Lemur food plants as options for forest restoration in Madagascar

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The outcome of restoration plantings depends on the selection of plant species and their traits. Regeneration could be facilitated and diversified by attracting native seed dispersers into the sites to be restored. To provide a basis for the selection of plant species that Lemur food plants could attract lemurs, the main seed dispersers in Madagascar, I compiled a list of known lemur food plants (LFP). A literature search revealed 204 data sources from 64 study sites on the exploitation of plants by 56 free-ranging lemur species. I aggregated the information, updated the taxonomy, and included further aspects, such as plant origin and life form, which may be of relevance for restoration. Lemur species exploited mainly fruits and leaves of 1,026 plant species (9.14% of all vascular plant species present in Madagascar), from 599 genera and 147 families. The data revealed many promising aspects for restoration, such as integrating the 10 most important LFP that are also used by people. The integration of LFP would increase the value of restoration areas for both animals and humans. Despite some limitations, the assembled database can provide assistance and guidance in the selection of plant species for restoration programs, whereby facilitating future regeneration may be accomplished passively through lemur seed dispersal.

Key words: conservation, facilitated regeneration, planting, primates, seed dispersal, species selection

Implications for Practice

- The unique biota of Madagascar is threatened by ongoing deforestation. Restoration efforts use only a limited number of tree species and lag behind those of other tropical countries in terms of scale and eligibility as model for best practice.
- Our knowledge of lemur food plants (LFP) has grown extensively over the past couple decades. Integrating this information into plant selection could diversify restoration or reforestation. Different plant traits can be considered to optimize species selection for restoration plantings.
- The incorporation of LFP can result in facilitated regeneration through faunal seed dispersal. Projects applying and studying this aspect are needed to improve both restoration and conservation outcomes.

Introduction

Forest restoration activities are “actions to re-instate ecological processes, which accelerate recovery of forest structure, ecological functioning and biodiversity levels towards those typical of climax forest” (Elliott et al. 2013, p. 12). These actions often include direct seeding or raising plants in a nursery and subsequent planting, with the selection of species determining the success of reforestation or restoration (Lamb et al. 2005). Plant traits that often play a role in species selection relate to performance, such as survival and growth (Birkinshaw et al. 2009). Further traits that can be considered are ecological, including the type of successional state the plant belongs to, traditionally pioneer or climax (Padilla et al. 2009; Elliott et al. 2013); adaptations to environmental conditions (Dreesen et al. 2002); life/growth form (e.g. herb, shrub, tree or liana) (Gómez-Aparicio 2009; Campbell et al. 2015); seed dormancy and mode of seed dispersal (e.g. autochorous [self-dispersal by dehiscent fruits], anemochorous [wind dispersal], or zoochorous [animal dispersal]) (Knowles & Parrotta 1995); the ability for nitrogen fixation, which improves soil quality and facilitates growth on poor soils (Chaer et al. 2011); and origin (native/introduced) and invasive properties (Gérard et al. 2015). Lastly, an important aspect that can play a role in species selection is related to the usage of plants, including whether humans are able to utilize them for timber, fruits, and oils (Manjaribe et al. 2013; Lavialle et al. 2015), or animals use them for food resources.
The unique biota of Madagascar does not only fulfill important ecosystem services and functions, but it also represents the country’s long-term capital for continuing income through tourism, therefore restoration of natural habitats should integrate strong conservation aspects for the endemic biota. Lemurs, the nonhuman primates endemic to Madagascar, play a special role in this aspect, serving as flagships for tourism. Currently, they comprise over 100 species, from 15 genera and 5 families. More than 90% of these species are categorized by the World Conservation Union Red List as threatened, that is, vulnerable, endangered, or critically endangered (World Conservation Union Red List as threatened, that is, vulnerable, endangered, or critically endangered (Raza et al. 2012; Gardner et al. 2018; Morelli et al. 2020). To alleviate and counter deforestation, a growing number of programs focus on reforesting or restoring destroyed or degraded landscapes, working at different scales, in Madagascar (Birkinshaw et al. 2009). However, restoration efforts are not yet as efficient and large scale as in other tropical countries, notably lacking projects that demonstrate best practices, and so local and national decision-makers are often reluctant to invest in restoration (Birkinshaw et al. 2013).

The list could provide a base of information to diversify tree plantations and to facilitate the restoration of forest ecosystems in Madagascar.

**Methods**

Over the past 60 years, extensive studies on the feeding ecology of free-ranging lemurs have been conducted. Most of these studies were designed to describe the animals’ feeding behavior via direct observations (e.g. Britt 2000), but there were also approaches that used feeding traces at plants (e.g. Meier & Rumpler 1987), analyzed feces and identified seeds of exploited plants (e.g. Moses & Semple 2011), or identified exploited plants via their DNA in feces (Quéméré et al. 2013). These studies provide lists of plant species and plant parts in the diet of lemur species.

To create the database, I aggregated published lists on LFP. Given the complexity of the criteria that had to be applied to compile a rigorous database, I only briefly summarize the methods here, while the approaches are described in detail in Supplement S1.
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Literature Search
The basis of my data collection was a literature search using the Web of Science Core Collection. The time span used was 1945 to 11 September, 2019. During the screening process, I found and included further publications containing information on LFP cited by others.

Data Entry and Updating
I entered information from selected data sources in the LFP database, if a plant exploited by a lemur was identified at least at the family level. Along with information on family/genus/species of lemur and plant, I entered information on exploited plant parts, study site, and forest type. I paid close attention to avoid data redundancy.

After the entry I checked and updated every lemur species name via the study site according to Mittermeier et al. (2010). With Tropicos (http://www.tropicos.org), a botanical database mainly of the tropics, I checked and updated every plant species/genus/family name. If it was not possible to assign a name unambiguously, I reduced the identification to the next higher taxonomic level. Furthermore, I checked all names for synonymy within the database. Though the Catalogue of the Plants of Madagascar(http://legacy.tropicos.org/Project/Madagascar), an additional database that is part of Tropicos, is taxonomically more up-to-date for plants from Madagascar, it does not include 81 plant species exploited by lemurs that are taxonomically valid according to Tropicos. To avoid the loss of information on these plant species, I used Tropicos as a basis for the taxonomy. To enable a consideration of this problem in further uses, I added the status of the taxonomy of plants from the Catalogue of the Plants of Madagascar to the notes in the database.

Analyses
I reclassified and harmonized the forest types following Moat and Smith (2007), and combined different localities of the same study area under a given name for the study site.

To gain a better understanding of lemurs’ exploitation of species from different plant families and genera, I calculated Pearson’s correlations between the number of exploited species (without synonyms) from different families/genera, and the number of published accepted species in these families/genera in Madagascar. I determined the latter with the Catalogue of the Plants of Madagascar from 25 February, 2020. To interpret the meaning of Pearson’s correlation coefficient (r), I used the effect size following Cohen (1992). Effect sizes are “small” with 0.1 less than or equal to r less than 0.3, “medium” with 0.3 less than or equal to r less than 0.5, and “large” with r greater than or equal to 0.5.

To take into account the effect of introduced or invasive plant species, I crosschecked all plant species with “The introduced flora of Madagascar” (Kull et al. 2012). I referred to all species matching between the LFP database and Kull et al. (2012) as “introduced,” and therewith included species with unconfirmed status of origin. This conservative approach was taken because some species with unconfirmed status are also classified as invasive, thus potentially having a negative effect on the environment. Furthermore, this allowed comparisons with Gérard et al. (2015), who made similar calculations for lemurs and other endemic vertebrate taxa in Madagascar.

I assigned the life form (e.g. tree, shrub, liana) to all plant species with online databases and publications.

I used QGIS 3.4.14 to compile a map of the study sites and related forest types, and IBM SPSS Statistics 26 to produce plots and correlations.

Definition of “Observations” and “Exploitation Observations”
The LFP database originates from more than 200 studies, in which different methods were applied. Thus, there was no measure of quantity that was used consistently in all studies. To analyze the quantity of events, for example, the quantity of feeding events on a certain plant species or a certain plant part, I used the categories observations and exploitation observations.

One observation corresponds to one row in the database, which contains the information of one lemur species exploiting one plant, in one study site, in one forest type. This one observation can include also one or several exploitation observations, which contain the information on the exploited plant part/s (one or several) and the life form/s (one or several) of the exploited plant. Observations and exploitation observations were entered irrespective of the frequency or duration of consumption described in a given study (Table 1).

For analyses concerning the study sites and forest types, lemur and plant taxonomy, I used observations. There are

| Data Source | Study Site | Forest Type | Lemur Species | Plant Species | Exploited Plant Part | Life Form |
|-------------|------------|-------------|---------------|---------------|----------------------|-----------|
| A           | Berenty    | Southwestern dry spiny forest-thicket | Lemur catta | Tamarindus indica | Fruit, leaves, flowers | Tree      |
| B           | Beza Mahafaly Special Reserve | Southwestern dry spiny forest-thicket | Lemur catta | Tamarindus indica | Fruit, leaves | Tree      |
| C           | Berenty    | Southwestern dry spiny forest-thicket | Lemur catta | Tamarindus indica | Fruit, leaves | Tree      |
| D           | Antserananomby | Western dry forest | Lemur catta | Tamarindus indica | Fruit, leaves, flowers | Tree      |

Table 1  Example of the organization of data in the LFP database. In the table, there are 4 observations, 10 exploitation observations of exploited plant part, and 4 exploitation observations of life form. No matter how often or how long, for example, Data source A has observed Lemur catta exploiting Tamarindus indica, the data would be included as depicted. An exemplary analysis of these data would indicate that 75% of observations were made in southwestern dry spiny forest-thicket, and 25% in western dry forest, and that the diet of lemurs includes 40% fruit, 40% leaves, and 20% flowers.
5,420 observations in the LFP database. For analyses concerning the diets of lemur genera, exploited parts in forest types, life forms, I used exploitation observations. There are 5,854 exploitation observations of plant parts in the database, and 4,455 exploitation observations of life forms.

A larger number of observations/exploitation observations alone does not mean necessarily that the observed event is more frequent than another. Rather, a larger number of observations/exploitation observations can also be the result of greater research intensity, and/or a larger number of different exploited plant species. It was impossible to separate these effects, and this must be considered while interpreting the results.

Results

Study Sites and Forest Types, Lemur and Plant Taxonomy

Study Sites and Forest Types. The LFP database contains 5,420 observations from 204 data sources (some referring to more than one study), published between 1962 and 2018 (Table S1, also available from https://doi.org/10.25592/uhhfdm.1021). The studies were conducted at 64 study sites across five forest types: humid forest (44.83%), western dry forest (18.71%), southwestern dry spiny forest-thicket (19.06%), littoral forest (9.56%), and “other” (7.84%) (Fig. 1; Table S2).

Lemur Species/Genera/Families. Observations include 56 lemur species, two Eulemur hybrid species, and one Microcebus species (identified only at the genus level), covering all 15 extant lemur genera and all 5 extant families (Fig. 2). Most of the observations (32.73%) are of Eulemur, followed by Propithecus (16.24%) and Lemur (13.32%). The top three of the species with most observations, Lemur catta, Propithecus verreauxi, and Eulemur rubriventer, together represent approximately one-fourth of all observations; the top 10 species (in order, L. catta, P. verreauxi, E. rubriventer, Eulemur rufifrons, Varecia variegata editorum, Eulemur coronatus, Eulemur macaco, Eulemur cinereiceps, Propithecus diadema, and Microcebus murinus) together represent approximately half of all observations.

Exploited Plant Species/Genera/Families. In all observations, the exploited plant is identified at the level of family, and furthermore in 97% at the genus level, and in approximately 58% at the species level. In total, 1,111 different plant species are exploited, constituting 600 different plant genera, and 147 different plant families. After considering the synonymy within the LFP database, 599 genera with 1,026 species are used for further analyses. From the 11,220 vascular plant species present in Madagascar, as estimated by Callmander et al. (2011), lemurs exploit 9.14%.

The 10 plant species with most observations and the 10 plant species exploited by most different lemur species differ only in one plant species (Table 2). Of the 11 species, Mangifera indica is naturalized and the status of Tamarindus indica and Strychnos spinosa is unconﬁrmed (Kull et al. 2012); however, the latter species seems to originate from Africa (POWO 2020).

Figure 1  Study sites with at least 10 observations, and related forest types (Moat & Smith 2007; “other” signifies a composition of different forest types occurring equally often at the site, see Supplement S1). Size of circles represents number of observations. The 10 study sites with most observations are labeled fully, abbreviations are explained in Table S2. For deﬁnition of observations see Methods: Deﬁnition of “Observations” and “Exploitation Observations.” Map compiled with QGIS 3.4.14. Sources of satellite image: Google satellite, SIO, NOAA, U.S. Navy, NGa, GECBO, Landsat/Copernicus, from 14 December, 2015.
The correlation between the number of exploited plant species and the number of published accepted species in Madagascar is weaker at the genus level compared with the family level (Figs. 3 & 4). The same applies to the effect size according to Cohen (1992), which is medium at the genus level and large at the family level. For the calculation, I selected the top 30 plant genera and families with the largest number of exploited species.

Origin and Invasive Status of Exploited Plant Species. The LFP database contains 102 introduced plant species. Of these, 18 are “cultivated,” 2 “introduced and indigenous,” 65 “naturalized” (including Lawsonia alba, which is a synonym of Lawsonia inermis), 7 “status unconfirmed,” and 10 “status unknown.”

Table 2 Top 10 of the plant species with most observations and top 10 plant species exploited by most different lemur species. For this calculation, the subspecies of Hapalemur griseus and Varecia variegata, the two hybrid species of Eulemur, and the Microcebus species identified only at the genus level were all treated as different species. Plant species in the same cell are synonymous within the LFP database. For definition of observations see Methods: Definition of “Observations” and “Exploitation Observations.” The complete table, including all plant species from the database, may be found in Table S3.

| Plant Species                        | Number of Observations | Plant Species                        | Number of Lemur Species |
|--------------------------------------|------------------------|--------------------------------------|-------------------------|
| Tamarindus indica                    | 53                     | Ficus pyrifolia, Ficus rubra         | 20                      |
| Strychnos spinosa, Strychnos madagascariensis, Strychnos vacuca | 33                     | Aphloia theiformis                   | 19                      |
| Canarium madagascariense, Canarium boivinii | 32                     | S. spinosa, S. madagascariensis, S. vacuca | 17                      |
| F. pyrifolia, F. rubra               | 31                     | Uapaca thouarsii, Uapaca ferruginea, Uapaca louvelii | 17                      |
| U. thouarsii, U. ferruginea, U. louvelii | 31                     | T. indica                            | 17                      |
| Gambeya boiviniana, Gambeya madagascariensis, Chrysophyllum boivinianum | 30                     | Ficus sorocoeoides, Ficus politoria | 16                      |
| Aphloia theiformis                   | 30                     | G. boiviniana, G. madagascariensis, C. boivinianum | 15                      |
| Ravenala madagascariensis            | 28                     | Mangifera indica                     | 15                      |
| Mangifera indica                     | 25                     | Ravenala madagascariensis            | 15                      |
| Ficus lutea, F. baronii              | 23                     | Canarium madagascariensis, C. boivinianum | 14                      |
unconfirmed, but probably native.” Of all introduced species listed by Kull et al. (2012), lemurs exploit 7.40%. Thirty-four of the 102 species are classified as invasive, which corresponds to 33.33%.

Approximately 40% of all Daubentonia madagascariensis observations are of introduced plant species, 30% for Prolemur simus, and 20% for Lemur catta (Fig. 5). For the genera Phaner, Mirza, and Indri, there are no observations of introduced plant species. The largest proportions of invasive species in the observations are found for Prolemur, Lemur, and Hapalemur species, with 12.50, 9.57, and 7.95%, respectively.

**Diets of Lemur Genera, Exploited Parts in Forest Types, Life Forms**

**Diets of Lemur Genera.** Of all exploitation observations of plant parts, 51.8% are fruit, 30.5% leaves, 10.0% flowers, 3.5% exudates, 2.2% seeds, 1.4% nectar, and 0.6% bark.

The lemur genera with the largest amount of available information on exploited plant parts are Eulemur (approximately 37%), which is mainly frugivorous, and Propithecus (14%) and Lemur (12%), which are mainly folivorous but also include high proportions of fruit in their diet (Figs. 6 & 7).

**Life Forms of Exploited Plant Species.** Concerning life forms, the exploitation observations of plant species are mainly classified as tree (approximately 54%), shrub (30%), and liana (7%). Of all plant species in the LFP database, 37% were assigned to more than one life form.

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**Discussion**

**Knowledge on Lemur Food Plants**

The LFP database, along with this analysis, constitute a comprehensive overview of LFP and their traits. In comparison with the most recent similar work by Birkinshaw and Colquhoun (2003), our knowledge has grown extensively. I detected 204 data sources providing non-redundant information, compared with 89 data sources in Birkinshaw and Colquhoun (2003). The number of 56 lemur species in the LFP database is twice as large as the number of lemur species whose diet was reported by...
This difference results both from the fact that studies on previously unstudied species have been conducted since 2003, and from taxonomic developments. At the time, Birkinshaw and Colquhoun (2003) recognized 45 lemur species, whereas Mittermeier et al. (2010), whose taxonomy I follow, recognized 96.

The taxonomic development is also reflected in the flora of Madagascar. Between 2003 and 2011, the number of recognized plant families has grown from 200 to 243 (Birkinshaw & Colquhoun 2003; Callmander et al. 2011). Similarly, the number of families observed to be exploited has grown to 147, compared with 118 in Birkinshaw and Colquhoun (2003). When unpublished datasets are considered, this number rises to 155 (Eppl ey et al. accepted 2019).

These findings suggest that further studies will continue to reveal additional families/genera exploited by lemurs. All studies were conducted at only 64 different sites, despite Madagascar having 98 terrestrial protected areas (Goodman et al. 2018). As protected areas outnumber the research sites that have been studied until now, it is obvious that there are still many unexplored areas.

**Frequent Food Plants, Exploitation of Introduced/Invasive Plants**

Though still incomplete, the LFP database can already help to determine frequently exploited plant taxa, which may be important as food for lemurs and thus could improve the ecological quality of restoration. The correlations between the number of exploited plant species and the number of published accepted species in Madagascar indicate a positive relationship at the family and genus level. Plant genera/families that differ from this relationship are either underrepresented or overrepresented in terms of numbers of exploited species. Examples of overrepresented genera, with at least 10 exploited species, are *Ficus*, *Albizia*, and *Terminalia*. Examples of overrepresented families, with at least 20 exploited species, are Moraceae, Clusiaceae, and Anacardiaceae.

A second approach to assess the frequency refers to the number of observations of plant genera/families exploited by lemurs. The largest numbers of observations are from the genera *Ficus* (246 observations), *Grewia* (155), and *Terminalia* (101), and from the families Fabaceae (204 observations), Rubiaceae (368), and Moraceae (334).

At the species level, the analysis indicates marked differences in relation to the variables “number of observations” and “number of lemurs species” exploiting these species. *Tamarindus indica* stands out with a large number of observations and lemurs species exploiting it. One reason is that this tree grows abundantly in Madagascar. In the southwest and south it typically dominates gallery forests (Sussman & Rakotozafy 1994; Williams 2006), representing a fallback food or keystone resource for *Lemur catta* (Budnitz & Dainis 1975; Sauther & Cuozzo 2009).

It is also remarkable that there are plant species exploited by approximately one-third of all lemur species (*Ficus pyrifolia*, *Ficus rubra*, *Aphloia theiformis*). Though the diversity of *Ficus* is lower in Madagascar than in other tropical regions in the Old World (Goodman & Ganzhorn 1997), lemur species seem to heavily rely on this genus. Among the species with most observations and the species exploited by most different lemur species, there are three *Ficus* species. Potential reasons for this reliance on *Ficus* are the huskless, small-seeded fruits and the inter- and intraspecies asynchronous fruiting (Bleher et al. 2003; Eppl ey et al. accepted 2019). A reason for the large number of lemur species exploiting *A. theiformis* could be its wide distribution throughout Madagascar (Danthu et al. 2010).

Among the plant species with most observations and the species exploited by most different lemur species, *Mangifera indica* is introduced, the status of *T. indica* and *Strychnos spinosa* is unconfirmed, and none are invasive according to Kull et al. (2012). Of all introduced plant species in Madagascar, lemur species exploit 7.40%, which is less than the percentage of all species exploited by lemur related to all species occurring in Madagascar (9.14%). Between the lemur genera there are large differences in the percentages of observations of introduced species, with 0 % for *Indri*, and over 40% for *Daubentonia*. The latter result may be due to the frequent study of this genus in cultivated areas. Of all introduced plant species that are exploited by lemurs, one-third is considered invasive according to Kull et al. (2012). This is a relatively large proportion, compared with the percentage of invasive plant species related to all introduced plant species in Madagascar (9.64%; Kull et al. 2012). The reason for this relatively large proportion can be the behavior of invasive plants, which reproduce over large distances and may act as pioneer species in fallow fields (Richardson et al. 2000; Kull et al. 2012). The result is supported by the findings of Gérard et al. (2015), who calculated the percentage of invasive plants related to all introduced plants exploited by endemic vertebrates in Madagascar at 28%.

**Problems and Limitations of the Interpretation**

The aggregation of studies in which different methods were applied leads to caveats and limitations in the interpretation. First, there was a lack of any consistent/standardized quantity measure used across all studies. To be able to integrate and interpret these data, I used observations and exploitation observations as measures, which are not without flaws (see Methods: Definition of “Observations” and “Exploitation Observations”). I illustrated the differences in number of observations and exploitation observations, respectively, for study sites, forest types, and lemur genera, to make them comprehensible. Second, some study designs do not intend to describe the exploitation of all different plant parts. This was primarily the case for studies on seed dispersal, which investigated only the exploitation of fruit and seeds (e.g. Razafindratsima et al. 2014). Due to the inclusion of such studies, it can be assumed that the results of the analyses are biased toward these plant parts.

Another problem relates to the result of the number of introduced plant species that are exploited. The method used to cross-check species at the level of varieties or species, respectively, led to an underestimation of the number of introduced species that are exploited by lemurs, as not all plants were identified at this
level. A prime example is the introduced genus *Eucalyptus* with nine observations, but none identified at the species level.

**Use for Restoration**

Connections between the LFP database and restoration activities can be easily drawn. Birkinshaw et al. (2009) and Manjaribe et al. (2013) analyzed survival and growth of seedlings from five of the 11 species with most observations and the species exploited by most different lemur species, to assess their suitability for restoration. Among them is *Aphloia theiformis*, a pioneer species that is not only lemur- but also bird-dispersed. In their study, all planted seedlings of this species survived 10 months, though their growth was relatively low compared with other species (Birkinshaw et al. 2009). *Uapaca thouarsii* proved environmentally tolerant and fast growing, thus being an alternative to introduced pioneer species for restoration (Manjaribe et al. 2013). Organic matter content of soil is affected positively by *Tamarindus indica*, but its roots and leaves can be allelopathic (Parvez et al. 2003; Fujij et al. 2004; Faust et al. 2015).

It is striking that all 11 species are used by the Malagasy people in a range of activities, adding another aspect that can play a role in species selection for restoration. *Uapaca louvelii* is used for timber (Lavialle et al. 2015), and *Ravenala madagascariensis* is used for house building (Rakotoarivelvo et al. 2014). The fruits/seeds of cultivated or wild *Strychnos spinosa*, *Mangifera indica*, and *Canarium madagascariense* are eaten (KJE Steffens 2018, personal observation; Styger et al. 1999). *Tamarindus indica* and *Ficus lutea* play roles in traditional ceremonies (Ranaivoson et al. 2015; Aumeeruddy-Thomas et al. 2018). The leaves/stem/bark of *A. theiformis*, *Ficus politoria*, *Ficus pyrifolia*, and *Chrysophyllum boivinianum* are used for traditional medicine (Rabearivony et al. 2015; Rakotoniaina et al. 2018). In fact, all of the species are likely used in some form for medical treatment, with some having multiple uses, for example, *T. indica* and *R. madagascariensis* are additionally used as food, for charcoal production, and to produce tools/utensils (Rakotoarivelvo et al. 2014; Ranaivoson et al. 2015).

If plants used by both animals and humans are selected for restoration, this could have various effects. Firstly, it could result in closer proximities between the two, potentially increasing the risk of zoonoses transmission (Ehlers et al. 2019). Tourism, as a source of income for local people, could profit from a facilitated accessibility to animals. It can be assumed, however, that there is already close contact between humans and wildlife in the highly anthropogenic landscape of Madagascar, as almost half of the remaining forest is closer than 100 m from the forest edge (Vieilledent et al. 2018). Secondly, a competitive situation may develop, for example, for limited fruits, between humans and animals. Regarding food crops, similar situations have been described for *Lemur catta* and *Eulemur mongoz* (LaFleur & Gould 2009; Nadhurou et al. 2017). With food trees like *M. indica* or *Litchi chinensis* planted for local consumption, however, the problem is less likely to arise as these species yield large quantities of fruits over a short period (Gérard et al. 2015). Such win-win situations could also arise when a species like *R. madagascariensis* is planted, which is pollinated by leums and used by humans for multiple purposes. Unfortunately, successful methods for harvesting this plant sustainably are absent (Rakotoarivelvo et al. 2014). This type of analysis and interpretation provides an example of what can be done with the data provided in the LFP database, by applying certain search criteria. The list of plant species possibly to be used in any one region will certainly depend on the plant species adapted to local conditions, the needs of the people, and the regional pool of lemur species.

Further traits that have to be considered in species selection for restoration are origin and invasive properties of plants. The results indicate that introduced plant species can be important food resources for lemurs. Together with their potential to grow fast, and to be used by humans in a range of activities, introduced plant species can constitute important components for restoration. But due to their varying effects on the native flora and fauna, they must be selected with caution (Manjaribe et al. 2013; Gérard et al. 2015; Lavialle et al. 2015).

Another trait that can play a role in species selection for restoration is life form of plants. Lemurs exploit mainly trees, shrubs, and lianas, which is associated with their largely arboreal lifestyle (Eppley et al. accepted 2019). While trees and shrubs are usually selected for restoration of degraded or destroyed forests, lianas are neglected, though their inclusion in restoration activities might be beneficial to biodiversity and ecological functioning of restored forests (Campbell et al. 2015).

**Facilitated Regeneration**

The results of this study support the possibility of a facilitated regeneration through the seed dispersal by lemurs. All lemur species include plants in their diet, and fruit is the most exploited part according to the LFP database. Moreover, most large seeds can be swallowed by these large vertebrates, and the gut-passage has influenced the germination success of seeds positively in some cases (Razafindratsima 2014). Only a minor proportion of species is known to be predominantly seed predators, including five species of *Propithecus* (Ganzhorn & Kappeler 1996; Hemingway 1998; Birkinshaw & Colquhoun 2003; Powysj & Mowry 2003; Patel 2014), *Indri indri* (Powysj & Mowry 2003), and *Daubentonia madagascariensis* (Andriamasimanana 1994).

It is obvious that seed dispersal is only the first step of forest regeneration, and that many different factors play a role in further steps like secondary seed dispersal or seed predation. However, seed dispersal is a prerequisite of natural regeneration; it influences invasion, range expansion, and gene flow in plant communities; in short, “without seed dispersal, ecosystems would disintegrate” (Nathan & Muller-Landau 2000; Holloway 2004, p. 114; Terborgh et al. 2008). That is why our knowledge on seed dispersal by primates should play a role in conservation efforts (Chapman & Dunham 2018). In doing so, it has to be considered that not only native species are dispersed, but also introduced invasive species like *Clidemia hirta*. The proliferation of this species may have positive effects in the short term, providing fruit year-round and luring the animals, but might also have detrimental effects on the forest in the long
term if it hinders regeneration of native tree species (Martinez 2010; Martinez & Razafindratsima 2014).

**Outlook**

There is a need for studies and applications of facilitated regeneration by lemurs, as only one restoration program has applied and reported on this to date (Holloway 2007; Martinez & Razafindratsima 2014). This need is reinforced in light of the commitments by the Malagasy government to the African Forest Landscape Restoration Initiative (AFR100), which aims to restore 4 million hectares by 2030 (Mansourian et al. 2016). Despite some knowledge gaps and limitations, the repertoire of plant species compiled in this article has the potential to be used in future restoration activities. The approach I applied in the creation of the LFP database was to repeatedly add traits of the plant species, like origin/invasive properties or life form. Following this, more aspects can be added in the future, to optimize the use of the database for species selection for restoration. By consulting the LFP database to select and plant species exploited by lemurs, these critically threatened, and in many ways valuable, primates could become part of their own conservation.

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Supporting Information

The following information may be found in the online version of this article:

Table S1. List of lemur food plants (LFP). Including lemur food plants (S1.1), data definitions. http://www.iucnredlist.org (accessed 29 Jan 2020).

Table S2. Study sites with geographic coordinates in decimal degrees, number of observations and label used in Figure 1.

Table S3. Plant species with number of observations and number of different lemur species exploiting these species.

Supplement S1. Detailed description of methods.

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