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Using Utilitarian Plants for Lemur Conservation

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Abstract
Nature and species conservation often conflict with intensive natural resource or land use. Many protected areas are too small for long-term conservation of viable vertebrate populations, especially in Madagascar, and forests are subject to exploitation for a variety of natural resources. Trying to exclude people from the use of these resources has not been successful during economic, natural, or political crises or when human population growth outruns any development effort. People need economic and other benefits, and conservation measures have to account for these needs. We compiled native and introduced tree, shrub, and herbaceous species used by both people and native vertebrates for three regions, covering the domains of the dry, transitional, and humid forest of Madagascar. We carried out semistructured interviews and group discussions in 12 different villages in each study region in November 2017. People listed 139 utilitarian plant taxa. Our literature search revealed that 72 of these plant species and 13 genera used by people, were also used by 208 different terrestrial vertebrates including 58 lemur species. Application of the Forest Landscape Restoration approach with a combination of exotic and native plant species used by both people and animals could increase the economic value of restored forest habitats for people, thus providing incentives for forest conservation. Plantations of mixed utilitarian trees and shrubs could be integrated into agricultural landscapes. Among land-living vertebrates, lemurs seem to benefit most from this approach. These measures might contribute to a successful array of biodiversity conservation in anthropogenic landscapes.

Keywords Agroforestry · Ethnobotany · Forest landscape restoration · Forest restoration · Madagascar · Strepsirrhines · Tree plantations

Introduction

The United Nations declared 2021–2030 the "Decade of Ecosystem Restoration," aiming to reverse degradation in ecosystems worldwide (Gann *et al.* 2019). This serves

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the achievement of international development targets as stated in the Sustainable Development Goals and more specifically in the New York Declaration on Forests and the Global Bonn Challenge concerning the protection and maintenance of forests across Africa. This political support is needed urgently to foster restoration in the world's biodiversity hotspots that have suffered from excessive habitat destruction, such as the native forests of Madagascar (Brinkmann *et al.* 2014; Harper *et al.* 2007; Waeber *et al.* 2015, 2016; Zinner *et al.* 2014). The African Forest Landscape Restoration Initiative (AFR100), a country-driven and African-led effort, aims to bring 100 million ha of forests and degraded forest landscape under restoration by 2030. As part of this Initiative, Madagascar has pledged to restore 4 million ha of degraded forest landscapes via the Forest Landscape Restoration approach by 2030.

Slash-and-burn agriculture remains the primary economic activity for many households, as opportunities for agricultural intensification are limited, and forested land is openly accessible in Madagascar (Gardner *et al.* 2016a, b; Hume 2006; Raharimalala *et al.* 2010; Styger *et al.* 2007). Over the past century, fallow periods became too short to ensure recovery of vegetation and soil conditions, resulting in increasing pressure on natural resources and declining agricultural productivity. The speed of fallow vegetation recovery and the changes in soil fertility of slash-and-burn cultivation sites has been well documented for a variety of sites (De Wilde *et al.* 2012; Gay-des-Combes *et al.* 2017; Klanderud *et al.* 2010; Leprun *et al.* 2009; Raharimalala *et al.* 2010; Styger *et al.* 2007; Zwartendijk *et al.* 2017). The restoration and transformation of fallow land to more productive permanent agricultural fields often failed, due to the high work load associated with sustainable cultivation techniques (manure and compost management) and further constraints such as limited resources for external inputs and marketing opportunities for agricultural products (Hume 2006).

At least in the eastern moist forests, natural forest gaps can regenerate well with native pioneer trees such as *Harungana madagascariensis* or *Dombeya* spp. (e.g., Martinez and Razafindratsima 2014). However, when the loss of tree cover is followed by landslides, mimicking slash-and-burn practices and fallow land, there are many cases in which the open land has been colonized by genera such as *Rubus* or *Aframomum* that form monospecific covers that seem to prevent the natural forest from regenerating (C. Welch, *pers. comm.*; Goodman *et al.* 2018). In the domain of the dry forest, regeneration after total clearance seems to follow three trajectories: natural forest regeneration (very slow), mostly monospecific stands of *Ziziphus* spp., or savannah covered by various grasses of limited value for livestock (Genini 1996). Thus, the species initiating a succession seem to be crucial for its further development.

Starting from degraded land that is no longer used by people, successions could be initiated with plants of possible use for people and the native fauna. To support the unique flora and fauna of biodiversity hotspots, forest restoration should favor native tree species. Yet, the profound local knowledge of indigenous plant species is still underexplored (e.g., Andriamparany *et al.* 2014) and from what is known scientifically, forest restoration with native trees is challenging due to higher costs, slower growth, and a lack of scientific species-specific knowledge of growth conditions (Birkinshaw *et al.* 2009; Lavialle *et al.* 2015). Also, given the high dependency of people on ecosystem services from forests and the pressure on forest resources by the rapidly growing human population, reforestation 'just for animals' may neither be acceptable for people nor sustainable (Gardner *et al.* 2016a, b). In contrast, reforestation using a handful of fast-growing tree species, such as various *Eucalyptus* and *Acacia* spp., has conservation value by providing the physical substrate for corridors and taking the pressure off the remaining forests (Andriamandimbiarisoa *et al*. 2015; De Wilde *et al*. 2012; Gérard *et al*. 2015; Irwin *et al*. 2010). However, these plantations do not contribute much to restoring functional habitats that can provide multiple ecosystem services. Thus, we are left with the inconsistency that, on the one hand, ecological forest restoration is good for the native fauna, but it provides too few ecosystem services for local people. On the other hand, plantations with exotic species provide financial revenues and some ecosystem services to local people, but too few benefits for animals. In response to this, many decision-makers have embraced the approach of Forest Landscape Restoration (FLR) in recent years, which seeks to reconcile biodiversity conservation and provision of ecosystem services for local people (Holloway 2003; Mansourian *et al*. 2017).

Our objective was to make better use of the local knowledge of the Malagasy inhabitants on the importance and usage of native plants and identify plant species of local importance that are also valuable for the native fauna. For this, we summarize the results of village surveys that could be relevant for forest restoration in three different regions of Madagascar, covering dry deciduous forest of the west, humid forest of the east, and a transition zone in the north of Madagascar. The goal of the study was to combine the human needs for forest resources and services with the objectives of nature and species conservation.

Methods

Study Area

We conducted the study in the regions of Menabe (Kirindy, western dry deciduous forest), Diana (transitional forest in the north of Madagascar), and Alaotra-Mangoro (Andasibe, eastern humid forest). Kirindy and Andasibe are villages associated with long-term biodiversity studies in these areas. We use these names in this publication as they are best known to people. Names of all villages and their coordinates are listed in the Electronic Supplementary Material [ESM] Table SI. All three study regions have experienced forest loss and forest fragmentation, making them important candidates for restoration (Figs. 1 and 2).

Menabe/Kirindy The Menabe region is part of the dry deciduous forest of coastal western Madagascar. The climate is characterized by pronounced seasonality with little or no rain from April to November, followed by a rainy season from December to March. Annual precipitation averages *ca.* 950 mm and has increased by about 0.5% per year since 1981. Mean annual temperature in Morondava is 24.7°C (Goodman *et al*. 2018; Sorg and Rohner 1996). The region suffers from one of the highest deforestation rates of the country (Zinner *et al*. 2014). Main crops are maize, cassava, groundnuts, and different bean varieties. Agriculture is based on slash and burn cultivation. Fallow land is colonized rapidly by secondary grassland or by *Ziziphus* spp., forming monospecific thickets (Genini 1996).

Diana The Diana region is located in northern Madagascar and represents a very heterogeneous region with annual rainfall ranging from 1000 to 2000 mm. The study

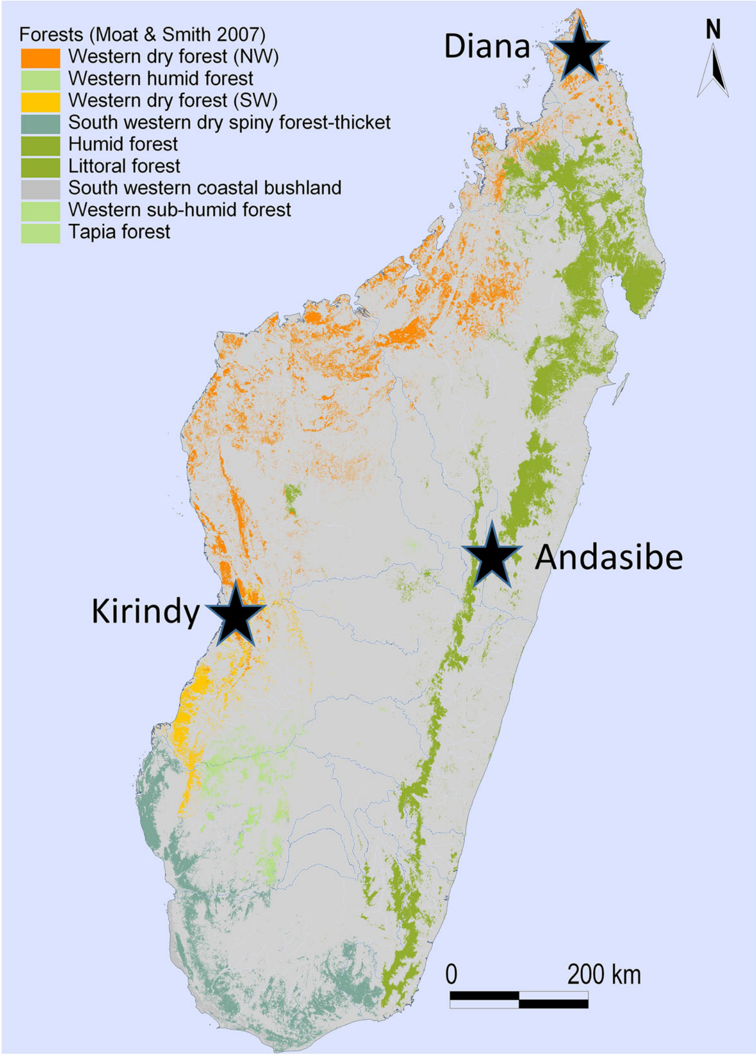

Fig. 1 Location of the selected study regions. Modified from Moat and Smith (2007).

villages are situated in the drier parts of the region dominated by deciduous forest with annual rainfall of about 1200 mm, falling mostly between November and April. Daily mean temperature fluctuates between 20° and 31°C (Goodman *et al.* 2018). The main crop is rice. Some villages generate income through community-based eucalyptus tree plantations, installed in 1996 to supply the regional capital with charcoal (GIZ/GREEN-Mad 2007).

Alaotra-Mangoro/Andasibe The study villages are located in the Andasibe region. Natural forest belongs to moist evergreen forest with around 1700 mm of rain per year, mostly falling between November and April. Daily mean temperature varies 14.5–23.6°C (Goodman *et al.* 2018). Rice is the most important crop.

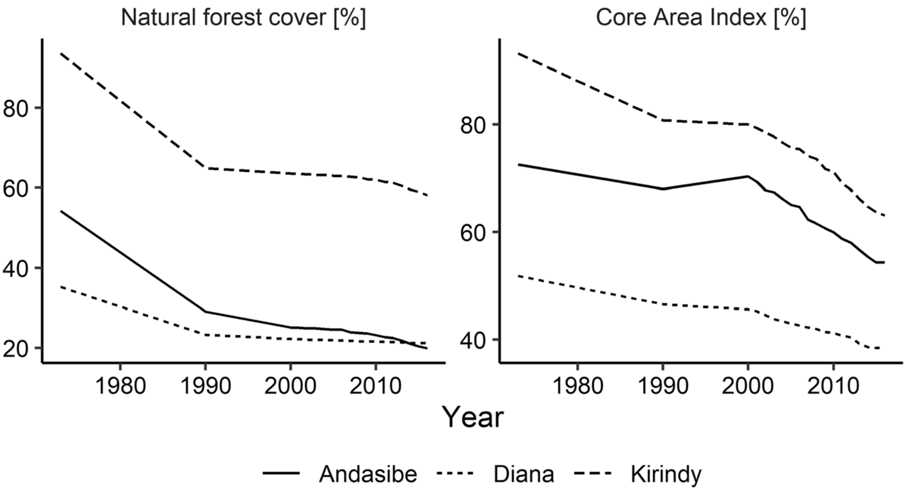

Fig. 2 Development of natural forest cover (left) and forest fragmentation (right) between 1973 and 2016 in three study regions in Madagascar. For 1973–2000, we used forest cover maps from Vieilledent *et al.* (2018). For 2001–2016, we produced annual forest cover maps by combining the forest cover map of the year 2000 provided by Vieilledent *et al.* (2018) and updated annual tree cover loss maps from Hansen *et al.* (2013). Forest fragmentation is expressed as the Core Area Index, that is, the ratio of forest core area to the total forest area in a study region. We calculated forest core area as the area that is further than a depth-of-edge distance of 90 m from the forest perimeter (McGarigal and Marks 1995).

Data Collection and Analysis

Based on recommendations of organizations working in the different areas (Diana: PAGE GIZ; Andasibe: Mitsinjo; Kirindy: Centre National de Formation, d'Education et de Recherche en Environnement et Forestière [CNFEREF]), we carried out surveys in 12 different villages in each study region in November 2017 (ESM Table SI). The mean (± standard deviation) number of inhabitants per village was 805 (± 494, $N = 10$) in Diana, 636 (± 450, $N = 12$) in Andasibe, and 1452 (± 875, $N = 12$) in Kirindy. The "village" survey was based on semistructured interviews and group discussions at the village level (Bernard 2011). We informed the president and village elders about the pending surveys prior to the actual meetings. The Malagasy authors of this study ran the meetings, supported by local staff. All communication was in Malagasy. Meetings were open to all villagers interested in participating, but we assured that at least half of the participants were not older than 50 years. We considered age important to avoid samples biased toward age groups with specific economic or management experiences (e.g., older people no longer involved in everyday activities). We did not consider gender. Both men and women participated in the surveys but participation was biased toward males. Separate discussions with men and women would have been desirable but could not be organized within the scope of the study. Questions concerned the use of natural resources, historical developments, socioeconomic, health, and cultural issues. We report only the use of natural resources here. For this, we asked people to name plants of local importance according to predefined categories that either contribute to ecosystem services (crops, cash-crops, medicinal plants, wood resources, nonwood products of the forest) or are unwanted invasive plants (weeds). In each category, we formulated questions without further specification, translated as follows:

Which plant products do you sell in the market? Which wild growing plants do people collect for food? Which medicinal plants do you use? What are the most important species used for charcoal? Are there plants (weeds) that you would like to get rid of? Which plants do you grow?

We translated local Malagasy plant species names into scientific names using personal knowledge and published lists (e.g., Schatz 2001; Sorg 1996). Plant vernacular names can vary between villages and even people from the same village. We did not consider plants for which a vernacular name resulted in more than two possible plant species, and species that could not be identified at least to the genus level.

We took information on plant use from the literature. We used the most up-to-date compilation of lemur food plants (Steffens 2020) to check whether lemurs consume any given plant species. We supplemented the data with data for other vertebrate taxa by searches in Web of Science, Google Scholar, books, and journals of regional relevance.

Ethical Note

Prior to the surveys, the president and village elders were informed about the intended surveys and asked for approval. The survey was carried out only with their consent. The identities of participants were not noted and therefore will not be disclosed. Participants were not pressured or forced to answer any question if they were not willing to.

Data Availability The datasets analyzed during the current study are available from the corresponding author on reasonable request.

Results

People named 240 different plant species of interest to them. Of these, we could identify 118 to species level. We identified a further 21 to the level of genera that were characteristic enough to be used for further analyses, such as *Adansonia* spp. (containing only endemic baobabs of Madagascar), *Dalbergia* spp. (also containing mostly endemic species of precious wood), or *Dioscorea* spp. (yam varieties found in native forests).

Of the 139 plant taxa mentioned in the village surveys that we could identify precisely enough to search the literature for their use by animals, 72 plant species and 13 genera were used by a total of 208 different terrestrial vertebrate species (Tables I and II). Apart from goats, cattle, introduced rats (*Rattus* sp.) and mice (*Mus* sp.) and the introduced myna (*Acridotheres tristis*) all other species are native to Madagascar. The literature database is most comprehensive for lemurs. It includes 58 lemur species associated with the plant species reported by the villagers. Most of the vertebrate species (131 out of 208) included were not in the “threatened” IUCN Red list categories (*Vulnerable*, *Endangered*, *Critically Endangered*), but 50 of the 58 lemur species included fell into one of the threatened categories.

Excluding weeds and crops, at least 56 plant taxa are of interest to people. These include native and introduced herbaceous and woody species. People listed only five

Table I Number of vertebrate species associated with plant taxa named as of interest to people in three study regions in Madagascar

	Food	Habitat	Food and habitat	Total	Number of threatened species and % (based on total) according to IUCN Red List
Amphibians	0	30	0	30	4 (13%)
Reptiles	4	20	3	21	6 (29%)
Birds	18	66	12	72	6 (8%)
Bats/flying foxes	3	9	3	9	3 (33%)
Lemurs	57	25	24	58	50 (86%)
Rodents	10	0	0	10	1 (10%)
Other mammals	6	3	1	8	0
Total	99	153	44	208	70 (33.7%)

"Other mammals" include tenrecs, shrews, carnivores, the bush pig, goats, and cattle. "Threatened" includes the IUCN Red List categories *Vulnerable*, *Endangered*, and *Critically Endangered*

herbaceous plants of value to them, which they do not plant on purpose. Woody species represent the majority of utilitarian plants, not planted specifically, but used opportunistically over the year (Fig. 3).

Discussion

Given the lack of investment options in Madagascar, fallow land taken out of the agricultural production could be used for conservation measures by initiating succession toward the restoration of native forests, including utilitarian plants at all successional stages. This would reduce the threat of succession being arrested at a certain stage. As it is unlikely that people will give up productive land for forest restoration our suggestion of using plants of dual use (usable by people and native animals) aims to restore fallow, unproductive land.

Once deforested, the first objective of restoration is likely to control soil erosion, maintain soil fertility, and grow pioneer plants that will provide the environment for seedlings of trees (Diemont *et al*. 2006; Klanderud *et al*. 2010). Herbs usually represent the first stages of natural succession (Raharimalala *et al*. 2010; Styger *et al*. 2007). Since herbaceous species are poorly represented in the data we compiled (Table II), we cannot speculate on the first steps of restoring fallow land. However, we are confident that local people have suggestions that can be followed. Later on, legume trees might be good candidates, as they fix nitrogen from the air. The multipurpose *Tamarindus indica* provides food and shelter for many native animal species and is a prime option for the drier parts of the country, although growth rates seem to be low (Ranaivoson *et al*. 2015). For humid forests, mango and litchi provide fruit for people and animals and *Harungana madagascariensis* is fast growing and can quickly cover degraded areas, providing food for birds and lemurs while serving medicinal purposes for humans (Birkinshaw *et al*. 2009; Rakotoarivelo *et al*. 2015; Steffens 2020). Adding

Table II Plants used by local people and other vertebrates in three study regions of Madagascar

Family	Species	Origin	Growth	Region	Importance for humans	Animal food	Animal habitat
Amaranthaceae	*Achyranthes aspera* L.	Introduced	Herb	North, east	Medicine, weed	Lemurs	
Amaranthaceae	*Chenopodium ambrosioides* (L.)	Introduced	Herb	East	Medicine	Lemurs	
Anacardiaceae	*Mangifera indica* L.	Introduced	Tree	North	Food, medicine, charcoal, cultivated crop	Lemurs, birds, bats	Lemurs, birds, reptiles, bats
Anacardiaceae	*Sclerocarya birrea* (A. Rich.) Hochst.	Native	Tree	North, west	Food,charcoal	Lemurs, bats	
Anacardiaceae	*Sorindeia madagascariensis* DC.	Native	Shrub, tree	North	Food	Lemurs	Lemurs
Annonaceae	*Annona muricata* L.	Introduced	Tree	North	Food, medicine	Lemurs	
Annonaceae	*Annona squamosa* L.	Introduced	Shrub, tree	North	Food, charcoal	Lemurs	
Apiaceae	*Centella asiatica* (L.) Urb.	Introduced	Herb	East	Medicine	Lemurs	
Apocynaceae	*Tabernaemontana coffeoides* Bojer ex A. DC	Native	Shrub, tree	North	Medicine	Lemurs	Lemurs
Arecaceae	*Cocos nucifera* L.	Introduced	Tree	North	Food, cultivated crop	Lemurs, reptiles	Lemurs, birds, reptiles, bats
Arecaceae	*Phoenix reclinata* Jacq.	Native	Shrub	West	Food	Lemurs	Lemurs
Asteraceae	*Bidens bipinnata* L.	Native	Herb	East	Weed	Lemurs	
Asteraceae	*Psiadia altissima* Benth. & Hook.f.	Native	Shrub, tree	East	Medicine	Lemurs	
Bignoniaceae	*Kigelianthe madagascariensis* (Baker) A. H. Gentry	Native	Shrub, tree	West	Medicine	Lemurs, birds	Birds
Boraginaceae	*Cordia lowryana* J. S. Mill.	Native	Tree	North	Medicine, food	Lemurs	
Bromeliaceae	*Ananas comosus* (L.) Merr.	Introduced	Herb	East	Cultivated crop	Lemurs	
Burseraceae	*Commiphora marchandii* Engl.	Native	Shrub	West	Medicine	Lemurs	
Canellaceae	*Cinnamosma fragrans* Baill.	Native	Shrub, tree	East, west	Medicine	Lemurs	

Table II (continued)

Family	Species	Origin	Growth	Region	Importance for humans	Animal food	Animal habitat
Caricaceae	*Carica papaya* L.	Introduced	Shrub, tree	North	Food, medicine, cultivated crop	Lemurs, bats	
Celastraceae	*Elaeodendron oliganthum* Baker	Native	Shrub, tree	North, east	Medicine	Lemurs	
Celastraceae	*Salacia madagascariensis* (Lam.) DC.	Native	Shrub, liana	East	Food	Lemurs	
Conolvulaceae	*Ipomoea batatas* (L.) Lam.	Introduced	Herb	North, east, west	Cultivated crop, weed	Lemurs	
Cucurbitaceae	*Citrullus lanatus* (Thunb.) Matsum. & Nakai	Introduced	Herb	North	Cultivated crop	Lemurs	
Cucurbitaceae	*Cucumis sativus* L.	Introduced	Liana	North, east	Cultivated crop	Lemurs	
Euphorbiaceae	*Euphorbia hirta* L.	Introduced	Herb	North	Weed	Lemurs	
Euphorbiaceae	*Manihot esculenta* Crantz	Introduced	Shrub	North, east, west	Cultivated crop	Lemurs, birds, others	Birds
Fabaceae	*Albizia lebbeck* (L.) Benth.	Introduced	Tree	North	Food	Lemurs, bats	Lemurs
Fabaceae	*Arachis hypogaea* L.	Introduced	Herb	North, east, west	Cultivated crop	Lemurs	
Fabaceae	*Cordyla madagascariensis* R. Vig.	Native	Tree	West	Food, charcoal	Lemurs	Lemurs, birds
Fabaceae	*Senna alata* (L.) Roxb.	Introduced	Herb, shrub	North	Weed	Lemurs	
Fabaceae	*Tamarindus indica* L.	Native	Tree	North, west	Food, medicine	Lemurs, birds, reptiles, bats	Lemurs, birds, reptiles, others, bats
Hypericaceae	*Harungana madagascariensis* Lam. ex Poir.	Native	Tree	North	Medicine	Lemurs	
Lauraceae	*Cassytha filiformis* L.	Native	Herb	North	Medicine	Lemurs	Lemurs
Lauraceae	*Persea americana* Mill.	Introduced	Shrub, tree	North	Food	Lemurs, bats	

Table II (continued)

Family	Species	Origin	Growth	Region	Importance for humans	Animal food	Animal habitat
Loganiaceae	*Strychnos madagascariensis* Poir.	Native	Shrub, tree	West	Food	Lemurs, others	Lemurs
Loganiaceae	*Strychnos spinosa* Lam.	Native	Shrub, tree	North	Food	Lemurs	
Malvaceae	*Adansonia suarezensis* H. Perrier	Native	Tree	North	Food	Lemurs, birds, bats	
Malvaceae	*Sida rhombifolia* L.	Introduced	Shrub	East	Weed	Lemurs	
Melastomataceae	*Clidemia hirta* (L.) D. Don	Introduced	Herb	East	Medicine, weed	Lemurs, birds	
Meliaceae	*Astrotrichilia asterotricha* (Radlk.) Cheek	Native	Shrub, tree	West	Medicine	Lemurs	
Meliaceae	*Azadirachta indica* A. Juss	Introduced	Tree	West	Medicine	Lemurs, bats	Lemurs
Meliaceae	*Neobeguea mahafaliensis* J.-F. Leroy	Native	Tree	West	Medicine	Lemurs, reptiles	Lemurs, birds
Moraceae	*Artocarpus heterophyllus* Lam.	Introduced	Tree	North	Food, medicine	Lemurs	Lemurs
Moraceae	*Ficus marmorata* Baker	Native	Shrub, tree	East	Medicine	Lemurs	
Moraceae	*Treculia perrieri* Jum.	Native	Tree	West	Food	Lemurs	
Myrsinaceae	*Maesa lanceolata* Forssk.	Introduced	Shrub, tree	East	Medicine	Lemurs, bats	
Myrtaceae	*Psidium guajava* L.	Introduced	Shrub, tree	North, east, west	Food, medicine	Lemurs, birds, bats	
Myrtaceae	*Syzygium cumini* (L.) Skeels	Introduced	Tree	East, west	Food	Lemurs	
Oleaceae	*Linociera tropophylla* H. Perrier	Native	Tree	West	Medicine	Lemurs	
Passifloraceae	*Passiflora ligularis* Juss.	Introduced	Liana	East	Food, medicine	Lemurs	
Phyllanthaceae	*Antidesma madagascariense* Lam.	Native	Shrub, tree	East	Medicine	Lemurs	Lemurs
Phyllanthaceae	*Securinega seyrigii* Leandri	Native	Tree	West	Food	Lemurs, reptiles	Lemurs, reptiles
Physenaceae	*Physena madagascariensis* Steud.	Native	Shrub, tree	North, west	Medicine	Lemurs	
Poaceae	*Cynodon dactylon* (L.) Pers.	Native	Herb	West	Weed	Reptiles	

Table II (continued)

Family	Species	Origin	Growth	Region	Importance for humans	Animal food	Animal habitat
Poaceae	*Oryza sativa* L.	Introduced	Herb	North, east, west	Cultivated crop	Lemurs, birds	Birds, reptiles, amphibians, bats
Poaceae	*Saccharum officinarum* L.	Introduced	Herb	East	Cultivated crop	Lemurs	Birds
Poaceae	*Zea mays* L.	Introduced	Herb	North, east, west	Cultivated crop	Birds	Birds
Polygonaceae	*Polygonum glabrum* Willd.	Introduced	Herb	East	Weed	Lemurs	
Pontederiaceae	*Eichhornia crassipes* (Mart.) Solms	Introduced	Herb	East	Medicine, weed	Lemurs, birds	
Rhamnaceae	*Ziziphus jujuba* Mill.	Introduced	Shrub, tree	North, west	Food, medicine, charcoal	Lemurs, bats	
Rosaceae	*Rubus alceifolius* Poir.	Introduced	Shrub	East	Weed	Lemurs	
Rubiaceae	*Mussaenda arcuata* Poir.	Native	Liana	West	Medicine	Lemurs	
Rubiaceae	*Paederia foetida* L.	Introduced	Liana	North	Medicine	Lemurs	
Rutaceae	*Cedrelopsis grevei* Baill.	Native	Shrub, tree	North, west	Medicine, food	Lemurs, reptiles	Lemurs
Rutaceae	*Citrus* × *aurantifolia* (Christm.) Swingle	Introduced	Shrub, tree	North	Cultivated crop	Lemurs	
Rutaceae	*Citrus* × *sinensis* L.	Introduced	Tree	East	Food	Lemurs	
Sapindaceae	*Cardiospermum halicacabum* L.	Native	Herb	West	Medicine	Lemurs	
Sapindaceae	*Litchi chinensis* Sonn.	Introduced	Tree	North	Food	Lemurs, birds, bats	Lemurs, bats
Sapotaceae	*Chrysophyllum boivinianum* (Pierre) Baehni	Native	Tree	East	Food	Lemurs	
Solanaceae	*Solanum lycopersicum* L.	Introduced	Herb	North	Cultivated crop	Lemurs	
Theaceae	*Camellia sinensis* (L.) Kuntze	Introduced	Shrub	East	Medicine	Lemurs	
Verbenaceae	*Lantana camara* L.	Introduced	Shrub	North, east	Medicine, weed	Lemurs, birds	
Plants identified only to genus level							
Asphodelaceae	*Aloe* sp.	Native	Herb, tree	North	Medicine	Lemurs	

Table II (continued)

Family	Species	Origin	Growth	Region	Importance for humans	Animal food	Animal habitat
Celastraceae	*Brexiella* sp.	Native	Shrub, tree	East	Food	Lemurs	
Combretaceae	*Terminalia* sp.	Native	Shrub, tree	West	Food	Lemurs, birds, reptiles	Lemurs
Dioscoreaceae	*Dioscorea* sp.	Native	Herb, liana	North, east	Food	Lemurs	
Fabaceae	*Acacia* sp.	Introduced, Native	Shrub, tree	North	Charcoal, cultivated crop	Lemurs, birds, bats	Lemurs, birds
Fabaceae	*Dalbergia* sp.	Native	Shrub, liana, tree	West	Food	Lemurs	Lemurs, reptiles
Loganiaceae	*Strychnos* sp.	Native	Shrub, liana, tree	West	Medicine, food	Lemurs	Lemurs
Malvaceae	*Adansonia* sp.	Native	Tree	West	Food	Lemurs, birds, others	Lemurs, birds, reptiles, bats
Moraceae	*Morus* sp.	Introduced	Tree	East	Medicine	Birds	
Musaceae	*Musa* sp.	Introduced	Herb	North, east	Food, cultivated crop	Lemurs, bats	Birds, reptiles, bats
Myrtaceae	*Eucalyptus* sp.	Introduced	Shrub, tree	North, east	Medicine, charcoal, cultivated crop	Lemurs, amphibians, bats	Lemurs, birds, amphibians, others, bats
Rosaceae	*Rubus* sp.	Introduced	Shrub, liana	East	Food		Birds
Solanaceae	*Solanum* sp.	Introduced, Native	Herb, shrub, liana tree	East	Cultivated crop	Lemurs, bats	

The first part of the table lists plants identified to species level and the second part plants that we could identify only to the genus level. Endemic plants are highlighted in bold

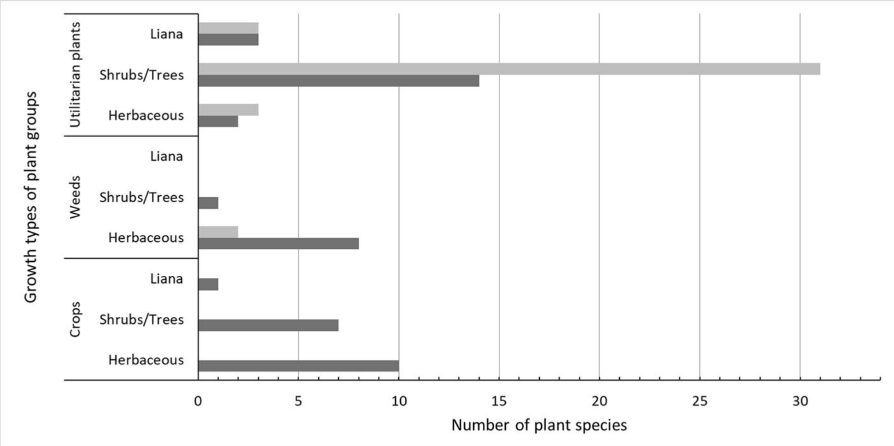

Fig. 3 Number of important plant species for local people and native vertebrates by growth form and plant group (crops, weeds, and utilitarian plants) in three study regions in Madagascar; dark grey = introduced plant species, light grey = native plant species.

plants with cultural and traditional values, such as tamarinds or baobabs, could further diversify the restoration and might add a "sense of place" component that protects forests beyond economic interests. In any case, it is crucial to come to a better understanding of the successional stages in regenerating Malagasy ecosystems by considering local knowledge (De Wilde *et al.* 2012; Ehrensperger *et al.* 2013; Gay-des-Combes *et al.* 2017; Klanderud *et al.* 2010; Leprun *et al.* 2009; Rabenantoandro *et al.* 2007; Raharimalala *et al.* 2010; Styger *et al.* 2007; Zwartendijk *et al.* 2017).

Adding native trees to reforestation projects has the potential to increase ecological complexity and ecosystem services (Brown *et al.* 2013; Ganzhorn 1987; Gérard *et al.* 2017; Holloway 2003; Lavialle *et al.* 2015; Martin *et al.* 2009, 2012; Rafidison *et al.* 2020; Zemp *et al.* 2019). However, they provide fewer direct financial benefits and risk adding disservices, such as antagonists to pollinators or increased herbivory (Wielgoss *et al.* 2014). Combining the various issues, we argue that forest rehabilitation using a mix of native and exotic species can be a good balance between benefits for people and benefits for the native fauna. By adding more native utilitarian plants or plants of cultural value, rehabilitated forests might be valued more by people and thus might have a higher chance of surviving and possibly developing into substitutes for the original forest (Fritz-Vietta *et al.* 2011). However, for such a balanced selection of rehabilitation species, we need to integrate scientific and local (practical) knowledge of the growth conditions and usage of native plants.

According to the present study, lemurs seem to be the group of vertebrates that would benefit most from this type of forest rehabilitation. Lemurs used almost all plant species we identified unambiguously and represented more than half of all vertebrates associated with utilitarian trees. More than 80% of these lemur species fall into one of the "threatened" IUCN Red List categories. This matches the general classification of lemurs as one of the most threatened taxa on earth (Schwitzer *et al.* 2014). The other vertebrate groups are poorly represented and mostly with species that are not considered threatened. This may be a sampling artefact, as few studies on nonlemur vertebrates have been completed in nonnative forests in these regions (Gardner *et al.* 2016a, b; Irwin *et al.* 2010; Martin *et al.* 2009, 2012; Ndriantsoa *et al.* 2017; Wilmé 2014).

An example of a reforestation project focusing not solely on the protection of species but also considering the needs of local people in southeast Madagascar was reported by Manjaribe *et al.* (2013). They planted a corridor consisting of three types of plants. The main part of the corridor consisted of plant species consumed by black-and-white ruffed lemurs (*Varecia variegata*), the remaining parts were divided into a timber and a nontimber tier, including plant species most frequently used by the local community for fuel production or construction, as well as a source of food or other products of commercial value. While there are plenty of examples of native animals using crop and forest plantations (e.g., Chapman *et al.* in press; Gardner *et al.* 2010; Irwin *et al.* 2010; Schwitzer *et al.* 2011), we are unaware of any example that explicitly uses plants of interest for people and animals alike and thus avoids the issue of the two "parties" competing for limited space. The plantation of utilitarian trees around the forestry station of Ampijoroa in northwestern Madagascar at colonial times, comes closest to the concept of multiuse plantations (fruit, timber, and other economic value trees) for people, but also designed to extend suitable habitat for lemurs (Ganzhorn and Abraham 1991).

Though utilitarian plants and crops offer a large, yet unexploited potential for restoration, care must be taken to avoid conflicts of interest. Though systematic surveys are lacking, anecdotal reports indicate that people in Madagascar do not tolerate animals eating their crops, such as *Hapalemur* spp. eating rice plants in the humid forests (Martinez 2008; T. Eppley, *pers. comm.*) or parrots and finches eating crops in the western part of Madagascar. Fruit trees seem to be less of a problem as long as people do not embark on industrial fruit production for the national or international market. In this context, mixed or fully utilitarian forests such as plantations or agro-forestry systems could benefit local communities and function as habitat extensions or corridors for vertebrates including lemurs. For example, lemurs use vanilla and cocoa plantations in northern Madagascar (Hending *et al.* 2018; Webber *et al.* 2020). However, when animals such as birds, flying foxes, or lemurs feed on fruits of trees also used by humans, they can transmit zoonotic diseases through contamination of fruits by feces. Diseases can range from salmonellosis to more dangerous viral diseases (Iehlé *et al.* 2007; Joffrin *et al.* 2020). This problem may not be as pronounced in plants used by people for medicinal purposes or charcoal production. Species targeted for wood or charcoal production or for the international furniture market may be good candidates to be used by many vertebrate species as well as by humans. These can include many species of precious wood, such as *Dalbergia* spp. that not only have suffered from illegal exploitation (the "rosewood crisis"; Wilmé *et al.* 2020) over the last few years, but have also traditionally been the most appreciated wood for cooking (Razafintsalama *et al.* 2014).

Apart from direct, unwanted, interactions with humans, vertebrates can contribute substantially to the dispersal of seeds and thus accelerate the invasion of species that may be of value to people and animals but are not wanted from a conservation point of view. These include neem trees (*Azadirachta indica*), guava (*Psidium guajava*), *Ziziphus* spp., or *Morus* spp. (Carrière *et al.* 2008; DeSisto *et al.* 2020; Kull *et al.* 2012). Moreover, many of the more than 20 plant taxa people listed as "weeds" (e.g., *Clidemia hirta*, *Lantana camara*, and *Rubus* spp.) are dispersed by frugivores. However, the perception of "weed" depends on context and might change over time (Kull *et al*. 2012; McConnell *et al*. 2015; Tassin and Kull 2015). For example, *Sorghum bicolor* (L.) Moench was planted as a crop well adapted to dry conditions in the west, but the harvests were compromised by birds and thus the cultivation was abandoned. Whatever was left in the region is now considered a "weed." *Clidemia hirta* is known as an invasive species that colonizes open areas quickly and park authorities make great efforts to remove it. Yet, *Clidemia hirta* allowed the frugivorous black-and-white ruffed lemur (*Varecia variegata*) to survive in forest fragments after a cyclone had blown down their fruit trees (Ratsimbazafy *et al*. 2002) and plays a major role in restoring rainforest in northern Madagascar (Martinez and Razafindratsima 2014). Similarly, guava (*Psidium guajava*) is invasive in parts of Madagascar, but this exotic plant was observed to play a key role in the survival of collared brown lemurs (*Eulemur collaris*) in the Mandena Conservation Zone, southeast Madagascar (Donati *et al*. 2020; Kull *et al*. 2012). Though not covered by the present study, the introduced *Opuntia* spp. is an example of repeated changes in its appreciation. Currently, this plant is considered an invasive weed in the dry parts of Madagascar but is used by lemurs and guaranteed the survival of people and their livestock during droughts in the past (Jolly 2004). It has recently been identified as a possible source of substantial economic income through the production of essential oils (Hänke *et al*. 2018), so may yet become desirable. *Acacia* spp. may include invasive species that are hard to control or remove once they have invaded natural systems, but not all species are invasive and as fast-growing legumes, that are fire resistant and retardant, they have a high potential to restore soil fertility and provide firewood from denuded areas. In many areas largely void of vegetation cover and with an exhausted seed bank, these "weeds," which are valuable to people, might be a first step to stop erosion, restore soil fertility (especially legumes), and thus provide the basis for the development of more complex ecosystems (Gay-des-Combes *et al*. 2017; Randriamalala *et al*. 2015; Zwartendijk *et al*. 2017).

To our knowledge, the concept of designing restoration projects focusing on plants to be used by humans and animals alike is lacking for Madagascar and other parts of the world. Although a thorough ecological and economic cost–benefit analysis must be made before applying the concept, the present study illustrates that there is a treasure of options and knowledge in the local human communities that should be paid more thorough attention.

Conclusion

The village surveys led to two major insights: First, there are many plant species of interest to people and native vertebrates alike, which could be used for restoration and that could provide economic income at various temporal scales, ranging from years (native yams) to decades and even centuries (native precious wood). The known diversity of possible plants is rarely used in restoration projects. Second, the surveys did not provide a complete list of plants that could be or were used by people. The whole aspect of honey production has not been considered (Eco-Services Consulting 2017; Fohavelo and Gulley 2000), and the medicinal plants mentioned in the surveys comprise only a fraction of the plants that people actually use (e.g., apart from their crops, people from Menabe listed 22 plants of value in the present compilation, while a previous study in the region described 151 species collected and used for many more different purposes [Favre 1990, 1996]). Similarly, an ethnobotanical study in 13 villages close to Andasibé reported 209 medicinal plants used by people (Rakotoarivelo *et al.* 2015) while our survey revealed only 34 species for the 12 villages we visited. Apart from the obviously incomplete sampling of information, we had to discard about a third of the data provided by the villagers because we could not link their names to our system. This exemplifies how little we know about the possibilities available. It also illustrates a huge, yet unexploited, knowledge that could be used for restoration without additional costs, except that of listening to local people (Marie *et al.* 2009).

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