology, and history, and offers details of potential research sites. We present "historical ecology" as a framework to aid future work, and argue that a refined understanding of the impact of human colonization can help create a nuanced chronology of environmental degradation that typifies Mauritius. Such detailed assessment is necessary to inform contemporary ecological conservation efforts. Finally, we argue that narratives of changing ecosystems and practice can help construct "usable pasts," often missing from historical records, for the multicultural populace of the island.

Keywords: biodiversity, extinction, environment, historical ecology, archeology, oceanic islands, enslavement, indenture

INTRODUCTION

Island colonization implies the permanent establishment of a community or colony rather than visitation, exploitation, or seasonal settlement. It is rare that we can distinguish between island colonization vs. seasonal settlement or sporadic activity within the archeological record, and definitions of colonization generally omit the intricacies of the "process" involved. This colonization process includes the landscape learning process (Rockman, 2003), visitation, resource exploitation and the gradual build-up of landscape knowledge, yet detailed study of the process of island colonization during colonialism is lacking.

The biogeographically divergent Indian Ocean staged the earliest examples of colonization and human maritime migrations. *Homo floresiensis* reached Flores between 840 KYA to 1 MYA

(Morwood et al., 1999; Brumm et al., 2010); crossings to Sahul were undertaken by at least 50 KYA (Bird et al., 2019) and possibly as early as 65 KYA (Clarkson et al., 2017). This early settlement chronology through Island South East Asia is contrasted by the colonization history of many open Indian Ocean islands; the Seychelles for example were one of the last places on earth to be settled, in AD 1770 (Fauvel, 1909; Cheke, 2010).

Settlement of Mauritius represents another recent colonization event. Following utilization by the Portuguese from 1506, and subsequent settlement by the Dutch in 1638 (Vaughan, 2005; Cheke and Hume, 2008), the island came under French occupation in 1715, and became British in 1810. During the 18th and 19th centuries Mauritius played a key role in the development of modern global Indian Ocean trade networks, serving as a hub for labor diasporas, and absorbing large numbers of individuals working on plantations. Consensus asserts that the island remained unoccupied until the arrival of Europeans due to its isolation in the Indian Ocean, and its distance from the East African coast. Research has tended toward that of its colonial history or the impact of humans on the island's natural environment and the reduction of native vegetation (Safford, 1997) and fauna, most famously the extinction of the dodo.

As the true scale of climatic and environmental disruption to island communities is increasingly acknowledged (Douglass and Cooper, 2020), the need to understand the process of colonization and disentangle this from the island's colonial history becomes clear. This paper is exploratory and aspirational, it presents initial research by the Mauritian Archeology and Heritage (MACH) project (Seetah, 2015) using a historical ecological approach to explore ways to understand island colonization under colonialism. The ability to better understand ecological change as a function of discrete human activity is identified as a major gap in current research on island conservation (Florens et al., 2012). We argue that historical ecology is a useable framework for an assessment of climatic and ecological impacts on Mauritius and present a summary of sites and their ecological context to consider the environmental and socio-political consequences of colonialism in the region, before presenting a conceptual framework for future research. Ultimately the aim of this paper is to explore how to produce "useable pasts" (Lane, 2010, p. 300) to inform future action and strategies for conservation, as well as our understanding of the lifeways of laboring peoples on the island.

For Mauritius, historical records have been extensively mined to recover evidence of ecological change following colonization (e.g., introductions and extinctions see Cheke, 2010, 2013). Archeological research has tended to focus on settlement development (Floore and Jayasena, 2010), and military installations (Summers and Summers, 2008), although more recent publications focus on the environmental contexts for a range of sites (see collection of articles in Seetah, in press). Initial, comprehensive, coring programs have been undertaken, but these have concentrated on Pleistocene to early Holocene transitions, with limited discussion of changes in recent centuries (de Boer et al., 2013a,b). The framework we propose could therefore help identify and respond to gaps in existing knowledge and promote new enquiry.

For example, from the literature we have reviewed and present in this paper, we identify several research questions that remain unanswered:

1. Aside from initial impacts on mangrove by the Dutch, what is the true scale of human activity on coastal ecosystems and ecology over time?
2. Can we accurately track the moving frontier of sugar production over time?
3. How did the differential impacts of commensals affect the island's ecology? What were the relationships between introduced species, and how did this exacerbate the decline of native fauna?
4. Similarly, what specific impacts affected endemic floras as plantations were established and developed?
5. Perhaps most importantly, can we identify the *main* driver of ecological degradation?

Focusing specifically on the last question, in this paper we tentatively test whether human demographics during the colonial period can be considered as a robust indicator of environmental impact through a combined assessment of historical trends and ecological proxies. Starting from the baseline hypothesis that "the greater the number of inhabitants, the greater the ecological impact" we explore the role of population size as a critical function for ecological degradation. In the process, we may observe population size—driven by colonial policy—does not have the strongest effect on ecological transformation of the island. Additionally, future research may reveal unexpected correlations between human population, forest clearance and biodiversity trends on colonized islands. Without understanding these relationships, it is difficult to fully understand lived experience of this landscape in the past, or, how best to conserve these landscapes in the present.

THEORIZING COLONIZATION DURING COLONIALISM

Research and debate on the first human colonization of oceanic islands have focused on events prior to AD 1500. This work has emphasized the seafaring technology of early watercraft, climatic drivers (Goodwin et al., 2014), and the motivation and timing for these voyages (Anderson, 1991; Wilmshurst et al., 2011). Post AD 1500, the emphasis shifts to focus on European expansion, framed around catastrophic impacts on indigenous populations and local biodiversity and ecology (Diamond, 2005). Colonization is considered in this paper as both a *de novo* episode involving initial occupation of a habitat, and a protracted transformative process over time. Under colonialism, distinguished here from colonization and describing hegemonic control of resources and peoples, the rate and scale of human impacts on ecosystems around the globe reached unprecedented levels.

Cases of staggered colonization, describing islands that were colonized relatively late compared to neighboring landmasses, can be found in the Caribbean, north African Atlantic coast, and South Pacific (Keegan and Diamond, 1987). *De novo* colonization of the Pitcairn Islands by settlers from the *Bounty* in 1798, and the

Galapagos in the 1800s, represent examples of colonization events during colonialism. However, nowhere is the paradox of late colonization—where conditions appear suitable for colonization, but the actual event only occurred recently—more pronounced than in the Indian Ocean. Fittingly termed "The Remote Island Enigma," this phenomenon typifies 28% of the small islands in the region (Anderson et al., 2018, p. 30–31).

Oceanic islands, specifically smaller ones, are characterized by a lower degree of ecological complexity on land (i.e., less extended trophic nets) compared to larger landmasses, and are particularly susceptible to ecological degradation following the introduction of exotic taxa and species (Fitzpatrick and Erlandson, 2018). Colonization invariably displaces or at least disrupts autochthonous populations. This disruptive process was deliberately exacerbated on those islands colonized during colonialism through practices that were designed to alter landscapes, promote globalized capitalism, and reconfigure human, animal, and plant populations.

Historical Ecology and Island Colonization

"Historical ecology" bridges historical and archeological research, forming an "interdisciplinary *long durée.*" It offers an ideal framework to investigate human ecosystems, political economies, intensification in agriculture and the impacts of other extractive industries. The framework is not focused on major transitions but rather "on the development of later communities who, while not the "first" to achieve some perceived milestone, could none the less be confidently linked to modern-day peoples in a more direct historical manner, thus producing a long-term record of continuity and change that may have resonance in the present" (Davies, 2010, p. 280). Emphasis is on spatial over temporal boundaries. It is our contention that historical ecology is particularly well suited to an island context like Mauritius, given the near-universal transformation of terrestrial and coastal zones within a short chronological span. Furthermore, the framework aims to situate the impact of all groups who influenced local ecology. In the absence of an indigenous population, all incoming peoples to Mauritius can be considered as colonizers.

We adapt Crumley's five processes (Crumley, 1994; see also Davies, 2010), identified as providing a set of unifying parameters that can be utilized within a historical ecology framework:

1. Human impacts: anthropogenic land cover changes, especially those modulated through technology.
2. Global impacts: local implications of global climatic systems, i.e., the monsoon.
3. Effective responses: the short- and long-term effective response to ecological modification, and the responding human impact.
4. Anticipated change: the nature and consequences of future ecological modification.
5. Potential change: anticipated modifications using a historical lens.

These processes guide survey and analytical methods to assess the nature of landscape change, i.e., in response to incipient and then rapidly intensified agriculture; the development of monocrop sugar production; the effects of commensals; how subsistence and settlements strategies of all groups impacted local ecology, and how activities associated with resource extraction and use, e.g., smelting, charcoal production, lime extraction, etc., led to landscape and soil degradation. There is a particular need to understand the ecological consequences of sugar production, situating these alongside the socio-political drivers that motivated local commercial enterprise. Understanding the underlying transformative ecological processes is critical to provide baseline climatic and environmental evidence, nested within the broader historic socio-economic context. Mitigation of past damage may be possible from the remnants of the highly fragmented and degraded local ecology. In summary, historical ecology provides a way to align major ecological colonization events, e.g., introductions, with the policies of colonialism. These can then be framed as part of subsequent short- and long-term environmental impacts to support future mitigation strategies.

STUDY AREA

The Mascarene Archipelago provides an ideal location to investigate the incipient, escalating, and long-term impacts of colonization and colonialism. These islands, the last major group to be colonized by humans, are especially important as they were genuine pristine ecosystems until a few centuries ago (Hume et al., 2013). In this context, Mauritius is a particularly useful case due to:

1. Its current biodiversity status and potential for conservation.
2. Its specific colonization history, with multiple waves of imperial groups, and distinct demographic flux that involved African, Indian, Malagasy, and Chinese peoples.
3. Its demographic and socio-political status as a long-standing democratic state with religious pluralism; high population density; dependency on imports and extractive commercialism (i.e., sugar, tourism, and fisheries), and a rapid rate of urbanization.
4. The potential to correct and mitigate future biodiversity degradation through sensitive policy.
5. The potential that the island can serve as a model for the 28% of IO islands, and other oceanic islands colonized during colonialism, and for other islands communities with colonial-period legacies.

The island's ecology has been the subject of extensive research, compared to most small islands in the Indian Ocean. Initially, this was motivated by a desire to understand colonial science. More recently, interest has been enthused by a fascination with the extinction of the dodo (Hume, 2006) and the current conservation status of the island's biota. Nonetheless, gaps in our understanding of the timing, rate, scale, and extent of historical degradative processes that affected the island remain. For example, how far into, and how quickly, did commensal species invade interior habitats?

A more profound gap is that scant attention has been paid to the actions of enslaved and indentured peoples. This ignores the agency of most of the population, indeed, the majority of the *colonizers*, who shaped the island's ecology. The Mauritian population of enslaved peoples grew steadily, reaching 60,000 in 1809, 80% of the island's inhabitants (Allen, 2012). During indenture, nearly half a million people migrated to the island in only 30–40 years. Absorbing such numbers, whilst undergoing extensive deforestation, and intensified agriculture, must have been spectacularly damaging to the island's entire ecosystem. It has been speculated that maroons and convicts may have contributed to the demise of the dodo, based on evidence of human mediated cut marks on dodo bones—a predominantly lowland bird—found in higher elevation cave shelters (Janoo, 2005). These suggestions, though contentious, at least stimulate us to consider the impacts of the global population of the island. Large gaps exist in our understanding of the damage to the maritime setting. Again, this is a topic where a more cohesive assessment of the actions of all groups would be useful. The post-emancipation period witnessed a migration of former enslaved individuals to the coast. Out of necessity, these individuals traded the plantation for a livelihood built on fishing the lagoon.

Geology, Topography, and Ecology

The Mascarenes were formed by volcanic activity, and constitute Réunion, Mauritius, and Rodrigues, as well as the Agalega Islands, Saint Brandon (also known as the Cargados Carajos), and Tromelin (**Figure 1**). Mauritius (centered on 20°20'S, 57°30'E) emerged from a hotspot to the southeast coast of Réunion (de Boer et al., 2013b) around 7.8 and 6.8 MYA (McDougall and Chamalaun, 1969). Volcanic activity, which ceased on the island around 25 KYA (Saddul, 2002), created successive island-and-lagoon ecosystems with fringing reef. These survive as fossilized reefs in various in-land locations, including Port Louis (**Figure 2**), and La Prairie in the southwest of the island. Mauritius is 64 km long in a north-north-east and south-south-west direction and 43 km across (1,865 km^2). The island's highest peak, Piton de la Petite Rivière Noire, rises to 828 m asl. Soils of the island developed overwhelmingly over basalt (Craig, 1934), with a high iron content, especially in the Terre Rouge region, with limited areas confined to the coasts with soils developing over coral sands or calcarenite. This iron rich soil negatively impacts the preservation of osteological remains and material artifacts, making sites like Mare aux Songes, a marshy Holocene faunal bone concentration, and Le Morne Old Cemetery, a burial ground situated on a sandy intertidal zone, key sites for assessing pre-human ecosystems, and demographic change during colonization. Humidity and moisture, rather than temperature, were key to local ecosystem stability during the Holocene (van der Plas et al., 2012; de Boer et al., 2013a). The island underwent periods of ecological flux during the Pleistocene and Holocene (van der Plas et al., 2012; de Boer et al., 2014), in cases resulting in mass mortality of local fauna (Rijsdijk et al., 2011, 2015). A marked increase in charcoal recovered

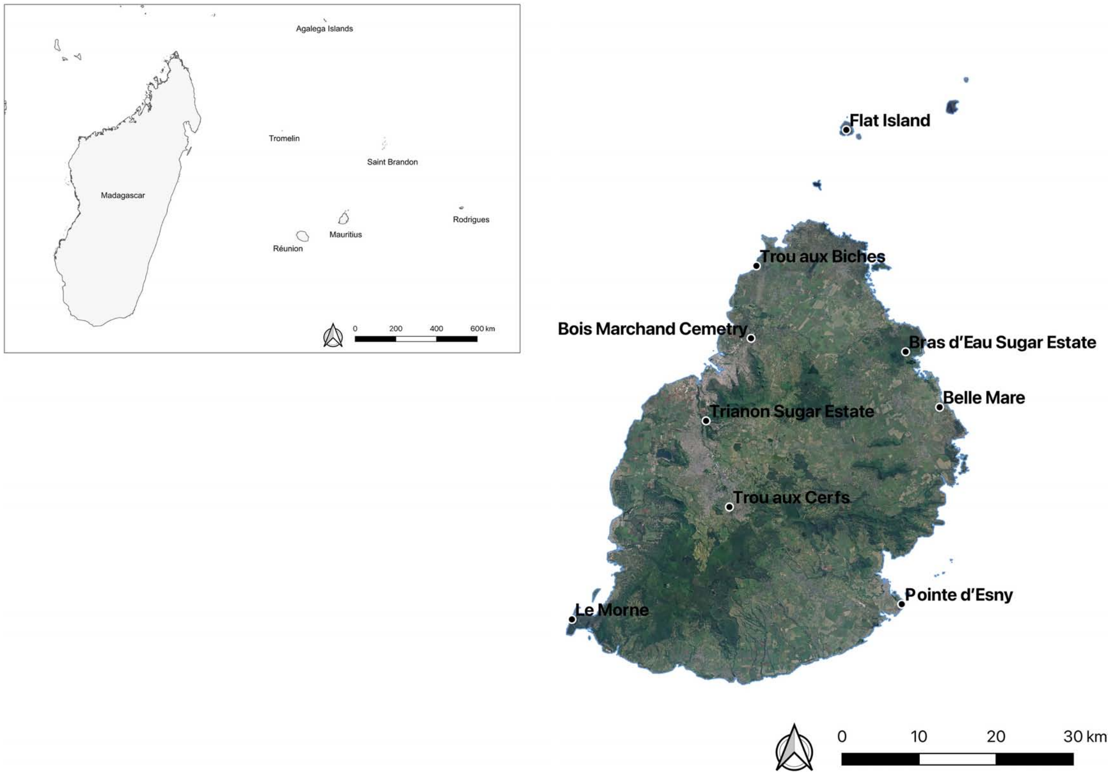

FIGURE 1 | Map of Mauritius with sites mentioned in text; inset situates the Mascarene Archipelago within the broader regional context.

FIGURE 2 | Fossil reef located in Port Louis, used during the colonial period as foundations for a hospital block attached to the immigration depot. This type of formation evidences the fringing reef that would have characterized the island as it formed during successive volcanic eruptions.

from soil cores taken from Kanaka Crater points to expanding human activity with colonization, alongside a rapid reduction in palm woodlands (de Boer et al., 2014). In tandem with deforestation and overall ecological degradation, a wide spectrum of introduced species, including pine (*Pinus* spp.), tea (*Camellia sinensis*), sugar cane (*Saccharum officinarum*) and many other fruiting and ornamental plants (de Boer et al., 2013b), have radically transformed the island's coastal and terrestrial landscape (Florens et al., 2016, 2017).

Conservation Status

Mauritius is a particularly complex case when attempting to assess the historical and evolving conservation status of the island. Although there is some debate as to the extent of forest on the island prior to colonization (de Boer et al., 2014), research suggests that Mauritius has lost some 95.6% of its original native vegetation landcover following human landing on the island (Hammond et al., 2015). What remains has been aptly described as a "confetti of fragments" (Florens et al., 2012). Because of the rate and scale of deforestation, relatively little is currently known about the dynamics of the natural ecosystem over time (Florens et al., 2012; de Boer et al., 2013b). Some 1,675 flowering plant taxa have been introduced (Kueffer and Mauremootoo, 2004), compared to 691 native species, of which nearly 40% are endemic (Baider et al., 2010). The establishment of the Jardin Botanique des Pamplemousses' by Pierre Poivre in 1770, renamed the Sir Seewoosagur Ramgoolam Botanic Garden post-independence in 1988, marked the creation of the first botanical garden in the southern hemisphere. The island also has an enviable record of botanical inventories (Bojer, 1837; Baker, 1877; Johnston, 1896; Vaughan, 1937; Baider et al., 2010). Remarkably, even with this history of cataloging, and despite the small size of the island, new native species of flora are still being discovered (Roberts et al., 2004; Baider et al., 2012), including not only relatively small herbaceous endemics (Florens and Baider, 2006; Pailler et al., 2020) but also much more conspicuous shrubs (Baider and Florens, 2016) and even larger trees (Baider and Florens, 2013; Byng et al., 2015). Important research on the impacts of anthropogenic activity on the island since colonization provides further cause for optimism, highlighting the uniquely rich and resilient nature of the local ecosystem. The wet forests of the island retain a density of woody plants, some 8,000 individual plants per ha (at least 1 cm stem diameter), and have the highest diversity index in the Mascarenes, and one of the highest for oceanic islands anywhere in the world. These facts, alongside the high rate of species endemism, and its position within the Madagascar and Indian Ocean islands biodiversity hotspots (Myers et al., 2000; Jenkins et al., 2013), all support the high priority for conservation (BGCI, 2021).

Colonization Processes and Colonial History

Adapting a historical ecology framework, the following emphasizes the onset of deforestation, establishment of plantations, rise of monocrop agriculture, and the development of modern infrastructures (Lane, 2010). This section is framed around the processes of colonization, emphasizing demography, species change, and initial, escalated, then profound ecological degradation, against a chronology of shifting colonial hegemony (**Figure 3**).

Initial Colonization

First settled in 1638, Mauritius was the earliest of the Mascarene islands to experience permanent habitation. It is a portent for other oceanic islands, epitomizing extreme and rapid anthropogenic landscape transformation wrought in less than four centuries (Florens, 2013). Why the island was not colonized earlier remains unknown. Mauritius is 2,000 km from the coast of East Africa, and 829 km from Madagascar. These two locations could have served as launching points for early visits. Earlier exploration has been suggested for the Phoenicians (Tooranwa, 2003, p. 21), and Swahili peoples (Allen, 1999, p. 9); however, there is no evidence to support this. Temporal variations in the monsoon, likely influenced the ability of early seafarers to cross the open ocean and navigate to the island. Maritime resources would have more than compensated for the absence of native land mammals as a food source. From at least the thirteenth century, Arab merchants allegedly visited, or at least knew of the island (Hume et al., 2013). In 1506, the Portuguese visited Mauritius and named it *Ilha do Cisne* (Island of the Swan), using it as a refreshing post (Grove, 1995, pp. 129–130). Neither of these groups settled. The Dutch reached the island in 1598, attempting a permanent settlement from 1638 at Vieux Grand Port. This first group of settlers constituted 25 men (Floore and Jayasena, 2010). They abandoned the island in 1658, re-settled in 1664, but only until 1710. The focus of the Dutch was the exploitation of coastal ebony forest (Carter, 2006, p. 807). They also brought some 300 enslaved individuals from Madagascar and Java, abandoning these people when they left the island. The ecological effects of these first settlement attempts may be assimilated to landnám (Islandic for land-taking), which typifies the early colonization of Iceland, with

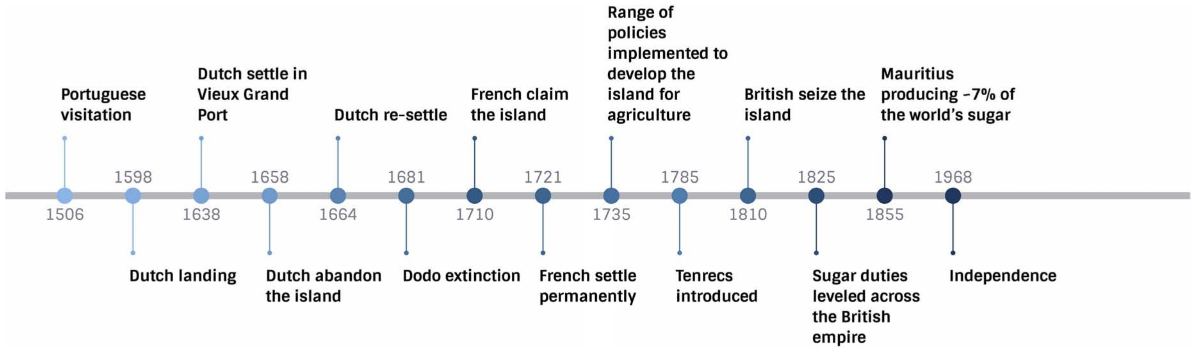

FIGURE 3 | Summary of main historical milestones catalyzing major ecological changes.

incipient forest clearance and sparse agricultural use, followed by abandonment and the spontaneous regeneration of secondary woodland (Smith, 1995). The number of inhabitants remained small during initial colonization. Despite this, the ecological impacts were profound. Deforestation of mangrove, as well as coastal ebony forests, characterized this early period, with ∼5% of the island's forests denuded (Rijsdijk et al., 2015) during this short timeframe. However, the impacts of invasive species appear to be more widespread. One reason that the Dutch settlement failed was due to plagues of rats destroying crops (Cheke and Hume, 2008, p. 80). This suggests that invasive rats were inadvertently introduced during visitation by the Portuguese, or from passing ships that were wrecked on the reefs (Grove, 1995, p. 130). Rats have a particularly detrimental impact on local ecosystems, especially one with a vertebrate fauna principally comprising birds and reptiles. It was also common practice for sailors to leave goats and pigs on islands in anticipation of culling this walking larder on future visits (Cheke, 2010). Both of these domesticates feralize easily, and pigs, in particular, impact ground nesting birds; indeed, no indigenous ground nesting birds survived the introduction of pigs (Cheke, 1987, p. 160).

The most infamous causality of this early colonization phase was the dodo. A unique mid-Holocene vertebrate bone concentration-Lagerstätte at Mare aux Songes, possibly the very first, youngest, and richest such bone bed discovered on an oceanic island (Rijsdijk et al., 2009), provides a snapshot of the Mauritian ecosystem about 4,000 years ago (Rijsdijk et al., 2011). Equally, this fossil assemblage provides a point of departure to consider the processes of extinction during colonization, and offers insights on how such evidence can inform future mitigation (Rijsdijk et al., 2015). Results from analysis of the Lagerstätte at Mare aux Songes show that the bed itself was created over a short 100-year timespan, suggestive of a mass mortality incident (Rijsdijk et al., 2011). Such events appear connected to localized climatic catastrophe (de Boer et al., 2014). The evidence shows that the dodo had survived thousands of years of cyclical climatic and volcanic extreme events (Rijsdijk et al., 2011, 2015); by the mid seventeenth century, the bird was extinct, a mere century following the discovery by Europeans (Roberts and Solow, 2003; Hume et al., 2004).

Escalating Colonization

For the next century, the island underwent an epoch of expanded terrestrial colonization. The French, who claimed the island in 1715 and settled permanently from 1721, had a more sustained impact on the island's ecology than the Dutch. From 1735, Governor Bertrand-François Mahé de La Bourdonnais initiated a range of policies to develop the island for agriculture. Principal amongst these was the introduction of cattle and water buffalo for traction. Cattle have both direct and indirect negative impacts on ecosystems. Corralling and maintaining herds lead to increased nitrogen from their waste, which often disproportionately benefit invasive alien plants and can impact lagoons in the form of runoff. When they forage, they create paths that facilitate dispersal of less physically robust commensals, such as goats, pigs, and cats, into habitats that would otherwise be difficult to access. This inadvertently exposes indigenous fauna and flora to new invasive species that have a greater negative impact on native ecosystems. Vast tracts of land were parceled and transformed into plantations.

The drastic transformation and deforestation of the hinterland also had a negative impact on the coast and lagoon. Without natural barriers, the torrential rains of cyclones pour the soils from the mountains into the rivers, which in turn carry sediments into the lagoon waters. The lagoons were further polluted and harmed by coastal urbanization and unsustainable fishing as Mauritius lacked pre-colonial artisanal fisheries (Houbert, 2009).

Enslaved Africans, Malagasy, and Indians were brought from French colonies, as well as the East Coast of Africa, and Madagascar (Allen, 2015, p. 22); a labor force engaged to irrevocably transform the island. Tenrecs, introduced around 1785, and which proliferated in the wild, were an important source of food for these laboring peoples (Cheke, 2010), which suggests a nutritional strategy that involved a degree of foraging. This activity may have had an impact on local native species, but it is more likely that introduced mammals such as monkeys were the target. Evidence from Le Morne, a cemetery used by enslaved and post-emancipated peoples around 1815, supports this with the recovery of deer bones found within a burial context.

Profound Colonization

Mauritius entered a penultimate chapter of colonization. Driven by one crop, sugar cane, the scale and rate of change increased exponentially, and encompassed the coastal and lagoon intertidal zones. French hegemony ended in 1810, when the British seized Mauritius, recognizing its strategic regional significance, but less interested in the island itself. The British instituted their own legal system, but virtually all other facets of life remained unchanged, including the plantocracy: the island remained French, but under British rule. This combination effectively merged imperial strengths, to the detriment of the island's ecosystem. An established understanding based on some 100 years of colonial science developed specifically to transform and align the ecosystem to French agricultural ideals, was integrated into the huge infrastructure and globalized trade network of the British empire. Sugarcane had been introduced by the Dutch, and was important to the French, but they also cultivated a variety of crops, and the Bras d'Eau sugar estate for example began as a working farm (Haines, 2019). For the British, sugar was the major cash crop (Walvin, 2019). The transformation of Mauritius into a sugar island is an exemplar of how policy can directly degrade ecology. In 1825, Britain leveled sugar duties throughout its empire. This catalyzed an unprecedented ecological and demographic transformation. Between 1855 and 57, an island of only 1,865 km^2 produced some ∼7% of the world's sugar (Allen, 2008, p. 152). Unlike other volcanic islands in the Mascarenes, or the granitic Seychelles, Mauritius has a relatively flat topography over a large surface area of the island. As important, and unlike nearby Réunion, it had at least two natural harbors, Port Louis (west coast) and Grand Port near Mahébourg (southeast), as well as numerous access points for small water vessels to disembark people.

The British administration coincided with the abolition of the trade in enslaved people. To meet labor demands for the rapidly escalating production of sugar, the British instituted The Great Experiment, replacing *forced* with *indentured* labor. This catalyzed one of the most rapid demographic transformations anywhere in the Indian Ocean (Kuczynski, 1948), with some 451,000 indentured migrant workers, mainly from India, forming this labor diaspora (Allen, 1999, p. 16).

Continued Ecological Transformation

Adopting a view that colonization is a protracted process, the island's chronology of ecological degradation has continued since independence from Britain in 1968, and is ongoing today. The new country emerged from colonial rule as a largely socialist nation. Since then, the ideals of capitalism have marched the island toward modernization, urbanization, and globalization. Independence was the point at which local laboring and mercantile groups rose to political power, but not ownership of the plantations. Some plantations, notably Bras d'Eau, are now state lands. However, estate divisions established during colonialism have largely remained in place to the modern day. In cases, this has placed a burden on both archeological heritage (Bakker and Odendaal, 2008), and conservation initiatives. However, as vast tracks of land are owned by French-descent Mauritians, who constitute just two percent of the overall population, there exists an opportunity to galvanize a relatively small proportion of the populace—but one with political influence as well as land ownership—into action. Moreover, this specific well-educated and globally connected group has often been vocal about the need for ecological sustainability (Le Breton, in press) and has been at the forefront of highlighting the need for better conservation strategies (Florens, 2013). Strides to evaluate and manage local flora and fauna, for example, through the establishment of the NGO the Mauritian Wildlife Foundation, have led to world-acclaimed successes with conservation of the Mauritian Kestrel and Pink Pigeon (Sodhi et al., 2011). However, despite these accomplishments, with the highest population density in Africa (Statista, 2020), the island's ecology will continue to degrade through human activity, and relative inactivity on the part of conservation (Florens, 2013; Sachs et al., 2021).

SURVEYING A LANDSCAPE CREATED BY COLONIALISM

Given the significant conservation status of Mauritius, and the potential of archeo-historic evidence, it is an ideal location to apply the principles of landscape historical ecology by assessing the ecological impacts of colonialism. We need to generate more baseline evidence, but these data need to be cohesive and better aligned with the long-term socio-political and demographic contexts that drove the changes observed in the archeo-historic record. Such data and evidence will best serve to influence policy and practice today. Improving the understanding of what drove biodiversity loss in the various groups of animals and plants over the period of human impact and how these varied through time and space as the various drivers wax and wane, can provide interesting insights in not only how to better protect what is left of one of the most highly threatened biodiversity in the world (BGCI, 2021), but also in restoring the ecosystems into their most functional state possible to ensure reinstating ecosystem services and long term conservation of biodiversity (Albert et al., 2021).

Here we present a broad-spectrum environmental reconnaissance strategy, initially motivated and funded by the Australian National University (PI: Prof. Atholl Anderson) for research focused on the potential early exploration of Mauritius. Sites initially surveyed included Flat Island, Trou aux Cerfs, and Le Morne. MACH subsequently continued several seasons of work on Flat Island, and Le Morne, as well as the remaining sites listed below. At the time of writing, 12 sites have been surveyed as part of the work of MACH. We concentrate on eight locations that have already provided, or have the potential to provide, evidence on the ecological context and change over time (see **Figure 1**).

As outlined above, the following summary of sites and themes emphasizes the relationships between landscape transformation, demographic flux, and colonial directives. This meets our mandate to disentangle and reveal the underlying ecological degradation aligned against the details of colonial chronology and changing policy. In both implicit and explicit ways, we attempt to synthesize work from Mauritius with Crumley's five unifying processes, i.e., human impacts; global impacts; effective responses; anticipated changes, and potential changes. Although some of the sites discussed below have actively been targeted for ecological evidence, our team has also responded to the needs of local heritage institutions requesting support and archeological expertise. In showcasing these sites, we anticipate stimulating new collaborative research focused on developing the historical ecology framework.

Sites and Themes Aligned With Crumley's Processes

1st Process, "Human Impacts"

Bras d'Eau National Park is located within a former estate, spanning some 5,000 acres (20.2 km^2), which has undergone numerous phases of ecological transformation due to agricultural intensification, use of local resources by laboring peoples, and as a consequence of both colonial and post-independence land management (Haines, 2019, 2021). The site is characterized by basalt outcrops; vesicular basalt also forms part of the fabric of the underlying soil. This geomorphology has historically been considered an impediment to agriculture, and a major effort of colonial practice on plantations was to direct enslaved and indentured peoples to stockpile the larger boulders, use medium stones to build walls, and cobbles for roads. Stonemasons also cut the basalt into blocks for buildings. This has had the effect of transforming, on a massive scale, the composition of the island's soil. However, despite the extensive landscape engineering that has occurred on Bras d'Eau, the large size of the site has meant that many areas exist that are ideal for ecological study, located well away from the developed part of the estate. Bras d'Eau retains an ancient ebony tree, which, along with pre-colonization specimens located in the southwest of the island, could be crucial for developing dating profiles.

Trianon was also a former sugar estate, inscribed in 1974 as a National Monument because of the presence of a series of barracks, built from basalt blocks, potentially used as dwellings or storage (Calaon et al., 2012; Seetah et al., 2015). This site has produced the first plant macrofossils indicative of imports and food culture (Seetah, 2015), as well as preliminary finds that point to cattle management.

Biogeography of commensals forms a focus of work concentrating on understanding how introduced species have, and continue, to adapt and alter the environment. By collaborating with a local pest control company, the MACH project has been collecting specimens of rats (*Rattus rattus* and *Rattus norvegicus*, the Indian musk shrew (*Suncus murinus*) from around the island, recording biogeographical evidence, and skeletonizing the specimens. These samples will then form the basis for molecular and geometric morphometric analysis to identify regional variation. Behavioral traits are also recorded. These data will be mapped onto evidence derived from archeological excavations.

Bras d'Eau typifies Crumley's "human impacts" by demonstrating the scale of transformative changes to promote agriculture mediated via technology. In this case, the technology was relatively basic, thus emphasizing the extent of direct human agency in landscape reconfiguration. Bras d'Eau also illustrates how legacies of colonial policy endured to cause ecological harm. Despite being listed as a national park and with some plantings of native and endemic species, it continued to be used for the propagation of exotics, such as mango, that have since completely altered much of the local landscape. Similarly, Trianon also illustrates the scale of change for agriculture, but is even more pertinent within the context of urbanization and development. The entire surrounding region now forms part of a major commercial center, new housing, and major transport developments. In the future, our work will seek to understand the nature of soil change from Trianon and Bras d'Eau as a consequence of agriculture. Understanding "human impacts" is also approached directly from demographic evidence (see future work, below), and indirectly, from the commensals brought to the island.

2nd Process, "Global Impacts"

Flat Island has been left relatively untouched by development with no modern roads or buildings; thus, the paleoecological context remains relatively undamaged. The islet is approx. 12 km from the northernmost tip of Mauritius and covers 253 ha. It was used as a quarantine station in the nineteenth century for humans and livestock. Surveys have identified several suitable areas for coring, but it was clear that mechanical equipment would be needed due to the high degree of basaltic inclusions in the soil.

Bois Marchand was the largest cemetery in the Indian Ocean when established in 1867, covering some 162 ha. As with Flat Island, this site was created in response to massive epidemics, in this case of malaria, which plagued the island from the 1850s. Invariably, these epidemics were a consequence of alterations to the landscape that allowed disease vectors to proliferate; the increased rate of mobility as ship technology improved, and the arrival of new groups of people who carried disease. Research at Bois Marchand has concentrated on recovery of human remains from the epidemics of the late 1860s. The site is also extremely valuable as it was established as a "garden cemetery" (Čaval, in press), which in tropical locations, favored the use of endemic flora (Mytum, 2003, 2004, p. 48). To our knowledge, no recent inventory of the cemetery flora has been done, despite the size and relatively untouched nature of a site established with a view to promulgate endemic plants.

Evidence of landscape change a program of coring is underway with colleagues from Reading University (Pluskowski et al., in press) focused on lakes and wetlands (e.g., the volcanic crater lake of Trou aux Cerfs, and the marshy areas of Le Morne) with potential for recovering sediment sequences containing records of paleoenvironmental and paleoclimatic change (**Figure 4**). This coring profile is being developed at the local scale (e.g., type of crops cultivated, introduction/extinction of plant species, phylogenetic studies, deforestation/burning, floral diversity and abundance, intensive sugar cane exploitation) and continental scales (e.g., history of paleocyclones). Silted lagoons and wetlands in the buffer zone of the Le Morne World Heritage Site provide an ideal location for developing research at the local scale, whilst lake sediments accumulated within Trou aux Cerfs crater

FIGURE 4 | Sediment core extracted from a freshwater marsh located near Belle Mare in 2016. Core analyzed by Dr. Alex Brown, Wessex Archeology based geoarcheologist, as part of initial research undertaken in partnership with Reading University. The core comprises an herbaceous peat (0–0.2 m), dark gray-brown detrital organic lake muds (0.2–0.57 m) overlying olive green silts (0.57 m +). Pollen was poorly preserved, although upper samples of the sequence did include aquatic pollen of *Potamogeton*, fern spores, along with variable quantities of microscopic charcoal.

offer the potential for investigating paleoclimatic change at the continental scale.

Assessing "global impacts" is driven from the view that Mauritius was a hub for the movement of large numbers of laboring peoples (Allen, 1999), and goods. Baseline evidence, from coral cores and other climate proxies will allow us to situate these actions against a chronology of local change that had regional resonance (see future work). Mauritius formed a node between the Indian, and Atlantic and Pacific oceans, both within the context of labor diaspora, and products. Understanding the transmission of disease at a regional scale, and the influence of global weather systems such as El Niño on local climate, are also key outcomes of studies under the umbrella of "global impacts."

3rd Process, "Effective Responses"

Le Morne was inscribed as a UNESCO World Heritage Site (WHS) in 2008, commemorating resistance to enslavement. Falling within the buffer zone of the WHS are several swamps and lagoon areas that likely preserve continuous and easily accessible sedimentary sequences of environmentally salient data. This kind of sequence is indicated for research on environmental and anthropogenic change at the local scale (e.g., introduction/extinction of plant taxa). This is particularly important given that the area was not subject to intensive sugar cropping. Thus, although established settlement has taken place since the period following emancipation, prior to this, the region was sparsely inhabited. Several seasons of survey and excavation in the area have led to the discovery of a cemetery used during and after the period of enslavement. Human remains provide evidence of regional demography (Fregel et al., 2014), and future work on settlements sites will help to reveal the food gathering strategies of individuals not directly attached to the plantation economy (Lightfoot et al., 2020).

Climate proxy evidence is also being collected from coastal areas where emerged portions of ancient coral reefs are evident, and possibly having formed during the last interglacial period (Eemian c. 130 ka BP) or connected with tectonic uplift. This predominantly geological topic can be developed in connection with the positioning of mines for coral extraction and lime production during the colonial period (Walker, 1962), which have had major degradative impacts. Indeed, old coral and calcarenite quarries, such as those at La Prairie, may be a source of cores for climate proxy evidence. The most promising avenue for climate proxy evidence comes from surveys in Pointe d'Esny and Trou aux Biches (see future work). Our team has identified several large corals in both locations, and existing cores are currently housed at the Mauritius Oceanographic Institute. Working with climate scientists Prof. Rob Dunbar and Dr. Neil Tangri from Stanford University, temperature logging instruments have also been placed in these locations to monitor sea temperature fluctuations over the last 5 years.

Other sites listed are obviously pertinent to our understanding of the response to ecological degradation. We focus on Le Morne because it provides evidence from a group that has very little presence in the historical record, and which is generally thought of as having little material culture. Thus, Le Morne helps us assess "effective response" from the view of enslaved people, at the time that the most profound ecological changes to the island were coinciding with massive social upheavals and demographic reconfiguration. Le Morne has also been a key site for modern activity to regenerate local mangrove forests (**Figure 5**). Clearly, we will need to integrate many locations to investigate this process. However, creating a profile of climatic and ecological changes within a well-defined chronology has particular value for the region of Le Morne as this remains an area of low population density, with evidence of the will to conserve the existing habitat. Most importantly, the region remains one of the poorest in Mauritius, and building local resilience should be a priority to support the local community.

4th Process, "Anticipated Change"

Trou aux Cerfs is the largest crater on the island and harbors a volcanic lake. It has been described as a monogenetic volcano with a central vent, formed during late stages of volcanic activity from 700 to 600 KYA (Saddul, 1995), and is now dormant. The crater is 614 m asl (Nel et al., 2012) forms a circular depression, with a diameter of some 350 m and 180 m at the outermost

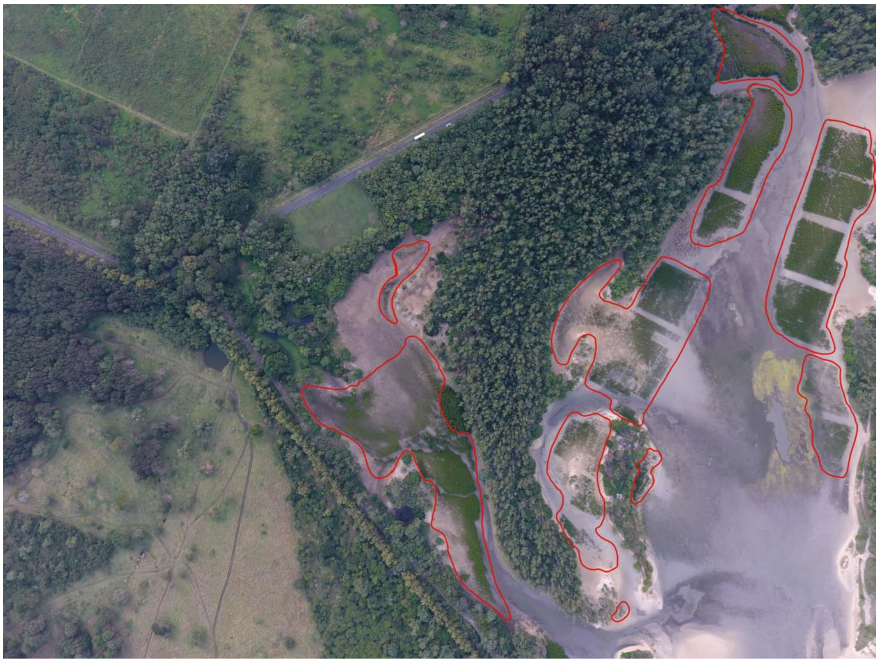

FIGURE 5 | Aerial image of mangrove regeneration; new mangrove evident as delineated and regular plantings (outlined in red). Drone image from 2017.

rim and base, respectively, and a depth of 80 m at the base (Johnson et al., 2010). Situated in a prominent portion of the island, and less affected by agricultural activities in proximity, the sedimentary sequence at the bottom of the crater is likely to provide continental-scale paleoclimatic records (e.g., cyclones, precipitation, temperature). In addition, any botanical records are likely less affected by human activity, although deforestation did occur in the post-war period and replanted with pine. These records would form useable comparisons with those accumulated in the lowlands and near the coast. Important results have been derived from cores extracted from Trou Kanaka (de Boer et al., 2013a,b, 2014) to the south of Trou aux Cerfs. Aligning evidence from a wider geographic profile of cores would provide baseline data from a broad sweep of the island, and more broadly for the archipelago and the Indian Ocean. The area immediately around the crater edge has a path ringing the entire perimeter, which would allow a relatively easy descent into the crater with hand-held coring equipment. An initial reconnaissance of the visible crater slope was made, identifying a minimum of six terraces. From this preliminary survey, an estimate of the minimum sediment accumulation on the volcano lake margin was possible, with the topmost sediment characterized by small angular basalt blocks.

This location brings evidence in support of understanding “anticipated changes” specifically with regards to how a continuation of sugar agriculture will further deteriorate local ecology, and also, escalating urbanization as Trou aux Cerfs is within a region, Curepipe, that has seen rapid development. The site is also critical to provide baseline evidence from which sustained mitigation strategies can be developed to support conservation.

5th Process, “Potential Change”

Impacts on the maritime context are being investigated through coastal reconnaissance and a large-scale program of mapping of underwater wrecks (Manfio and Seetah, in press; Manfio and von Arnim, 2020, p. 505). Coastal reconnaissance has mainly been undertaken as foot surveys, circumnavigating the island. This was conducted to understand topography, coastal morphology, erosion, and land use. The integration of these data with archive records in GIS systems is providing information on coastal transformation and use over the centuries. In addition, ethnographic study of traditional boats, local seafaring practices, boat types, and their regional differences is ongoing to better understand the development of incipient seafaring traditions and cultural affinity with coastal and lagoon environments.

The maritime context is critical for assessing how multiple uses of the coast over time will impact, and change, what is arguably one of the island’s most important natural resources, the lagoon. New developments in aquaculture are already providing economic benefits. Additionally, new uses of the coast for activities associated with tourism, the exploitation of deep-sea fishing resources, and the fact that Mauritius remains an important nautical thoroughfare, all continue a long history of marine exploitation. These diverse uses are radically evolving, and there is a pressing need to situate the heritage context into this dynamic equation to avoid loss of a significant cultural resource. Over 800 historical shipwrecks have been recorded from archival records and surveys in the waters around Mauritius. From this substantial database, GIS mapping is underway integrating historical, archeological, as well as environmental data to help local government manage this heritage resource, protect the wrecks, and mitigate potential impacts on the lagoon environment as the lagoon comes under increasing pressure (Manfio and von Arnim, 2020).

Table 1 summarizes the section above aligned with the historical ecology framework. As can be seen, overlap is unavoidable and anticipated.

Future Work

In concluding this section on the ongoing work of MACH, the following summarizes future projects that would support the development of a landscape historical ecology framework.

Prehistory of Mauritius

New research is needed to develop a preliminary model for sea-level change and emerged land in the Mascarene Plateau (Norder et al., 2018), back to the LGM period (Last Glacial Maximum, c. 18 ka BP), when sea level was as much as 130 m below present-day levels, and beyond. Understanding of how the prehistoric sea-level changes influenced the region's biota is evolving. For example, in Mauritius and elsewhere, recent findings (Norder et al., 2018) have showed that single island endemism in some groups (flowering plants and mollusks) are best explained by longer-lasting sea-level stands, instead of the lowest sea-level stands achieved during glaciations. In Mauritius, it has been suggested that, during the last glaciation, Flat Island, along with other islets off the north coast, was connected to Mauritius (Strahm, 1993). Also, changes in palaeo-currents in the Indian Ocean and historical navigation tracks (Vincent, 1998) need to be considered. These datasets would help define potential sea-routes and investigate the possibility and impact of early visitation. Future research may involve the identification of coral reef emergence points and the definition of their position above sea level, inclination, and mapping.

Priorities of Human Colonization

Priorities of human colonization are being investigated through the analysis of both modern and ancient DNA. An initial exploratory study with 100 individuals sampled from a cross section of the island's peoples revealed a highly admixed contemporary population (Fregel et al., 2014). This has motivated a larger study currently under investigation. Ancient sampling from cemeteries in Le Morne and Bois Marchand has provided the first concrete scientific evidence for the origins of the enslaved and indentured diasporas (Fregel et al., 2015).

Climate Proxy Evidence

Climate proxy evidence Trou aux Cerfs has the potential of providing a long paleocyclone and paleoclimatic record from the center of the island. A minimum of six terraces were observed on the lowest portion of the volcano mouth. A 250 cm long stick was manually driven into the lake sediments from the top of the lowest terrace providing an estimate of the minimum sediment accumulation on the volcano lake margin. When trying to hammer in a PVC pipe we were prevented by angular basalt blocks (10 s of cm) and could only recover the top 30 cm of the sequence that will be used to test proxy presence/preservation. Proper coring equipment is needed to recover a suitable sequence. Pointe d'Esny in the south and Trou aux Biches in the north, two coastal sites, form part of surveys to identify suitable *Porites* corals that can be cored to generate proxy data on climate and ecological changes over the last 200–300 years. Fossilized coral and reef have been identified from Port Louis, a coral reef profile reaching c. 4 m asl. A 1 m deep channel filled with cross-bedded sand-sized bioclasts characterizes the top of the profile (**Figure 2**). On Flat Island, a coral reef platform 2 m asl has been recorded, which coincides with the position of a jetty and graveyard in Plage Verte.

Dating

Dating should form a major focus of research, given that the C14 profile for the last 300 years, particularly in tropical climates, is poor (Higham, pers. comm.). Dating profiles are being developed from coral (Seetah, 2018; Pluskowski et al., in press) and ecofacts as part of the work of MACH (focused on the historical period) to complement the extensive dating undertaken on sediment core to study climate variability and ecology (mainly pre-colonial) (de Boer et al., 2014) and mid-Holocene fauna (Rijsdijk et al., 2011). In the future, these studies could be knitted into a comprehensive regional database, such as is currently being undertaken for Mediterranean Africa (Lucarini et al., 2020). Dendrochronology profiles, challenging in tropical climates, are being developed in collaboration with colleagues at the Mauritius Herbarium, and from single large specimens, such as the ebony tree from Bras d'Eau (**Figure 6**). Mauritius presents several preserved wildlife areas where ebony and other hardwood trees as old as 500 years. may still be found, e.g., Brise Fer forest. Starting from the study of those trees, a new dendrochronological reference curve can be built, which can be used for paleoclimatic purposes, as well as for tracking historical wood trade routes, particularly relevant for ebony. However, research is needed to check the viability of ebony trees for dendrochronology; growth rings may be too thin as the diameter of a 400 yr old ebony tree can be as

FIGURE 6 | A wood core extracted from an endemic ebony tree for dendrochronology, Bras d'Eau Sugar Estate. Although banding of the rings is faint, typical of tropical hardwoods, the image illustrates the potential for use of this species as part of a dendrochronology dating program.

TABLE 1 | Sites and themes nested within Crumley's five historical ecology processes.

Historical ecology processes	Site	Theme
Humans impacts	Bras d'Eau; Trianon	Priorities of arrival; commensals
Global impacts	Pointe d'Esny and Trou aux Biches (baseline data); Bois Marchand and Flat Island (disease)	Landscape change (regional)
Effective responses	Le Morne (coastal regeneration)	Dating (future work); climate proxies
Anticipated change	Trou aux Cerfs (baseline data)	
Potential change		Maritime context

narrow as 40 cm. A recently funded and government-approved 16-month long project (PI: VF) is currently gathering stem diameter growth rate of thousands of forest trees (each previously measured 4–20 years ago), that will provide data useful to calibrate age of native tree species using their trunk diameter. Permission has also been granted to core hundreds of individuals and the cores will be available for further dating methods of the trees using dendrochronology and carbon-14 dating. The cores will also be available to be used to infer past climatic conditions like droughts that would have happened during the lifetime of the sampled trees. A dendrochronology program should be developed in parallel with sediment studies. A small but important series of palaeoecological studies undertaken on cores from upland and lowland settings cover the last 38,000 years (van der Plas et al., 2012; de Boer et al., 2013a,b, 2014). These studies provide a valuable long-term perspective on vegetation responses to past climate change and the environmental impact of colonization, though evidence for the latter is largely restricted to sequences from upland settings. The evidence for human impact in upland sequences currently has no lowland parallel due to absent and/or poor pollen preservation from deposits covering the period of human colonization and settlement of Mauritius. Pollen was largely absent from the Mare Tatos sequence covering the last 500 years (de Boer et al., 2014), while at Mare aux Songes, the infilling of the marsh with dolerite boulders (a malaria control measure) largely disturbed the last 4,000 years of deposits (de Boer et al., 2015). A preliminary coring initiative in 2016 with a collaborating team from Reading University recovered sequences from lowland wetlands at Point D'Esny in the south and Belle Mare close on the east coast. Pollen was poorly preserved in both sequences, though the upper samples from Belle Mare included aquatic pollen of *Potamogeton*, fern spores and variable quantities of microscopic charcoal (**Figure 4**). Unfortunately, no short-lived plant macrofossils suitable for radiocarbon dating were observed. However, given the dating profiles developed from the coring programs mentioned above, we are confident that suitable samples for C14 will be recovered from future coring operations (see Pluskowski et al., in press for a more comprehensive discussion).

Spatial Analysis of Anthropogenic Landcover Change

Spatial analysis of anthropogenic landcover change satellite images can be used to detect land clearing, land-use, and agriculture-triggered landscape change (Sheth et al., 2010). Such information can be integrated to investigate human impact, in relation to the introduction and extinction of plants and animal species.

DISCUSSION

Investigating historic human ecology provides a way to assess and understand a major transformative event in the recent past, global colonialism, which has greatly transformed the Earth system. Mauritius, with its defined physical boundaries, limited local resources, and the relatively recent and well-documented history of human colonization and corresponding impacts, falls within the category of islands that offer the ideal conditions for understanding the complex historical interweaving between humans and the surrounding environment (Norder et al., 2017). A historical ecology framework allows researchers to move beyond the limits of ecological concepts (Lane, 2010, p. 31), as well as existing archeological research focused on the "when," rather than "how and why." The Remote Island Enigma illustrates one example of the fundamental differences between early and recent island colonization events, and the specificities of the Indian Ocean vs. other oceanic basins. For Mauritius, colonization during colonialism typifies colonization of small places driven by global forces; an entirely different context to colonization by the original seafarers. Landscape historical ecology provides a useable framework to investigate topics that underpin this essential connection between local and global. Principal amongst these is to track the rate and scale, the moving frontier, of growth in sugar production; the differential impacts of commensals on the island's ecology, and the relationships between introduced and endemic floras as plantations were established and developed.

For each of these topics, it is evident that the historical evidence, describing policies, populations, and providing a clear chronology, must be well integrated with the physical evidence of demographic, climatic, and ecological fluctuations. In this way, there is a possibility to disentangle the discrete aspects of this period of massive social, political, and ecological upheaval. Such a broad integrative strategy is essential if we are to mitigate the ongoing climatic and ecological damage facing this and other island nations and promote resilience and recovery of biodiversity and ecosystems through ecological restoration initiatives.

Creating useable pasts is an essential driver of landscape historical ecology. Beyond its historical value, this approach may provide insight for current challenges i.e., extinctions, biodiversity loss, social justice, pandemics, etc., to promote

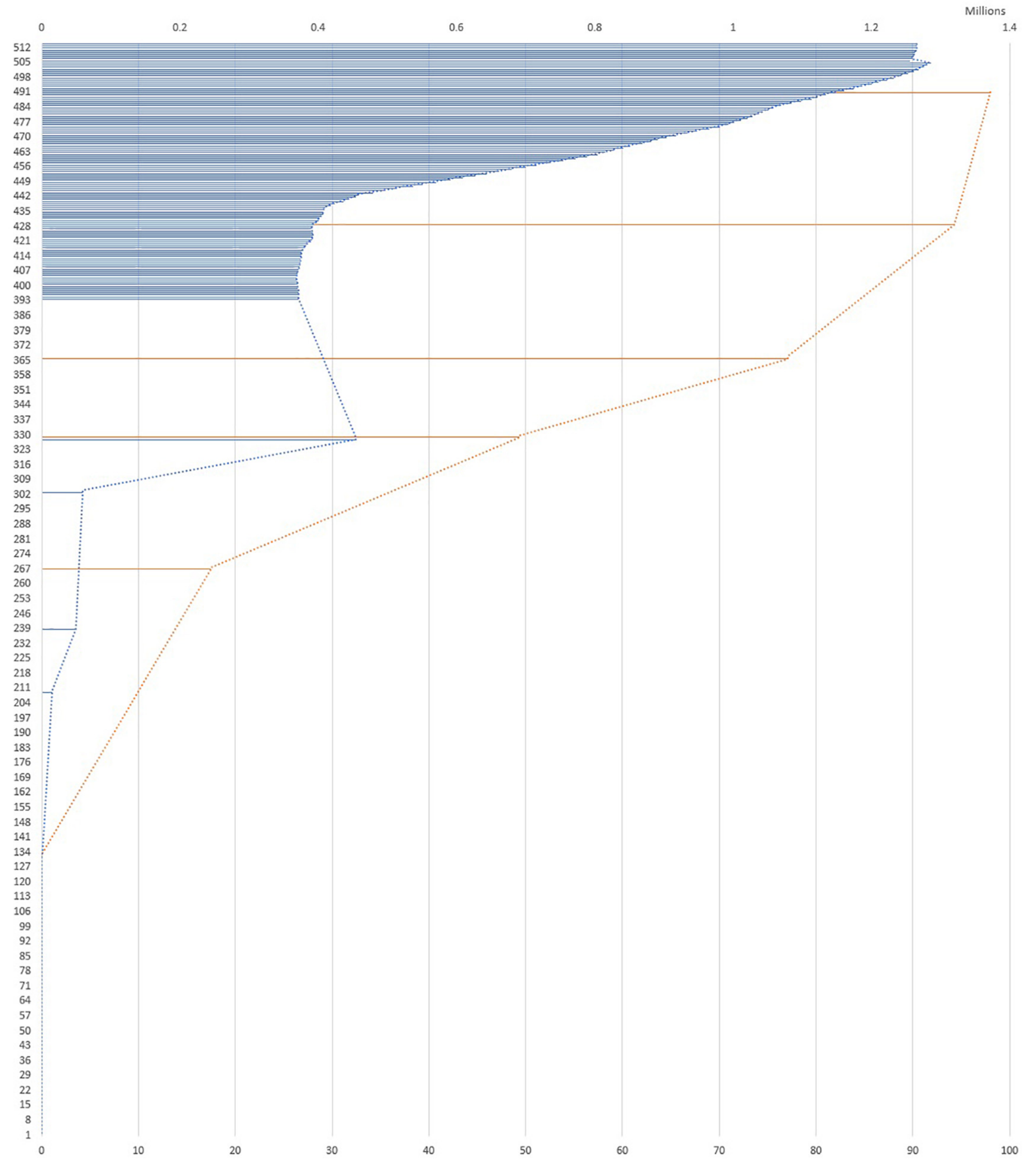

FIGURE 7 | Model aligning human population growth (blue line, millions of people) with forest loss (red line, percent of forest loss). Source data for population development of Mauritius since 1900 are from Statistics Mauritius (https://statsmauritius.govmu.org/SitePages/Index.aspx https://statsmauritius.govmu.org/SitePages/Index.aspx) and from and United Nations Demographic Yearbook (https://unstats.un.org/unsd/demographic/products/dyb/default.htm). Figures up to 1945 are for the island of Mauritius only. The island of Rodrigues is included thereafter. Figures prior to 1900 were retrieved from Norder et al., 2017. Forest clearance data: based on Norder et al., 2017: forest clearance is derived from forest cover in six historical maps from 1638 onward [See Figure 2 in Norder et al. (2017)]. Timeline is represented on the *Y*-axis, where Year 1 corresponds to CE 1507 corresponding to the first possible landing on the Island by the Portuguese, and Year 514 is CE 2020).

sustainability. Adopting an applied approach to the creation and utility of a useable past, we present a summary of how one major question could be usefully addressed. Establishing the priority of demography vs. policy as a function of ecological degradation would serve as a valuable repository that could be applied within the context of contemporary mitigation.

In our conceptual model, historical data are reported on the *Y*-axis, providing the chronological framework of colonization, and ecological/human proxy data on the *X*-axis, providing information of human impact on and contribution to the island's ecosystem. The *X*-axis, "Ecological Impact," would be a function of the different strands of evidence collected from the project. These include, but may not be limited to:

- Human demography/pressure, i.e., derived from historical records.
- Estimated loss of forest cover (in hectares), i.e., derived from pollen diagrams (data on forest clearance, e.g., by the Dutch).

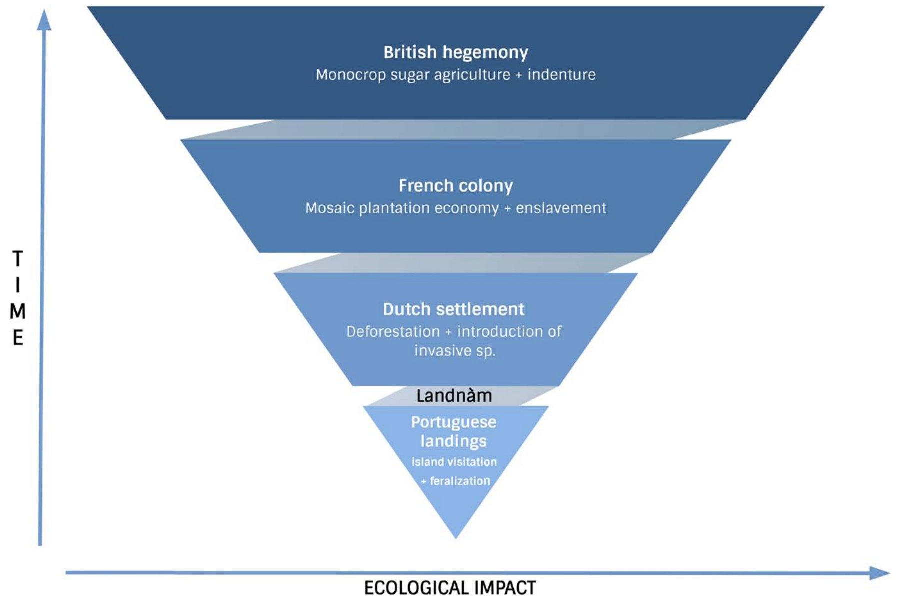

FIGURE 8 | A linear conceptual model aligning colonization process and colonial history.

- Estimated extension of cleared vegetation, i.e., derived from pollen diagrams (data on extension of sugar cane fields, e.g., by the French).
- Fluctuations in flora biodiversity, i.e., derived from pollen diagrams (number of plant native/endemic vs. introduced taxa).
- Extractive pressure:
    - Estimate mass of wooden resources extracted, i.e., derived from pollen diagrams from ebony.
    - Estimate mass of sugar from cane, i.e., derived from pollen diagrams and/or historical records of sales.
- Local diet and food, e.g., nutritional trophic level for different populations from isotope analysis (Lightfoot et al., 2020).
- Migration, e.g., demographic data from aDNA (Fregel et al., 2014).
- Fire frequency records, i.e., derived from microcharcoal remains in cores.

These lines of evidence may be represented independently on the *X*-axis, or as a single value, derived for the combination of different parameters into a single function. Extracting one case example from the above, human population size and the impacts on forest, and using readily available data for illustrative purposes only, **Figure 7** provides a revealing graphic representation for human pressure on the island's flora.

Four periods can be observed:

Period 1: Year ca. 1–130 (ca. CE 1507–1638): Virtually no impact between the Portuguese visit and the establishment of the Dutch colony with the first community of enslaved people.

Period 2: Year 131–329 (ca. CE 1638–1835): Demography and deforestation progress with a similar trend: demography grows to c. 450,000, and deforestation extends over 50% of the land.

1835: abolition of slavery and introduction of indentured labor

Period 3: Year 330–429 (ca. CE 1836–1935): There is a marked decoupling between demography and deforestation. While demography stabilizes around 400,000 (cf. United Kingdom demographic policies). On the other hand, deforestation doubles over the same period, extending over c. 95% of the land.

Period 4: Year 430 to present (c. 1935–1997): The trend is inverted compared to Period 3. While demography increases from c. 400,000–1,250,000 people, deforestation extends marginally to 95.6% of the land.

As this model suggests, population size may be considered as a critical proxy for ecological degradation in the early phases of colonization. However, the correlation between human population and deforestation, weakens over time, with lower human populations in the nineteenth and twentieth centuries causing more deforestation than larger present-day populations. Qualifying how and why ecological transformations occurred will require a deeper understanding of human behavior and ecological change, based on the detailed study and correlation of different social and ecological parameters. The graph will alter significantly as further parameters are integrated, possibly leading to unexpected emerging patterns. Ultimately, this approach will allow us to produce models as depicted in **Figure 8**. This simple conceptual model aligns a range of actors and functions. It will obviously evolve as actual, and more, data are utilized.

CONCLUSION

Mauritius was a genuine pristine ecosystem until a few centuries ago. Through three distinct phases of imperial rule, it underwent massive demographic and ecological flux. In attempting to re-create European landscapes and science in tropical lands, the colonial elite established the first botanical gardens in the southern hemisphere, one of the earliest meteorological societies, and recorded reams of data on local ecology and climate to better understand how to develop local agriculture. The impressive work on the dodo has provided an important corpus of evidence on the island's pre-human ecosystem, native biogeography and extinction, and the pressures on native fauna and flora since human habitation. Thus, large repositories of historical evidence, and a growing body of research on paleoclimate and paleoecology, form a foundation for new research framing human historical ecology. However, we still do not understand in detail how and why the island transformed so quickly.

There are major gaps in our studies of colonization when that process occurs in tandem with colonialism. Few places outside of the Indian Ocean have experienced the dual forces of colonization and colonialism together; for the Indian Ocean, however, this coupled system characterizes nearly one-third of the ocean's islands. Thus, a different approach is needed, one that asks different questions, utilizes history, including oral traditions, to build context, and one which integrates the agency of all colonizing peoples.

The human dimension was critical, but this remains a major omission in our research on the island's past. The island had a once-pristine ecology, but was not—as Mark Twain has often been misquoted as saying—paradise. During colonialism, everyone was galvanized to work toward the same goal and there was scant attention paid to conservation. Although in Mauritius some of the first efforts to protect native forests for ecosystem services (water regulation) were made, enforcement failed to support these good intentions. No one seems to have considered the island as home; enslaved people justifiably sought to escape, laborers were contracted to return to their respective homelands, and Europeans had little desire to migrate to this colony, not least because of the risk of disease. Without an indigenous population, the core practices of landscape change were never challenged. The machine of colonialism was powered by large numbers of individuals all essentially aligned in their efforts to transform and exploit the land for profit. Conversely, without an indigenous population, developing new practices for sustainable use of resources since independence has no precedence, and will take time and knowledge. That knowledge will have to come from a deeper understanding of the underlying process of change, which historical records alone cannot provide. Moreover, the how and why, rather than the when, has greater utility for descendent communities in Mauritius.

Few locations around the world offer this level of evidence, and mitigation of past damage is still possible. If successful remediation can be achieved through the approaches outlined above in combination with allied studies, the island could serve as both portent and beacon for other small islands around the world.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary material, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

All authors listed have made a substantial, direct, and intellectual contribution to the work, and approved it for publication.

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The Global and Western Indian Ocean Dispersal of House Geckos From Asia Using Historical and Mitochondrial DNA Perspectives

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Seven species of house geckos occur across the scattered islands of the Indian Ocean. Two of these, *Hemidactylus frenatus* and *H. parvimaculatus* are both widespread and possess distribution profiles that suggest pre-European, or perhaps natural dispersal to some islands. Of these, only *H. frenatus* currently has sufficient molecular data to begin exploring dispersal patterns. This species is one of the most successful reptile colonists, as demonstrated by its global, pantropical distribution. While in some areas, such as Australia and continental South America, its dispersal patterns are both recent and well-known, early historical records of *Hemidactylus* in the Indian Ocean islands suggest earlier and/or potentially non-human-mediated dispersals. Here, we reviewed the historical literature and combined those reports with an assessment of mitochondrial DNA diversity of a global sampling of *H. frenatus* samples that included modern and museum specimens. Our results corroborate previous studies and demonstrate the relatively high diversity within this species' native range in Southeast Asia. In addition, the phylogenetic analysis suggests both a potential cryptic species complex, as well as global geographic structuring of different *H. frenatus* mitochondrial lineages. This has important implications for many comparative studies of this complex. Frequent and ongoing dispersals and colonizations complicate the identification of potentially older migration patterns. Further assessments including additional samples and analyses of additional genetic markers are necessary to disentangle older from more recent dispersals within this intriguing species.

Keywords: *H. frenatus*, house gecko, phylogenetics, evolution, human-mediated dispersal

INTRODUCTION

As the global human population has grown, so have the number of plant and animal species that we have collectively translocated beyond the boundaries of their natural distributions. These range expansions, combined with population and range contractions of many endemic native species have led to a generalized pattern of global biotic homogenization (Olden et al., 2004), and this phenomenon has accelerated with the commensurate increase in international shipping, human travel, and cargo movement (Mooney and Cleland, 2001). Importantly, determining whether a species's distribution has been influenced by people is not always straightforward since long-distance, non-human-mediated dispersal has been demonstrated in a wide range of species (de Queiroz, 2005). The majority of studies that have focused on range expansions resulting from human-mediated transport have often done so with a view toward using these taxa as a proxy for understanding human migration pathways and trade networks. As a result, they have focused on those specific taxa that have been most closely interwoven into human societies, and on which people have become most reliant.

In addition to the common domestic animals (Frantz et al., 2019; Perri et al., 2021) and plants (da Fonseca et al., 2015), as well as animals introduced as game, numerous additional commensal species have also dispersed as a result of their association with people but in a less deliberate fashion. Classic animal examples include rats, mice and house shrews (*Suncus murinus*), all of which have been the subject of genetic (Duplantier et al., 2002; Tollenaere et al., 2010; Aplin et al., 2011; Brouat et al., 2014; Ohdachi et al., 2016) and archeological (Cucchi et al., 2020) studies investigating their dispersal beyond their native distributions, including across the Western Indian Ocean (Cheke, 2010). A comprehensive survey of taxa whose current distributions have been manipulated by people in Island Southeast Asia, for example, revealed scores of animal species that have been transported between islands over the past 10,000 years (Heinsohn, 2003). Likewise, movements of both wild, commensal and domesticated animals and plants across and around the Indian Ocean from Asia to East Africa and Madagascar have also been reviewed (Boivin et al., 2013).

Here, we explored the patterns of transport and dispersal using commensal geckos, a somewhat neglected species in animal movement studies, despite the fact that they are widespread and easily transported (Jones et al., 2013). Although there are more than 165 species within the genus *Hemidactylus* (Agarwal et al., 2021), the majority are restricted to small-ranging habitats in South Asia. Approximately 10 species, including the house geckos *H. mabouia* from Africa and the Asian *H. frenatus*, have achieved intercontinental distributions (Weterings and Vetter, 2018), while *H. parvimaculatus* reached many Indian Ocean islands. However, because the review by Weterings and Vetter (2018) regarding invasive *Hemidactylus* did not re-assess older identifications, the Indian Ocean distributions are not reliable for '*H. mabouia*' or '*H. brookii*' (= *H. parvimaculatus*).

Hemidactylus frenatus is the most widely introduced gecko in the world (Weterings and Vetter, 2018), and though native to tropical Asia and the Indian subcontinent, it has been identified on islands and continents spanning the globe (McKay and Milenkaya, 2020). Adaptations that permit this species to establish populations in new locations include: the females' ability to store viable sperm for up to a year (Yamamoto and Ota, 2006); their hardshelled eggs' resistance to immersion in seawater (Hsu et al., 2021) and the capability to reproduce year-round in tropical zones (McKay and Phillips, 2012). Furthermore, they lay eggs in crevices in objects, and are therefore often accidentally transported in cargo or baggage (Weterings and Vetter, 2018, ASC pers. obs.). These features also increase their potential to remain undetected and undamaged in transit in the past on both ancient sailing vessels and on modern shipping containers. None of these characters alone, however, explain why this species, and others such as *H. mabouia* and *H. parvimaculatus*, but not their numerous congeners, have been such successful colonists.

While the spread of *H. frenatus* throughout the Pacific was first described in association with troop and supply movements during World War II (Case and Bolger, 1991), this species has also been suggested as a proxy to understand older human movements, at least across the Indian Ocean (Cheke, 2010; Boivin et al., 2013). The observation that distinct haplogroups coexist across some of these islands (Rocha et al., 2010), together with their curious distribution on remote atolls suggests they may have arrived in a series of different events (Cheke, 2010). Given the modern widespread distribution of gecko species within tropical and subtropical ecotones, commensal geckos in general, and *H. frenatus* specifically, represent excellent models to investigate the unintentional human-mediated movement of a widespread commensal reptile. One of the problems hindering the genetic approach to understanding the spread of geckos is the use of different markers in independent studies, which precludes efforts to comprehensively and simultaneously analyze all the available data.

Here, in order to characterize the distribution of specific house gecko populations, we applied two different approaches. First, we established both the time frame and geographic distribution of house geckos in the Indian Ocean by reviewing the historic literature and early descriptions and collections of geckos in the region. We then extracted DNA and sequenced a 463 bp fragment of the mitochondrial cytochrome *b* gene from 111 museum and modern specimens of the most widespread and genetically diverse house gecko species, derived from over 70 locations representing 36 countries (**Supplementary Table 1**). Using the obtained sequence alignment, we constructed phylogenetic trees and assessed the geographic partitioning of the individuals assigned to well-supported clades. These combined approaches, including the increased resolution afforded by genetic signatures, allowed us to identify specific populations and lineages of Asian house geckos across their global and Indian Ocean distributions. These data also allowed us to discuss the results in light of human-mediated movement of taxa writ large.

RESULTS AND DISCUSSION

Historical Accounts of the Distribution of Commensal Geckos in the Indian Ocean

In addition to *H. frenatus*, six other species of house geckos, mostly small gray or brown, largely facultatively anthropophilic animals, inhabit the historically uninhabited remote islands of the Indian Ocean. None of the volcanic islands of Mascarenes and Comoros, nor the continental fragments (Madagascar and the granitic Seychelles), much less the numerous atolls of the western Indian Ocean (**Figure 3**), have been connected to any continent for upward of 60 million years, and therefore either natural or

FIGURE 1 | An image of seven geckos drawn by Charles Alexandre Lesueur in 1803. The *Hemidactylus parvimaculatus* from Coëtivy is bottom right (Cheke, 2009). Although it is a female without preano-femoral pores, the pattern of tubercles and the undertail scalation detailed in the side-sketch closely match photographs and details for *parvimaculatus* in Mahony's (2011) review of *brookii* group geckos.

human-mediated over water dispersal are necessary to explain their distribution.

Of the seven, two, *Hemidactylus platycephalus* and the *H. mabouia-mercatorius* complex are Afro-Malagasy species (Rocha et al., 2010), which historically were merged within the polyphyletic umbrella species '*H. mabouia*' (Louette et al., 2004; Rocha et al., 2010; Agarwal et al., 2021). Of these, only *H. mercatorius* seems to have spread beyond the immediate area (Madagascar, Comoros, Aldabra group, Farquhars), to the granitic Seychelles and, unexpectedly, to Platte, but only recently via human agency (Gerlach, 2007; Rocha et al., 2009a). For example, although Boulenger (1909) reported "*H. mabuia*" on Mahé in 1905 (specimen confirmed by Cheke (1984) as *H. mercatorius*), it probably did not establish a population since it was not detected again there until 1995, and in 2002 on Frégate (Gerlach, 2007). Platte, a low coral island, is infrequently visited by zoologists, and it is possible that *H. mercatorius* may have been long established. *H. parvimaculatus* was initially misidentified as *H. mercatorius* (Vinson and Vinson, 1969) in the Mascarenes, but true *mabouia*/*mercatorius* was absent in the Mascarenes (Cheke and Hume, 2008; Cole, 2008) until discovered in Réunion in 2010, with molecular data suggesting their recent introduction from either the Comoros, the Seychelles or the East African coast (Sanchez et al., 2012), the most likely of these being Mayotte (Comoros), also still a French territory.

Of the other five species, one is Pacific, and four are Asian in origin, but with differing dispersal histories. *Lepidodactylus lugubris* is a parthenogenic Pacific species with apparently endemic Indian Ocean clones (Ineich, 1999), which suggests a long-established natural dispersal via drift. This species is also the least associated with humans, and only occurs on the most easterly of the islands including Rodrigues, the Chagos group, and Coëtivy (Gerlach, 2007; Cheke and Hume, 2008; Cole, 2009). Boulenger (1909) reported specimens of *L. lugubris* collected in 1905 from both Mahé and Praslin in the granitic Seychelles, but it has not been reported since (Gerlach, 2007), and no specimens exist in the United Kingdom Natural History Museum collections (Cheke, 1984), so this record may have been made in error. *L. lugubris* does occur sympatrically in houses in Rodrigues with three other gecko species (ASC pers. obs.), and it has also recently been found on St. Brandon/Cargados Carajos (Nik Cole, pers. comm. to ASC, 2020), directly in the path of the South Equatorial Current (New et al., 2005).

Parthenogenic *Hemiphyllodactylus typus,* only found in the Mascarenes, is not usually associated with buildings (Grégory et al., 2007) and was first reported in 1948 (Vinson and Vinson, 1969; Deso et al., 2020). Two studies (Grégory et al., 2007; Deso et al., 2020) however, suggested that given the difficulty in observing this species, it may have escaped notice and be native in the Mascarenes, especially since it appears to favor the native forest habitat. This narrative would require oceanographically difficult cross-equatorial drifting. Another Asian gecko species, *Gehyra mutilata*, is widespread in the Indian Ocean, but lacks sufficient genetic variation in this region to identify its geographical origins (Rocha et al., 2009b). *G. mutilata* is strictly commensal and is unlikely to have survived on islands where the human presence was only fleeting. Therefore, even if cross-ocean mariners introduced the species unintentionally, a temporary human stopover would not be sufficient for the species to maintain a presence. In fact, this species failed to establish a population on Aldabra until there was a permanent human presence at a research station (Cheke, 1984; Gerlach, 2007).

The final two species, *Hemidactylus frenatus* and *H. parvimaculatus,* are both facultative commensals, with distributions, histories and genetic signatures that warrant further investigation. Both of these species, common in southern India and Ceylon/Sri Lanka (Daniel, 2002; Das and de Silva, 2005), have long-term established populations in the Maldives where *H. frenatus* was likely introduced on multiple occasions (Agarwal et al., 2019). When the first faunal collections were made in the Maldives by the Stanley Gardiner expedition of 1899-1900, H. *frenatus* was widespread throughout, but *parvimaculatus* (as '*H. gleadovii*') was only collected on Hulule, Male Atoll (Laidlaw, 1902). People from Sri Lanka are known to have settled on numerous occasions, so the presence of *H. parvimaculatus* is not unexpected, and *H. frenatus* could also have arrived from long-standing trading (Maloney, 1980; Litster, 2016) with ports to the east.

The Maldives are long-inhabited islands, possibly from 1400 BCE (Maloney, 1980; Jaufar, 2019), though Litster (2016, 2020) is more cautious about BCE dates, suggesting probable early stopover use, if not settlement. The oldest confirmed direct radiocarbon date is remarkably late, 249–393 CE, evidently after the cowry-shell (*Monetaria moneta*) trade for currency was well-established. While they could be the source of gecko populations elsewhere, it is the presence of geckos on further-flung islands first encountered by humans more recently, in the last 1,500 years, mostly the last 500, that concern us here.

Hemidactylus parvimaculatus

Hemidactylus parvimaculatus is part of the Indo-Asian *H. brookii* complex, and was only recognized as a separate species in 2010; the natural range of the species being the island of Sri Lanka and also southern India (Bauer et al., 2010). Although not reported in Mauritius until 1818 (Cheke and Hume, 2008) (as '*H. brookii*'), and still absent from the granitic Seychelles (Gerlach, 2007), it was collected on then uninhabited isolated sand cay of Coëtivy in 1803. Coëtivy, discovered in 1771 (Lionnet, 1972), was first settled in 1811 (de Froberville, 1848), though it had been visited on various occasions by Seychellois and French/Mauritians (Toussaint, 1967) seeking free coconuts and turtles. This specimen was illustrated in a remarkable watercolor of seven geckos by Baudin expedition artist Charles-Alexandre Lesueur (Collection Lesueur, Muséum du Havre MS 78-115; reproduced in Cheke (2009); **Figure 1**); the species was also collected in 1905 on the remote atoll of Desroches in the Amirantes (Boulenger, 1909; as *H. brookii*), and was still present in 1981 (Gardner, 1986).

Its presence on these isolated low islands is anomalous, and is unlikely to result from natural drift (it would be a unique cross-equatorial case of sea drift in the Indian Ocean). It is also unlikely to have been brought from Mauritius, whence the Seychelles and their outer islands were settled, as it would have shown up on the much more populated main granitic islands, where it is still absent (Gerlach, 2007; Rocha et al., 2009a). It is therefore possible that it arrived via Austronesian cross-ocean mariners traveling via Sri Lanka or the Maldives - the species does not occur in these travelers' source areas (Sumatra, Borneo). The species was not found on Desroches in 2005 despite targeted searches (Rocha et al., 2009a) - only *frenatus*, absent in 1905, (Boulenger, 1909 contra Gerlach, 2007) but present in 1981 (Cheke, 1984; Gardner, 1986) was identified, nor has it been rediscovered on Coëtivy (Cheke, 1984; Gardner, 1986). A more likely source is the Maldives: Maldivian folklore recounts tales of boats lost at sea ending up in remote islands, so, although the islands are not specifically named (apart from Chagos; Romero-Frías, 1999; Romero-Frias, 2012), this could be the source of *H. parvimaculatus* on Desroches and Coëtivy.

One story, *Hoïïavai* (= Chagos in Maldivian; Litster, 2016), was based on a 17th century BCE case of a fishing vessel wrecked in the Chagos, and its crew rescued to tell the tale (Romero-Frias, 2012). Although some Portuguese ships had been wrecked on the northern Chagos banks in the mid-late 16th century, they were traders heading for the East Indies and back (Wenban-Smith and Carter, 2016), so would have been unlikely to have carried *parvimaculatus*. The same applies to the first known deliberate landing on Egmont in 1605 by an English party traveling east (Wenban-Smith and Carter, 2016). There is no evidence of any European landing on Diego Garcia until much later. *H. parvimaculatus* also occurs on Moheli and Anjouan (Comoros) (Vences et al., 2004; Rocha et al., 2005; Hawlitschek et al., 2011), and all three Mascarenes (Vinson and Vinson, 1969; as '*H. mercatorius*'; Vences et al., 2004), but not Madagascar (Glaw and Vences, 2007).

Two clades are present in the Mascarenes (Vences et al., 2004; Rocha et al., 2005), and one extends to the Comoros, potentially indicating invasion events from different source populations. Although Austronesian and subsequent pre-European cross-ocean trading from c.800 BCE (Cheke, 2010; Boivin et al., 2013) is a possible source of the Comorian clade (with back-spread to Réunion later), a post-European origin of both clades is probably more likely since the Comoros was formerly administered colonially from Réunion. There is no reason to suppose that *Hemidactylus* spp. in the Mascarenes arrived other than accidental transport post-European contact since there is no evidence of pre-European landings in this group (Cheke and Hume, 2008; Cheke et al., 2017).

Hemidactylus frenatus

The most complex and interesting case is that of the common house gecko *Hemidactylus frenatus*. Although its almost universal presence on Indian Ocean islands suggests a generalized, probably anthropogenic distribution, there are numerous anomalies within this apparently uniform pattern. Rocha et al.'s (2010) statement that this species is 'present throughout Indian Ocean islands without any signs of geographical structure' overlooked the fact that some structure is evident in both this and previous papers (Vences et al., 2004; Rocha et al., 2005) as discussed below.

House geckos tend only to be reported by naturalists, and not by mariners or explorers, so it is unsurprising that the first Indian Ocean record is not until c.1770 when Philibert Commerson's artist Paul Jossigny drew a *Hemidactylus frenatus* from Mauritius; the previously unpublished image is preserved in the Muséum National d'Histoire Naturelle in Paris (Cheke and Hume, 2008), reproduced by Bour (2015); **Figure 2**. A report (Hoffstetter, 1946) identifying some gecko subfossils as *H. frenatus* was made in error; the bones were those of the osteologically similar endemic gecko *Cyrtodactylus* (now *Nactus) serpensinsula* (Arnold, 2009), extinct on the Mauritian mainland, and only discovered alive on offshore islets after Hoffstetter's study. Despite intensive fossil collection across different Indian Ocean islands (Aldabra, Reunion, Mauritius, Madagascar and Seychelles), where other gekkonid species have been identified (Cheke and Hume, 2008; Hume, 2004; Hume et al., 2018) there are no known subfossils of *Hemidactylus* spp. in the Indian Ocean, suggesting that a natural and old (pre-human) colonization is unlikely.

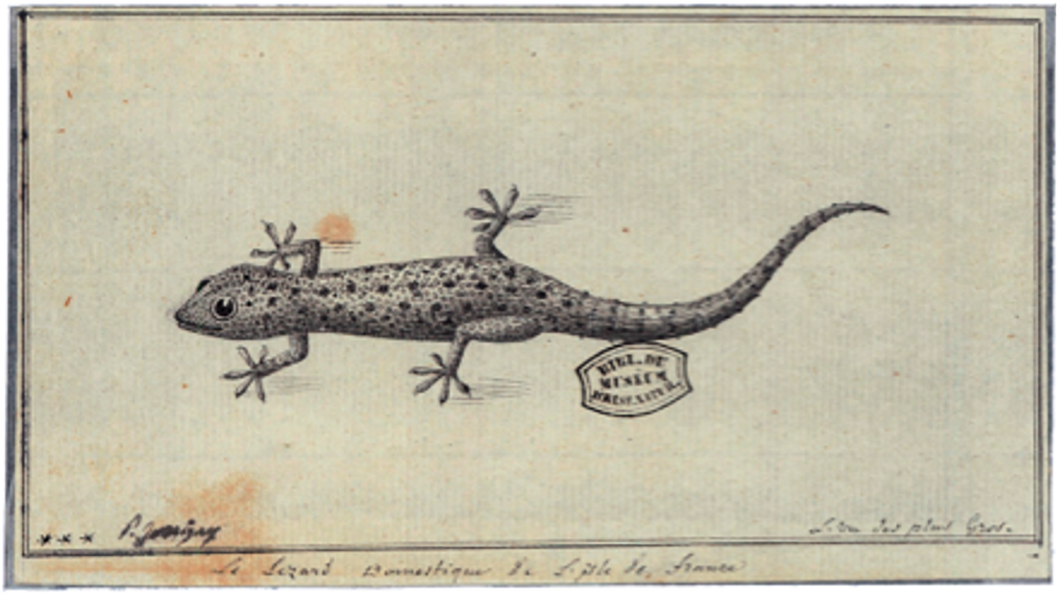

FIGURE 2 | An image of *Hemidactylus frenatus,* Mauritius. Sketch by Paul Philippe Sanguin de Jossigny c.1770 (from Bour (2015)).

The interesting aspects of *frenatus* are its curious distribution on outlying atolls and sand cays of the Seychelles (**Figure 3**) – the species is widespread on these islands which have only small agricultural (coconut) or, more recently, tourist-related settlements. Despite this, the species was absent on the much more populated, visited and biologically known granitic islands until the 1990s (Gerlach, 2007), barring a doubtful record from "the Seychelles" (island unspecified) in 1863 (Peters and von der Decken, 1869).

H. frenatus occurs, or occurred, on many low islands and atolls visited by the 1905 Stanley Gardiner/Percy Sladen Trust expedition (Boulenger, 1909; Cheke, 1984). There are no earlier records since, other than Rémire (Amirantes; collection in 1882; Günther, 1884), no-one had previously collected lizards on these islands. The expedition found them on Bird (central Seychelles), Poivre, Rémire and Desroches (Amirantes), Sirène and 'Establishment' [= Raphael] (St. Brandon), Diego Garcia, Salomon group, *Peros* Banhos group and possibly Egmont (Chagos), but none were identified on the granitic islands. This species has subsequently been found on several other low islands: Platte, Alphonse, Desnoeufs, African Banks (Cheke, 1984; Gerlach, 2007), Agalega (Cheke and Lawley, 1983; Webster and Cadinouche, 2013), and belatedly reconfirmed on St. Brandon (Nik Cole, pers. comm. 2020). The species was, and remains (Cheke, 1984; Gerlach, 2007), absent on more westerly atolls closer to Madagascar, where *H. mercatorius* was, and is, present (Farquhars, Aldabra, Cosmoledo, Astove) (Boulenger, 1909), and where the currents favor transport northwest from Madagascar, and at times effectively north/north-east via the SECC (Peng et al., 2015; Hawlitschek et al., 2017).

While commonly found in houses, *H. frenatus* is found living in rocks and trees on islands inhabited only by seabirds in the Amirantes' (Gardner, 1986), leading him to agree with Cheke (1984) that this distribution was due to natural sea-drift from the east. However, that does not explain why the drift missed the granitic islands (but hit Bird further north), and carried the geckos further west to the Amirantes. The fullest flow of the South Equatorial Current runs south of the Seychelles Bank (New et al., 2005), which might have impacted the Amirantes more than the granitics, which would also be 'protected' (in a sense) by the shallow bank diverting the flow around it. Unlike many of the atolls, the granitic islands have other native lizards including geckos, but pre-existing reptiles have never been known to prevent its establishment elsewhere, and *H. frenatus* is known to aggressively out compete other similarly sized geckos (e.g., Cole et al., 2005; Dame and Petren, 2006; Newbery and Jones, 2007; Csurhes and Markula, 2009).

Hemidactylus frenatus is also widespread in Madagascar (Glaw and Vences, 2007) and is present on all four Comoro islands (Louette et al., 2004; Hawlitschek et al., 2011). Unlike the oceanic high islands and atolls (Maldives excepted), these have been inhabited for well over a millennium (Crowther et al., 2016; Anderson et al., 2018b), but reptile collections, apart from one Malagasy chameleon, only date from the mid-19th century BCE (Andriamialisoa and Langrand, 2003; Hawlitschek et al., 2011). Hence, there is no historical basis for insight into the means or date of arrival of the species there. Some consider three, or all four, species of *Hemidactylus* in the Comoros to have been introduced (Vences et al., 2004; Hawlitschek et al., 2011) but given the distribution and habitat preferences (Hawlitschek et al., 2011, 2017), the evidence for *mercatorius* and especially *platycephalus* remains ambiguous.

In summary, from the seven largely commensal house gecko species that today inhabit Indian Ocean islands, only the early records of both *H. parvimaculatus* and *H. frenatus* across some isolated islands suggest the possibility of early (pre-European) colonizations or even natural dispersals. Of these, *H. frenatus* is undoubtedly the widest distributed and most abundant across the

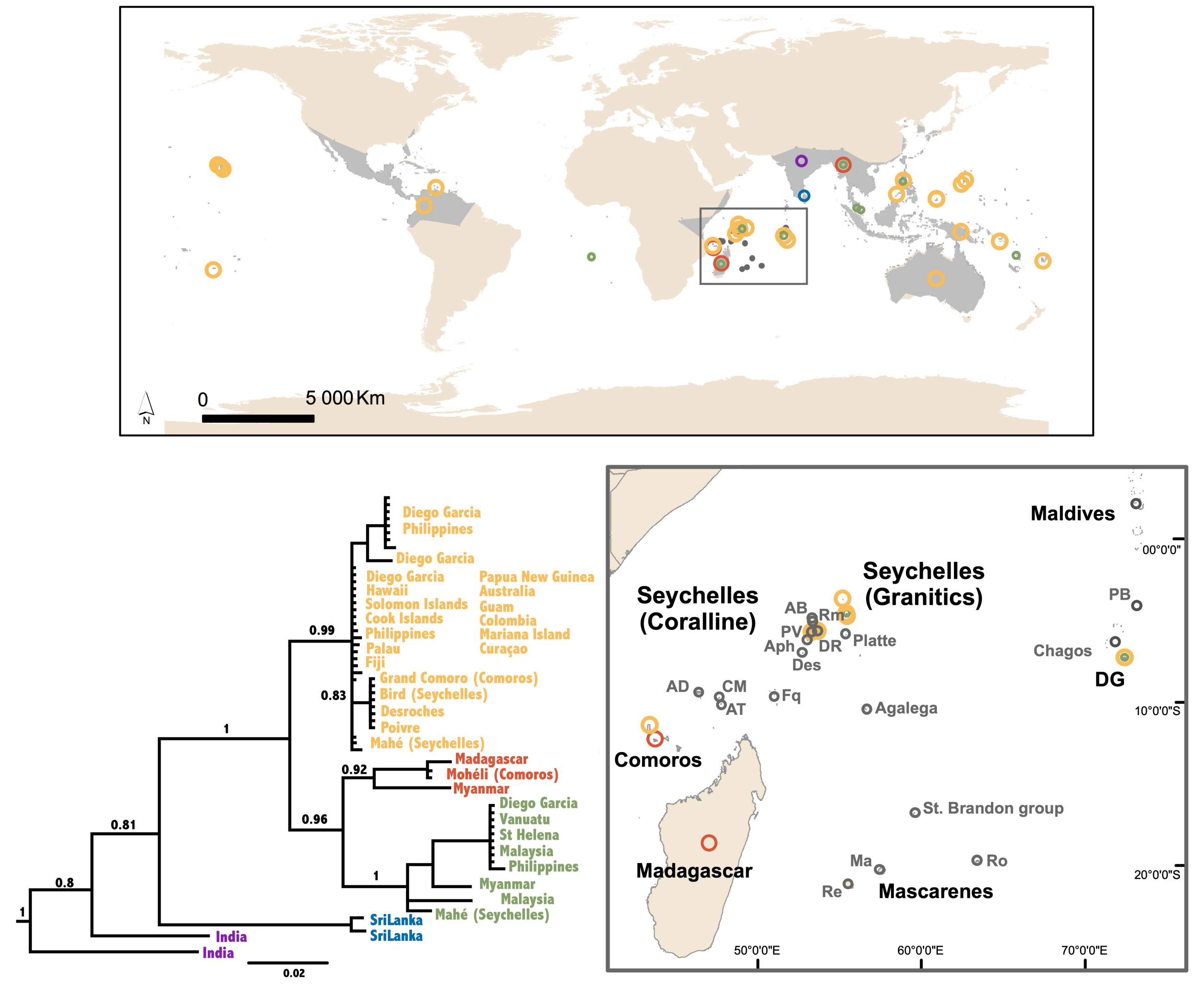

FIGURE 3 | (Top) A map showing the location of modern and museum samples that yielded sufficient DNA to be included in this study. The colors on the map mirror those of the clades on the phylogenetic tree depicting the relationships of the Cytochrome *b* lineages. The light gray shading denotes the modern distribution of *H. frenatus* retrieved from GBIF records and converted into polygons (GBIF.org; 29 November 2021- GBIF Occurrence download https://doi.org/10.15468/dl.s8w3sw). **(Bottom left)** A schematic representation of the Bayesian consensus tree (full tree in **Supplementary Figure 1**). Branches leading to the outgroups are not shown and posterior probabilities are shown for the main branches only. Tips are labeled with the different localities where samples from each lineage originate, and are color-coded to match the distribution maps. **(Bottom Right)** An inset depicting the relevant locations across the Western Indian Ocean discussed in the main text. Location acronyms are as follows: Reunion (Re); Mauritius (Ma), Rodrigues (Ro), *Peros* Baños (PB), African Banks (AB), Rémire (Rm), Poivre (PV), Desroches (DR), Alphonse (Aph), Desnoeufs (Des), Farquars (Fq), Aldabra (AD), Cosmoledo (CM) and Astove (AT). St. Brandon group including Sírene and Establishment (= Île Raphael).

Western Indian Ocean (and globally), and we therefore tried to gather a comprehensive widespread set of samples that allowed for an exploration of the geographic distribution of its genetic variation, and possibly shed some light into this species's (early or modern) dispersal patterns.

Molecular Evidence for Global *Hemidactylus frenatus* Dispersal and Distribution

Several recent studies have attempted to resolve colonization patterns across parts of the range of *H. frenatus* using mtDNA sequences. Vences et al. (2004) analyzed partial 16S rRNA sequences from individuals from Madagascar, Grand Comoro, the Andaman islands, Mauritius, Rodrigues and Sri Lanka and considered this to show "low genetic differentiation . . . with no recognizable phylogeographical structure, indicating recent colonization or introductions." Rocha et al. (2005) focused on the Comoro islands, and likewise, did not identify any notable structure with the same 16S rRNA marker.

Using partial 12S rRNA and Cytochrome *b* (CYTB) gene sequences to examine the origin of South American populations, Torres-Carvajal (2015) found no variation across Ecuador, Colombia, Hawaii and Papua New Guinea, although these were highly distinct from lineages in Myanmar/Burma and India. Tonione et al. (2011) also identified high diversity within the tiny island of Moorea, French Polynesia, based on Cytochrome Oxidase 1 (CO1) sequences, and Agarwal et al. (2019) determined the probable origin of *H. frenatus* from the Maldive Islands to be from Southeast Asia. Both these latter studies proposed multiple introductions, and the need for improved sampling of potential source populations to unravel colonization patterns.

At least five lineages have now been identified within *H. frenatus*, and geographic structure is present. In addition to the Indian and Sri Lankan lineages, the worldwide (Indian, Pacific and Atlantic Ocean islands) samples analyzed here fit clearly into three well-supported clades. One (red in **Figure 3**) is present in both Myanmar and the Western Indian Ocean (WIO) islands of Madagascar and Comoros (Moheli), another (green) is found both in southeast Asia (Vanuatu, Philippines, Malaysia, Myanmar) as well as across some WIO islands (Diego Garcia, the Seychelles -Mahé- and Madagascar) and also in the Atlantic Ocean island of St. Helena. The third (yellow) is also widespread across the Pacific and Indian Ocean islands.

Since we sequenced samples from the main 16S rRNA haplogroups in the Western Indian Ocean, we were able to match these three lineages of CYTB to the different haplogroups described in Rocha et al. (2010). Although structure was, unsurprisingly, previously less obvious using the more conserved locus than with CYTB, these three lineages are also reflected in 16S data. In this way, the yellow clade corresponds to 16S haplotypes H4-H7 and H10, the red clade to Comoros and Madagascar H8 and H9, and the green clade, to remaining haplotypes from Mahé (represented by H2 - sample 2MA21).

We did not sample additional South American localities, but extrapolating from Torres-Carvajal (2015), South American localities from Colombia to Ecuador (including Galapagos) all belong to the yellow lineage, which is further present also at least in Myanmar (Tonione et al., 2011). In addition, though not all lineages can be unambiguously associated with the ones in Agarwal et al. (2019), some correspondence is evident (e.g., lineage A from (Agarwal et al., 2019) with the blue lineage here, both solely in Sri Lanka). The remaining lineages are not comparable, highlighting the diversity harbored by this taxa, especially in Southeast Asia.

Given this, and the number of lineages identified in other studies with other mitochondrial loci (e.g., Tonione et al., 2011), it seems likely that additional lineages remain unidentified from Southeast Asia. With highly divergent lineages present in India and Sri Lanka, supporting their Indian origin (Bansal and Karanth, 2010), at least three of the lineages spread eastward and westward, giving rise to their modern global distribution. Contrary to its colonization across continental South America, which seems to have been recent and involved mostly a single lineage (Case and Bolger, 1991; Case et al., 1994; Torres-Carvajal, 2015), Tonione et al. (2011) identified three lineages within Moorea, a small island in French Polynesia, and similarly, Western Indian Ocean islands overall currently harbor at least three different lineages of this species.

As with many other widespread species of *Hemidactylus* assessed with genetic methods, including *H. mabouia* (Agarwal et al., 2021) and *H. fasciatus* (Wagner et al., 2014), *H. frenatus* appears to be a species complex. Variation between the samples from mainland India and Sri Lanka and the island populations ranges up to 14 and 11%, respectively, which is as high as the divergence between pairs of reptile (Harris, 2002) and mammalian (Allen et al., 2020) species as measured using CYTB sequences. Variation between the main lineages within the Indian Ocean islands ranges between 7.0 and 8.5%, which in some small archipelagos such as Diego Garcia (and in the Seychelles) co-occur, highlighting the intricacy of the phylogeography of *H. frenatus*.

These current patterns highlight both the high levels of diversity, particularly within the native range, and suggest a high number of colonization events required to explain their current distribution. All five primary lineages are currently found in India, Sri Lanka and/or Myanmar, but without a comprehensive sampling across this area and an increased number of markers with various levels of resolution, the timings of the different Western Indian Ocean island colonizations remain unknown. While there is yet no clear evidence for natural and old colonization events (e.g., differentiated lineages endemic from certain islands or groups), it does appears is possible that this species has been transported in multiple waves, perhaps initially in pre-European times, but that these few early dispersals are now predominantly obscured by a much greater number of recent and ongoing translocations associated with modern transportation networks.

The patterns revealed here related to the three primary lineages identified allow for the development of provisional and testable hypotheses. The widespread ‘yellow’ lineage (**Figure 3**) occurs on scattered atolls of the coralline Seychelles. *H. frenatus*, however, was not present on the islands from which these atolls were colonized when they were first sampled in the 19th century. In addition, the yellow lineage still does not occur in Mauritius, and *H. frenatus* was only confirmed in the granitic Seychelles (Mahé) in the 1990s. Since this lineage occurs widely, both on the mainland and in the islands of Wallacea and the Pacific, it is likely to have been present in Sumatra and Borneo when the Austronesian voyagers colonized Madagascar and the Comoros. No archeological remains have been found to confirm that they crossed mid-ocean (Anderson et al., 2018a). Geckos could still have been dispersed either via shipwrecks that did not result in an archeological signature, or via lost mariners who strayed from the Maldives (Agarwal et al., 2019).

The ‘red’ lineage’s presence in the Indian Ocean only on Madagascar and the Comoros (Rocha et al., 2010), could match the profile of Indian trade with East Africa and Madagascar/Comoros in the medieval and early modern period (Boivin et al., 2013). Specifically, the geographic distribution could be correlated with the distribution of the introduced Indian civet *Viverricula indica* found in Madagascar, Comoros, the East African islands of the Zanzibar group, and Socotra (Gaubert et al., 2017), but nowhere else in the western Indian Ocean. The third (green) lineage could correspond to more modern trade and travel (notably to formerly isolated Diego Garcia), which may also be responsible for the yellow lineage's dispersal to Australia and the Pacific.

Higher resolution datasets, through either greater number of targeted markers such as SNPs or the retrieval of complete mitochondrial and nuclear genomes, are required to further investigate the lineage splits and chronology of these different dispersals, but the patterns presented are suggestive, and the use of these commensal species as tracers for early human movements merits further consideration. This approach would be significantly improved though denser sampling of mainland southeast Asia and the other suggested sources of all the lineages.

Furthermore, determination of dispersal patterns based on any single molecular marker, such as mtDNA, needs to be treated with caution. In Southern Europe, patterns of minimal variation in mtDNA in two unrelated gecko species conflicted with nuclear markers, suggestive of a "selective sweep" that could obscure phylogeographic history based on mtDNA (Rato et al., 2010, 2011). A higher than usual nDNA/mtDNA diversity pattern was also identified in *H. frenatus* (Tonione et al., 2011), which certainly warrants further investigation and highlights the need to interpret cautiously the phylogeographic patterns based on mtDNA.

Finally, it appears from the current data that some gecko species and lineages are significantly more amenable to human translocation, or are more efficient at establishing colonies thereafter. From the greater than 165 currently recognized species of genus *Hemidactylus*, ten have intercontinental distributions, with two that are widely present in Western Indian Ocean islands, *H. mabouia-mercatorius* complex and *H. frenatus,* among the five most widespread and invasive *Hemidactylus* (Rocha et al., 2010; Weterings and Vetter, 2018).

As noted earlier, geckos have specific characteristics that make them efficient colonizers, but the characteristics that make some species especially effective remain unknown. Several studies have suggested that thermal physiology may play a role. Thus, an investigation of thermal tolerances in widespread species, relative to those with more restricted ranges may be revealing. Clearly *H. frenatus* is able to colonize what is thought to be less optimal habitat (McKay and Milenkaya, 2020), and there is some evidence for increased cold tolerance in invasive populations (Lapwong et al., 2021). On the other hand, *H. frenatus* showed no evidence of increased boldness which is often (although not necessarily) associated with invasive species (Nordberg et al., 2021).

The identification of likely "cryptic species" within both *H. mabouia* species-complex and *H. frenatus*, however, complicates the situation, since it becomes unclear if the same lineages have been compared, or if some lineages have unique characteristics. Modeling approaches, to determine potential ranges, and the impact of climate change (e.g., Rödder et al., 2008), as well as analyses of diet, behavior and other ecological variables, may benefit from determining which lineages within these diverse species are being compared. The sequence dataset presented in this study may form a useful comparative framework for such future assessments.

CONCLUSION

Atypical distribution patterns of *H. parvimaculatus* and *H. frenatus* on outlying atolls and sand cays of the Seychelles, coupled with an historic absence on the more populated islands are compatible with a hypothesis of early, pre-European or even natural, colonization patterns. We attempted to verify this for *H. frenatus* using analysis of CYTB sequence data from modern and museum specimens. Our results highlight high diversity across its native range, indicating that it is a potential species complex, as well as the multiple translocation events needed to explain its current distribution. Ultimately, while it was not possible to clearly define their patterns and timings without a greatly increased sampling across its native range, it remains tempting to hypothesize that they reflect the different routes and timings of human dispersals across the region, while accepting that older patterns may be obscured by frequent and ongoing recent colonization events. Increased sampling of both specimens and genomic variation is a promising way to further investigate these questions and to better understand the reasons underlying some geckos' extreme colonizing capabilities.

METHODS

Initially, 97 tissue samples of *Hemidactylus frenatus* were analyzed: 51 specimens were obtained from museum collections (Field Museum, Chicago; British National History Museum, London; Smithsonian, Washington DC), and 46 modern specimens were collected in the field by Dr. J. Chris Hillman and Solomon Pomerantz (Sealinks Project). Museum samples were mainly stored in ethanol or formalin, while the modern tissue samples were dried. To enable the data collected here to be directly compared with the phylogeographic patterns obtained by Rocha et al. (2010), 14 samples representing distinct haplogroups based on 16S rRNA sequences from this earlier work were re-extracted and included in this study. An additional 15 specimens (including two outgroups) were included from GenBank (**Supplementary Table 1**).

All samples excluding those previously analyzed by (Rocha et al., 2010) were analyzed in the facilities at the Archeology Department of Durham University. For these, DNA extractions were performed using Qiagen Microkit following the manufacturers' instructions. A 463 bp region of the mitochondrial cytochrome b was amplified and sequenced in one fragment, in 25 ul reactions (1U of Sigma Jump Start Taq (0.2 ul), 10 mM primers (0.625 ul each), 25 mM $MgCl_2$ (4 ul), 10* Buffer (2.5 ul) 25 mM dNTP mix (0.25 ul) with 1 ul DNA extract and made upt to volume with H_2O) and annealing temperatures of 58-59°C. Due to the fact that many specimens were from museum samples, specific primers were designed (5′-3′): CTAATGATCCTCCGCAAAGC and AATCCGCCTCAAATTCACTG, based on the sequence of the whole mtDNA of *Hemidactylus frenatus* (Accession number NC_012902). For the specimens previously analyzed by Rocha et al. (2010), universal Cytochrome *b* primers (GluDG and Cytb2H - (Palumbi, 1996) were used to amplify a fragment that was 417 bp, missing the last 46 bp relative to the remaining samples. Conditions were as above, but using 1U of MyTaq and the associated Mastermix Buffer, and with an annealing temperature of 50°C. These PCRs were carried out in the laboratories at CIBIO, University of Porto. Sequencing reactions were carried out using both primers by the DNA Sequencing Service at the School of Biological and Biomedical Sciences at Durham University, while those from CIBIO were purified and sequenced using a commercial company (Genewiz, Germany).

While all of the samples from Rocha et al. (2010) could be amplified, due to the known issues of extracting DNA from museum specimens, and especially those stored in formalin, (reviewed in Hykin et al. (2015), only one "old" museum sample yielded DNA, and in total only 64 samples were successfully sequenced (information detailed in **Supplementary Table 1**). Electropherograms were manually inspected and corrected, and manually aligned using both Geneious R6 version (Kearse et al., 2012) and BioEdit (Hall, 1999). All showed typical mtDNA base composition, and could be translated into expected amino acid sequences for the gene. Regarding the ingroup (*H. frenatus*), the alignment had 106 variable and 74 parsimony informative sites. New sequences were submitted to GenBank (accession numbers OL880471-OL880521).

Phylogenetic analyses were performed by construction of Bayesian trees using MrBayes version 3.2.2 (Ronquist et al., 2012). The best-fit nucleotide substitution model, selected in jModelTest2 (Darriba et al., 2012) under the AIC criterion was the HKY + G model. The analysis was run for 5,000,000 generations, with a sample frequency of 5,000 and with a burn-in period of 25%, with remaining trees used to infer a consensus tree and calculate Bayesian Posterior Probabilities. A Maximum likelihood (ML) approach was also employed to estimate a phylogeny, using PhyML 3.0 (Guindon et al., 2010), both for defining the most appropriate model of molecular evolution under the AIC criteria, and producing a phylogeny. The chosen model was again the HKY + G model, and support for the phylogenetic tree was inferred with 1,000 bootstrap replicates. The phylogenetic trees were imported to FigTree v.1.4.2 (Rambaut, 2014) for graphical visualization and editing. Two divergent species from the genus, *Hemidactylus shihraensis* and *Hemidactylus dawudazraqui*, were used as outgroups. The full resulting tree (BI consensus; complete tips labeled) with bootstraps and posterior probabilities is shown on **Supplementary Figure 1**.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material,** further inquiries can be directed to the corresponding author/s.

ETHICS STATEMENT

Permits for fieldwork and tissue collection were obtained from SBS (Seychelles Bureau of Standards) for Seychelles specimens (granted to SR and DJH). Permission to sample museum specimens was secured from the museums after a destructive application process.

AUTHOR CONTRIBUTIONS

ASC, and GL conceived of the study. ASC collected and analyzed historical records. SR, AT, and DJH extracted DNA and generated and analyzed mitochondrial sequences. SR, AT, GL, DJH, and ASC wrote the manuscript with contributions from all authors.

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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.2022.791762/full#supplementary-material

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