People, Lemurs and Utilitarian Plants of the Littoral Forests in Southeast Madagascar



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Abstract

Tropical forests support a diversity of plants. Many of them are threatened, emphasising that their shared use by people and wildlife may benefit their conservation. Litt forests of southeast Madagascar, home to seven threatened lemur species, provide the Antanosy people with natural resources. In the early 2000s, protected areas were established in two regions that historically incurred different levels of anthropogenic pressures: Sainte Luce and Mandena. We explored the local use of plants as medicine, construction materials and firewood, and examined the overlap of plants used by people and the red-collared brown lemur (Eulemur collaris), the largest lemur in this ecosystem and an important seed disperser. Between July and October 2018, 60 adults (30 women, 30 men) participated in semi-structured interviews. Our findings show 122 plants are locally used as medicines, 60 as construction materials, and 71 as firewood. Of all utilitarian plants, 52 were confirmed in this lemur's diet. Sainte Luce participants reported they used a higher diversity of species in all three categories. Western medicines were available and preferred to medicinal plants, but the choice also often depended on the health condition being addressed. Firewood was preferred to charcoal for cooking. Resource restrictions of the protected areas has negatively affected the local people. Local ethnobotanical knowledge reflects the importance of plants, while differences in plant use of the two communities reflect differences in biodiversity and socio-economic circumstances. Emphasising this interdependence, especially in forest restoration, could be a path towards conservation of plants, lemurs, and people, as well as traditional livelihoods.

Keywords Ethnobotany \cdot Ethnoprimatology \cdot *Eulemur collaris* \cdot Lemur \cdot Livelihoods \cdot Red-collared brown lemur \cdot Traditional medicine

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Introduction

Tropical forests support an immense diversity of plant species (Janzen 1970; Balick *et al.* 1996). People residing within these ecosystems often rely on forest plants for food, medicine, construction materials, or cooking fuel (Byron and Arnold 1999; Ingram *et al.* 2005; Asprilla-Perea and Diaz-Puente 2019). Numerous plant species used by people are also found in the diet of local wildlife (Krief *et al.* 2005; Felton *et al.* 2010; Petroni *et al.* 2017; Mukherjee *et al.* 2011), including frugivorous non-human primates (hereafter "primates"). The value of the seed dispersal activities of these these animals, especially of utilitarian species, has been recognised as an argument for primate conservation, not only due to its importance for forest regeneration, but also where plant species of importance to humans are concerned (Lambert 1998; Chapman and Dunham, 2018; Steffens, 2020).

Human activities are a major driver of environmental change and biodiversity loss (Gardner et al. 2009; Morris 2010). Among the main causes is selective logging (Hall and Bawa 1993; Hill and Harner 2004; Dent and Wright 2009; Putz et al. 2012). Additionally, people rely on various non-timber forest products (NTFPs), such as medicinal plants, firewood, or weaving materials (Panayotou and Ashton 1992; Shackleton and Shackleton 2004). It was long thought that people's use of NTFPs had little ecological impact. However, due to NTFPs' increasingly recognised economic importance (Shackleton and Shackleton 2004), this is not necessarily true. Furthermore, NTFPs often have cultural significance (Posey 1999; Cocks and Wiersum 2003). Consequently, identifying cultural keystone species (i.e., species that shape people's cultural identity, as reflected in their importance in people's diets, pharmacopoeias, construction activities, and/or spiritual practices) (Garibaldi and Turner 2004) and using them in forest restoration might motivate support of local communities for forest conservation (Brandt et al. 2013). People's livelihoods are often based in natural resources, some of which are also important to the wildlife. One of the ways to support the local people and the wildlife is through emphasising their shared use of natural resources (Kinnaird 1992; Krief et al. 2005; Felton et al. 2010; Petroni et al. 2017).

One of the most frequently explored examples of utilitarian plants are medicinal plants (van Wyk and Wink 2018). Traditional medicine incorporates use of natural resources to prevent, treat, or heal human diseases and ailments, often as a part of a ritual, and combined with spiritual beliefs (Smith-Hall *et al.* 2012). It is an important part of many countries' traditions and culture (Quansah 2005). Many people throughout the tropics, especially those living in rural areas, rely on medicinal plants. This is mostly due to cultural preference, the effectiveness of medicinal plants, or limited access to Western medical resources (Balick *et al.* 1996). Species used in construction can also have a socio-cultural value, which depends on their physical traits and their local recognition (Brandt *et al.* 2013). Moreover, higher intensity, quality, and exclusivity of use add to plants' sociocultural value (Turner 1988).

Madagascar is a biodiversity hotspot (Myers *et al.* 2000), with a high degree of microendemism (Wilmé *et al.* 2006; Callmander *et al.* 2011). However, as is

the case for other tropical and subtropical countries, Madagascar is facing biodiversity loss. Forests are cleared to make space for agriculture, which is the main livelihood activity in many parts of the country. Sainte Luce and Mandena littoral forests of southeastern Madagascar are among the most threatened ecosystems in the world (Bollen and Donati 2006), and only around 10% of the original forest remains (Consiglio et al. 2006). To mitigate biodiversity loss, protected areas were created in Mandena (in 2002) and Sainte Luce (2005). People living near these areas were previously reported to use 58% of all tree species, the uses of which varied from medicinal plants to construction materials, firewood, and food (Lowry et al. 1999; Ingram et al. 2005b; Razafindraibe et al. 2013). However, these lists were not previously compared to the lists of plant species found in the diet of local wildlife. Comparing the two is important, as it might reveal overlaps that could inform wildlife conservation activities, while also considering the needs of the local people. Medicinal plants are locally of high importance, and their use is typically prescribed by traditional healers, known as ombiasa. According to local beliefs, spiritual forces govern people's lives, and any violation of spiritual rules may result in bad spirit possession or serious illness (Lyon and Hardesty 2005). Traditional healers' activities, however, depend on the availability of medicinal plants (Lyon and Hardesty 2012). Although Western medicines are becoming increasingly available in the region, previous reports showed that they are rarely used, because people doubted their effectiveness (QMM 2001). NTFPs are locally also used as cooking fuel. Firewood and charcoal are the primary sources of energy. While 90% of the rural population relies on firewood, living trees are not felled for this purpose — instead, people collect deadwood and fallen branches (QMM 2001). This has little impact on the forest structure and diversity (Ingram and Dawson 2006). In contrast, charcoal production is a more destructive practice, and has led to large-scale deforestation, which is detectable from satellite imagery and aerial photographs (Ingram and Dawson 2006). Charcoal use is more prevalent among urban populations (e.g., in Fort Dauphin) and migrants coming from the south of Madagascar (e.g., the Antandroy), who make the charcoal locally and are also responsible for the high degree of forest loss in Mandena (QMM 2001; Ingram and Dawson 2006; Ganzhorn et al. 2007).

Sainte Luce and Mandena are two of the littoral forests growing on sandy soil (Vincelette *et al.* 2007), located in the Anosy region. Due to unsustainable extraction of forest resources, prior to the establishment of protected areas, Mandena was more degraded than Sainte Luce (Bosser and Rabevohitra *et al.* 1996; Dumetz 1999; Bollen and Donati 2006). Both forests are home to the red-collared brown lemur (*Eulemur collaris*). This is an Endangered lemur species found only in the southeast of Madagascar (Donati *et al.* 2020), where it inhabits lowland semi-montane humid forests and littoral forests. It is the largest lemur species in the littoral forest. Due to its body size, this predominantly frugivorous lemur (Donati *et al.* 2007a) is probably the exclusive disperser of many large-seeded plants (Bollen et al. 2004). Therefore, these animals are uniquely important for various plant species' regeneration, while also playing a role in overall forest regeneration patterns (Račevska 2020). In this study, we cross-reference people's use of plants with that of the red-collared brown lemur, document and compare the use of plants by people living in the two areas,

and discuss how local plant uses might have changed since the protected areas were established. We first explore the importance and the value of the plants to the local people, and then consider their relationship to the ecology of the red-collared brown lemur. We address the following questions:

- 1. Which plants are used as medicine, construction materials, and firewood by people in Sainte Luce and Mandena?
- 2. What are the details of medicinal plant use (i.e., which parts of the plants are used, and how the medicine is prepared)? What medical issues are they used to treat?
- 3. Do people from Sainte Luce and Mandena use Western medicines? If so, what are the preferred ways of treating illnesses (medicinal plants or Western medicine), and why?
- 4. Do people from Sainte Luce and Mandena use charcoal? If so, do they prefer it to firewood?
- 5. Are there any other uses of plants related to local livelihoods?
- 6. How many plant species within each category examined (i.e., medicine, construction material, firewood) are also found in the diet of the red-collared brown lemur?

Methods

Study Sites

Sainte Luce (24°45' S, 47°11' E) and Mandena (24°57' S, 47°0' E) (Fig. 1) are similar in botanical composition (Rabenantoandro et al. 2007; Campera et al. 2014), yet different in their historical degrees of anthropogenic use, lemur community composition, current mining pressure, and proximity to Fort Dauphin (25°02' S, 46°59' E), the capital of the Anosy region. In Sainte Luce, the designated protected area consists of five fragments, which became protected in 2005 and cover 747 ha. Sainte Luce is located about 35 km from Fort Dauphin. In Mandena, two joined fragments comprise the Mandena Conservation Zone, established in 2005 and spanning over 230 ha. It is located about 10 km from Fort Dauphin. Prior to becoming protected, Mandena was more degraded than Sainte Luce (Bosser and Rabevohitra et al. 1996; Dumetz 1999). In 1986, the QMM mining company (QIT Madagascar Minerals), a subsidiary of the Rio Tinto mining company, began operating in the area, and was expected to continue for the following 40 years (Rio Tinto 2017). In Mandena, the mining company also established a tree nursery for endemic species, and a plantation of fast-growing exotic species, such as Acacia sp. and Eucalyptus sp. intended for local use as timber and firewood (Vincelette et al. 2003). The creation of protected areas, the introduction of exotics and the associated changes in resource management have most probably affected local people's resource use and livelihoods, but no studies have been published on the details of it. While some activities, such as hunting, logging, and charcoal production, became prohibited when the protected areas were established, certain resources, such as medicinal plants and firewood, can be collected with a permit obtained from the community-level forest association (Communautés de Base, or COBA). Mining commenced in Mandena in 2009, but



Fig. 1 The littoral forests of Sainte Luce and Mandena (Madagascar), and the focal villages of the study. (Mandena villages, *top to bottom*: Mangaiky, Betaligny, and Ampasy Nahampoana; Sainte Luce villages, *left to right*: Ambandrika, Ampanasatomboky, and Manafiafy).

at the time of publication, Sainte Luce is still in the pre-mining phase. Both Sainte Luce and Mandena are inhabited by the red-collared brown lemur, Thomas's dwarf lemur (*Cheirogaleus thomasi*), and the southern woolly lemur (*Avahi meridionalis*). Sainte Luce forest fragments are also home to the Anosy mouse lemur (*Microcebus tanosi*), while the Ganzhorn's mouse lemur (*Microcebus ganzhornii*), southern bamboo lemur (*Hapalemur meridionalis*) and greater dwarf lemur (*Cheirogaleus major*) are found in Mandena.

Study Population and Sample

The Anosy region is among the most isolated and economically poor regions of Madagascar (Vincelette *et al.* 2007). Most of the region's population is engaged in subsistence agriculture and fishing (Vincelette *et al.* 2007; Račevska 2020), but agricultural productivity is seasonal and low. Because of the region's isolation and poverty, local people are heavily reliant on the forest for livelihoods (Ingram *et al.* 2005; Razafindraibe *et al.* 2013), which has led to substantial destruction and degradation of the littoral forests over the last 50 years (Dumetz 1999; QMM 2001). In addition to agriculture, fishing, and collecting forest resources, some community members

are employed by the QMM, while other work as teachers, forest guides for researchers and tourists, or guards at the tourist lodges (Ingram *et al.* 2005b; Evers and Seagle, 2012; Kraemer 2012; Račevska 2020). In Sainte Luce, some of the women earn income through embroidery (project "Stitch Sainte Luce", a cooperative supported by the local NGO "SEED Madagascar"). Our participants came from six villages, three in each area (Ambandrika, Ampanasatomboky, and Manafiafy) and three villages in Mandena (Ampasy Nahampoana, Betaligny, and Mangaiky) (Fig. 1). We chose these focal villages because of their proximity to the protected forest fragments. All participants were residents in the focal villages.

Data Collection

Sixty adults (ten from each focal village) participated in the study. Participants' selfreported ages ranged from 24 years to 90 years in Mandena (median = 39.0, IQR = 24.0), and from 28 years to 80 years in Sainte Luce (median = 44.5, IQR = 30.0). We designed semi-structured interviews (Bernard 2017) and administered them between April and October 2018. To ensure equal representation of women and men in the sample, we selected participants using quota sampling (Newing 2010). All interviews were conducted by the first author and a local Antanosy translator (n = 3), and took place in participants' homes. All participants spoke the local Antanosy dialect of Malagasy, in which the interviews were conducted. We framed our questions about uses of plants within a broader discussion about local use of natural resources, which included questions about lemurs inhabiting the littoral forest, hunting, fishing, and people's perceptions of conservation and socioeconomic development more generally. Participants' answers were translated into English to allow immediate follow-up questions. To document which species were used, we used the free listing technique (Albuquerque et al. 2014; Oliveira et al. 2019), in which we asked participants to name all the plants they knew and used as medicine, construction material, or firewood. If participants stated that they did not know or use any other species in any of the three categories, we used nonspecific prompting (Albuquerque et al. 2014). We identified all plants by their vernacular names, while we obtained their scientific names from the published literature (Bollen 2003; Ingram and Dawson 2006; Rabenantoandro et al. 2007; Ganzhorn et al. 2007; Donati et al. 2007a, 2011, 2020).

To understand local use of medicinal plants, we asked participants whether they used medicinal plants. If their answer was positive, we asked them to list each species they used, along with details of their use — i.e., plant part used (e.g., leaves, bark, roots, etc.), how the medicine was prepared, and which condition/s it treated. We include all answers provided by our participants, including culturally understood illnesses such as *hevo* — a culturally understood childhood illness, involving a range of symptoms such as diarrhoea, dehydration, stomach ache, high temperature, prickly oral cavity, soft fontanel and a general state of weakness (SEED Madagascar 2012). In addition, we inquired about the participants' use of Western medicines. We also asked which type they preferred, and why. To find out about plants used as construction materials, we asked the participants to list all plants they used for

construction of their homes, and to identify which of those they considered most important. Finally, we surveyed participants' use of firewood or charcoal as cooking fuel. If participants used firewood, we asked them to list all species they used. If participants answered that they also used charcoal, we asked them which they preferred, and why. To compare the plant species used by people and those previously confirmed in the diet of the red-collared brown lemur, we use several lemur diet datasets (i.e., Bollen 2003; Donati *et al.* 2007a, 2011, 2020; Račevska 2020; Račevska, unpublished data).

Ethical Note

The University Research Ethics Committee of Oxford Brookes University granted the ethical approval. The datasets generated and analysed during the current study are not publicly available due to them containing sensitive information about human participants, but are available from the corresponding author on reasonable request.

Data Availability Before data collection began, each translator signed a confidentiality agreement, wherein it was stated that any of the gathered information would not be discussed with any third parties. For each participant, we noted their age, gender and the name of their village as identifying factors. We did not ask for participants' signatures due to low levels of literacy in the area. We emphasised the anonymous nature of the study and data confidentiality, also making sure that all participants understood they did not have to answer any question that they did not want to answer, without disclosing the reason. We obtained separate consent for the interviews to be audio recorded, the purpose of which was, as we explained to each participant, to ensure a higher accuracy when documenting their responses. After the interview, the first author transcribed each recording and translated it with the help of a translator.

Results

All of the people interviewed in this study (n = 60) used plants as medicine (122 plants), construction materials (59 plants), and cooking fuel (71 plants). They named a total of 191 plants, 50 (26%) of which were used for more than one purpose. Additionally, ten women from Sainte Luce (67%) and six from Mandena (40%) reported collecting sedge (*Lepironia mucronata*), locally known as mahampy. Using the traditional "over/under" technique, they weave sedge into different types of products (i.e., mats, hats, and baskets), which they subsequently sell to earn additional income.

Medicinal Plants

Plants are used as medicine in Sainte Luce (29 or 97% of participants) and Mandena (24 or 80% of participants). Of the 122 plants used for medicinal purposes, we were able to identify 49 (40%) to species level (Table S1). The number of reported

species was higher in Sainte Luce (n = 92) than in Mandena (n = 51), with an overlap of 21 species. The most commonly reported plant in both areas was the Madagascan periwinkle (Catharanthus roseus). This flowering plant is used by a third of Sainte Luce and Mandena participants to treat stomach problems (Table S1). In Sainte Luce, a plant locally known as fagnota (Monathotaxus sp.) was reported with equal frequency. Tea made from its leaves is used to alleviate stomach and heart problems, while a paste made from its powdered roots and water is believed to help with bad spirit possession. As one participant explained, "Fagnota has a bad smell. If you put it under the person's nose, the bad spirit goes". The same participant also used fagnota to relieve bad luck: "If you are unlucky, mix the powder with water and put it all over your body to lose the bad luck". In both Sainte Luce and Mandena, most medicinal plants were used for treating digestion issues (Sainte Luce: n = 34or 40%; Mandena: n = 15 or 29%). Most participants also reported using Western medicines (n = 29, or 97% of each sub-sample). Sainte Luce participants reported using 25 Western medicines, the most common being paracetamol (n = 24, or 83%) and amoxicillin (n = 17, or 59%). Western medicines were primarily used as painkillers (n = 34, or 59% of participants) to alleviate headache, toothache, and other body pain. Participants from Mandena reported using 13 types of western medication, with paracetamol (n = 15, or 52%) and amoxicillin (n = 4, or 14%) the most commonly used. While some participants preferred to use Western medicines, others preferred to rely on medicinal plants, and some stated that their choice depended on the condition they needed to treat (Fig. 2).

People in both Sainte Luce and Mandena preferred Western medicines to medicinal plants. An explanation for the preference was provided by four Sainte Luce participants (35%) and four Mandena participants (45%). The most commonly given reason was their perception of Western medicines as stronger and fasterworking than the medicinal plants (Fig. 3). Western medicines are available in the



Fig. 2 Participants' preferences of medicinal plants and Western medicines in Sainte Luce (n = 29) and Mandena (n = 29). Two participants did not provide an answer. Madagascar, April–October 2018.



Fig. 3 Reasons given to explain people's preference of Western medicines over medicinal plants in Sainte Luce (n = 10) and Mandena (n = 13). Madagascar, April–October 2018.

surveyed villages, or from travelling salespeople. Although not all villages have doctors or hospitals, both are reportedly available in the nearby villages and towns. However, many people found them too expensive. As they explained, sometimes their only option is to sell their chickens to pay for the medication. As one participant illustrated, "I prefer medicinal plants because I do not have to buy them. If I have a stomach ache, I spend 50,000 ariary to buy medication for it" (9.55 GBP).

Participants who preferred medicinal plants explained that this was because collecting plants from unprotected areas, such as fragments outside the conservation zones or within their villages, is free (Figure 4). Collection of medicinal plants is



Fig.4 Reasons given to explain people's preference for medicinal plants over Western medicines in Sainte Luce (n = 5) and Mandena (n = 6). Some participants provided multiple answers. Madagascar, April–October 2018.

also allowed from the protected area with a permit. One participant who used both medicinal plants and Western medicines explained that he uses medicinal plants "for simpler illnesses, like stomach pain". Another stated that in situations when Western medicines are not instantly available, "plants are the first aid". There are also culturally understood ailments that participants believe cannot be treated with Western medicines. As one participant explained, "When a doctor cannot treat me, the witch doctor recognises that it is a bad spirit". Another participant revealed that "Doctors do not have any medication to treat *hevo*". Medicinal plants are also considered more practical, and without side effects. As one participant explained: "Medicinal plants can treat a lot of diseases, and Western medicines have a bad impact on me — if I take too many, I get stomach problems".

Plants Used as Construction Materials

Using forest species as construction materials is common in both areas (29, or 97%) of participants in each area). Sainte Luce participants reported using 38, and Mandena participants 36 different plants as construction materials (Table S2). In both areas, the only participants who reportedly did not use plants in this way were women. The extent of the anthropogenic pressure on the forest for the extraction of plants used for construction is illustrated by a participant who disclosed that "It can take up to 80 trees to build a house.". The most frequently reported species in Sainte Luce was Ravenala madagascariensis. Roofs are made using its dried leaves, while its trunk is sometimes used in wall construction. Some participants (n = 5, or 17% in Sainte Luce and n = 8, or 28% in Mandena) mentioned that not being able to access timber species in the protected area negatively impacted them. A few participants (two, or 7% in Sainte Luce, and three, or 10% in Mandena) stated they were unable to find the native species they used to obtain from the now protected areas elsewhere. More participants (15, or 52% in Sainte Luce and 14, or 48% in Mandena) mentioned how generally not being able to obtain forest resources from the protected area negatively impacted their livelihoods. One participant explained that while some of these species grow in the unprotected areas (i.e., S7), the trees are not as strong as they are in the protected areas because they are too young. In Mandena, participants relied more on the introduced, faster growing species (i.e., Eucalyptus sp.), despite their perceived lower quality and reduced longevity. The species used most often is *E. citriodora*. As one participant described, this species is "good for roof, but not for the floor because it is too soft".

Plants Used as Firewood

In both Sainte Luce and Mandena, dead wood collected from the forest was the most frequently used cooking fuel. Participants used 71 different species in this way, but only seven (10%) of these species were used in both Sainte Luce and Mandena (Table S3). More species were named by Sainte Luce participants (n = 48) than Mandena participants (n = 30). However, many participants, especially

in Mandena (n = 12, or 40%; compared to n = 4, or 13% in Sainte Luce) did not name particular tree species, stating that the species did not matter, and they would use any dead wood they found. Most Sainte Luce participants preferred using firewood (n = 29, or 97%) to charcoal (n = 1, or 3%). In Mandena, the preference for firewood (n = 23, or 77%) was lower than in Sainte Luce, but higher than the preference for charcoal (n = 7, or 23%). In Sainte Luce, the most frequently reported species used as firewood were *Asteropeia multiflora* and *A. micraster*, while Mandena participants most frequently reported using *Eucalyptus citriodora* (Fig. 5).

The majority of Sainte Luce participants preferred to use firewood rather than charcoal because it was considered customary. As one participant explained, "It is a habit inherited from the ancestors". By contrast, charcoal, along with the stove needed for its use, the participants often perceived as too expensive. "A bag costs 3,000 ariary" (0.64 GBP). The most common explanation for firewood preference in Mandena was that firewood is cheaper than charcoal, a bag of which costs up to 6,000 Malagasy Ariary (1.28 GBP). One participant reported that, to cook a single meal, they would need around five pieces of charcoal, costing around 200 Malagasy Ariary (0.038 GBP). Moreover, there were other reasons for not using charcoal. As one participant explained, "Charcoal requires living wood to be made, I do not like it. You need to chop down living trees".

Four of the Sainte Luce participants used charcoal, but only one of them preferred it as cooking fuel. The most common explanation for preferring charcoal was that it is an easier cooking method. As participants explained, "I do not need to blow in the fire. It is easy, I can leave it". Only Mandena participants reported making charcoal themselves. They explained they made it in their village, mainly using introduced species, such as *Eucalyptus citriodora* (n = 5) or *E. robusta* (n = 1), or fruit trees such as *Litchi chinensis* (n = 3), *Mangifera indica* (n = 2) or *Artocarpus heterophyllus* (n = 1).



Fig. 5 Explanations of why people prefer firewood over charcoal as cooking fuel in Sainte Luce (n = 26) and Mandena (N=21). Madagascar, April–October 2018.

Utilitarian Species Found in the Diet of the Red-Collared Brown Lemur

Out of 191 different plants used by people in this study, 52 (27%) are also found in the diet of the groups of the red-collared brown lemur studied in Sainte Luce and Mandena. We were able to identify 45 of these plants (87%) at the species level. Of the 52 total plant types, the red-collared brown lemur ate fruit of 42 (81%). These are used locally as construction materials (n = 34), firewood (n = 29) and traditional medicine (n = 20) (Table I). While not all species' conservation status is known, nine (17%) are classified as Vulnerable or Endangered (IUCN Red List 2021) (Table I).

When we consider only the utilitarian plants identified at the species level, the percentage of species belonging to each examined category in the diet of the red-collared brown lemur is still substantial (Table II).

Discussion

The findings of this study reveal that medicinal plants and western medicines are reported as being used more frequently in the region than has previously been documented (Norscia and Borgognini-Tarli 2006; Lyon & Hardesty 2012). However, participants' decisions about whether to use traditional or Western medicines often depend on the medical issue to be addressed. While people in Sainte Luce use native species as construction materials, many participants from Mandena reported a switch to introduced species, such as *Eucalyptus* sp. Some of the participants also reported that their livelihoods have been negatively affected by the resource restrictions of the protected areas. The forest resources they used to collect in the protected areas, which they are now unable to access, are reportedly difficult for them to find elsewhere. All participants stated they used firewood as cooking fuel and were less selective of plants used for this purpose. The majority preferred firewood to charcoal, mostly because it is more affordable. The importance of local traditions and ancestors was evident in many participants' choices throughout. Of the plants used by people in this study, the red-collared brown lemur inhabiting the Sainte Luce and Mandena protected areas fed on 52 (this does not account for the seasonal differences in their diet). The shared use of plants by people and wildlife should inform the conservation efforts for these plant species.

Medicinal Plants

Before this study, very little had been published on the Anosy people's use of plants. Of the plant uses we examined, medicinal plants were the most numerous category. While the medicinal use of some of these species is known from published literature (e.g., Ingram *et al.* 2005b; Norscia and Borgognini-Tarli 2006), use of many others has not previously been recorded, and the number of medicinal plants documented here is higher than in the previous studies. Sainte Luce

Table IUtilitarian species in the diet ofOctober 2018	of the red-collared brov	/n lemurs in Sainte	Luce and Mandena. Plants whose fruit	is eaten are presented in bold . Mi	ladagascar, April–
Scientific name	Local name	Conservation status	Use	Area	Diet data set
Anthostema madagascariense	bamby	LC	construction	SL	6
Asteropeia multiflora	fanola fotsy	LC	medicine; construction; firewood	SL, MND; SL, MND; SL	2, 6
Beilschmiedia madagascariensis	resonjo	LC	firewood	SL	1, 2, 6
Bembicia unifiora	bemalemy	LC	firewood	SL	1, 2, 6
Brochoneura acuminata	mafotra	LC	construction	MND	1, 2, 6
Burasaia madagascariensis	farisaty	LC	medicine	SL	9
Buxus madagascarica	haramboanjo	LC	construction; firewood	SL	1, 2
Cabucala madagascariensis	tandrokosy	LC	medicine	SL	9
Campnosperma micranteium	roandria	LC	medicine	SL, MND	1, 2, 6
Scolopia erythrocarpa	lampivahatry	EN	construction; firewood	SL, MND; SL	1, 2, 3, 4, 6
Clerodendrum sp.	fantsikohy	ı	construction	MND	1, 2
Cynometra cloiselii	mampay	ı	firewood	SL	1, 2, 3, 4, 6
Dillenia triquetra	varikanda	LC	construction	SL	1, 2, 4
Diospyros myriophylla	hazomainty	LC	construction; firewood	SL, MND; SL	1, 2, 6
Dracaena reflexa var. nervosa	falinandro	LC	medicine	SL	9
Dypsis prestoniana	boaka	VU	medicine	SL, MND	3,6
Dypsis sp.	raotry	ı	medicine; construction	SL; SL, MND	6
Embelia incumbens	taratasy	ı	medicine	MND	9
Saldinia littoralis	mangavoa	ı	construction	SL	1, 2, 6
Erythroxylum sp.	fangora	ı	medicine	SL	2
Ficus megapoda	aviavi	ı	medicine	SL	1, 2
Ficus pyrifolia	nonoky	ı	medicine	MND	1, 2
Ficus guatterüfolia	fihamy	ı	medicine	SL, MND	9
Grisollea sp.	zambo	ı	firewood	SL	1, 2

Table I (continued)					
Scientific name	Local name	Conservation status	Use	Area	Diet data set
Homalium albiflorum	voakazoala	LC	construction; firewood	SL	2, 3, 4
Homalium louvelianum	ramirisa	νU	construction; firewood	SL	1, 2
Intsia bijuga	harandrato	NT	medicine; construction; firewood	SL, MND; SL, MND; SL	1, 2
Leptolaena paucifiora	fonto	LC	construction	SL, MND	1, 2
Homalium planiflorum	hazofotsy	LC	construction	MND	9
Macaranga sp.	makaranga	ı	firewood	MND	1, 2, 6
Neotina isoneura	sagnira	LC	medicine; construction	MND	2
Noronhia emarginata	belavenoky	LC	construction; firewood	SL	1, 2, 6
Noronhia ovalifolia	zorafotsy	EN	construction; firewood	SL	3
Ocotea racemosa	varongy	LC	construction	MND	4,6
Phyllarthron licifolium	zahambe	EN	construction; firewood	SL	9
Plectronia densiflorum	fanstikahitry	LC	construction; firewood	SL	1, 2, 6
Poupartia chapelieri	sisikandrongo	LC	construction	SL	3,6
Psidium guajava	goavy	ı	medicine; construction; firewood	SL, MND; MND; MND	1, 2, 5
Psorospermum brachypodum	haronga	٨U	medicine; firewood	SL, MND; MND	1, 2
Ravenala madagascariensis	ravenala	LC	construction; firewood	SL, MND; SL	1, 2, 3, 4, 5
Sarcoleana sp.	vondroza	ı	construction; firewood	SL, MND; SL	1,2
Neocussonia rainaliana	vonsilana	EN	firewood	MND	1, 2
Schizolaena elongata	fotondahy	LC	construction, firewood	SL	3, 6
Scolopia orientalis	zoramena	VU	construction, firewood	SL	9
Suregada baronii	kalavelo	ı	medicine	SL	2
Symphonia verrucosa	hazingy	LC	construction	SL, MND	1, 2
Syzygium emirnense	rotry	LC	medicine, construction, firewood	SL; SL, MND; SL, MND	1, 2, 3, 4, 5, 6

Table I (continued)					
Scientific name	Local name	Conservation status	Use	Area	Diet data set
Tambourissa purpurea	ambora	ГС	construction, firewood	SL; SL, MND	1, 2, 4
Terminalia fatraea	katrafa	LC	medicine, construction, firewood	SL, MND; SL; SL	3, 6
<i>Uapaca</i> sp.	voapaky		construction, firewood	SL, MND; SL, MND	1, 2, 3, 4, 5, 6
Vepris elliotii	ampoly	LC	medicine, construction, firewood	SL; SL, MND; SL	1, 2, 3, 4, 5
Vitex tristis	nofotrakoho	EN	construction, firewood	SL; SL	1, 2, 5, 6
1. Dožavicko 2020. 7. Dožavicka	muhlishad data: 3. Danat	at al 2007a. 4. Dan	oti at al 2011. 5. Donoti at al 2020b. 6.	. Bollan 2003	

1: Račevska 2020; 2: Račevska, unpublished data; 3: Donati et al. 2007a; 4: Donati et al. 2011; 5: Donati et al. 2020b; 6: Bollen 2003 *LC-Least Concern; VU - Vulnerable; EN - Endangered; SL - Sainte Luce; MND - Mandena.

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participants named a higher diversity of plants used as medicine than Mandena participants, which might be related to differing levels of past forest degradation of the two areas, with Mandena being more heavily degraded (Bosser and Rabevohitra et al. 1996; Dumetz 1999; Bollen and Donati 2006). The most frequently used species in both Sainte Luce and Mandena was the Madagascan periwinkle (Catharanthus roseus). This perennial flowering plant, common across tropical countries, is used in traditional medicine in most of its natural range. It is also one of the most researched medicinal plants, whose components are used in the treatment of numerous medical conditions: from headaches and diabetes to different types of cancer (Arora et al. 2010; Mishra and Verma 2017). The wide use of medicinal plants matches the results of previous studies (Lyon and Hardesty 2012; Ingram et al. 2005b; Norscia and Borgonini-Tarli 2006; Razafindraibe et al. 2013; Hogg et al. 2013). Across numerous African countries, traditional medicine is the primary source of medication for many people (Abdullahi 2011). However, our findings show a higher reliance on and preference for Western medicines than previously reported from the study area (QMM 2001). Most participants in this study were not concerned with the availability of Western medicines, but with their affordability. Many believed Western medicines were generally more effective than medicinal plants. In contrast, medicinal plants are free and - according to our participants abundant. This is in line with previous research from Madagascar and other African countries (Sofowora 1996; Neudert et al. 2017). What seems to be of equal, if not greater importance, is that medicinal plants are a part of the local cultural heritage. Even though they are the least represented among the utilitarian plants found in the diet of the red-collared brown lemur (Tables I and II), their value to the local people makes their conservation important.

The use of Western medicine and traditional healing seem well integrated in Sainte Luce and Mandena, but while both types of medicine are widely used, their use is not interchangeable. Many participants explained that their choice depends on the medical condition being treated. For example, diseases of the reproductive system, skin issues, culturally understood illnesses, and issues which are believed to be the result of spirit possession are only treated using medicinal plants. This illustrates the role of traditional healers, whose knowledge is highly revered in the Antanosy culture (Lyon and Hardesty 2005). It is locally believed that violating spiritual rules can cause serious diseases and spiritual possessions. Regardless of their faith, most Malagasy people believe in spirit possession, but those with non-traditional religious beliefs trust that their religious faith will protect them from it (Lyon and Hardesty 2005).

Table IIUtilitarian plants andthe percentage of each categoryused by the red-collared brownlemurs in Sainte Luce andMandena.Madagascar, April –October 2018		Number of plants	Percentage used by the red-collared brown lemurs
	Medicine	49	41%
	Construction	45	76%
	Firewood	50	58%

Construction Materials, Firewood and Other

Using trees as construction materials was equally common in Sainte Luce and Mandena, but Sainte Luce participants reported using a higher diversity of plants than Mandena participants. While some of the plants are only present in one of the two areas, the reason for this difference could also be attributed to the differences in their availability. As species become less prevalent, so does their use. Since construction plants are the most numerous category among the utilitarian plants found in the diet of the red-collared brown lemur (Tables I and II), a decrease in their prevalence in the forest could also affect the lemurs. Several species of palms, such as Beccariophoenix madagascariensis and Dypsis saintelucei, previously used by people in Sainte Luce (Hogg et al. 2013), have in some fragments experienced population size decreases of 46% and 66% respectively (Hyde Roberts et al. 2020). Neither of the two once commonly used species were reported as being used currently by any of our participants. Furthermore, some participants mentioned no longer being able to find their preferred species outside of the protected areas where timber extraction is banned. It is difficult to assess the extent of this issue, as we did not ask this guestion specifically. One participant's remark about trees in unprotected areas being too young and therefore insufficiently strong is most probably related to the anthropogenic pressures, due to which the more desirable trees (i.e., the older and stronger ones) of the same species already having been extracted.

While people's reliance on introduced species has increased in Mandena, some participants considered them to be of lower quality than native ones they used previously. This is similar to the results of a study conducted near the Analalava reserve in the east of Madagascar, which showed that local people ranked native species more highly for wood quality as compared with introduced species (Lavialle et al. 2015). Despite being regarded by some of our participants as of inferior quality, Eucalyptus species are widely used as construction material (Table II). In east Madagascar, E. robusta ranked highest in timber hardness and rot resistance among the introduced species (Lavialle et al. 2015). One of the participants in this study commented that houses built from E. robusta need to be rebuilt every 7 years, whereas houses built using native species lasted 40 years (Lavialle et al. 2015). In the Morogoro region of Tanzania, study participants ranked E. tereticornis highly as a construction material (Krog et al. 2005). Despite some of our Mandena participants' emphasis on loss of tradition, switching to introduced species could be the only way to conserve the littoral forests, while simultaneously increasing the sustainability of local people's lives and forest-related livelihoods.

Plantations of exotic species planted in the appropriate area can reduce the pressure on the natural forest (Sedjo and Botkin 1997; Gérard *et al.* 2015; Konersmann *et al.* 2021). Studies have also shown that socio-cultural value of timber species increases with the increase of their availability and accessibility (Thomas *et al.* 2009; Brandt *et al.* 2013). This suggests that these exotic species might become more valued in Mandena, as their use becomes more common. Cultural heritage is of great importance in the region, so coping with change is inevitably complex. Evidence that people in Mandena are switching to using introduced species is a reason for hope in the longevity of forest protection. Conservation

education and outreach may be necessary to help support the transition and bridge the difference between tradition and what is realistically possible.

When it comes to cooking, firewood is reported as the most frequently used fuel type in both Sainte Luce and Mandena. Many of the species used as firewood were also found in the diet of the red-collared brown lemur (Tables I and II). Sainte Luce participants listed a higher number of species used in this way. Similarly with the situation with other utilitarian plants, this could also be related to different species' availability between Sainte Luce and Mandena, previous habitat degradation (Bosser and Rabevohitra *et al.* 1996; Dumetz 1999; Bollen and Donati 2006), or the higher reliance of Mandena participants on charcoal as cooking fuel. Overall, more plants were used as firewood than as construction materials, and participants tended to be less selective about their choice in this category. The diversity of species used as construction materials and firewood were higher in this study than previously reported (Ingram *et al.* 2005b). High dependence on firewood was also reported in different parts of northwest and east Madagascar, where 98% of households used firewood (Harvey *et al.* 2014).

Despite fewer people using charcoal in both Sainte Luce and Mandena, this practice is more common in Mandena, where charcoal is made using wood from fruit and introduced tree species growing within the village areas. This differs from the previously reported charcoal production, which was done by the Antandroy migrants and mainly using forest species to produce charcoal in the forest (QMM 2001; Ingram et al. 2005b; Rasolofoharivelo 2007). This was among the primary sources of deforestation in Mandena (Donati et al. 2007b). However, those studies were conducted between 12 and 18 years ago, and local circumstances may have changed since then. Most participants preferred firewood to charcoal, stating that using firewood is not only their cultural heritage, but also a more affordable option. Use of charcoal seems to be reserved for the comparatively more well-off urban population (QMM 2001), as is the case in many parts of Africa (Kersten et al. 1998; Tabuti et al. 2003; Arnold et al. 2006; Woollen et al. 2016; Ndegwa et al. 2020) and southeast Asia (Sovacool 2013; Win et al. 2018). As one of the Mandena participants disclosed, it is not uncommon for charcoal producers to sell all the charcoal they make to increase their income, and use firewood themselves. This is consistent with previous reports showing that the main benefit of charcoal production among rural farmers across sub-Saharan Africa is income generation (Zulu and Richardson 2013).

In terms of other plant uses related to income increase, sedge weaving was the most commonly mentioned one in this study, and as reported in earlier studies, weaving and selling sedge products is a common way of supplementing household income in both Sainte Luce and Mandena (Evers and Seagle 2012; Hogg *et al.* 2013). Sedge mats are of cultural importance to both women and men, and used in many aspects of daily life, for example to shroud corpses (Holloway and Short 2014).

Utilitarian Species Used by the Red-Collared Brown Lemur

We showed that the red-collared brown lemur feeds on 52 utilitarian plants (27%) used by the participants of this study. This lemur is the largest currently extant lemur

species inhabiting the littoral forest fragments of southeast Madagascar. It is mainly frugivorous (Donati et al. 2007a), and an important seed disperser of numerous plant species, for some of which it might be the exclusive disperser in this ecosystem (Bollen et al. 2004; Donati et al. 2007b). We found that the red-collared brown lemur consumed fruits of 42 utilitarian plants (Table II), and could play a role in their dispersal. Of the utilitarian species revealed in this study, Uapaca sp., C. cloiselii, P. densiflorum, S. emirnense, F. megapoda and F. pyrifolia, P. guayava, R. madagascariensis, and V. eliotti make up significant proportions of the red-collared brown lemurs' diet, but showed variation between seasons and years (Račevska 2020; Donati et al. 2020b). The diets of 56 lemur species, published over 204 studies, include mainly fruits and leaves of 1026 plants, or 9% of all vascular plants in Madagascar (Steffens 2020). However, not all plant species are equivalent in terms of importance as food sources. Lemur diets show seasonal variation, and while some plants might constitute preferred food items, others may represent fallback foods, consumed in periods of food scarcity, when favoured or more nutritional food items are unavailable (Marshall and Wrangham 2007; Marshall et al. 2009; Sauther and Cuozzo 2009). Seasonality relates to diet and behavioural patterns (Stevenson et al. 2000), both of which are likely to affect seed dispersal - not only in terms of when any plant species' seeds are dispersed, but also where (i.e., how far from the parent tree). This will probably impact seed survival and seedling recruitment (Muller-Landau and Hardesty 2005), and in the long term, forest structure and diversity. The red-collared brown lemur is predominantly frugivorous year-round (Donati et al. 2007a, 2011), and typically copes with periods of food scarcity by extending its home range size (Campera et al. 2014). However, its dietary diversity tends to be lower in the dry season (Račevska 2020), when the littoral forest shows a fruiting bottle-neck (Donati et al. 2007a; Campera et al. 2014). While some plants tend to be more represented in its diet (Bollen 2003; Račevska 2020; Donati et al. 2020b), their specific proportions vary between years, as forest productivity fluctuates. For example, R. madagascariensis, C. cloiselii, D. presoniana, V. eliotti, T. fratraea, S. elongata, H. albiflorum, P. chapelieri, and N. ovalifolia are utilitarian plants that were indicated as particularly important for the red-collared brown lemurs' diet in the lean season (Donati et al. 2007a). Understanding this lemur's seed dispersal in greater detail might therefore have important implications for the synergy of sustainable human resource goals and forest management initiatives.

Many of the plant species important to lemurs and people might be facing extinction: a 2021 report by the Botanic Gardens Conservation International revealed that 1840 tree species Madagascar are threatened, 1828 of them endemic (BGCI 2021). The same report showed that 53% of all endemic tree species have at least one use for local people: most of them are used as timber, while other common uses include firewood and medicine. Of the utilitarian species documented in this study, conservation status information was available for only 27 medicinal plants, 42 species used as construction materials, and 43 species used as firewood. The majority were classified as Least Concern (IUCN Red List 2021) (Tables S1, S2, and S3). Out of all the species whose use by both people and lemurs we documented in this study, and for which their conservation status was available (73%), less than 10% (i.e., 8%) have stable population trends (IUCN Red List 2021). These numbers are worrying, but emphasising plants' common use by people and other animals might facilitate their conservation through the encouragement of sustainable use to ensure their future availability for human and nonhuman users. Forest protection can have a negative impact on local people (Coad *et al.* 2008), but reforestation using plants of cultural or economic value might contribute to higher local involvement in and support of forest restoration (Ingram *et al.* 2005). While this would help secure local livelihoods, it would also benefit plant species protection.

Focusing restoration efforts on plant species with value to both people and the wildlife (e.g., Konersmann *et al.* 2021) differs from the more common strategy of working towards reducing people's reliance on forest resources of high importance to the wildlife. A reforestation project in Kianjavato (southeast Madagascar) combined species consumed by the black and white ruffed lemur (*Varecia variegata*) with commercially important species (Manjaribe *et al.* 2013). The three-tiered corridors have different intended uses: the permanent tier (not intended for harvest), the timber tier (indented for sustainable harvest of species locally used as construction material and firewood), and the non-timber tier (comprising fruit and commercially important species). Even introduced species, such as *Psidium guayave*, can be highly beneficial for native wildlife that feeds on them, as well as people for whom these plants may have economic importance (Gérard *et al.* 2015; Kull *et al.* 2013).

Studies elsewhere showed that an overlap between plant species eaten by primates and used by people is not uncommon. Tana River mangabeys (*Cercocebus galeritus*) consume the fruit and seeds of the *Phoenix reclinata* palm, used by human communities living near the Tana River in Kenya (Kinnaird 1992). As both the people's and the mangabeys' reliance on this palm is substantial, Kinnaird argued that regulating offtake rates would be beneficial to both people and mangabeys. Woolly spider monkeys (*Brachyteles arachnoides*) in Intervales State Park, São Paulo (Brazil) feed on 25% of medicinal plants used by people living nearby (Petroni *et al.* 2017). The diet of chimpanzees (*Pan troglodytes*) in the Kibale National Park (Uganda) included 21% of plants used in traditional medicine locally (Krief *et al.* 2005). Plants typically harvested for timber in La Chonta (Bolivia) were found to make up 50% of the diet of Peruvian spider monkeys (*Ateles chamek*) inhabiting the unlogged area (Felton *et al.* 2010).

As the red-collared brown lemur's diet includes species used as medicine, construction materials, and firewood, emphasising this lemur's interdependence with local people could benefit its conservation. For example, incorporating a range of utilitarian and lemur food species into conservation projects (e.g., establishing buffer zones, habitat corridors, and habitat restoration projects) could provide benefits to both lemurs and people (Gérard *et al.* 2015; Steffens 2020; Konersmann *et al.* 2021; Hyde Roberts, personal communication). Since there is little overlap between the fruits people and lemurs eat, as the red-collared brown lemurs do not feed on human crops and people largely do not consume the forest fruits eaten by the lemurs (Račevska 2020), competition over these resources is unlikely. Red-collared brown lemurs are one of several lemur species inhabiting the littoral forest ecosystem. Future studies should therefore aim to reveal potential overlaps between the utilitarian species and those found in other lemurs' diets. While the conservation status of the majority of plants documented in this study needs examining, it is clear that even their local extinction could have a significant impact on both the lemurs and the people who share this landscape.

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Author Contributions ER, CMH and GD designed the study. HTL helped adapt the questionnaire to the local context. ER and HTL collected the data. ER analysed the data and wrote the manuscript. CMH and GS provided guidance on the analyses, and editorial advice throughout the production of the manuscript.

Declarations

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

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