Forest restoration integrating needs of the local human population and facilitated regeneration via lemur seed dispersal in Madagascar

Dissertation

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Kim Jakob Ezra Steffens

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Reviewers:

Prof. Dr. Jörg Ganzhorn, Universität Hamburg

Prof. Dr. Kathrin Dausmann, Universität Hamburg

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SUMMARY

One of the main threats for biodiversity on earth is the destruction of tropical forests. Tree plantings as countermeasures often merely increase the area covered by trees, but do not include ecological aspects and biodiversity conservation. Therefore, restoration efforts that consider these aspects are needed, but when targeted at conservation only they may neglect resource needs of the local human population. Also, these efforts are time-consuming and costly.

In Madagascar, where patterns of forest and biodiversity loss are reflected, we aim to develop a restoration concept that integrates biodiversity conservation with human needs. Further, we aim to explore the role that facilitated regeneration through seed dispersal by lemurs might play in such restoration.

In the first step, I compiled a database of lemur food plants, to facilitate their inclusion in restoration plantings. The plant species that were most heavily exploited by lemurs are all used by the local people in a variety of ways, offering a great potential for their use in the restoration of diverse forests, both in terms of biology and ecosystem services. In a second step, we studied the seed dispersal ecology and habitat utilization of crowned lemurs (*Eulemur coronatus*) in a degraded habitat in the Oronjia New Protected Area, northern Madagascar. The lemurs' habitat use was associated with vegetation structures such as tree density, yet the animals used heavily degraded areas and forest edges. Moreover, they dispersed about one-third of all plant species known to occur in Oronjia - 20 of which appear to rely on crowned lemurs as sole dispersers - and had an overall positive impact on germination. We suggest reestablishing small habitat patches with crucial vegetation structures as a conservation measure. Using these patches as corridors or extensions of habitat, lemurs and other animals could disperse seeds into restoration areas, thereby diversifying these and accelerating natural regeneration. In a last step, we investigated the utilization of plant species by the local human population in three different regions in Madagascar, and by different vertebrate groups. There is considerable overlap between humans and vertebrates' use of plant species, revealing first, the potential of these plant species to be used in the Forest Landscape Restoration Approach that aims to reconcile conservation and human well-being, and second, the largely unexplored but great treasure of knowledge of the local people.

This dissertation may contribute to advance restoration that benefits animals and humans. For this, more applications are urgently needed, which may also be included in conventional tree plantings, such as plantations, in small steps. Risks of disease transmission between humans and animals and possible competitive situations should be considered. The results of this dissertation seem particularly relevant considering that now is the UN Decade on Ecosystem Restoration.

ZUSAMMENFASSUNG

Eine der Hauptursachen für den globalen Verlust von Biodiversität ist die Zerstörung von tropischen Wäldern. Konventionelle Baumpflanzungen erhöhen zwar die mit Bäumen bedeckte Fläche, tragen aber wenig zum Erhalt von Biodiversität bei. Deshalb sind Maßnahmen zur Wiederherstellung von Wäldern notwendig, die ökologische Aspekte und damit den Naturschutz einbeziehen. Solche Maßnahmen sind allerdings zeit- und kostenaufwändig, und nicht notwendigerweise vereinbar mit Ressourcenbedürfnissen der lokalen Bevölkerung.

Diese Dissertation hat zum Ziel, ein Konzept zur Wiederherstellung von Wäldern in Madagaskar zu entwickeln, das sowohl den Aspekt des Naturschutzes als auch die Bedürfnisse der lokalen Bevölkerung einbezieht. Des Weiteren soll die Samenausbreitung durch Lemuren untersucht werden, die die natürliche Regeneration beschleunigt, und damit eine Rolle in der Wiederherstellung vielfältiger Waldökosysteme spielen könnte.

Im ersten Schritt habe ich eine Datenbank mit Nahrungspflanzen von Lemuren zusammengestellt, um die Einbindung dieser Pflanzen in Baumpflanzungen zu ermöglichen. Die Analyse legte offen, dass die wichtigsten Nahrungspflanzen von Lemuren auch von der madagassischen Bevölkerung auf vielfältige Art und Weise genutzt werden. Damit haben diese Pflanzenarten ein großes Potential für die Wiederherstellung vielfältiger Wälder, sowohl in biologischer Hinsicht als auch bezogen auf Ökosystemdienstleistungen. Im zweiten Schritt haben wir die Samenausbreitung und Habitatnutzung von Kronenmakis (*Eulemur coronatus*) in einem degradierten Wald im Schutzgebiet Oronjia, im Norden Madagaskars, untersucht. Die Kronenmakis breiteten fast ein Drittel aller vorkommenden Pflanzenarten aus und die Ausbreitung hatte insgesamt einen positiven Effekt auf die Keimung dieser Pflanzen. Die Habitatnutzung war mit Vegetationsstrukturen wie zum Beispiel der Baumdichte assoziiert, dennoch nutzten die Tiere stark degradierte Bereiche und auch Waldränder. Als Schutzmaßnahme schlagen wir deshalb die Wiederherstellung von kleinen Waldbereichen vor, die die notwendigen Vegetationsstrukturen enthalten. Diese Bereiche könnten die Tiere als Korridore oder Erweiterung ihres Habitats nutzen, und durch ihre Samenausbreitung zu deren Diversifizierung und beschleunigter Regeneration beitragen. In einem letzten Schritt haben wir mithilfe von Umfragen in Dörfern drei verschiedener Regionen Madagaskars eine Liste von Nutzpflanzen zusammengestellt. Diese haben wir auf ihre Funktion als Habitat oder

Nahrung für verschiedene Vertebratengruppen untersucht. Ein Großteil der Nutzpflanzen wies dabei auch eine Funktion für endemische Vertebraten auf, was wiederum deren Potential zur Wiederherstellung vielfältiger Wälder aufzeigt. Weiterhin wurde deutlich, wie viel bisher unterforschtes Wissen die lokale Bevölkerung über die Nutzung von Pflanzen innehat.

Das in dieser Dissertation entwickelte Konzept kann dazu beitragen, Wälder wiederherzustellen, die Menschen und Tieren nutzen. Dazu muss es unbedingt weitere Anwendung finden, die auch in kleinen Schritten in konventionelle Pflanzungen von Bäumen, wie Baumplantagen, integriert werden kann. Dabei sollten Risiken der Krankheitsübertragung zwischen Menschen und Tieren, und der möglichen Konkurrenz um Ressourcen beachtet werden. Die Ergebnisse dieser Arbeit scheinen besonders relevant, da sie in der „UN Decade on Ecosystem Restoration“ erscheint.

GENERAL INTRODUCTION

The destruction of tropical forests is one of the main factors for the ongoing global biodiversity loss (Butchart et al., 2010; Hoffmann et al., 2010; Sala et al., 2000). The proportion of tropical forest that is already destroyed, however, is outweighed by the proportion that is degraded to different degrees, even though many different definitions of forest degradation exist and it is harder to measure than total destruction (International Tropical Timber Organization, 2002; Lund, 2009). Further, the strongholds of extant biodiversity, the so-called primary forests, have not generally been spared from human disturbance or even deforestation, these occurred just long enough in the past, so their traces are no longer evident (Chazdon, 2003, 2014; Gibson et al., 2011).

Today, more than 90% of the forest area worldwide is covered by forest that has regenerated naturally (FAO, 2020). Therefore, there is not only a far-reaching impact of humans on forests, but also a great potential for their natural regeneration. This potential however can be impaired by anthropogenically induced barriers such as fires or the introduction of invasive species (Elliott et al., 2013). But even without these barriers, it can take about 80 to 150 years for a forest to reach a status that supports maximum biodiversity and biomass. From the human perspective this is a long time, especially given the persistent and accelerating human population growth and their resource needs, which are the ultimate reasons for the destruction of tropical forests (Elliott et al., 2013). To accelerate natural regeneration, or at least increase the area covered by trees, it is thus necessary to apply restoration or reforestation.

While reforestation refers to “actions that return any kind of tree cover to deforested land”, restoration activities are defined as “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). Both of these actions usually include some kind of tree planting.

Plantations as an option for reforestation

In many tropical countries, tree planting is often based on a small number of introduced, fast-growing tree species from genera like *Eucalyptus* and *Pinus,* whose properties and cultivation techniques are well-known, resulting in large monocultural plantations (Brancalion et al., 2020; Shono et al., 2007; Stanturf et al., 2013). Such plantations make up about 70% of all planted forests in Africa, and *Pinus* is already ranking among the top five genera with the highest volume of growing stock (FAO, 2020). While plantations can be highly productive and profitable, they have several disadvantages compared to natural forests (Clough et al., 2016; Meijaard et al., 2018; Stanturf et al., 2013). These “artificial ecosystems” are in general more susceptible to disturbances compared with natural ecosystems, for example, they are prone to storm damages, pest infestations and diseases (Aguín et al., 2013; Elmqvist et al., 2003; Meyer et al., 2016; Morimoto et al., 2019, p. 436). Also, they may facilitate the establishment and spread of alien and invasive plant species, due to the phylogenetic homogenization of local plant communities, and the introduced plant species from tree plantings themselves hold the potential to invade and harm native plant communities (Carrière & Randriambanona, 2007; Krumm & Vítková, 2016; Kusuma et al., 2018). Finally, plantations usually have little value for biodiversity conservation, they offer less ecosystems services to people than natural forests, and they store less carbon, which is important in terms of climate change (Chazdon, 2008; Clough et al., 2016; Elliott et al., 2013; Lamb et al., 2005).

Forest loss and plantations in Madagascar

Madagascar is a prime example of a country harboring a unique and diverse fauna and flora with a large proportion of endemics, and the threatening of these by the destruction of tropical forest (Ganzhorn et al., 2001; Myers et al., 2000). Between 1950 and 2000, about 40% of the forest cover of Madagascar has been lost (Harper et al., 2007). Also, the patterns of tree planting as introduced above are reflected in Madagascar, where native tree species are often neglected due to missing knowledge on their properties and cultivation techniques, or due to slower growth compared to exotic species, both leading to more time and higher financial investment needed for their implementation (Birkinshaw et al., 2009, 2013; Ganzhorn, 1987; Vincelette et al., 2007). While natural forests are used in a much wider range of activities and provide more ecosystem services, plantations offer economic benefits to local people, who use their wood to produce charcoal, as firewood or for construction, which can reduce pressure on resources from natural forests (Carrière & Randriambanona, 2007; Gérard et al., 2015; Lavialle et al., 2015). Beyond that, monocultural and intensively used plantations are of no or little use to endemic plant and animal species of Madagascar (Ganzhorn, 1987; Hending et al., 2020; Ramanamanjato & Ganzhorn, 2001). Some old plantations on the other hand, which have not been cut for several decades, offer rich undergrowth as well as an intermediate canopy layer that is used by some lemur species - primates endemic to Madagascar - for feeding, traveling and resting (Ganzhorn, 1987). The same is true for cacao and vanilla agroecosystems, where less intensively used plantations and those closer to natural forests support more diversity (Hending et al., 2018, 2020; Webber et al., 2020).

Forest Landscape Restoration (FLR)

Obviously, the more natural a forest system is, the more diversity it can support. From this point of view, those tree plantings that implemented only native species and resembled natural forests would be best for conservation. However, experiences in Madagascar have shown that measures targeted only at nature conservation while disregarding the needs of the local human population cannot be successful, as forest resources are of high socio-economic importance for the people (Gardner et al., 2013, 2016; Mansourian et al., 2017).

An approach that combines ecological restoration with supporting livelihoods of local people is Forest Landscape Restoration, which is defined as “a planned process that aims to regain ecological integrity and enhance human well-being in deforested or degraded forest landscapes” (WWF/IUCN, 2000, p. 2). One option to implement FLR in Madagascar could be to plant tree species of use for animals and humans alike. In this way, people might be motivated to participate in planting and maintenance, making reforestation and restoration more sustainable. In addition, the ever-shrinking habitat of animals would be expanded again, and their seed dispersal could accelerate natural regeneration in tree plantings, thereby diversifying these and lowering financial and temporal investment (Holloway, 2004; Styger et al., 1999; Wunderle Jr., 1997).

Role of seed dispersal and its evolution

Seed dispersal plays a key role in plant and animal ecology and evolution: it is the base for the regeneration of many plants, and impacts plant colonization, invasion and distribution, demography, community structure and ultimately biodiversity (Bascompte & Jordano, 2007; Jordano et al., 2011; Levin et al., 2003; Martinez & Razafindratsima, 2014; Schupp et al., 2010; Terborgh et al., 2002; Wang & Smith, 2002). There are three hypotheses that aim to explain the advantage of seed dispersal, and thus its evolutionary origin (Howe & Smallwood, 1982).

Following the *Escape Hypothesis*, mortality of seeds and seedlings due to predators, pathogens or competition is density dependent; the dispersal of seeds away from the mother plant should reduce the density and thus increase the probability of seed and seedling survival. Following the *Colonization Hypothesis*, habitats are always subject to disturbances and changes, which result in the development of new, untouched habitats. Dispersal should allow plants to colonize these habitats, increasing their distribution and survival. Following the *Directed Dispersal Hypothesis*, dispersers may deposit seeds non-randomly at microhabitats that are especially suited for the germination and survival of the seed and seedling (Howe & Smallwood, 1982).

Even though empirical evidence suggests that the ecology of many plants can be best described by the *Escape Hypothesis*, the three hypotheses are not mutually exclusive, and plant species could benefit in more than one or even in all three forms described by the hypotheses (Levin et al., 2003; Wenny, 2001). The recruitment patterns of plants ultimately depend on several different factors, including fecundity of the mother plant, seed disperser characteristics, intra- and interspecific competition, type and density of pathogens and predators, and deposition site conditions (Nathan & Casagrandi, 2004).

Seed dispersal agents

The main agents involved in seed dispersal are animals (zoochory), wind (anemochory), water (hydrochory) and the plant itself (autochory; Howe & Smallwood, 1982; van der Pijl, 1982). Zoochory is mediated by many different vertebrate taxa, including mainly mammals (e.g, the sambar deer (*Rusa unicolor*; Brodie et al., 2009)) and birds (e.g., the Chaco chachalaca (*Ortalis canicollis*; Donatti et al., 2011)), but also reptiles (e.g., the red-footed tortoise (*Geochelone carbonaria*; Strong & Fragoso, 2006)), fishes (e.g., the Tambaqui (*Colossoma macropomum*; Anderson et al., 2011)) and, though extremely rarely, amphibians (the Izecksohn's Brazilian treefrog (*Xenohyla truncata*; da Silva et al., 1989)) (Herrera, 2008). Invertebrates may also play a role in seed dispersal, as secondary dispersers (e.g., the ant species *Aphaenogaster swammerdami* (Böhning-Gaese et al., 1999; Dausmann et al., 2008) or dung beetles (Coleoptera species from the families Scarabaeidae, Geotrupidae and Aphodiidae (Andresen, 2002))). While primary seed dispersal is the first movement of a seed away from its origin at the plant, secondary dispersal are movements following primary dispersal (Muller-Landau & Hardesty, 2005).

Forms of seed dispersal

Morphological adaptations of fruits and seeds may be used to infer the agent responsible for the dispersal of a plant species (van der Pijl, 1982). Viscid and hooked seeds or fleshy fruits for example point to animal dispersal, the former representing adaptations to external dispersal via their attachment to fur or feathers (epizoochory), and the latter to internal dispersal via being swallowed and subsequently defecated, spit out or regurgitated (endozoochory) (Herrera, 2008; Sorensen, 1986; van der Pijl, 1982). In woody plants, endozoochory through frugivorous vertebrates is by far the most widespread system of seed dispersal. Especially tree species in tropical forests are adapted to this system, between 51% and 98% of them are offering fleshy fruits, depending on the type of forest (Herrera, 2008; Howe & Smallwood, 1982).

Madagascar's frugivore community

In comparison with other tropical regions, Madagascar's community of vertebrate species involved in endozoochory is peculiar. Despite the island's great biodiversity, its frugivore community is species-poor, with only about 30 species, the majority being lemurs (Albert-Daviaud et al., 2018). Both the low diversity and the relation of primate species numbers to bird/ bat species numbers is contrasting compared to other tropical regions and Old World islands, where frugivore diversity is much higher and dominated by birds, followed by bats, and then primates (Fleming et al., 1987). Hypotheses that aim to explain the low frugivore diversity on Madagascar are the food availability hypothesis, which suggests that fruits may be unsuitable as basic food resource due the unpredictability of rainfall and thus varying phenology of forests, and the nutritional hypothesis suggesting that nitrogen content of fruits in Madagascar was too low to meet protein requirements of primates and allow a larger diversification of their frugivore community (Dewar & Richard, 2007; Donati et al., 2017).

Frugivorous lemurs surpass frugivorous birds and bats not only in terms of species richness, but also in biomass (Wright et al., 2005), and they are able to swallow and defecate larger seeds than the latter groups. Therefore, they seem to act as the most important seed dispersers on Madagascar, though research on birds and bats is limited (Razafindratsima, 2014). But fruit exploitation and seed dispersal are not limited to lemurs classified as frugivores: fruit is the plant part that is exploited by most different lemur species, and many of these defecate seeds undamaged; only *Propithecus* spp., *Indri indri*, and *Daubentonia madagascariensis* are known to be predominantly seed predators (Andriamasimanana, 1994; Birkinshaw & Colquhoun, 2003; Ganzhorn & Kappeler, 1996; Hemingway, 1998; Patel, 2014; Powzyk & Mowry, 2003; Ramananjato et al., 2020).

Conservation of ecological functions

The populations of all extant lemur species are declining due to habitat destruction through the conversion of forests to agricultural fields or logging and wood harvesting, as well as hunting and trapping (Estrada et al., 2017; IUCN 2021). While the impact of total destruction of forest on lemurs as forest-dwellers is obvious, knowledge on the impact of degradation on the animals' ecology and health is still limited in Madagascar. Yet, it was shown that slight disturbances can lead to lemur population density and species richness increases, while heavier disturbances can lead to density decrease and extinctions (Burivalova et al., 2015; Ganzhorn et al., 1997; Irwin et al., 2010). To obtain further insights, more studies in anthropogenically modified habitats such as degraded forests are needed (Ganzhorn, 1987; Irwin et al., 2010; Isabirye-Basuta & Lwanga, 2008).

Not only when species go extinct, but already when their population densities decline, ecological functions such as seed dispersal are lost (Valiente-Banuet et al., 2015). In comparison with the primate regions of Africa, Asia and South America, Madagascar is projected to undergo the largest changes in its primate species community, which are mainly attributable to the predicted extinction of broad groups of folivorous and frugivorous lemurs (Jernvall & Wright, 1998). Today there are plant species that are missing extant dispersers, which strongly impairs their chances for survival and may even trigger extinction cascades (Albert-Daviaud et al., 2020; Federman et al., 2016; Pedrono et al., 2013). For conservation, it is thus important to understand the consequences of the loss of seed dispersal by lemurs on regeneration and survival of plant species (Ganzhorn et al., 1999; Moses & Semple, 2011; Sato, 2012). Thinking constructively, it might be possible to use lemur seed dispersal to ensure survival of plants. One possibility to implement this idea in conservation measures might be to integrate lemurs into forest restoration concepts (Holloway, 2004; Ramananjato et al., 2020; Razafindratsima & Razafimahatratra, 2010).

Aim and overview of dissertation

With my dissertation I aim to explore, first, the possibility of integrating needs of animals and humans in restoration activities in Madagascar, and second, the role that facilitated regeneration via lemur seed dispersal might play in these.

In the *first chapter*, I provide an overview of lemur food plants. To this aim, I carried out an extensive literature search to compile publications on food-related behavior of lemurs. From these publications, I extracted information about the lemur species, the plants and plant parts they feed on, and study sites. After applying recent taxonomic revisions of lemur and plant species, I used this database to analyze lemur species' diets, most heavily exploited plant species, and plant species' characteristics such as origin and life form. Also, I explored human uses of the plant species that were most heavily used by lemurs. The objective of this study is to facilitate the inclusion of lemur food plants into restoration activities.

The next two chapters are focused on the ecology of crowned lemurs (*Eulemur coronatus*). We investigated the species' seed dispersal ecology (*second chapter*) and its habitat utilization and demands on vegetation structures (*third chapter*) in a dry degraded forest habitat in northern Madagascar. Specific questions we pose in the *second chapter* relate to seed dispersal quantity (e.g., How many seeds are dispersed? How many plant species are dispersed?) and quality (e.g., How are seeds affected by the gut passage? How does this influence their germination success and time?). In the *third chapter*, we ask whether it is possible to link habitat use by crowned lemurs to structural vegetation characteristics described on a small scale, or vegetation productivity on a larger scale. The objectives of this study are to understand the influence of lemurs on regeneration in a degraded forest, to facilitate their inclusion into restoration activities, and to predict possible positive and negative effects this may have.

While the first three chapters start from the animals' perspective, the *fourth chapter* does so from the humans' perspective. Here, we examine the utilization of plants by local communities in three culturally and climatically different regions of Madagascar. The plants that are for example being used as medicine, food or to produce charcoal, were subsequently analyzed for their function as food or habitat for vertebrates. The objectives of this study are to explore and highlight the knowledge of local people about plant utilization, and to advance the Forest Landscape Restoration approach including plant species of benefit to humans and animals.

Publications used for the dissertation

Chapter 1

Steffens, K. J. E. (2020). Lemur food plants as options for forest restoration in Madagascar. *Restoration Ecology*, 28(6), 1517–1527. https://doi.org/10.1111/rec.13234

Chapter 2

Steffens, K. J. E., Sanamo, J., & Razafitsalama, J. (accepted). The role of lemur seed dispersal in restoring degraded forest ecosystems in Madagascar. *Folia Primatologica*.

Chapter 3

Steffens, K. J. E., Sanamo, J., Razafitsalama, J., & Ganzhorn, J. U. (submitted). Utilization of degraded habitats by a frugivorous primate in northern Madagascar: implications for forest restoration. *Animal Conservation*.

Chapter 4

Konersmann, C., Noromiarilanto, F., Ratovonamana, Y. R., Brinkmann, K., Jensen, K., Kobbe, S., Köhl, M., Kuebler, D., Lahann, P., Steffens, K. J. E., & Ganzhorn, J. U. (2021). Using utilitarian plants for lemur conservation. *International Journal of Primatology*. https://doi.org/10.1007/s10764-021-00200-y

Further publications associated with the dissertation

Eppley, T. M., Hoeks, S., Chapman, C. A., Ganzhorn, J. U., Hall, K., Owen, M. A., et al. (submitted). Descending from the trees: factors favoring transitions to terrestriality in arboreal primates. *Proceedings of the National Academy of Sciences of the United States of America.*

Eppley, T. M., Steffens, K. J. E., Colquhoun, I. C., & Birkinshaw, C. (in press). Lemur food plants. In S. M. Goodman (Ed.), *The New Natural History of Madagascar*. Princeton: Princeton University Press.

Fiedler, P. M. A., De Lapparent, A., Razafitsalama, J., Sanamo, J., Steffens, K. J. E., & Ganzhorn, J. U. (2021). Secondary seed removal in a degraded forest habitat in Madagascar. *Scientific Reports*, 11, 16823. https://doi.org/10.1038/s41598-021-96306-7

Müller, P. J., Noromiarilanto, F., Razafindrafarasoa, B., Totorobia, D. A., Jaomaharitra, S., Andriamihamina, A. F., Razafitsalama, J., Birkinshaw, C., & Steffens, K. J. E. (submitted). Relating resource management and income diversity to economic development of communities around the Oronjia New Protected Area, northern Madagascar. *Madagascar Conservation & Development*.

References

Aguín, O., Sainz, M. J., Ares, A., Otero, L., & Pedro Mansilla, J. (2013). Incidence, severity and causal fungal species of *Mycosphaerella* and *Teratosphaeria* diseases in *Eucalyptus* stands in Galicia (NW Spain). *Forest Ecology and Management*, *302*, 379–389. https://doi.org/10.1016/j.foreco.2013.03.021

Albert-Daviaud, A., Buerki, S., Onjalalaina, G. E., Perillo, S., Rabarijaona, R., Razafindratsima, O. H., Sato, H., Valenta, K., Wright, P. C., & Stuppy, W. (2020). The ghost fruits of Madagascar: Identifying dysfunctional seed dispersal in Madagascar's endemic flora. *Biological Conservation*, *242*, 108438. https://doi.org/10.1016/j.biocon.2020.108438

Albert-Daviaud, A., Perillo, S., & Stuppy, W. (2018). Seed dispersal syndromes in the Madagascan flora: The unusual importance of primates. *Oryx*, *52*(3), 418–426. https://doi.org/10.1017/S0030605317001600

Anderson, J. T., Nuttle, T., Saldaña Rojas, J. S., Pendergast, T. H., & Flecker, A. S. (2011). Extremely long-distance seed dispersal by an overfished Amazonian frugivore. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1723), 3329–3335. https://doi.org/10.1098/rspb.2011.0155

Andresen, E. (2002). Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology*, *27*, 257–270. https://doi.org/10.1046/j.1365-2311.2002.00408.x

Andriamasimanana, M. (1994). Ecoethological study of free-ranging Aye-Ayes (*Daubentonia madagascariensis*) in Madagascar. *Folia Primatologica*, *62*, 37–45. https://doi.org/10.1159/000156761

Bascompte, J., & Jordano, P. (2007). Plant-animal mutualistic networks: The architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 567–593. https://doi.org/10.1146/annurev.ecolsys.38.091206.095818

Birkinshaw, C., Andrianjafy, M., & Rasolofonirina, J.-J. (2009). Survival and growth of seedlings of 19 native tree and shrub species planted in degraded forest as part of a forest restoration project in Madagascar's highlands. *Madagascar Conservation & Development*, *4*(2), 128–131. https://doi.org/10.4314/mcd.v4i2.48653

Birkinshaw, C., & Colquhoun, I. C. (2003). Lemur food plants. In S. M. Goodman & J. P. Benstead (Eds.), *The Natural History of Madagascar* (pp. 1207–1220). Chicago: The University of Chicago Press.

Birkinshaw, C., Lowry II, P. P., Raharimampionona, J., & Aronson, J. (2013). Supporting target 4 of the global strategy for plant conservation by integrating ecological restoration into the Missouri Botanical Garden's conservation program in Madagascar. *Annals of the Missouri Botanical Garden*, *99*(2), 139–146. https://doi.org/10.3417/2012002

Böhning-Gaese, K., Gaese, B. H., & Rabemanantsoa, S. B. (1999). Importance of primary and secondary seed dispersal in the Malagasy tree *Commiphora guillaumini*. *Ecology*, *80*(3), 821–832. https://doi.org/10.2307/177020

Brancalion, P. H. S., Amazonas, N. T., Chazdon, R. L., Melis, J., Rodrigues, R. R., Silva, C. C., Sorrini, T. B., & Holl, K. D. (2020). Exotic eucalypts: from demonized trees to allies of tropical forest restoration? *Journal of Applied Ecology*, *57*(1), 55–66. https://doi.org/10.1111/1365-2664.13513

Brodie, J. F., Helmy, O. E., Brockelman, W. Y., & Maron, J. L. (2009). Bushmeat poaching reduces the seed dispersal and population growth rate of a mammal-dispersed tree. *Ecological Applications*, *19*(4), 854–863. https://doi.org/10.1890/08-0955.1

Burivalova, Z., Bauert, M. R., Hassold, S., Fatroandrianjafinonjasolomiovazo, N. T., & Koh, L. P. (2015). Relevance of global forest change data set to local conservation: case study of forest degradation in Masoala National Park, Madagascar. *Biotropica*, *47*(2), 267–274. https://doi.org/10.1111/btp.12194

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., … Watson, R. (2010). Global biodiversity: indicators of recent declines. *Science*, *328*(5982), 1164–1168. https://doi.org/10.1126/science.1187512

Carrière, S. M., & Randriambanona, H. (2007). Biodiversité introduite et autochtone: Antagonisme ou complémentarité? Le cas de l'eucalyptus à Madagascar. *Bois et forêt des Tropiques*, *292*(2), 5–21.

Chazdon, R. L. (2003). Tropical forest recovery: legacies of human impact and natural disturbances. *Perspectives in Plant Ecology, Evolution and Systematics*, *6*(1–2), 51–71. https://doi.org/10.1078/1433-8319-00042

Chazdon, R. L. (2008). Beyond deforestation: restoring forests and ecosystem services on degraded lands. *Science*, *320*(5882), 1458–1460. https://doi.org/10.1126/science.1155365

Chazdon, R. L. (2014). *Second growth: the promise of tropical forest regeneration in an age of deforestation*. Chicago: The University of Chicago Press.

Clough, Y., Krishna, V. V., Corre, M. D., Darras, K., Denmead, L. H., Meijide, A., Moser, S., Musshoff, O., Steinebach, S., Veldkamp, E., Allen, K., Barnes, A. D., Breidenbach, N., Brose, U., Buchori, D., Daniel, R., Finkeldey, R., Harahap, I., Hertel, D., … Scheu, S. (2016). Land-use choices follow profitability at the expense of ecological functions in Indonesian smallholder landscapes. *Nature Communications*, *7*(1), 13137. https://doi.org/10.1038/ncomms13137 da Silva, H. R., de Britto-Pereira, M. C., Caramaschi, U., & de Britto-Pereira, M. C. (1989). Frugivory and seed dispersal by *Hyla truncata*, a neotropical treefrog. *Copeia*, *1989*(3), 781–783. https://doi.org/10.2307/1445517

Dausmann, K. H., Glos, J., Linsenmair, K. E., & Ganzhorn, J. U. (2008). Improved recruitment of a lemur-dispersed tree in Malagasy dry forests after the demise of vertebrates in forest fragments. *Oecologia*, *157*(2), 307–316. https://doi.org/10.1007/s00442-008-1070-6

Dewar, R. E., & Richard, A. F. (2007). Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences*, *104*(34), 13723–13727. https://doi.org/10.1073/pnas.0704346104

Donati, G., Santini, L., Eppley, T. M., Arrigo-Nelson, S., Balestri, M., Boinski, S., Bollen, A., Bridgeman, L., Campera, M., Carrai, V., Chalise, M., Lewis, A., Hohmann, G., Kinnaird, M., Koenig, A., Kowalewski, M., Lahann, P., McLennan, M., Nekaris, K. A., & Ganzhorn, J. U. (2017). Low levels of fruit nitrogen as drivers for the evolution of Madagascar’s primate communities. *Scientific Reports*, *7*, 14406. https://doi.org/10.1038/s41598-017-13906-y

Donatti, C. I., Guimarães, P. R., Galetti, M., Pizo, M. A., Marquitti, F. M. D., & Dirzo, R. (2011). Analysis of a hyper-diverse seed dispersal network: modularity and underlying mechanisms. *Ecology Letters*, *14*(8), 773–781. https://doi.org/10.1111/j.1461-0248.2011.01639.x

Elliott, S., Blakesley, D., & Hardwick, K. (2013). *Restoring Tropical Forests: A Practical Guide*. Kew: Royal Botanic Gardens.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., & Norberg, J. (2003). Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment*, *1*(9), 488–494. https://doi.org/10.2307/3868116

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K. A.-I., Nijman, V., Heymann, E. W., Lambert, J. E., Rovero, F., Barelli, C., Setchell, J. M., Gillespie, T. R., Mittermeier, R. A., Arregoitia, L. V., de Guinea, M., Gouveia, S., Dobrovolski, R., … Li, B. (2017). Impending extinction crisis of the world’s primates: why primates matter. *Science Advances*, *3*(1), e1600946. https://doi.org/10.1126/sciadv.1600946

FAO. (2020). *Global Forest Resources Assessment 2020*. Rome: Food and Agriculture Organization of the United Nations. https://doi.org/10.4060/ca9825en

Federman, S., Dornburg, A., Daly, D. C., Downie, A., Perry, G. H., Yoder, A. D., Sargis, E. J., Richard, A. F., Donoghue, M. J., & Baden, A. L. (2016). Implications of lemuriform extinctions for the Malagasy flora. *Proceedings of the National Academy of Sciences*, *113*(18), 5041–5046. https://doi.org/10.1073/pnas.1523825113

Fleming, T. H., Breitwisch, R., & Whitesides, G. H. (1987). Patterns of tropical vertebrate frugivore diversity. *Annual Review of Ecology and Systematics*, *18*, 91–109.

Ganzhorn, J. U. (1987). A possible role of plantations for primate conservation in Madagascar. *American Journal of Primatology*, *12*, 205–215. https://doi.org/10.1002/ajp.1350120208

Ganzhorn, J. U., Fietz, J., Rakotovao, E., Schwab, D., & Zinner, D. (1999). Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology*, *13*(4), 794–804. https://doi.org/10.1046/j.1523-1739.1999.98245.x

Ganzhorn, J. U., & Kappeler, P. M. (1996). Lemurs of the Kirindy Forest. In J. U. Ganzhorn & J.-P. Sorg (Eds.), *Ecology and economy of a tropical dry forest in Madagascar* (pp. 257–274). Göttingen: German Primate Center.

Ganzhorn, J. U., Lowry, P. P., Schatz, G. E., & Sommer, S. (2001). The biodiversity of Madagascar: one of the world’s hottest hotspots on its way out. *Oryx*, *35*(4), 346–348. https://doi.org/10.1046/j.1365-3008.2001.00201.x

Ganzhorn, J. U., Malcomber, S., Andrianantoanina, O., & Goodman, S. M. (1997). Habitat characteristics and lemur species richness in Madagascar. *Biotropica*, *29*(3), 331–343. https://doi.org/10.1111/j.1744-7429.1997.tb00434.x

Gardner, C. J., Jasper, L. D., Eonintsoa, C., Duchene, J.-J., & Davies, Z. G. (2016). The impact of natural resource use on bird and reptile communities within multiple-use protected areas: evidence from sub-arid southern Madagascar. *Biodiversity and Conservation*, *25*(9), 1773–1793. https://doi.org/10.1007/s10531-016-1160-4

Gardner, C. J., Nicoll, M. E., Mbohoahy, T., Oleson, K. L. L., Ratsifandrihamanana, A. N., Ratsirarson, J., René de Roland, L.-A., Virah-Sawmy, M., Zafindrasilivonona, B., & Davies, Z. G. (2013). Protected areas for conservation and poverty alleviation: experiences from Madagascar. *Journal of Applied Ecology*, *50*(6), 1289–1294. https://doi.org/10.1111/1365-2664.12164

Gérard, A., Ganzhorn, J. U., Kull, C. A., & Carrière, S. M. (2015). Possible roles of introduced plants for native vertebrate conservation: the case of Madagascar. *Restoration Ecology*, *23*(6), 768–775. https://doi.org/10.1111/rec.12246

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Lovejoy, T. E., & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature*, *478*(7369), 378–381. https://doi.org/10.1038/nature10425

Harper, G. J., Steininger, M. K., Tucker, C. J., Juhn, D., & Hawkins, F. (2007). Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation*, *34*(4), 325–333. https://doi.org/10.1017/S0376892907004262

Hemingway, C. A. (1998). Selectivity and variability in the diet of Milne-Edwards’ sifakas (*Propithecus diadema edwardsi*): implications for folivory and seed-eating. *International Journal of Primatology*, *19*, 355–377. https://doi.org/10.1023/A:1020344018670

Hending, D., Andrianiaina, A., Maxfield, P., Rakotomalala, Z., & Cotton, S. (2020). Floral species richness, structural diversity and conservation value of vanilla agroecosystems in Madagascar. *African Journal of Ecology*, *58*(1), 100–111. https://doi.org/10.1111/aje.12682

Hending, D., Andrianiaina, A., Rakotomalala, Z., & Cotton, S. (2018). The use of vanilla plantations by lemurs: encouraging findings for both lemur conservation and sustainable agroforestry in the Sava region, northeast Madagascar. *International Journal of Primatology*, *39*(1), 141–153. https://doi.org/10.1007/s10764-018-0022-1

Herrera, C. M. (2008). Seed dispersal by vertebrates. In C. M. Herrera & O. Pellmyr (Eds.), *Plant-Animal Interactions: An Evolutionary Approach,* 5th edition (pp. 185–208). Malden, Oxford, Victoria: Blackwell Science.

Hoffmann, M., Hilton-Taylor, C., Angulo, A., Böhm, M., Brooks, T. M., Butchart, S. H. M., Carpenter, K. E., Chanson, J., Collen, B., Cox, N. A., Darwall, W. R. T., Dulvy, N. K., Harrison, L. R., Katariya, V., Pollock, C. M., Quader, S., Richman, N. I., Rodrigues, A. S. L., Tognelli, M. F., … Stuart, S. N. (2010). The impact of conservation on the status of the world's vertebrates. *Science*, *330*(6010), 1503–1509. https://doi.org/10.1126/science.1194442

Holloway, L. (2004). Ecosystem restoration and rehabilitation in Madagascar. *Ecological Restoration*, *22*(2), 113–119. https://doi.org/10.3368/er.22.2.113

Howe, H. F., & Smallwood, J. (1982). Ecology of seed dispersal. *Annual Review of Ecology and Systematics*, *13*(1), 201–228. https://doi.org/10.1146/annurev.es.13.110182.001221

International Tropical Timber Organization. (2002). *ITTO guidelines for the restoration, management and rehabilitation of degraded and secondary tropical forests*. Yokohama: International Tropical Timber Organisation.

Irwin, M. T., Wright, P. C., Birkinshaw, C., Fisher, B. L., Gardner, C. J., Glos, J., Goodman, S. M., Loiselle, P., Rabeson, P., Raharison, J.-L., Raherilalao, M. J., Rakotondravony, D., Raselimanana, A., Ratsimbazafy, J., Sparks, J. S., Wilmé, L., & Ganzhorn, J. U. (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation*, *143*(10), 2351–2362. https://doi.org/10.1016/j.biocon.2010.01.023

Isabirye-Basuta, G. M., & Lwanga, J. S. (2008). Primate populations and their interactions with changing habitats. *International Journal of Primatology*, *29*(1), 35–48. https://doi.org/10.1007/s10764-008-9239-8

IUCN (2021). *The IUCN Red List of Threatened Species*. Version 2021-1. https://www.iucnredlist.org, Accessed on 03 June 2021.

Jernvall, J., & Wright, P. C. (1998). Diversity components of impending primate extinctions. *Proceedings of the National Academy of Sciences*, *95*(19), 11279–11283. https://doi.org/10.1073/pnas.95.19.11279

Jordano, P., Forget, P.-M., Lambert, J. E., Böhning-Gaese, K., Traveset, A., & Wright, S. J. (2011). Frugivores and seed dispersal: mechanisms and consequences for biodiversity of a key ecological interaction. *Biology Letters*, *7*(3), 321–323. https://doi.org/10.1098/rsbl.2010.0986

Krumm, F., & Vítková, L. (2016). *Eingeführte Baumarten in europäischen Wäldern: Chancen und Herausforderungen*. Freiburg: European Forest Institute.

Kusuma, Y. W. C., Rembold, K., Tjitrosoedirdjo, S. S., & Kreft, H. (2018). Tropical rainforest conversion and land use intensification reduce understorey plant phylogenetic diversity. *Journal of Applied Ecology*, *55*(5), 2216–2226. https://doi.org/10.1111/1365-2664.13201

Lamb, D., Erskine, P. D., & Parrotta, J. A. (2005). Restoration of degraded tropical forest landscapes. *Science*, *310*(5754), 1628–1632. https://doi.org/10.1126/science.1111773

Lavialle, J., Carrière, S. M., Miandrimanana, C., Tilahimena, A., Birkinshaw, C., & Aronson, J. (2015). Complementarity of native and introduced tree species: exploring timber supply on the east coast of Madagascar. *Madagascar Conservation & Development*, *10*, 137–143. https://doi.org/10.4314/mcd.v10i3.6

Levin, S. A., Muller-Landau, H. C., Nathan, R., & Chave, J. (2003). The ecology and evolution of seed dispersal: a theoretical perspective. *Annual Review of Ecology, Evolution, and Systematics*, *34*(1), 575–604. https://doi.org/10.1146/annurev.ecolsys.34.011802.132428

Lund, H. G. (2009). *What is a degraded forest?* Gainesville: Forest Information Services.

Mansourian, S., Stanturf, J. A., Derkyi, M. A. A., & Engel, V. L. (2017). Forest Landscape Restoration: increasing the positive impacts of forest restoration or simply the area under tree cover? *Restoration Ecology*, *25*(2), 178–183. https://doi.org/10.1111/rec.12489

Martinez, B. T., & Razafindratsima, O. H. (2014). Frugivory and seed dispersal patterns of the red-ruffed lemur, *Varecia rubra*, at a forest restoration site in Masoala National Park, Madagascar. *Folia Primatologica*, *85*, 228–243. https://doi.org/10.1159/000363408

Meijaard, E., Garcia-Ulloa, J., Sheil, D., Carlson, K. M., Wich, S. A., Juffe-Bignoli, D., & Brooks, T. M. (2018). *Oil palm and biodiversity: A situation analysis by the IUCN Oil Palm Task Force*. Gland: IUCN. https://doi.org/10.2305/IUCN.CH.2018.11.en

Meyer, F. E., Shuey, L. S., Naidoo, S., Mamni, T., Berger, D. K., Myburg, A. A., van den Berg, N., & Naidoo, S. (2016). Dual RNA-sequencing of *Eucalyptus nitens* during *Phytophthora cinnamomi* challenge reveals pathogen and host factors influencing compatibility. *Frontiers in Plant Science*, *7*, 191. https://doi.org/10.3389/fpls.2016.00191

Morimoto, J., Nakagawa, K., Takano, K. T., Aiba, M., Oguro, M., Furukawa, Y., Mishima, Y., Ogawa, K., Ito, R., Takemi, T., Nakamura, F., & Peterson, C. J. (2019). Comparison of vulnerability to catastrophic wind between *Abies* plantation forests and natural mixed forests in northern

Japan. *Forestry: An International Journal of Forest Research*, *92*(4), 436–443. https://doi.org/10.1093/forestry/cpy045

Moses, K. L., & Semple, S. (2011). Primary seed dispersal by the black-and-white ruffed lemur (*Varecia variegata*) in the Manombo forest, south-east Madagascar. *Journal of Tropical Ecology*, *27*, 529–538. https://doi.org/10.1017/S0266467411000198

Muller-Landau, H. C., & Hardesty, B. D. (2005). Seed dispersal of woody plants in tropical forests: concepts, examples and future directions. In D. Burslem, M. Pinard, & S. Hartley (Eds.), *Biotic Interactions in the Tropics* (pp. 267–309). Cambridge: Cambridge University Press. https://doi.org/10.1017/CBO9780511541971.012

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, *403*(6772), 853–858. https://doi.org/10.1038/35002501

Nathan, R., & Casagrandi, R. (2004). A simple mechanistic model of seed dispersal, predation and plant establishment: Janzen-Connell and beyond. *Journal of Ecology*, *92*(5), 733–746. https://doi.org/10.1111/j.0022-0477.2004.00914.x

Patel, E. R. (2014). Silky sifaka *Propithecus candidus* Grandidier, 1871. In C. Schwitzer, R. A. Mittermeier, A. B. Rylands, L. A. Taylor, F. Chiozza, E. A. Williamson, J. Wallis, & F. E. Clark (Eds.), *Primates in Peril: The World's 25 Most Endangered Primates 2012-2014* (pp. 38–43). Bristol: IUCN SSC Primate Specialist Group (PSG), International Primatological Society (IPS), Conservation International (CI), Bristol Zoological Society (BZS).

Pedrono, M., Griffiths, O. L., Clausen, A., Smith, L. L., Griffiths, C. J., Wilmé, L., & Burney, D. A. (2013). Using a surviving lineage of Madagascar's vanished megafauna for ecological restoration. *Biological Conservation*, *159*, 501–506. https://doi.org/10.1016/j.biocon.2012.11.027

Powzyk, J. A., & Mowry, C. B. (2003). Dietary and feeding differences between sympatric *Propithecus diadema diadema* and *Indri indri*. *International Journal of Primatology*, *24*, 1143–1162. https://doi.org/10.1023/B:IJOP.0000005984.36518.94

Ramanamanjato, J.-B., & Ganzhorn, J. U. (2001). Effects of forest fragmentation, introduced *Rattus rattus* and the role of exotic tree plantations and secondary vegetation for the conservation of an endemic rodent and a small lemur in littoral forests of southeastern Madagascar. *Animal Conservation*, *4*(2), 175–183. https://doi.org/10.1017/S1367943001001202

Ramananjato, V., Rakotomalala, Z., Park, D. S., DeSisto, C. M. M., Raoelinjanakolona, N. N., Guthrie, N. K., Fenosoa, Z. E. S., Johnson, S. E., & Razafindratsima, O. H. (2020). The role of nocturnal omnivorous lemurs as seed dispersers in Malagasy rain forests. *Biotropica*, 00:1-8. https://doi.org/10.1111/btp.12789

Razafindratsima, O. H. (2014). Seed dispersal by vertebrates in Madagascar's forests: review and future directions. *Madagascar Conservation & Development*, *9*(2), 90–97. https://doi.org/10.4314/mcd.v9i2.5

Razafindratsima, O. H., & Razafimahatratra, E. (2010). Effect of red ruffed lemur gut passage on the germination of native rainforest plant species. *Lemur News*, *15*, 39–42.

Sala, O. E., Chapin III, F. S., Armesto, J. J., Berlow, E., Bloomfield, J., Dirzo, R., Huber-Sanwald, E., Huenneke, L. F., Jackson, R. B., Kinzig, A., Leemans, R., Lodge, D. M., Mooney, H. A., Oesterheld, M., LeRoy Poff, N., Sykes, M. T., Walker, B. H., Walker, M., & Wall, D. H. (2000). Global biodiversity scenarios for the year 2100. *Science*, *287*(5459), 1770–1774. https://doi.org/10.1126/science.287.5459.1770

Sato, H. (2012). Frugivory and seed dispersal by brown lemurs in a Malagasy tropical dry forest. *Biotropica*, *44*(4), 479–488. https://doi.org/10.1111/j.1744-7429.2011.00838.x

Schupp, E. W., Jordano, P., & Gómez, J. M. (2010). Seed dispersal effectiveness revisited: a conceptual review. *New Phytologist*, *188*(2), 333–353. https://doi.org/10.1111/j.1469-8137.2010.03402.x

Shono, K., Cadaweng, E. A., & Durst, P. B. (2007). Application of assisted natural regeneration to restore degraded tropical forestlands. *Restoration Ecology*, *15*(4), 620–626.

Sorensen, A. E. (1986). Seed dispersal by adhesion. *Annual Review of Ecology and Systematics*, *17*, 443–463.

Stanturf, J. A., Vance, E. D., Fox, T. R., & Kirst, M. (2013). *Eucalyptus* beyond its native range: environmental issues in exotic bioenergy plantations. *International Journal of Forestry Research*, *2013*, 463030. https://doi.org/10.1155/2013/463030

Strong, J. N., & Fragoso, J. M. V. (2006). Seed dispersal by *Geochelone carbonaria* and *Geochelone denticulata* in northwestern Brazil. *Biotropica*, *38*(5), 683–686. https://doi.org/10.1111/j.1744-7429.2006.00185.x

Styger, E., Rakotoarimanana, J. E. M., Rabevohitra, R., & Fernandes, E. C. M. (1999). Indigenous fruit trees of Madagascar: potential components of agroforestry systems to improve human nutrition and restore biological diversity. *Agroforestry Systems*, *46*, 289–310. https://doi.org/10.1023/A:1006295530509

Terborgh, J., Pitman, N., Silman, M., Schichter, H., & Núñez V., P. (2002). Maintenance of tree diversity in tropical forests. In D. J. Levey, W. R. Silva, & M. Galetti (Eds.), *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation* (pp. 1-17). Wallingford: CAB International. https://doi.org/10.1079/9780851995250.0001

Valiente-Banuet, A., Aizen, M. A., Alcántara, J. M., Arroyo, J., Cocucci, A., Galetti, M., García, M. B., García, D., Gómez, J. M., Jordano, P., Medel, R., Navarro, L., Obeso, J. R., Oviedo, R., Ramírez, N., Rey, P. J., Traveset, A., Verdú, M., & Zamora, R. (2015). Beyond species loss: the extinction of ecological interactions in a changing world. *Functional Ecology*, *29*(3), 299–307. https://doi.org/10.1111/1365-2435.12356

van der Pijl, L. (1982). *Principles of seed dispersal in higher plants*. New York: Springer.

Vincelette, M., Rabenantoandro, J., Randrihasipara, L., Randriatafika, F., & Ganzhorn, J. U. (2007). Results from ten years of restoration experiments in the southeastern littoral forests of Madagascar. In J. U. Ganzhorn, S. M. Goodman, & M. Vincelette (Eds.), *Biodiversity, Ecology and Conservation of Littoral Ecosystems in Southeastern Madagascar, Tolagnaro (Fort Dauphin)* (pp. 337–354). Washington: Smithsonian Institution.

Wang, B. C., & Smith, T. B. (2002). Closing the seed dispersal loop. *Trends in Ecology & Evolution*, *17*(8), 379–386. https://doi.org/10.1016/S0169-5347(02)02541-7

Webber, A. D., Solofondranohatra, J. S., Razafindramoana, S., Fernández, D., Parker, C. A., Steer, M., Abrahams, M., & Allainguillaume, J. (2020). Lemurs in cacao: presence and abundance within the shade plantations of northern Madagascar. *Folia Primatologica*, *91*, 96–107. https://doi.org/10.1159/000501987

Wenny, D. G. (2001). Advantages of seed dispersal: a re-evaluation of directed dispersal. *Evolutionary Ecology Research*, *3*, 51–74.

Wright, P. C., Razafindratsita, V. R., Pochron, S. T., & Jernvall, J. (2005). The key to Madagascar frugivores. In J. L. Dew & J. P. Boubli (Eds.), *Tropical Fruits and Frugivores: The Search for Strong Interactors* (pp. 121–138). Dordrecht: Springer.

Wunderle Jr., J. M. (1997). The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management*, *99*, 223–235. https://doi.org/10.1016/S0378-1127(97)00208-9

WWF/IUCN. (2000). *Forests reborn—A workshop on forest restoration*. Report on the WWF/IUCN International Workshop on Forest Restoration, Segovia, Spain.

CHAPTER I

Lemur food plants as options for forest restoration in Madagascar

RESTORATION ECOLOGY
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RESEARCH ARTICLE

Lemur food plants as options for forest restoration in Madagascar

Kim J. E. Steffens

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 plantscould 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

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Author contribution: KJES conceived and designed the research, analyzed the data, wrote and edited the manuscript.

[1]Department of Biology, Institute of Zoology, University of Hamburg, Martin-Luther-King Platz 3, 20146 Hamburg, Germany
[2]Address correspondence to K. J. E. Steffens, email kimsteffens1@gmail.com

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(Gérard et al. 2015). Depending on the context, the combination of several of these traits determines the attractiveness of plant species for restoration plantings.

In the context of Madagascar, ongoing deforestation threatens its exceptional flora and fauna (Myers et al. 2000; Harper et al. 2007). One of the drivers for this situation is the poverty of the Malagasy population, with 77.8% living on less than 1.90 $ per day (World Bank 2017). The Malagasy people are thus highly dependent on natural resources for food and medicines, often produced through shifting agriculture practices, and for wood that can be used as timber, firewood, and charcoal (Rakotomanana et al. 2013). Even in protected areas, which have exponentially increased since the beginning of this century, these anthropogenic pressures, including hunting, remain (Razafimanahaka 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 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 2019), making Madagascar a top priority in terms of protecting primate diversity (Schwitzer et al. 2014; Estrada et al. 2017). Lemurs play an important role in plant pollination and seed dispersal, allowing for the healthy functioning of Malagasy forest ecosystems, and should be considered in restoration decisions (Kress et al. 1994; Bakker et al. 1996; Razafindratsima 2014). By global comparisons, Madagascar sticks out because it lacks the species-rich guilds of frugivores that dominate most other forest ecosystems throughout the tropics and subtropics (Fleming et al. 1987; Reed & Fleagle 1995; Wright 1999; Kissling et al. 2009; Donati et al. 2017). While frugivores can account for up to 80% of the mammal biomass in other tropical forests (Terborgh 1986), Madagascar has only a handful of frugivorous bird species, three fruit bat species, and some rodents that may cache seeds and thus contribute to seed dispersal (Goodman & Sterling 1996; Albert-Daviaud et al. 2018), and while these species may be important, they have not been widely studied in Madagascar (Goodman et al. 1997; Böhning-Gaese et al. 1999; Bollen & Van Elsacker 2002; Rakotomanana et al. 2003; Picot et al. 2007; Andrianaivoarivelo et al. 2011; Oleksy et al. 2017).

There are no exclusively frugivorous extant lemur species, but many of these species eat fruits and therefore represent the dominant group of frugivores on the island. Their importance in evolutionary terms is illustrated by the fact that the majority of Malagasy fruits are adapted to lemur dispersal (Albert-Daviaud et al. 2018, 2020; Nevo et al. 2019). Under the present conditions, lemurs are essential seed dispersers, especially for large-seeded plant species that cannot be swallowed or transported by most other taxa (Razafindratsima 2014).

Given this critical information, one could potentially achieve a positive, self-sustaining effect by planting species regularly exploited by lemurs. These plants would not only contribute to conservation by offering food and habitat resources, but they would also entice lemurs from neighboring forests into restoration sites, where they would deposit seeds via their feces, thereby accelerating and enriching natural regeneration (Dew & Wright 1998; Razafindratsima & Razafimahatratra 2010; Moses & Semple 2011; Razafindratsima & Martinez 2012; Sato 2012; Elliott et al. 2013; Martinez & Razafindratsima 2014; Ramananjato et al. 2020). The idea of facilitated forest restoration through primate seed dispersal has received little attention (Chapman & Dunham 2018), and so far this idea has only been applied and monitored in one Madagascar restoration program, established in the Masoala National Park in the northeastern part of the country (Holloway 2007). In 1997, this program strategically planted species of food trees of *Varecia rubra* to entice the lemurs into restoration sites, thus promoting seed dispersal. As hoped for, these lemurs dispersed seeds into the restoration sites, while also using unexpectedly low vegetation structures, and occasionally feeding under an open canopy (Martinez 2010; Martinez & Razafindratsima 2014).

For this study, I compiled a database of known lemur food plants (LFP) in Madagascar (Table S1, also available at https://doi.org/10.25592/uhhfdm.1021). The database includes information on study locations and forest types; studied lemur families/genera/species; exploited plant families/genera/species; life forms, origin, and invasive properties of exploited plant species, and their specific exploited parts.

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.

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-do-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

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.

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

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).

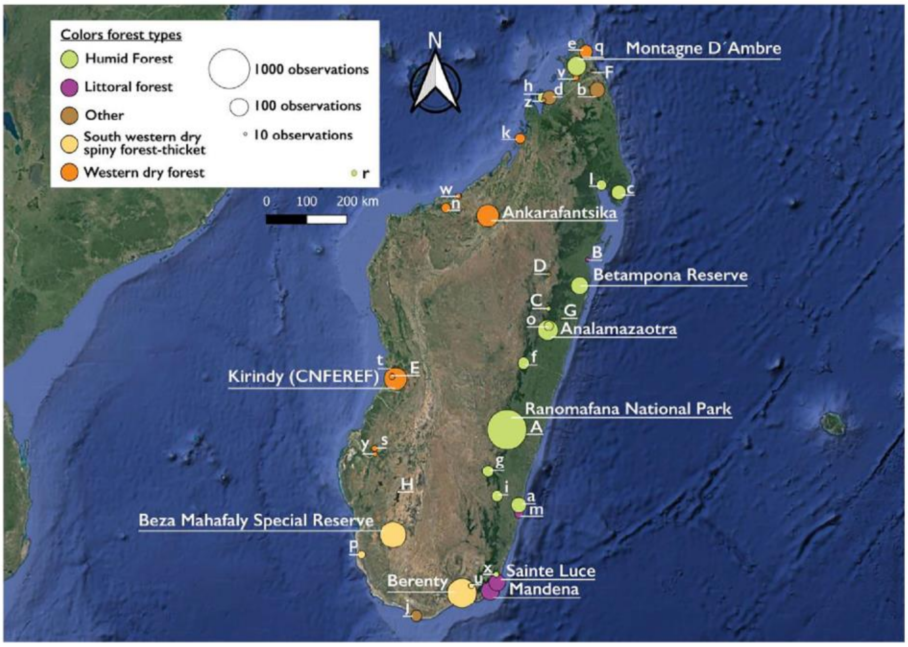

Figure 1 Study sites with at least 10 observations, and related forest types (Moat & Smith 2007; "other" signifies a composition of different forest types occurring equally often at the site, see Supplement S1). Size of circles represents number of observations. The 10 study sites with most observations 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, GEBCO, Landsat/Copernicus, from 14 December, 2015.

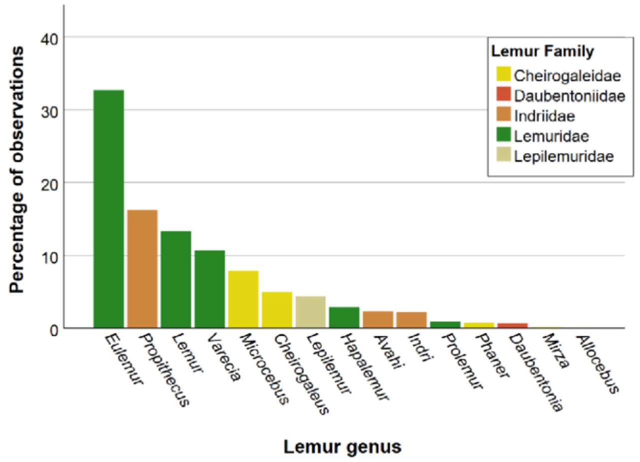

Figure 2 Percentage of observations for each lemur genus (not visible: *Mirza* represents 0.09% of observations, *Allocebus* 0.02%). For definition of observations see Methods: Definition of "Observations" and "Exploitation Observations."

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

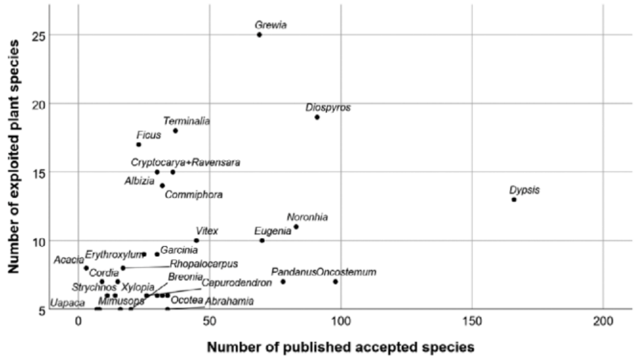

Figure 3 Correlation between the number of exploited plant species and the number of published accepted species (in *Catalogue of the Plants of Madagascar*), in the 30 genera with the largest number of exploited species. Pearson's correlation is significant at a level of significance of 5% ($n = 30$, $r = 0.389$, $p = 0.033$).

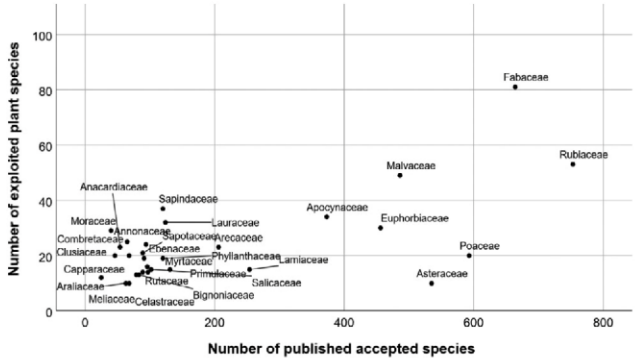

Figure 4 Correlation between the number of exploited plant species and the number of published accepted species (in *Catalogue of the Plants of Madagascar*), in the 30 families with the largest number of exploited species. Pearson's correlation is significant at a level of significance of 5% ($n = 30$, $r = 0.640$, $p = 0.000$).

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 vacacoua	33	*Aphloia theiformis*	19
Canarium madagascariense, Canarium boivinii	32	*S. spinosa, S. madagascariensis, S. vacacoua*	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 soroceoides, 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 madagascariense, C. boivinii*	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.

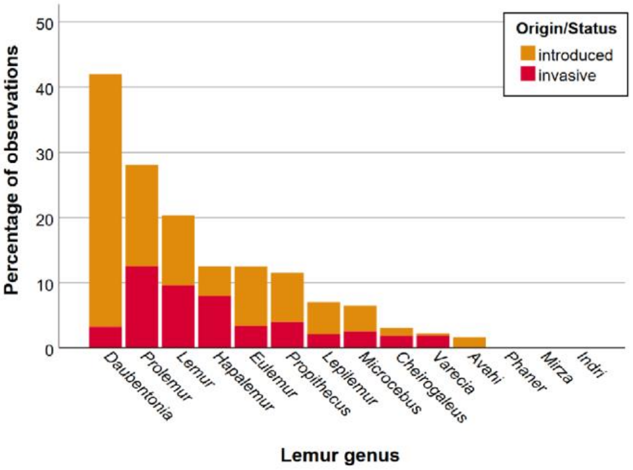

Figure 5 Percentage of observations of introduced/invasive plant species, related to all observations of plant species, for each lemur genus (*Allocebus* missing, because no observations are reported at the plant species level for this genus). For definition of observations see Methods: Definition of "Observations" and "Exploitation Observations."

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

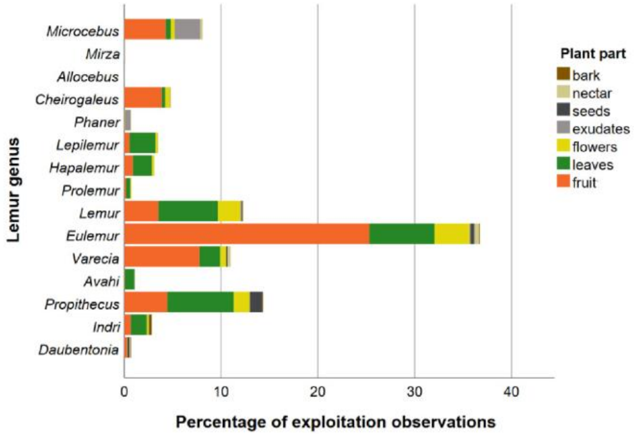

Figure 6 Percentage of exploitation observations of each plant part in each genus, related to all exploitation observations in all genera (not visible: *Mirza* and *Allocebus* together constitute 0.1%). The plant part fruit includes ripe fruit, unripe fruit, exocarp, skin, fruit pulp, flesh, whole fruit, aril, pod; leaves include young leaves, mature leaves, old leaves, leaf base, leaf tip, petiole, leaf bud, shoot, stem, pith, other green parts of the plant not included in the other categories; flowers include petals, blossom, inflorescence, flower buds, pollen; exudates include sap, gum; seeds include seed coat; and bark includes wood. For definition of exploitation observations see Methods: Definition of "Observations" and "Exploitation Observations."

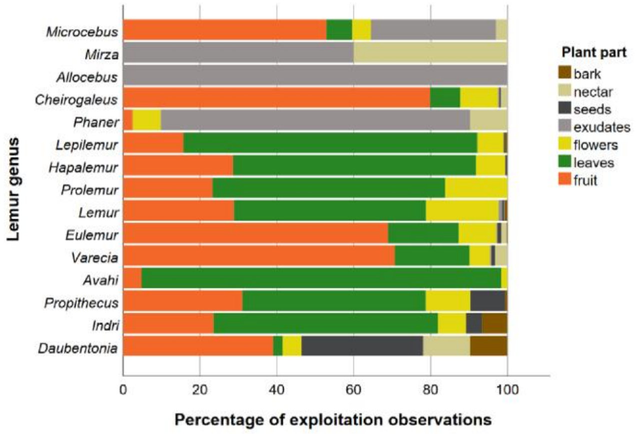

Figure 7 Dietary composition of plant parts for each lemur genus. For definition of exploitation observations see Methods: Definition of "Observations" and "Exploitation Observations."

Birkinshaw and Colquhoun (2003). 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 (Eppley 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 lemur species" exploiting these species. Tamarind (*Tamarindus indica*) stands out with a large number of observations and lemur 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), lemurs 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; Eppley 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, lemurs exploit 7.40%, which is less than the percentage of all species exploited by lemurs 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; Fujii 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 (Rakotoarivelo 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 (Rakotoarivelo 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 lemurs and used by humans for multiple purposes. Unfortunately, successful methods for harvesting this plant sustainably are absent (Rakotoarivelo 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; Powzyk & Mowry 2003; Patel 2014), *Indri indri* (Powzyk & 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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Literature Cited

Albert-Daviaud A, Buerki S, Onjalalaina GE, Perillo S, Rabarijaona R, Razafindratsima OH, Sato H, Valenta K, Wright PC, Stuppy W (2020) The ghost fruits of Madagascar: identifying dysfunctional seed dispersal in Madagascar's endemic flora. Biological Conservation 242:108438

Albert-Daviaud A, Perillo S, Stuppy W (2018) Seed dispersal syndromes in the Madagascan flora: the unusual importance of primates. Oryx 52:418–426

Andriamasimanana M (1994) Ecoethological study of free-ranging Aye-Ayes (*Daubentonia madagascariensis*) in Madagascar. Folia Primatologica 62: 37–45

Andrianaivoarivelo RA, Ramilijaona OR, Racey PA, Razafindrakoto N, Jenkins RKB (2011) Feeding ecology, habitat use and reproduction of *Rousettus madagascariensis* Grandidier, 1928 (Chiroptera: Pteropodidae) in eastern Madagascar. Mammalia 75:69–78

Aumeeruddy-Thomas Y, Rafidison VM, Kjellberg F, Hossaert-McKey M (2018) Sacred hills of Imerina and the voyage of *Ficus lutea* Vahl (Amontana) in Madagascar. Acta Oecologica 90:18–27

Bakker JP, Poschlod P, Strykstra RJ, Bekker RM, Thompson K (1996) Seed banks and seed dispersal: important topics in restoration ecology. Acta Botanica Neerlandica 45:461–490

Birkinshaw C, Andrianjafy M, Rasolofonirina J-J (2009) Survival and growth of seedlings of 19 native tree and shrub species planted in degraded forest as part of a forest restoration project in Madagascar's highlands. Madagascar Conservation & Development 4:128–131

Birkinshaw C, Colquhoun IC (2003) Lemur food plants. Pages 1207–1220. In: Goodman SM, Benstead JP (eds) The natural history of Madagascar. The University of Chicago Press, Chicago, Illinois

Birkinshaw C, Lowry PP II, Raharimampionona J, Aronson J (2013) Supporting target 4 of the global strategy for plant conservation by integrating ecological restoration into the Missouri Botanical Garden's conservation program in Madagascar. Annals of the Missouri Botanical Garden 99:139–146

Bleher B, Potgieter CJ, Potgeiter CJ, Johnson DN, Böhning-Gaese K (2003) The importance of figs for frugivores in a South African coastal forest. Journal of Tropical Ecology 19:375–386

Böhning-Gaese K, Gaese BH, Rabemanantsoa SB (1999) Importance of primary and secondary seed dispersal in the Malagasy tree *Commiphora guillaumini*. Ecology 80:821–832

Bollen A, Van Elsacker L (2002) Feeding ecology of *Pteropus rufus* (Pteropodidae) in the littoral forest of Sainte Luce, SE Madagascar. Acta Chiropterologica 4:33–47

Britt A (2000) Diet and feeding behaviour of the black-and-white ruffed lemur (*Varecia variegata variegata*) in the Betampona Reserve, eastern Madagascar. Folia Primatologica 71:133–141

Budnitz N, Dainis K (1975) *Lemur catta*: ecology and behavior. Pages 219–236. In: Tattersall I, Sussman RW (eds) Lemur biology. Plenum Press, New York

Callmander MW, Phillipson PB, Schatz GE, Andriambololonera S, Rabarimanarivo M, Rakotonirina N, Raharimampionona J, Chatelain C, Gautier L, Lowry PP II (2011) The endemic and non-endemic vascular flora of Madagascar updated. Plant Ecology and Evolution 144:121–125

Campbell MJ, Edwards W, Odell E, Mohandass D, Laurance WF (2015) Can lianas assist in rainforest restoration? Tropical Conservation Science 8: 257–273

Chaer GM, Resende AS, Campello EFC, de Faria SM, Boddey RM (2011) Nitrogen-fixing legume tree species for the reclamation of severely degraded lands in Brazil. Tree Physiology 31:139–149

Chapman CA, Dunham AE (2018) Primate seed dispersal and forest restoration: an African perspective for a brighter future. International Journal of Primatology 39:427–442

Cohen J (1992) A power primer. Psychological Bulletin 112:155–159

Danthu P, Lubrano C, Flavet L, Rahajanirina V, Behra O, Fromageot C, Rabevohitra R, Roger E (2010) Biological factors influencing production of xanthones in *Aphloia theiformis*. Chemistry & Biodiversity 7:140–150

Dew JL, Wright PC (1998) Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. Biotropica 30:425–437

Donati G, Santini L, Eppley TM, Arrigo-Nelson S, Balestri M, Boinski S, et al. (2017) Low levels of fruit nitrogen as drivers for the evolution of Madagascar's primate communities. Scientific Reports 7:14406

Dreesen D, Harrington J, Subirge T, Stewart P, Fenchel G (2002) Riparian restoration in the southwest: species selection, propagation, planting methods, and case studies. Pages 253–272. In: Dumroese RK, Riley LE, Landis TD (eds) National proceedings: forest and conservation nursery associations-1999, 2000, and 2001. USDA Forest Service, Fort Collins, Colorado

Ehlers J, Poppert S, Ratovonamana RY, Ganzhorn JU, Tappe D, Krüger A (2019) Ectoparasites of endemic and domestic animals in Southwest Madagascar. Acta Tropica 196:83–92

Elliott S, Blakesley D, Hardwick K (2013) Restoring tropical forests: a practical guide. Royal Botanic Gardens, Kew, United Kingdom

Eppley TM, Steffens KJE, Colquhoun IC, Birkinshaw C (accepted, 2019) Lemur food plants. In: Goodman SM (ed) The natural history of Madagascar. 2nd edition. The University of Chicago Press, Chicago, Illinois

Estrada A, Garber PA, Rylands AB, Roos C, Fernandez-Duque E, Di Fiore A, et al. (2017) Impending extinction crisis of the world's primates: why primates matter. Science Advances 3:e1600946

Faust S, Hanisch S, Buerkert A, Joergensen RG (2015) Soil properties under manured *Tamarindus indica* in the littoral plain of South-Western Madagascar. Arid Land Research and Management 29:167–179

Fleming TH, Breitwisch R, Whitesides GH (1987) Patterns of tropical vertebrate frugivore diversity. Annual Review of Ecology and Systematics 18:91–109

Fujii Y, Shibuya T, Nakatani K, Itani T, Hiradate S, Parvez MM (2004) Assessment method for allelopathic effect from leaf litter leachates. Weed Biology and Management 4:19–23

Ganzhorn JU, Kappeler PM (1996) Lemurs of the Kirindy Forest. Pages 257–274. In: Ganzhorn JU, Sorg J-P (eds) *Ecology and economy of a tropical dry forest in Madagascar. Primate report 46–1*. German Primate Center, Göttingen, Germany.

Gardner CJ, Nicoll ME, Birkinshaw C, Harris A, Lewis RE, Rakotomalala D, et al. (2018) The rapid expansion of Madagascar's protected area system. Biological Conservation 220:29–36

Gérard A, Ganzhorn JU, Kull CA, Carrière SM (2015) Possible roles of introduced plants for native vertebrate conservation: the case of Madagascar. Restoration Ecology 23:768–775

Gómez-Aparicio L (2009) The role of plant interactions in the restoration of degraded ecosystems: a meta-analysis across life-forms and ecosystems. Journal of Ecology 97:1202–1,214

Goodman SM, Ganzhorn JU (1997) Rarity of figs (*Ficus*) on Madagascar and its relationship to a depauperate frugivore community. Revue d'Écologie (La Terre et la Vie) 52:321–329

Goodman SM, Ganzhorn JU, Wilmé L (1997) Observations at a *Ficus* tree in Malagasy humid forest. Biotropica 29:480–488

Goodman SM, Raherilalao MJ, Wohlhauser S (eds) (2018) Les aires protégées terrestres de Madagascar: leur histoire, description et biote/ The terrestrial protected areas of Madagascar: their history, description, and biota. Association Vahatra, Antananarivo, Madagascar

Goodman SM, Sterling EJ (1996) The utilization of *Canarium* (Burseraceae) seeds by vertebrates in the RNI d'Andringitra, Madagascar. Pages 83–89. In: Goodman SM (ed) *A floral and faunal inventory of the eastern slopes of the Réserve naturelle intégrale d'Andringitra, Madagascar: with reference to elevational variation*. Fieldiana: zoology, new series 85. Field Museum of Natural History, Chicago, Illinois.

Harper GJ, Steininger MK, Tucker CJ, Juhn D, Hawkins F (2007) Fifty years of deforestation and forest fragmentation in Madagascar. Environmental Conservation 34:325–333

Hemingway CA (1998) Selectivity and variability in the diet of Milne-Edwards' sifakas (*Propithecus diadema edwardsi*): implications for folivory and seed-eating. International Journal of Primatology 19:355–377

Holloway L (2004) Ecosystem restoration and rehabilitation in Madagascar. Ecological Restoration 22:113–119

Holloway L (2007) Targeting sustainable options for restoring natural capital in Madagascar. Pages 64–75. In: Aronson J, Milton SJ, Blignaut JN (eds) Restoring natural capital: science, business, and practice. Island Press, Washington DC

Kissling WD, Böhning-Gaese K, Jetz W (2009) The global distribution of frugivory in birds. Global Ecology and Biogeography 18:150–162

Knowles OH, Parrotta JA (1995) Amazonian forest restoration: an innovative system for native species selection based on phenological data and field performance indices. Commonwealth Forestry Review 74: 230–243

Kress WJ, Schatz GE, Andrianifahanana M, Morland HS (1994) Pollination of *Ravenala madagascariensis* (Strelitziaceae) by lemurs in Madagascar: evidence for an archaic coevolutionary system? American Journal of Botany 81:542–551

Kull CA, Tassin J, Moreau S, Ramiarantsoa HR, Blanc-Pamard C, Carrière SM (2012) The introduced flora of Madagascar. Biological Invasions 14: 875–888

LaFleur M, Gould L (2009) Feeding outside the forest: the importance of crop raiding and an invasive weed in the diet of gallery forest ring-tailed lemurs (*Lemur catta*) following a cyclone at the Beza Mahafaly Special Reserve, Madagascar. Folia Primatologica 80:233–246

Lamb D, Erskine PD, Parrotta JA (2005) Restoration of degraded tropical forest landscapes. Science 310:1628–1,632

Lavialle J, Carrière SM, Miandrimanana C, Tilahimena A, Birkinshaw C, Aronson J (2015) Complementarity of native and introduced tree species: exploring timber supply on the east coast of Madagascar. Madagascar Conservation & Development 10:137–143

Manjaribe C, Frasier CL, Rakouth B, Louis EE Jr (2013) Ecological restoration and reforestation of fragmented forests in Kianjavato, Madagascar. International Journal of Ecology 2013:726275

Mansourian S, Razafimahatratra A, Ranjatson P, Rambeloarisao G (2016) Novel governance for forest landscape restoration in Fandriana Marolambo, Madagascar. World Development Perspectives 3:28–31

Martinez BT (2010) Forest restoration in Masoala National Park, Madagascar: the contribution of the red-ruffed lemur (*Varecia rubra*) and the livelihoods of subsistence farmers at Ambatoladama. PhD Dissertation. University of Minnesota, Minneapolis, Saint Paul, Crookston, Duluth, Morris, Rochester.

Martinez BT, Razafindratsima OH (2014) Frugivory and seed dispersal patterns of the red-ruffed lemur, *Varecia rubra*, at a forest restoration site in Masoala National Park, Madagascar. Folia Primatologica 85:228–243

Meier B, Rumpler Y (1987) Preliminary survey of *Hapalemur simus* and of a new species of *Hapalemur* in eastern Betsileo, Madagascar. Primate Conservation 8:40–43

Mittermeier RA, Louis EE Jr, Richardson M, Schwitzer C, Langrand O, Rylands AB, et al. (2010) Lemurs of Madagascar. 3rd edition. Conservation International, Bogotá, Colombia

Moat J, Smith P (2007) Atlas of the vegetation of Madagascar. Royal Botanic Gardens, Kew, England

Morelli TL, Smith AB, Mancini AN, Balko EA, Borgerson C, Dolch R, et al. (2020) The fate of Madagascar's rainforest habitat. Nature Climate Change 10:89–96

Moses KL, Semple S (2011) Primary seed dispersal by the black-and-white ruffed lemur (*Varecia variegata*) in the Manombo forest, South-East Madagascar. Journal of Tropical Ecology 27:529–538

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Nadhurou B, Righini R, Gamba M, Laiolo P, Ouledi A, Giacoma C (2017) Effects of human disturbance on the mongoose lemur *Eulemur mongoz* in Comoros: implications and potential for the conservation of a critically endangered species. Oryx 51:60–67

Nathan R, Muller-Landau HC (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. Trends in Ecology & Evolution 15:278–285

Nevo O, Razafimandimby D, Valenta K, Jeffrey JAJ, Reisdorff C, Chapman CA, et al. (2019) Signal and reward in wild fleshy fruits: does fruit scent predict nutrient content? Ecology and Evolution 9:10534–10543

Oleksy R, Giuggioli L, McKetterick TJ, Racey PA, Jones G (2017) Flying foxes create extensive seed shadows and enhance germination success of pioneer plant species in deforested Madagascan landscapes. PLoS One 12: e0184023

Padilla FM, Ortega R, Sánchez J, Pugnaire FI (2009) Rethinking species selection for restoration of arid shrublands. Basic and Applied Ecology 10:640–647

Parvez SS, Parvez MM, Fujii Y, Gemma H (2003) Allelopathic competence of *Tamarindus indica* L. root involved in plant growth regulation. Plant Growth Regulation 41:139–148

Patel ER (2014) Silky sifaka *Propithecus candidus* Grandidier, 1871. Pages 38–43. In: Chiozza F, Clark FE, Mittermeier RA, Rylands AB, Schwitzer C, Taylor LA, Wallis J, Williamson EA (eds) Primates in peril: the world's 25 most endangered primates 2012–2014. IUCN SSC Primate Specialist Group (PSG), International Primatological Society (IPS), Conservation International (CI), Bristol Zoological Society (BZS), Arlington, Virginia

Picot M, Jenkins RKB, Ramilijaona O, Racey PA, Carrière SM (2007) The feeding ecology of *Eidolon dupreanum* (Pteropodidae) in eastern Madagascar. African Journal of Ecology 45:645–650 (accessed June 01, 2020).

Plants of the World Online (POWO) (2020) Facilitated by the Royal Botanic Gardens, Kew. http://www.plantsoftheworldonline.org/

Powzyk JA, Mowry CB (2003) Dietary and feeding differences between sympatric *Propithecus diadema diadema* and *Indri indri*. International Journal of Primatology 24:1143–1162

Quéméré E, Hibert F, Miquel C, Lhuillier E, Rasolondraibe E, Champeau J, et al. (2013) A DNA metabarcoding study of a primate dietary diversity and plasticity across its entire fragmented range. PLoS One 8:e58971

Rabearivony AD, Kuhlman AR, Razafiariso ZL, Raharimalala F, Rakotoarivony F, Randrianarivony T, et al. (2015) Ethnobotanical study of the medicinal plants known by men in Ambalabe, Madagascar. Ethnobotany Research and Applications 14:123–138

Rakotoarivelo N, Razanatsima A, Rakotoarivony F, Rasoaviety L, Ramarosandratana A, Jeannoda V, et al. (2014) Ethnobotanical and economic value of *Ravenala madagascariensis* Sonn. In eastern Madagascar. Journal of Ethnobiology and Ethnomedicine 10:57

Rakotomanana H, Hino T, Kanzaki M, Morioka H (2003) The role of the velvet asity *Philepitta castanea* in regeneration of understory shrubs in Madagascan rainforest. Ornithological Science 2:49–58

Rakotomanana H, Jenkins RKB, Ratsimbazafy J (2013) Conservation challenges for Madagascar in the next decade. Pages 33–39. In: Raven PH, Sodhi NS, Gibson L (eds) Conservation biology: voices from the tropics. John Wiley & Sons, Ltd., Oxford, United Kingdom

Rakotoniaina EN, Donno D, Randriamampionona D, Harinarivo HL, Andriamaniraka H, Solo NR, et al. (2018) Insights into an endemic medicinal plant species of Madagascar and Comoros: the case of Famelona (*Chrysophyllum boivinianum* (Pierre) Baehni, Sapotaceae family). South African Journal of Botany 117:110–118

Ramananjato V, Rakotomalala Z, Park DS, DeSisto CMM, Raoelinjanakolona NN, Guthrie NK, et al. (2020) The role of nocturnal omnivorous lemurs as seed dispersers in Malagasy rain forests. Biotropica 1–8.

Ranaivoson T, Brinkmann K, Rakouth B, Buerkert A (2015) Distribution, biomass and local importance of tamarind trees in South-Western Madagascar. Global Ecology and Conservation 4:14–25

Razafimanahaka JH, Jenkins RKB, Andriafidison D, Randrianandrianina F, Rakotomboavonjy V, Keane A, et al. (2012) Novel approach for quantifying illegal bushmeat consumption reveals high consumption of protected species in Madagascar. Oryx 46:584–592

Razafindratsima OH (2014) Seed dispersal by vertebrates in Madagascar's forests: review and future directions. Madagascar Conservation & Development 9:90–97

Razafindratsima OH, Jones TA, Dunham AE (2014) Patterns of movement and seed dispersal by three lemur species. American Journal of Primatology 76:84–96

Razafindratsima OH, Martinez BT (2012) Seed dispersal by red-ruffed lemurs: seed size, viability, and beneficial effect on seedling growth. Ecotropica 18:15–26

Razafindratsima OH, Razafimahatratra E (2010) Effect of red ruffed lemur gut passage on the germination of native rainforest plant species. Lemur News 15:39–42

Reed KE, Fleagle JG (1995) Geographic and climatic control of primate diversity. Proceedings of the National Academy of Sciences 92:7874–7,876

Richardson DM, Pysek P, Rejmanek M, Barbour MG, Panetta FD, West CJ (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6:93–107

Sato H (2012) Frugivory and seed dispersal by brown lemurs in a Malagasy tropical dry forest. Biotropica 44:479–488

Sauther ML, Cuozzo FP (2009) The impact of fallback foods on wild ring-tailed lemur biology: a comparison of intact and anthropogenically disturbed habitats. American Journal of Physical Anthropology 140:671–686

Schwitzer C, Mittermeier RA, Johnson SE, Donati G, Irwin M, Peacock H, et al. (2014) Averting lemur extinctions amid Madagascar's political crisis. Science 343:842–843

Styger E, Rakotoarimanana JEM, Rabevohitra R, Fernandes ECM (1999) Indigenous fruit trees of Madagascar: potential components of agroforestry systems to improve human nutrition and restore biological diversity. Agroforestry Systems 46:289–310

Sussman RW, Rakotozafy A (1994) Plant diversity and structural analysis of a tropical dry forest in southwestern Madagascar. Biotropica 26:241–254

Terborgh J (1986) Community aspects of frugivory in tropical forests. Pages 371–384. In: Estrada A, Fleming TH (eds) Frugivores and seed dispersal. Springer, Dordrecht, The Netherlands

Terborgh J, Nuñez-Iturri G, Pitman NCA, Valverde FHC, Alvarez P, Swamy V, et al. (2008) Tree recruitment in an empty forest. Ecology 89:1757–1768

Vieilledent G, Grinand C, Rakotomalala FA, Ranaivosoa R, Rakotoarijaona J-R, Allnutt TF, et al. (2018) Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. Biological Conservation 222:189–197

Williams JT (2006) Introduction, taxonomy, description and distribution. Pages 1–12. In: El-Siddig K, Gunasena HPM, Prasad BA, Pushpakumara DKNG, Ramana KVR, Vijayanand P, Williams JT (eds) Tamarind. *Tamarindus indica*. Southampton Centre for Underutilised Crops, Southampton, United Kingdom

World Bank (2017) World development indicators 2017. World Bank, Washington DC

World Conservation Union (2019) The IUCN red list of threatened species. Version 2019–3. http://www.iucnredlist.org (accessed 29 Jan 2020).

Wright PC (1999) Lemur traits and Madagascar ecology: coping with an Island environment. Yearbook of Physical Anthropology 42:31–72

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 sources (S1.2) and other literature cited (S1.3).

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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Chapter 1 author contributions

I hereby confirm that Kim J. E. Steffens designed the study and carried out a literature search to collect the data. He analyzed the data and wrote the manuscript.

Jörg Ganzhorn

Prof. Dr. Jörg Ganzhorn

CHAPTER 2

The role of lemur seed dispersal in restoring degraded forest ecosystems in Madagascar (accepted by *Folia Primatologica*)

Kim J. E. Steffens[a], Justin Sanamo[b], Jeremi Razafitsalama[c]

[a] Department of Biology, Institute of Zoology, Universität Hamburg, Martin-Luther-King Platz 3, 20146 Hamburg, Germany

[b] Département Sciences de la Nature et de l'Environnement, Facultés des Sciences, Université d'Antsiranana, Antsiranana 201, Madagascar

[c] Missouri Botanical Garden Antsiranana, BP 268, Antsiranana 201, Madagascar

ABSTRACT

Anthropogenic disturbances lead to the degradation or destruction of tropical forests, with negative consequences for flora, fauna, and local people. Restoration plantings may compensate these impacts, but time and financial expenditures are high. Thus, priority is often given to plantations of a few introduced species that have little value for conservation. Animal seed dispersal may diversify and accelerate regeneration of restoration plantings, thereby lowering their costs. We studied seed dispersal quantity and quality of crowned lemurs (*Eulemur coronatus*) in a highly degraded forest in northern Madagascar, conducting behavioural observations and germination experiments and describing dispersed plant species' characteristics. Crowned lemurs were highly frugivorous, dispersing a large number of seeds and plant species. While there were negative effects of gut passage on germination, the positive effects of pulp removal outweighed these, resulting in an overall positive effect on regeneration. Our study confirmed that effects of gut passage are dependent on the dispersed plant species. We found 20 plant species, including three threatened with extinction, whose only dispersers in Oronjia seem to be crowned lemurs. We conclude that lemurs play important roles in protecting plant species and maintaining healthy ecosystems through seed dispersal, and that *E. coronatus* is a key species in this respect. In addition, if lemurs were included in restoration, they would disperse a diversity of plant species that cannot be matched by conventional restoration plantings. Their influence would facilitate the regeneration of some, but not all plant species. Negative effects, like the spread of invasive species through seed dispersal by lemurs, must also be considered.

Keywords: Conservation, Facilitated regeneration, Diet, Primates, True lemurs

1. INTRODUCTION

Over the last century Africa has become the global “deforestation hotspot”, with the highest deforestation rate among all continents (FAO, 2020: 125). It is estimated that Madagascar’s forest cover decreased by 40% between 1950 and 2000 (Harper et al., 2007). While a lot of tropical forest has already been lost, there is even more forest area that is now degraded to different degrees, exceeding the area that is still covered with original forest (International Tropical Timber Organization, 2002, 2020). Forest degradation and its impact on diversity can be difficult to measure due to its variable intensity and appearance, and exact estimates for the extent of degradation in Madagascar’s forest are missing (Asner et al., 2004; Burivalova et al., 2015). Nevertheless, the consequences of anthropogenic disturbances are generally negative for flora and fauna, illustrated by the fact that entire ecosystems and their inhabitants were already threatened with extinction many years ago (Ganzhorn et al., 2001; Irwin et al., 2010). Population declines and species extinctions do not only reduce species diversity, but also disrupt ecological interactions and thus functional diversity, or from the human perspective, ecosystem services (Chazdon, 2008; Valiente-Banuet et al., 2015).

Restoration activities may compensate or reverse the consequences of deforestation and degradation, but restoration with native tree species is time consuming, costly, and the information on peculiarities of the region and adaptations of plants to the local conditions are rarely available (Pareliussen et al., 2006; Chazdon, 2008; Birkinshaw et al., 2009). That is why simple reforestation with very few well-known and usually introduced species, such as *Eucalyptus* spp., is often given priority: In Africa nearly 70% of all planted forests belong to these plantations, which may offer short-term financial benefits for the people, but are of little value for conservation (FAO, 2020; Konersmann et al., 2021).

In Madagascar, lemurs play important roles in ecological interactions as predator and prey species, pollinators, and seed dispersers (Soma, 2006; Heymann, 2011; Razafindratsima, 2014; Goodman & Ganzhorn, in press). Seed dispersal is essential for plant ecology and evolution, as it provides the basis for the regeneration of many plants, and impacts plant colonization, invasion and distribution, demography, community structure and thus species diversity (Terborgh et al., 2002; Wang & Smith, 2002; Schupp et al., 2010; Jordano et al., 2011; Martinez & Razafindratsima, 2014).

From a conservational perspective it is important to understand the consequences that lemur population declines or extinctions have on ecosystems, through the loss of the function of seed dispersal and its impact on regeneration (Ganzhorn et al., 1999; Crowley et al., 2011; Federman et al., 2016; Albert-Daviaud et al., 2018, 2020). From the same perspective, but turning the argument around, seed dispersal by lemurs might be an important contribution to the restoration of ecosystems. To this end, planting activities could include species to attract lemurs and foster their seed dispersal to facilitate regeneration, thereby lowering the costs for restoration (Wunderle Jr., 1997; Styger et al., 1999; Holloway, 2004; Razafindratsima & Razafimahatratra, 2010; Razafindratsima & Martinez, 2012; Martinez & Razafindratsima, 2014; Ramananjato et al., 2020; Steffens, 2020).

To explore the possibilities of facilitated restoration in degraded forests through seed dispersal, studies on the dispersers' ecology and behaviour in these forests are indispensable. However, primate field research is highly biased towards species and study sites: Between 2011 and 2015 for example, only four different study sites accounted for nearly 50% of research field stays in Madagascar, probably because they are easily accessible and provide research facilities (Bezanson & McNamara, 2019). These sites, including Ranomafana National Park, Berenty Private Reserve, Kirindy Forest National Park and Ankarafantsika National Park, harbour relatively intact habitats, therefore more applied studies in anthropogenic habitats such as degraded forests are needed (Ganzhorn, 1987; Irwin et al., 2010; Goodman et al., 2018).

In order to provide the basis for the integration of lemurs into restoration activities, this study aims to describe the "seed dispersal quantity and quality" (Schupp, 1993) of crowned lemurs (*Eulemur coronatus*) in a highly degraded forest in northern Madagascar. Specific questions we aim to answer are: What is the proportion of fruits in the animals' diet? How many seeds and plant species are dispersed, and how are characteristics like seed size, plant origin and invasiveness? How do crowned lemurs handle fruits and seeds, and how is seed condition, as well as germination success and time, affected by the gut passage?

2. METHODS

2.1 Study site

We conducted the study in the southeastern part of the Oronjia New Protected Area (between 12°16´17´´ S – 12°16´53´´ S and 49°23´10´´ E – 49°23´53´´ E; WGS84), about 15 km east of Antsiranana in northern Madagascar. The vegetation of the study site consists of western dry deciduous forest (Moat & Smith, 2007). Due to former anthropogenic pressures, like charcoal production, forest clearance for cultivation, selective tree cutting, and military use, the forest is highly degraded (Goodman et al., 2018). Its height rarely reaches more than 8 m, the leaf concentration is highest between 0.2 and 2 m, and in many areas taller vegetation is absent (Missouri Botanical Garden, 2015).

2.2 Equipment with radio-collars

In April 2018, five individuals of crowned lemurs were anaesthetized with 15 mg Telazol® (Tiletamine HCl and Zolazepam HCl, 100 mg/mL, zoetis, United States), administered by remote injection. This was done by a team led by E. E. Louis, Jr. (Omaha's Henry Doorly Zoo and Aquarium), including F. Randrianasolo, G. Nalinirina, T. F. Razafimanjato, H. E. Razafimahatratra and J. R. Rakotonomenjanahary. Each animal was equipped with a brass collar carrying a TW-3 radio tag by biotrack, weighing together ca. 16.7 g, or 1.2% of the mean body weight. Afterwards, we administered 6 mL of electrolyte solution (Veterinary lactated ringer's injection USP, manufactured for Abbott laboratories) subcutaneously, to avoid dehydration. Animals were kept in cloth bags in the shade until they fully recovered, and released at the place of their capture. The same procedure was carried out in April 2019, to detach the radio-collars. The mean body weight of adult crowned lemurs was 1364 g (*SD*= 127; *N*= 7), the mean body length, measured from occipital to basis of the tail, was 30.6 cm (*SD*= 4.2; *N*= 7), the mean tail length, measured from basis to tip of tail, was 47.4 cm (*SD*= 1.8; *N*= 7).

In the Oronjia forest it would be impossible to locate and follow crowned lemurs without collars, as their abundance is very low, the animals are timid, and forest undergrowth is very dense with few trails. To be able to collect enough seeds for the germination experiment, containing different plant species (see 2.3), and to be able to accumulate enough observation time to allow the exclusion of seasonal or other biases, it was thus crucial to equip the study animals with radio-collars and habituate them.

2.3 Data collection

The data collection focused on two groups of crowned lemurs with sizes of 5-7 (group A) and 8-14 (group B) individuals. Group B was often weakly cohesive, showing strong fluctuation in size especially in the dry season, as it was found before for *E. coronatus* (Freed, 1996).

We habituated the lemurs to our presence, for one month. By that time, group A was fully habituated, and group B semi-habituated. In behavior surveys, we followed one group of lemurs and conducted all-occurrence sampling of their feeding-related behaviour (Zuberbühler & Wittig, 2011). Using binoculars, we observed which item was consumed and, in case of plant parts, which species. We measured duration of feeding bouts, which we defined as the time that at least one individual of the observation group was consuming food. We conducted the surveys from mid-June 2018 to mid-April 2019, from dawn to 1130 h and/or from 1430 h to dusk. We had to intermit the surveys from 1130 h to 1430 h for logistical reasons, as well as during the night, because the forest undergrowth is difficult to penetrate and also impairing visibility of our study animals. The mean observation time per day, which we calculated by using only days with two surveys carried out of the same group, was 6.7 h (*SD*= 0.6; *N*= 33) for group A and 4.0 h (*SD*= 1.6; *N*= 27) for group B. The total observation time, the time we observed at least one individual of the two groups, adds up to 527 h. During this time, we took a GPS point every five minutes with a handheld GPS (Garmin GPSMAP 64s).

2.3.1 Feces collection

During the surveys we collected fresh feces, either located by observing a defecation event, or by checking the ground at places where animals stayed for at least 15 minutes. When we could clearly assign a dropping to an individual, we put it in a separate plastic bag, otherwise we combined all droppings within a radius of 1.5 m into one plastic bag. We treated each bag as one sample in further analysis.

Within 48 hours following the collection we washed the feces in a sieve with 1x1 mm openings (Stevenson, 2000; Sato, 2012). We identified seeds that had fallen through and were held back with the help of our own reference collection of seeds (Photograph: Fig. S1; Bollen & van Elsacker, 2002), but counted only the seeds held back (> 1 mm length; Razafindratsima & Martinez, 2012). If more than 100 seeds of one species occurred in a sample, we estimated numbers. Not all dispersed seeds and the associated plants could be identified on the species level, but they could be clearly differentiated as morphospecies. Thus, independent of the level of identification, the species/ morphospecies are from now on treated as species.

We checked the seeds condition, differentiating between intact, damaged by lemur (showing dental damage/ being destructed) and damaged by insects (showing small holes)/ rotten preceding ingestion/ malformed. Further, we assessed ripeness of seeds, differentiating between ripe (usually hard and fully developed) and unripe (usually soft, not fully developed and differently coloured).

2.3.2 Germination experiment

We planted intact seeds from feces in a tree nursery, under controlled, semi-shaded conditions (Photograph: Fig. S2). From the same plant species, we planted whole fruits (from now on "fruit") and seeds manually extracted from fruits ("extracted") as controls (Dew & Wright, 1998; Moses & Semple, 2011; Sato, 2012). This experimental design was intended to mimic the influence animals can have on germination, via removing the fruit pulp and passing seeds through their gastro-intestinal tract (Samuels & Levey, 2005). By comparing the treatments *extracted* and *fruit*, it is possible to determine the effect of removing the fruit pulp that can have inhibitory effects on germination (1). These inhibitory effects include the blocking of biochemical processes responsible for germination and making the light regime and osmotic pressure unfavourable for germination (reviewed in Traveset et al., 2007). By comparing the treatments *feces* and *extracted*, it is possible to determine the effect of the gut passage, which can be mechanical and/or chemical (2). By comparing *feces* and *fruit*, it is possible to determine both effects together (1+2; Samuels & Levey, 2005).

While collecting fruits for the experiments, we picked fruits from different plant individuals wherever possible - either directly from the plant or from the ground - to balance possible genetic effects. We only planted fruits and seeds extracted from fruits that were ripe and intact, which we assessed visually and olfactorily. Before planting, we measured the longest side ("length") of seeds from feces/ seeds extracted from fruits/ whole fruits to the nearest mm with a calliper (15-20 seeds/fruits per species; Moses & Semple, 2011).

For planting, we filled polyethylene bags having drainage holes, with a mixture of two parts forest soil and one part dung, following recommendations by local tree nursery workers. We placed each seed/fruit in a single bag, and planted 15-20 seeds per treatment of each plant species, depending on availability. In total, we planted 47 different plant species.

We monitored the plantings at least every third day, and watered them depending on weather conditions, so that the soil never dried out completely. We weeded the plantings regularly. When the first part of the seedling (cotyledon/ stalk) appeared aboveground, we noted this as date of germination. We planted seeds between June 2018 and April 2019, and continued the monitoring until October 2019.

2.4 Analysis

We performed calculations and generated plots in R (version 4.0.1; R Core Team 2020) and IBM SPSS Statistics (version 26). To calculate home ranges we used the R package "AdehabitatHR" (Calenge, 2006).

2.4.1 Seed dispersal quantity and dispersed species' characteristics

Diet

We calculated the proportion of different food items in the diet of both lemur groups together. This was done by dividing the duration of feeding bouts on each item by the total duration of feeding bouts on all items.

Number of seeds dispersed

By dividing the total number of seeds found in feces by the total observation time and then by the mean group size, we calculated the number of seeds dispersed per hour of observation and individual of lemur. By multiplying this value with the mean observation time per day, we calculated the number of seeds dispersed per "observation day" and individual of lemur (1). To relate this number to the area used by the animals, we calculated home range sizes by use of multiple convex polygons, including all GPS points taken during behaviour surveys. By dividing the mean group size by the home range size, we calculated the population density in individuals per square kilometre without considering overlap between the two groups' home ranges (2), following Sato (2012). Multiplying the results 1 and 2, we calculated the number of seeds dispersed per square kilometre and observation day (3). We calculated step 1 - 3 separately for the two groups. To obtain an estimate for the whole population of lemurs, we took the mean of the results of step 3.

Fruit and seed sizes

We calculated mean seed length of plant species whose seeds were dispersed and mean fruit length of plant species whose fruits were swallowed, and classified species means in the size categories “small” (<5 mm), “medium” (5-10 mm) and “large” (>10 mm), following Dew and Wright (1998). As “swallowed” we considered fruits that we observed to be swallowed at least occasionally in one piece.

Distribution of dispersed plant species

We looked up the distribution for all dispersed plants we were able to identify at the species level in the *Catalogue of the Vascular Plants of Madagascar* (Madagascar Catalogue 2021). All distribution statuses other than “endemic”, “native but not endemic” and “naturalized” were pooled to “other”, these included “Africa”, “Comoros, Africa” and one species that was not included in the catalogue.

2.4.2 Seed dispersal quality: Germination success and time

We firstly analysed the data at the community level, for all 47 plant species together, and afterwards at the species level, for each species separately. Not all seeds are statistically independent, as they may have been defecated by the same individual of lemur or collected from the same plant. We treated them nonetheless as independent during analysis, as we assume that variations within the treatments are small compared to variations between treatments, following Razafindratsima and Martinez (2012).

Using Chi-square independence tests, we analysed whether germination success (%) depends on the seed source (Sato, 2012). If there were no cells with expected frequencies lower than 5, we calculated Pearson’s chi-square test, otherwise we calculated Fisher’s exact test. If these global tests were significant ($p < 0.05$), we carried out Bonferroni-corrected pairwise comparisons between the three treatments.

To analyse whether germination time (d) depends on the seed source, we used either ANOVA (global test) and Tukey HSD post hoc tests (Moses & Semple, 2011), if homogeneity of variances was given according to Levene’s test, or Welch-Test (global test) and Games-Howell post hoc tests, if homogeneity was not given. We ignored violations of the normal distribution assumption for ANOVA, because it is robust against these (Schmider et al., 2010).

3. RESULTS

3.1 Seed dispersal quantity and dispersed species' characteristics

3.1.1 Diet

The lemurs fed mainly on fruit (81.9%) - including ripe (59.7%) and unripe (22.3%) fruit - and to a lesser extent on leaves (8.3%), flowers (6.6%) and nectar (2.7%) (Fig. 1). They rarely fed on invertebrates (0.3%) and honey, fungi, soil and a propagule (together 0.2%).

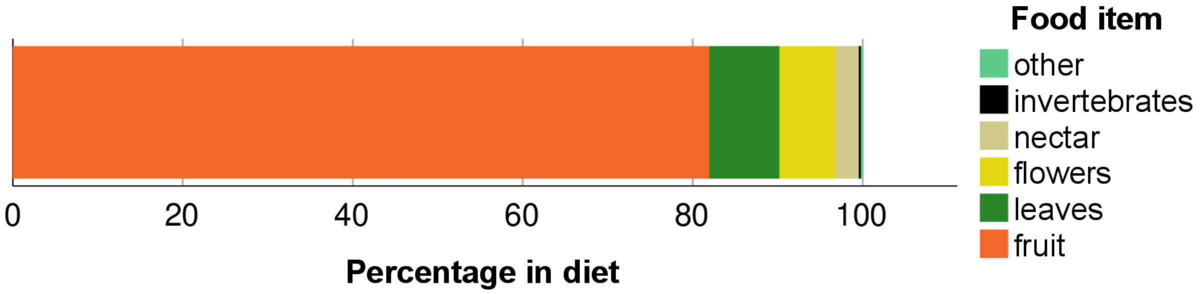

Figure 1 Percentage of different items in the diet of crowned lemurs in Oronjia, calculated by use of the duration of feeding bouts, which are defined as the time we observed at least one individual of the survey group feeding.

3.1.2 Number of seeds dispersed

In total we collected 993 feces samples, and 97% of these contained seeds. The mean number of seeds dispersed by the lemur groups per km2 and observation day was 698 (*SD*= 430; *N*= 2 groups). This number can be seen as an estimate for the whole population.

3.1.3 Fruit and seed size

The mean fruit length of plant species whose fruits were swallowed was 13.3 mm (*SD*= 7.2; *N*= 35), with 2.9% of species having small fruits, 31.4% having medium sized fruits, and 65.7% having large fruits (Table S1). The mean seed length of plant species whose seeds were dispersed was 10.3 mm (*SD*= 5.6; *N*= 56), with 21.4% of species having small seeds, 30.4% having medium sized seeds, and 48.2% having large seeds. The largest seeds dispersed are those of *Abrahamia suarezensis*, with a mean length of 27 mm (*SD*= 2; *N*= 19).

3.1.4 Number and distribution of dispersed plant species

Group A dispersed 70 plant species and group B dispersed 58 plant species, altogether they dispersed 80 plant species. Per observation day, the lemurs dispersed on average 6.0 (*SD*= 3.1;

N= 33; group A) and 5.9 (*SD*= 3.7; *N*= 27; group B) plant species. Of all 80 plant species 52 could be identified on the species level. Of the latter, 28 (54%) are endemic to Madagascar, 15 (29%) are native but not endemic, 4 (8%) are naturalized, and 5 (10%) have another distribution according to the *Catalogue of the Vascular Plants of Madagascar* (Fig. 2; Table S1; Madagascar Catalogue 2021). Of all species neither endemic nor native to Madagascar *Lantana camara* and *Ziziphus spina-christi* are invasive according to Kull et al. (2012), as they produce reproductive offspring over distance (Richardson et al., 2000).

According to the IUCN Red List (IUCN, 2021), 26 (50%) of the 52 plants identified on species level are of Least Concern, 1 (2%) is Near Threatened, 6 (12%) are Vulnerable, 1 (2%) is Endangered, and 18 (35%) are not included (Table S1).

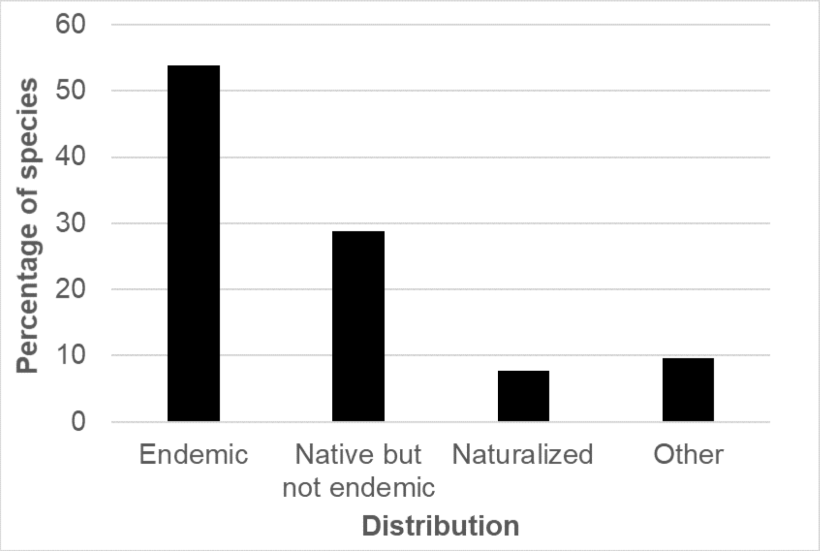

Figure 2 Percentage of dispersed plant species with different distributions according to the *Catalogue of the Vascular Plants of Madagascar* (Madagascar Catalogue 2021).

3.2 Seed dispersal quality

3.2.1 Seed condition

Most of the fecal clumps were loosely cohesive, and scattered by falling through the vegetation. The majority of seeds defecated by lemurs were intact (28,623 seeds; 94%), minor proportions were damaged by lemurs (1,172; 4%), or damaged by insects/ rotten/ malformed (594; 2%). Of both the intact seeds and seeds damaged by lemurs, 97% were ripe, and 3% were unripe.

3.2.2 Germination success

For all 47 plant species together, there was a significant relation between seed source (from feces, whole fruit or seeds extracted from fruits) and germination success (Pearson's $\chi 2$= 28.937; *df*= 2; *N*= 2,805; $p < 0.001$). Germination success was higher for extracted seeds compared to seeds from feces (Bonferroni-corrected pairwise comparisons; $p < 0.01$) and fruit ($p < 0.001$). Between seeds from feces and whole fruits there was no significant difference (p= 0.066) (Fig. 3).

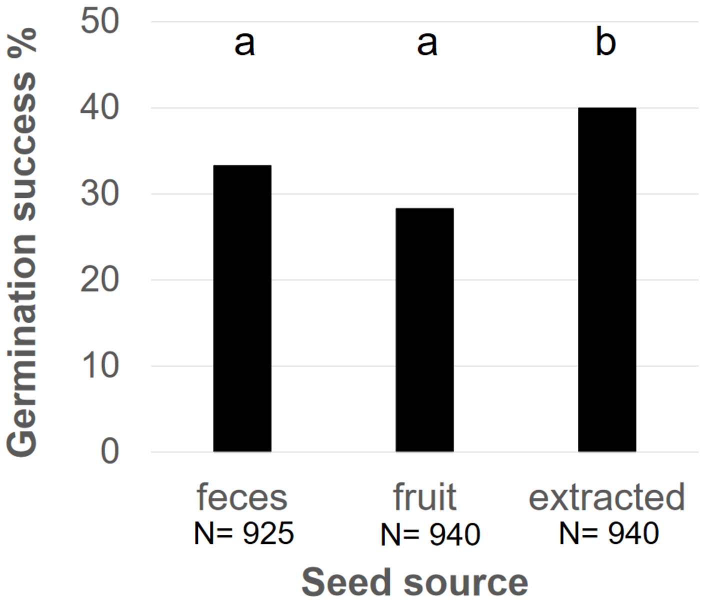

Figure 3 Relation between seed source and germination success for all 47 plant species together. Number of seeds planted within each treatment is given as N. Seed sources with the same letter above the bars were not significantly different at α= 0.05.

Within the single species, global tests revealed a significant relationship between seed source and germination success for 18 species, for 26 species the result was not significant, and for three species testing was not possible as they showed no germination (Table 1). The germination success of feces and extracted was higher than of fruit in the majority of significant multiple comparisons (6 of 10, and 10 of 12 significant multiple comparisons, respectively). The germination success of feces was lower than of extracted in all significant multiple comparisons between these two treatments (7 comparisons).

Table 1 Germination success percentages and statistical comparison of germination success between the seed sources feces, fruit, and extracted for different plant species. If there was no germination, statistical analysis with Chi-square independence test was not possible. Superscript letters show the results of Bonferroni-corrected pairwise comparisons, percentages carrying the same letter were not significantly different at α= 0.05. Please note that numbers following plant species names are not logically ordered (e.g., *Diospyros* sp. 3), but allow comparisons with other published research.

Plant species	**Germination success feces %**	**Germination success fruit %**	**Germination success extracted %**	**Global test**	**Test statistic**	***df***	***N***	***p***
Abrahamia suarezensis	84^{a}	20^{b}	95^{a}	Pearson's χ2	29.205	2	59	< 0.001
Allophylus sp.	5	0	0	Fisher's exact	1.851	2	60	n.s.
Ampelocissus sphaerophylla	$45^{a,b}$	50^{a}	10^{b}	Pearson's χ2	8.352	2	60	< 0.05
Azima tetracantha	63	70	70	Pearson's χ2	0.295	2	56	n.s.
Berchemia discolor	95	65	70	Fisher's exact	6.204	2	60	n.s.
Capuronia benoistii	5	0	0	Fisher's exact	1.851	2	60	n.s.
Carissa sp.	5^{a}	30^{a}	80^{b}	Pearson's χ2	24.677	2	60	< 0.001
Cinnamosma madagascariensis	80^{a}	0^{b}	100^{a}	Pearson's χ2	46.667	2	60	< 0.001
Cissus lanea	10	15	0	Fisher's exact	3.030	2	60	n.s.
Cissus microdonta	40	45	55	Pearson's χ2	0.938	2	60	n.s.
Cordia lowryana	0^{a}	15^{a}	60^{b}	Fisher's exact	17.517	2	55	< 0.001
Cordia myxa	68	65	90	Fisher's exact	3.999	2	59	n.s.
Diospyros aculeata	95^{a}	20^{b}	90^{a}	Pearson's χ2	32.503	2	60	< 0.001
Diospyros analamerensis	80^{a}	25^{b}	80^{a}	Pearson's χ2	17.062	2	60	< 0.001
Diospyros cf. *olacinoides*	25^{a}	30^{a}	0^{a}	Fisher's exact	7.922	2	60	< 0.05
Diospyros perrieri	55	30	55	Pearson's χ2	3.348	2	60	n.s.
Diospyros sp. 3	5^{a}	80^{b}	15^{a}	Pearson's χ2	29.850	2	60	< 0.001
Diospyros sp. 7	10	10	5	Fisher's exact	0.622	2	60	n.s.
Erythroxylum platyclados	0	0	0	not possible			60	
Erythroxylum rignyanum	30^{a}	50^{a}	90^{b}	Pearson's χ2	15.204	2	60	< 0.001
Ficus sp. 3	0	10	5	Fisher's exact	1.921	2	60	n.s.
Flacourtia ramontchi	0^{a}	45^{b}	100^{c}	Pearson's χ2	40.178	2	60	< 0.001
Garcinia verrucosa	100^{a}	40^{b}	100^{a}	Fisher's exact	27.543	2	60	< 0.001
Grewia lapiazicola	5	0	0	Fisher's exact	1.851	2	60	n.s.
Grewia sp. 1	5	5	5	Fisher's exact	0.432	2	60	n.s.
Landolphia sp.	55	30	65	Pearson's χ2	5.200	2	60	n.s.
Lantana camara	5	25	25	Fisher's exact	3.763	2	60	n.s.
Macphersonia gracilis	74	45	45	Pearson's χ2	4.270	2	59	n.s.
Mystroxylon aethiopicum	56^{a}	35^{a}	15^{a}	Pearson's χ2	6.901	2	58	< 0.05
Olax dissitiflora	60	50	35	Pearson's χ2	2.536	2	60	n.s.
Operculicarya sp. 1	5	0	10	Fisher's exact	1.921	2	60	n.s.
Operculicarya sp. 2	50	20	20	Pearson's χ2	5.714	2	60	n.s.
Petchia sp.	0	0	0	not possible			60	
Phyllanthus casticum	0	0	0	not possible			60	
Pyrostria antsirananensis	15	5	5	Fisher's exact	1.541	2	60	n.s.
Rhopalocarpus suarezensis	15	0	20	Fisher's exact	4.471	2	60	n.s.
Salacia madagascariensis	5^{a}	45^{b}	80^{b}	Pearson's χ2	22.941	2	60	< 0.001
Senna petersiana	3^{a}	70^{b}	60^{b}	Pearson's χ2	13.749	2	60	< 0.01
Strychnos madagascariensis	75^{a}	0^{b}	60^{a}	Pearson's χ2	25.455	2	60	< 0.001
Terminalia ankaranensis	15	0	0	Fisher's exact	4.329	2	60	n.s.
Terminalia calcicola	26^{a}	0^{a}	0^{a}	Fisher's exact	8.709	2	59	< 0.01
Terminalia mantaly	25^{a}	$55^{a,b}$	70^{b}	Pearson's χ2	8.400	2	60	< 0.05
Tricalysia ovalifolia	10	35	25	Fisher's exact	3.534	2	60	n.s.
Trilepisium sp.	45	75	70	Pearson's χ2	4.450	2	60	n.s.
Verbenaceae 4	15	5	0	Fisher's exact	3.111	2	60	n.s.
Xanthocercis madagascariensis	95	90	90	Fisher's exact	0.622	2	60	n.s.
Ziziphus spina-christi	0	25	10	Fisher's exact	5.728	2	60	n.s.

3.2.3 Germination time

For all plant species together, there was a significant difference in germination time between the seed sources (Welch-ANOVA $F = 25.703$; $df_1 = 2$; $df_2 = 562.364$; $p < 0.001$). Germination time was lower for feces compared to fruit (Games-Howell post hoc test; $p < 0.001$) and extracted compared to fruit ($p < 0.001$), between feces and extracted there was no significant difference ($p = 0.164$) (Fig. 4).

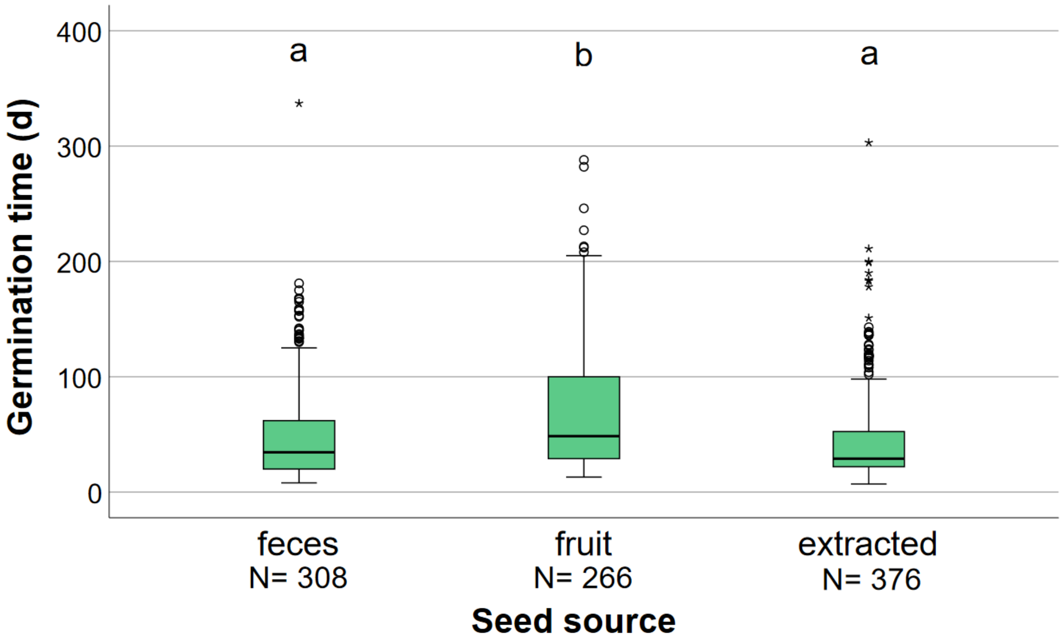

Figure 4 Relation between germination time in days and seed source for all 47 plant species together. Number of germinated seeds is given as N. Seed sources with the same letter above the boxes were not significantly different at $\alpha = 0.05$. Lines within boxes mark median values, the boxes span the interquartile range between 1st and 3rd quartile. Circles mark outliers farther than 1.5 interquartile ranges from the nearer edge of the box, asterisks mark outliers farther than 3 interquartile ranges, and whiskers extend to minimum or maximum values that are not outliers (Weinberg & Abramowitz, 2008).

Within the single species, global tests revealed significant differences in germination time between the different seed sources for 14 species, for 26 species the result was not significant, and for 14 species testing was not possible as their germination success was too low (Table 2). The germination time of feces and extracted was lower than of fruit in all but one significant post-hoc test (7 of 8, and 6 of 6 significant post-hoc tests, respectively). The germination time of feces was lower than of extracted in 2 of 3 significant post-hoc tests and higher in the one remaining.

Table 2 Mean germination time in days (bold) and statistical comparison of germination time between the seed sources feces, fruit, and extracted for different plant species. If no or too few individuals of a species germinated, statistical analysis with ANOVA/ Welch-Test was not possible. Superscript letters show the results of post-hoc tests (ANOVA: Tukey HSD, Welch-Test: Games-Howell), germination times carrying the same letter were not significantly different at α= 0.05. In case of plant species that showed germination of only two seed sources, superscript letters show the results of global tests. Please note that numbers following plant species names are not logically ordered (e.g., *Diospyros* sp. 3), but allow comparisons with other published research.

Plant species	Mean germination time (d); *SD*; *N* feces	Mean germination time (d); *SD*; *N* fruit	Mean germination time (d); *SD*; *N* extracted	Global test	Test statistic	*df*1	*df*2	*p*
Abrahamia suarezensis	**10**^{a}; SD= 2.1; N= 16	**16.8**^{b}; SD= 3.8; N= 4	**9.9**^{a}; SD= 3.2; N= 19	ANOVA	10.111	2	36.00	< 0.001
Allophylus sp.	**62**; SD= NA; N= 1	N= 0	N= 0	not possible				
Ampelocissus sphaerophylla	**122.9**; SD= 43; N= 9	**109.4**; SD= 56.9; N= 10	**181**; SD= 4.2; N= 2	ANOVA	1.753	2	18.00	n.s.
Azima tetracantha	**24.6**; SD= 3.8; N= 10	**23.4**; SD= 4.6; N= 14	**26.4**; SD= 10.2; N= 14	ANOVA	0.662	2	35.00	n.s.
Berchemia discolor	**44.9**; SD= 19.4; N= 19	**46.7**; SD= 11.6; N= 13	**44.6**; SD= 20.2; N= 14	ANOVA	0.056	2	43.00	n.s.
Capuronia benoistii	**70**; SD= NA; N= 1	N= 0	N= 0	not possible				
Carissa sp.	**25**; SD= NA; N= 1	**33.8**; SD= 3.8; N= 6	**27.5**; SD= 9.5; N= 16	ANOVA	1.347	2	20.00	n.s.
Cinnamosma madagascariensis	**44.7**; SD= 4.6; N= 16	N= 0	**37.6**; SD= 15.7; N= 20	ANOVA	3.070	1	34.00	n.s.
Cissus lanea	**113.5**; SD= 40.3; N= 2	**121**; SD= 55.5; N= 3	N= 0	ANOVA	0.026	1	3.00	n.s.
Cissus microdonta	**128.5**; SD= 19; N= 8	**110.9**; SD= 23.9; N= 9	**120.5**; SD= 9.5; N= 11	Welch-Test	1.363	2	12.50	n.s.
Cordia lowryana	N= 0	**93**^{a}; SD= 116.1; N= 3	**21.5**^{b}; SD= 5.5; N= 12	ANOVA	5.849	1	13.00	< 0.05
Cordia myxa	**57.9**; SD= 36.5; N= 13	**74.6**; SD= 11.2; N= 13	**74.1**; SD= 34; N= 18	Welch-Test	1.209	2	22.26	n.s.
Diospyros aculeata	**11.6**^{a}; SD= 1.5; N= 19	**26.8**^{a,b}; SD= 8.2; N= 4	**15.8**^{b}; SD= 5.2; N= 18	Welch-Test	10.773	2	7.01	< 0.01
Diospyros analamerensis	**21.2**; SD= 3.4; N= 16	**23.2**; SD= 6.3; N= 5	**22.9**; SD= 3.5; N= 16	ANOVA	0.995	2	34.00	n.s.
Diospyros cf. *olacinoides*	**113.6**; SD= 17.5; N= 5	**144.2**; SD= 53.3; N= 6	N= 0	ANOVA	1.484	1	9.00	n.s.
Diospyros perrieri	**22.3**^{a}; SD= 8.8; N= 11	**31.8**^{b}; SD= 9.5; N= 6	**16**^{a}; SD= 2.9; N= 11	ANOVA	9.239	2	25.00	< 0.001
Diospyros sp. 3	**181**; SD= NA; N= 1	**158.9**; SD= 34.8; N= 16	**198**; SD= 14.1; N= 3	ANOVA	1.874	2	17.00	n.s.
Diospyros sp. 7	**91.5**; SD= 4.9; N= 2	**190**; SD= 1.4; N= 2	**199**; SD= NA; N= 1	not possible				
Erythroxylum platyclados	N= 0	N= 0	N= 0	not possible				
Erythroxylum rignyanum	**21.2**^{a}; SD= 6.6; N= 6	**37.8**^{b}; SD= 10; N= 10	**27.2**^{a}; SD= 5.9; N= 18	Welch-Test	7.683	2	11.99	< 0.01
Ficus sp. 3	N= 0	**68.5**; SD= 57.3; N= 2	**44**; SD= NA; N= 1	not possible				
Flacourtia ramontchi	N= 0	**64.2**^{a}; SD= 30.2; N= 9	**28.9**^{b}; SD= 9.7; N= 20	Welch-Test	11.824	1	8.76	< 0.01
Garcinia verrucosa	**45.4**^{a}; SD= 17.4; N= 20	**159.8**^{b}; SD= 92.2; N= 8	**41.3**^{a}; SD= 14.2; N= 20	Welch-Test	6.454	2	15.79	< 0.01
Grewia lapiazicola	**30**; SD= NA; N= 1	N= 0	N= 0	not possible				
Grewia sp. 1	**175**; SD= NA; N= 1	**174**; SD= NA; N= 1	**84**; SD= NA; N= 1	not possible				
Landolphia sp.	**47.5**^{a}; SD= 13.8; N= 11	**127.8**^{a}; SD= 71.1; N= 6	**60.6**^{a}; SD= 23.4; N= 13	Welch-Test	4.579	2	10.85	< 0.05
Lantana camara	**141**; SD= NA; N= 1	**120**; SD= 20.7; N= 5	**174**; SD= 78.4; N= 5	ANOVA	1.113	2	8.00	n.s.
Macphersonia gracilis	**29.6**^{a}; SD= 12.9; N= 14	**63**^{b}; SD= 14.8; N= 9	**50.6**^{a,b}; SD= 23; N= 9	Welch-Test	15.484	2	15.42	< 0.001
Mystroxylon aethiopicum	**31.5**^{a}; SD= 3.9; N= 10	**43.4**^{b}; SD= 5.5; N= 7	**50**^{b}; SD= 5.2; N= 3	ANOVA	24.262	2	17.00	< 0.001
Olax dissitiflora	**69.8**^{a}; SD= 17.2; N= 12	**40.7**^{b}; SD= 7.5; N= 10	**39**^{b}; SD= 6.3; N= 7	ANOVA	20.312	2	26.00	< 0.001
Operculicarya sp. 1	**46**; SD= NA; N= 1	N= 0	**9**; SD= 2.8; N= 2	not possible				
Operculicarya sp. 2	**102.5**; SD= 39.7; N= 10	**101.5**; SD= 63.4; N= 4	**57**; SD= 12; N= 4	ANOVA	1.791	2	15.00	n.s.
Petchia sp.	N= 0	N= 0	N= 0	not possible				
Phyllanthus casticum	N= 0	N= 0	N= 0	not possible				
Pyrostria antsirananensis	**201.3**; SD= 118.9; N= 3	**150**; SD= NA; N= 1	**119**; SD= NA; N= 1	not possible				
Rhopalocarpus suarezensis	**29.7**; SD= 1.2; N= 3	N= 0	**66.5**; SD= 56.3; N= 4	ANOVA	1.221	1	5.00	n.s.
Salacia madagascariensis	**23**; SD= NA; N= 1	**68**; SD= 55.4; N= 9	**30.5**; SD= 25.9; N= 16	ANOVA	2.832	2	23.00	n.s.
Senna petersiana	**42.7**; SD= 16.8; N= 3	**23.1**; SD= 10.4; N= 14	**35.5**; SD= 37.2; N= 12	ANOVA	1.135	2	26.00	n.s.
Strychnos madagascariensis	**57.8**; SD= 21.9; N= 15	N= 0	**67.3**; SD= 20.5; N= 12	ANOVA	1.332	1	25.00	n.s.
Terminalia ankaranensis	**105.3**; SD= 49.7; N= 3	N= 0	N= 0	not possible				
Terminalia calcicola	**61.8**; SD= 24.2; N= 5	N= 0	N= 0	not possible				
Terminalia mantaly	**60.4**^{a,b}; SD= 18.9; N= 5	**90.9**^{a}; SD= 50.8; N= 11	**56.3**^{b}; SD= 17.8; N= 14	ANOVA	3.402	2	27.00	< 0.05
Tricalysia ovalifolia	**105.5**; SD= 74.2; N= 2	**143.3**; SD= 16.6; N= 7	**81.6**; SD= 24.5; N= 5	Welch-Test	9.403	2	2.35	n.s.
Trilepisium sp.	**25**^{a,b}; SD= 5.7; N= 9	**28.7**^{b}; SD= 6.3; N= 15	**23.6**^{a}; SD= 4; N= 14	ANOVA	3.404	2	35.00	< 0.05
Verbenaceae 4	**34.3**; SD= 10; N= 3	**44**; SD= NA; N= 1	N= 0	not possible				
Xanthocercis madagascariensis	**22.4**^{a}; SD= 9.5; N= 19	**28.3**^{b}; SD= 3.2; N= 18	**25.7**^{a,b}; SD= 4.7; N= 18	ANOVA	3.861	2	52.00	< 0.05
Ziziphus spina-christi	N= 0	**83.8**; SD= 11.3; N= 5	**89**; SD= 38.2; N= 2	Welch-Test	0.036	1	1.07	n.s.

4. DISCUSSION

4.1 Seed dispersal quantity in comparison with other lemurs

Eulemur is among the most frugivorous genera of lemurs, alongside *Cheirogaleus* and *Varecia*, even though dietary switching, i.e. feeding on alternative food sources in times of scarcity, occurs among members of this genus (Hemingway & Bynum, 2005; Federman et al., 2016; Sato et al., 2016; Steffens, 2020). In Oronjia crowned lemurs fed mainly on fruit (81.9%), ranking them second highest in the order of the most frugivorous species within the genus of true lemurs (*Eulemur*) (Sato et al., 2016). This is in line with results of other field studies in the rainforest of Montagne d'Ambre, where crowned lemurs also fed mainly on fruits (81.9% and 92.0%, respectively; Freed, 1996; Chen et al., 2015). A high percentage of fruits in the diet, along with seed swallowing, can be seen as the very basic premises for contributing to seed dispersal. Both of these premises were given for crowned lemurs, in contrast to other lemur species that either do not include fruits in their diet (e.g. *Avahi meridionalis*; Norscia et al., 2012) or are seed predators, masticating seeds (e.g., *Propithecus diadema*; Dew & Wright, 1998).

Nearly all feces samples we collected from crowned lemurs contained seeds (i.e., 97%). This large proportion was also found for *Eulemur fulvus* (97%; Sato, 2012), while the feces of *Varecia rubra* and *V. variegata* contain lower proportions of seeds (70%; Moses & Semple, 2011; 90%; Razafindratsima & Martinez, 2012). Although common brown lemurs (*E. fulvus*) and crowned lemurs belong to the same genus, the number of seeds dispersed by their populations per day differs more than an order of magnitude (9,854 seeds * km^{-2} * d^{-1} - Sato, 2012; 698 seeds * km^{-2} * d^{-1} - this study). The population of *V. rubra* dispersed an even lower number of 151 seeds * km^{-2} * d^{-1} (Moses & Semple, 2011). Obviously, the number of seeds that are dispersed by a population per day is hardly comparable between different species and studies. It should differ depending on the study and analysis methods, the population density, as well as the size of defecated seeds. Also, our result probably underestimates the actual number of dispersed seeds, as we cannot exclude having missed defecation events or dropped seeds during the feces collection.

4.2 Dispersed species' characteristics and secondary seed dispersal in Oronjia

Crowned lemurs dispersed a large number of species (80), totalling about 28% of all plant species known to occur in Oronjia according to Goodman et al. (2018). These numbers were lower for other true lemurs, except one species: *E. rufifrons* dispersed 25 plant species or about 3% of all plant species known to occur in Ranomafana National Park, *E. rubriventer* dispersed 26 species, also about 3% of all plant species known to occur in Ranomafana National Park, *E. fulvus* dispersed 70 species or about 13% of all plant species known to occur in Ankarafantsika National Park, *E. macaco* dispersed 57 species or 16% of all plant species known to occur in Lokobe National Park, and *E. collaris* dispersed 100 species or 39% of all plant species known to occur in the forests of Sainte Luce (Birkinshaw, 2001; Bollen et al., 2004; Rabenantoandro et al., 2007; Sato, 2012; Razafindratsima et al., 2014; Goodman et al., 2018). However, it has to be considered that such direct comparisons between results from different studies may be limited in their validity due to possible differences in methodological aspects, such as sampling method, effort, and timing. All studies though, except Bollen et al. (2004) studying *E. collaris*, were based on habituation, followed by behavioural observation, feces collection and analysis; and were carried out in both seasons, with a comparable or higher sampling effort than our study (Table S2). Therefore, these aspects do not seem to be responsible for the larger number of species dispersed by crowned lemurs. The study of Bollen et al. (2004) on *E. collaris* is hardly comparable with the other studies, as they applied different sampling methods, which is why the sampling effort could not be determined.

Most of the species dispersed by crowned lemurs are endemic, but two invasive species were also dispersed, which might have a negative impact on the local plant community. There are further examples of the dispersal of invasive species by lemurs, with potential or measured negative impact on local plant communities (Martinez & Razafindratsima, 2014; DeSisto et al., 2020). On the other hand, introduced and invasive species may serve as fallback food in times of resource scarcity, and may even contribute to protecting lemur species from extinction (LaFleur & Gould, 2009; Gérard et al., 2015; DeSisto et al., 2020; Donati et al., 2020).

While crowned lemurs exploited and dispersed fruits and seeds of a wide spectrum of lengths, the majority was large, which is a common phenomenon among true lemur species (*E. fulvus*, *E. rubriventer*: Dew & Wright, 1998; *E. macaco*: Birkinshaw, 2001; *E. collaris*: Bollen et al., 2004; *E. fulvus*: Sato, 2012). Bats and birds on the other hand usually disperse small seeds (Razafindratsima, 2014), the largest bird-dispersed seed found in Madagascar is about 12 mm long (Bleher & Böhning-Gaese, 2001; Albert-Daviaud et al., 2020). We found 20 plant species dispersed by lemurs with a mean seed length larger than 12 mm, which thus might solely depend on *E. coronatus* for seed dispersal in Oronjia. Two of these, *Rhopalocarpus suarezensis* and *Capurodendron nodosum* are Vulnerable, and one, *Diospyros analamerensis*, is Endangered (IUCN, 2021). Similar results from studies on common brown lemurs show that 23 large-seeded plant species seemingly depend solely on *E. fulvus* (Sato, 2012), and that in fragments without *E. fulvus*, lemur-dispersed tree species regenerated less than expected by the abundance of adult trees (Ganzhorn et al., 1999).

Besides the endemic vertebrates, introduced species might also play a role in the dispersal of large seeds. In Oronjia, the fruits of *Sclerocarya birrea* are consumed by zebus (*Bos taurus indicus*), who roam freely through the forest, and seeds are defecated intact. Therefore, cattle seem to play a major role in the dispersal and regeneration of this species (Rakotondraparany & Andriambeloson, 2015). Further research in this sector would be highly valuable to understand a possible influence of introduced animals, such as bush pig (*Potamochoerus larvatus*) and goat (*Capra hircus*) that occur in Oronjia, on seed dispersal and regeneration. Secondary seed dispersal, which might follow after the seeds have been dispersed by lemurs, obviously plays a subordinate role in the degraded habitat of Oronjia, where the rodent fauna seems to be depleted (Fiedler et al., 2021). However, we observed dung beetles moving bowls of crowned lemur feces that also contained seeds. In Amazonia, the effects that dung beetles have on seed dispersal and regeneration of seeds from primate feces are well established (Estrada & Coates-Estrada, 1991; Andresen, 2002a, 2002b). This research has yet to be conducted in Madagascar, though its dung beetle community is exceptionally diverse (Wirta et al., 2010).

4.3 Seed dispersal quality: Influence on seed condition and germination

Most of the seeds (94%) defecated by crowned lemurs were intact, which is less than the percentage of seeds defecated intact by *E. fulvus* (99.5%; Sato, 2012), but more than the percentages defecated intact by *E. rubriventer* (93%) and *E. rufifrons* (69%; published as *Eulemur fulvus rufus*; Overdorff and Strait, 1998). Explanations for these differences in seed condition after defecation might be a different abundance of seeds prone to destruction or already damaged pre-ingestion in the diet, or a different tendency to masticate seeds. Methodological differences cannot be excluded as an explanation either, as definitions of “intact” and “damaged” may differ between studies. A general problem in determining the percentage of intact seeds in feces samples is that destructed seeds might be not detected due to a strong decomposition. Thus, the percentage of damaged seeds we found is probably an underestimation of the real value. This is also supported by the fact that crowned lemurs fed on unripe fruits in about one fourth of our fruit exploitation observations. Unripe fruits can contain unripe seeds that are not yet fully developed and hard (Janzen, 1983; but see Cruz-Tejada et al., 2018). In the diet of other populations of crowned lemurs, proportions of one third of unripe and two thirds of ripe fruits were found (Freed, 1996; Chen et al., 2015).

This must be considered when assessing seed dispersal quality via feeding observations, as unripe seeds might be destroyed when fed upon, or they might not yet be able to germinate.

In the germination experiments for all plant species together, extracted seeds showed the highest germination success and lowest germination time. Compared to this, feces seeds showed a lower germination success and a similar germination time. Thus, the gut passage negatively influences germination success, while it has no impact on germination time. In comparison with the seeds within fruits, seeds from feces showed a higher germination success and a lower germination time, though only the second difference was significant. It seems that the negative influence of gut passage on germination is exceeded by a positive influence, which is caused by the removal of the fruit pulp and its inhibitory effects (reviewed in Traveset et al., 2007). This influence is confirmed by the marked differences in germination success and time between the extracted and fruit treatment, and may positively affect the plants' fitness, not only through increased and early emergence but also through a reduced susceptibility to pathogens (Lambert, 2001; Verdú & Traveset, 2005).

Another reason for the lower germination success of seeds from feces compared to seeds extracted from fruits might be failures in selecting intact seeds for the experiment. While there were no problems to select intact and ripe extracted seeds, for seeds from feces samples it was difficult to do so occasionally, as seeds that were passed by lemurs regularly showed changes in colour. These changes might be induced by the gut passage or pre-ingestion events, e.g. a mould infestation, and they might also mask that the seeds were possibly unripe upon the time of ingestion.

Within the single plant species, those patterns of germination are generally reflected; however, there are species showing contrasting patterns. This is in line with the results of other germination studies, in which germination of different treatments differed between the single plant species defecated by *Eulemur fulvus* or *Varecia rubra* (Razafindratsima & Razafimahatratra, 2010; Sato, 2012). When comparing the effects of different dispersing species, a corresponding effect at the disperser level can be observed: Studies on lemurs, Asian macaques and neotropical primates found mixed results, different disperser species either had a negative, neutral or positive impact on germination success and time (Razafindratsima, 2014; Fuzessy et al., 2016; Tsuji & Su; 2018). These findings can be explained by various characteristics that different dispersers and dispersed plants have, such as "morphological and physiological traits, as well as retention times in the gut", and "seed size, pulp composition, seed coat thickness, texture", respectively (Traveset et al., 2007: 82, 85). As these characteristics determine the extent of scarification of the seed during gut passage, they determine its germination (reviewed in Traveset et al., 2007).

To our knowledge, among all studies on germination of lemur-dispersed seeds with at least one control treatment, we included the largest number of different plant species (47), while other studies included a maximum of 16 species (Dew & Wright, 1998; Moses & Semple, 2011; Razafindratsima & Martinez, 2012; Sato, 2012). Therefore, the design of future studies that investigate the influence of gut passage and removal of the fruit pulp should always include a variety of plant species, as the germination depends not only on the treatment, but also on the species. Furthermore, the results of one primate species or disperser in general cannot be easily transferred to other species, also within the same genus.

4.4 Conclusions

Considering its seed dispersal quantity and quality characteristics, and in comparison with other lemurs, *E. coronatus* appears to be a key species for seed dispersal. The fact that 20 plant species, including three threatened with extinction, are dispersed only by crowned lemurs in Oronjia, illustrates the important role of lemur seed dispersal in protecting plant species.

Our results have important implications for the purpose of including lemurs in forest restoration activities. As the germination depends on the dispersed plant species, some species would regenerate better. For the aim of facilitating regeneration, it would beneficial to include these strongly-germinating species in planting activities. In addition, the diversity of plant species dispersed by lemurs is unmatched by conventional restoration efforts (Holloway, 2000; Birkinshaw et al., 2009; Manjaribe et al., 2013).

Thus, apart from playing an important role in maintaining diverse forest ecosystems in Madagascar, seed dispersal by lemurs may diversify restoration plantings. Yet, when planting species to attract lemurs to restoration sites, negative effects like the spread of invasive and potentially harmful species must be considered as well.

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Statement of Ethics

All capture and anaesthetization protocols were approved by the Institutional Animal Care and Use Committee (IACUC) of Omaha's Henry Doorly Zoo and Aquarium (97-001, 12-101), and were in accordance with research permits number 80/18/MEEF/SG/DGF/DSAP/SCB.Re and 300/18/MEEF/SG/DGF/DSAP/SCB.Re, issued by the "Direction du système des aires protégées" Antananarivo, Madagascar.

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Author contributions

KJES contributed to conceptualization, formal analysis, funding acquisition, investigation, methodology, project administration, resources, supervision, visualization and writing of this work. JS contributed to investigation, methodology, project administration, supervision and revision of this work. JR contributed to investigation, project administration, resources and revision of this work.

Conflict of interest statement

The authors have no conflicts of interest to declare.

Data availability statement

Most of the data included in Appendix/ Supplement tables. Further enquiries can be directed to the corresponding author.

REFERENCES

Albert-Daviaud A, Buerki S, Onjalalaina GE, Perillo S, Rabarijaona R, Razafindratsima OH, et al. (2020). The ghost fruits of Madagascar: Identifying dysfunctional seed dispersal in Madagascar's endemic flora. *Biological Conservation* 242: 108438.

Albert-Daviaud A, Perillo S, Stuppy W (2018). Seed dispersal syndromes in the Madagascan flora: The unusual importance of primates. *Oryx* 52: 418-426.

Andresen E (2002a). Dung beetles in a Central Amazonian rainforest and their ecological role as secondary seed dispersers. *Ecological Entomology* 27: 257-270.

Andresen E (2002b). Primary seed dispersal by red howler monkeys and the effect of defecation patterns on the fate of dispersed seeds. *Biotropica* 34: 261-272.

Asner GP, Keller M, Pereira Jr R, Zweede JC, Silva JNM (2004). Canopy damage and recovery after selective logging in Amazonia: Field and satellite studies. *Ecological Applications* 14: 280-298.

Bezanson M, McNamara A. (2019). The what and where of primate field research may be failing primate conservation. *Evolutionary Anthropology: Issues, News, and Reviews* 28: 166-178.

Birkinshaw C (2001). Fruit characteristics of species dispersed by the black lemur (*Eulemur macaco*) in the Lokobe Forest, Madagascar. *Biotropica* 33: 478-486.

Birkinshaw C, Andrianjafy M, Rasolofonirina J-J (2009). Survival and growth of seedlings of 19 native tree and shrub species planted in degraded forest as part of a forest restoration project in Madagascar's highlands. *Madagascar Conservation & Development* 4: 128-131.

Bleher B, Böhning-Gaese K (2001). Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia* 129: 385-394.

Bollen A, van Elsacker L (2002). Feeding ecology of *Pteropus rufus* (Pteropodidae) in the littoral forest of Sainte Luce, SE Madagascar. *Acta Chiropterologica* 4: 33-47.

Bollen A, van Elsacker L, Ganzhorn, JU (2004). Relations between fruits and disperser assemblages in a Malagasy littoral forest: A community-level approach. *Journal of Tropical Ecology* 20: 599-612.

Burivalova Z, Bauert MR, Hassold S, Fatroandrianjafinonjasolomiovazo NT, Koh LP (2015). Relevance of global forest change data set to local conservation: Case study of forest degradation in Masoala National Park, Madagascar. *Biotropica* 47: 267-274.

Calenge C (2006). The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. *Ecological Modelling* 197: 516-519.

Chazdon RL (2008). Beyond deforestation: Restoring forests and ecosystem services on degraded lands. *Science* 320: 1458-1460.

Chen KS, Li JQ, Rasoarahona J, Fousseni F, Manjaribe C (2015). Diet and seed dispersal by *Eulemur coronatus* (Gray, primates and Lemuridae) in the Amber Mountain National Park, Madagascar. *International Journal of Biology* 7: 20-31.

Crowley BE, Godfrey LR, Irwin MT (2011). A glance to the past: Subfossils, stable isotopes, seed dispersal, and lemur species loss in southern Madagascar. *American Journal of Primatology* 73: 25-37.

Cruz-Tejada DM, Acosta-Rojas DC, Stevenson PR (2018). Are seeds able to germinate before fruit color ripening? Evidence from six Neotropical bird-dispersed plant species. *Ecosphere* 9: e02174.

DeSisto CMM, Park DS, Davis CC, Ramananjato V, Tonos JL, Razafindratsima OH (2020). An invasive species spread by threatened diurnal lemurs impacts rainforest structure in Madagascar. *Biological Invasions* 22: 2845-2858.

Dew JL, Wright PC (1998). Frugivory and seed dispersal by four species of primates in Madagascar's eastern rain forest. *Biotropica* 30: 425-437.

Donati G, Campera M, Balestri M, Barresi M, Kesch K, Ndremifidy K, et al. (2020). Life in a fragment: Evolution of foraging strategies of translocated collared brown lemurs, *Eulemur collaris*, over an 18-year period. *American Journal of Primatology* 82: e23106.

Estrada A, Coates-Estrada R (1991). Howler monkeys (*Alouatta palliata*), dung beetles (Scarabaeidae) and seed dispersal: Ecological interactions in the tropical rain forest of Los Tuxtlas, Mexico. *Journal of Tropical Ecology* 7: 459-474.

FAO (2020). *Global forest resources assessment 2020 - Main report*. Rome, Food and Agriculture Organization of the United Nations.

Federman S, Dornburg A, Daly DC, Downie A, Perry GH, Yoder AD, et al. (2016). Implications of lemuriform extinctions for the Malagasy flora. *Proceedings of the National Academy of Sciences* 113: 5041-5046.

Fiedler PMA, De Lapparent A, Razafitsalama J, Sanamo J, Steffens KJE, Ganzhorn JU (2021). Secondary seed removal in a degraded forest habitat in Madagascar. *Scientific Reports* 11: 16823.

Freed BZ (1996). *Co-occurrence among crowned lemurs (*Eulemur coronatus*) and Sanford's lemur (*Lemur fulvus sanfordi*) of Madagascar*. PhD dissertation, Washington University.

Fuzessy LF, Cornelissen TG, Janson C, Silveira FAO (2016). How do primates affect seed germination? A meta-analysis of gut passage effects on neotropical plants. *Oikos* 125: 1069-1080.

Ganzhorn JU (1987). A possible role of plantations for primate conservation in Madagascar. *American Journal of Primatology* 12: 205-215.

Ganzhorn JU, Fietz J, Rakotovao E, Schwab D, Zinner D (1999). Lemurs and the regeneration of dry deciduous forest in Madagascar. *Conservation Biology* 13: 794-804.

Ganzhorn JU, Lowry PP, Schatz GE, Sommer S. (2001). The biodiversity of Madagascar: One of the world's hottest hotspots on its way out. *Oryx* 35: 346-348.

Gérard A, Ganzhorn JU, Kull CA, Carrière SM (2015). Possible roles of introduced plants for native vertebrate conservation: The case of Madagascar. *Restoration Ecology* 23: 768-775.

Goodman SM, Ganzhorn JU (in press) Predation on lemurs. In *The new natural history of Madagascar* (Goodman SM, ed.). Princeton, New Jersey, Princeton University Press.

Goodman SM, Raherilalao MJ, Wohlhauser S (2018). *Les aires protégées terrestres de Madagascar: Leur histoire, description et biote / The terrestrial protected areas of Madagascar: Their history, description, and biota.* Antananarivo, Association Vahatra.

Harper GJ, Steininger MK, Tucker CJ, Juhn D, Hawkins F (2007). Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation* 34: 325-333.

Hemingway CA, Bynum N (2005). The influence of seasonality on primate diet and ranging. In *Seasonality in primates: Studies of living and extinct human and non-human primates* (Brockman DK, van Schaik CP, eds.), pp 57-104. Cambridge, Cambridge University Press.

Heymann EW (2011). Florivory, nectarivory, and pollination—A review of primate-flower interactions. *Ecotropica* 17: 41-52.

Holloway L (2000). Catalysing rainforest restoration in Madagascar. In *Diversité et endémisme à Madagascar - Diversity and endemism in Madagascar* (Lourenço WR, Goodman SM, eds.), pp. 115-124. Paris, Mémoires de la Société de Biogéographie.

Holloway L (2004). Ecosystem restoration and rehabilitation in Madagascar. *Ecological Restoration* 22: 113-119.

International Tropical Timber Organization (2002). *ITTO guidelines for the restoration, management and rehabilitation of degraded and secondary tropical forests.* ITTO Policy Development Series, 13. Yokohama, International Tropical Timber Organization.

International Tropical Timber Organization (2020). *Guidelines for forest landscape restoration in the tropics*. ITTO Policy Development Series, 24. Yokohama, International Tropical Timber Organization.

Irwin MT, Wright PC, Birkinshaw C, Fisher BL, Gardner CJ, Glos J, et al. (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation* 143: 2351-2362.

IUCN (2021). *The IUCN Red List of Threatened Species. Version 2020-3.* https://www.iucnredlist.org (accessed March 5, 2021)

Janzen DH (1983). Physiological ecology of fruits and their seeds. In *Physiological plant ecology III* (Lange OL, Nobel PS, Osmond CB, Ziegler H, eds.), pp 625-655. Berlin, Heidelberg, New York, Springer-Verlag.

Jordano P, Forget P-M, Lambert JE, Böhning-Gaese K, Traveset A, Wright SJ (2011). Frugivores and seed dispersal: Mechanisms and consequences for biodiversity of a key ecological interaction. *Biology Letters* 7: 321-323.

Konersmann C, Noromiarilanto F, Ratovonamana YR, Brinkmann K, Jensen K, Kobbe S, et al. (2021). Using utilitarian plants for lemur conservation. *International Journal of Primatology*. https://doi.org/10.1007/s10764-021-00200-y

Kull CA, Tassin J, Moreau S, Ramiarantsoa HR, Blanc-Pamard C, Carrière SM (2012). The introduced flora of Madagascar. *Biological Invasions* 14: 875-888.

LaFleur M, Gould L (2009). Feeding outside the forest: The importance of crop raiding and an invasive weed in the diet of gallery forest ring-tailed lemurs (*Lemur catta*) following a cyclone at the Beza Mahafaly Special Reserve, Madagascar. *Folia Primatologica* 80: 233-246.

Lambert JE (2001). Red-tailed guenons (*Cercopithecus ascanius*) and *Strychnos mitis*: Evidence for plant benefits beyond seed dispersal. *International Journal of Primatology* 22: 189-201.

Madagascar Catalogue (2021). *Catalogue of the Vascular Plants of Madagascar.* Missouri Botanical Garden, St. Louis, U.S.A. & Antananarivo, Madagascar. http://legacy.tropicos.org/Project/Madagascar (accessed May 12, 2021).

Manjaribe C, Frasier CL, Rakouth B, Louis Jr EE (2013). Ecological restoration and reforestation of fragmented forests in Kianjavato, Madagascar. *International Journal of Ecology* 2013: 726275.

Martinez BT, Razafindratsima OH (2014). Frugivory and seed dispersal patterns of the red-ruffed lemur, *Varecia rubra*, at a forest restoration site in Masoala National Park, Madagascar. *Folia Primatologica* 85: 228-243.

Missouri Botanical Garden (2015). *Plan d’aménagement et de gestion de la Nouvelle Aire Protégée Oronjia*. Missouri Botanical Garden Madagascar.

Moat J, Smith P (2007). *Atlas of the vegetation of Madagascar*. Kew, Royal Botanic Gardens.

Moses KL, Semple S (2011). Primary seed dispersal by the black-and-white ruffed lemur (*Varecia variegata*) in the Manombo forest, south-east Madagascar. *Journal of Tropical Ecology* 27: 529-538.

Norscia I, Ramanamanjato J-B, Ganzhorn JU (2012). Feeding patterns and dietary profile of nocturnal southern woolly lemurs (*Avahi meridionalis*) in southeast Madagascar. *International Journal of Primatology* 33: 150-167.

Overdorff DJ, Strait SG (1998). Seed handling by three prosimian primates in southeastern Madagascar: Implications for seed dispersal. *American Journal of Primatology* 45: 69-82.

Pareliussen I, Olsson EGA, Armbruster WS (2006). Factors limiting the survival of native tree seedlings used in conservation efforts at the edges of forest fragments in upland Madagascar. *Restoration Ecology* 14: 196-203.

R Core Team (2020). *R: A language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rabenantoandro J, Randriatafika F, Lowry II PP (2007). Floristic and structural characteristics of remnant littoral forest sites in the Tolagnaro area. In *Biodiversity, ecology and conservation of littoral ecosystems in southeastern Madagascar, Tolagnaro (Fort Dauphin)* (Ganzhorn JU, Goodman SM, Vincelette M, eds.), pp. 65-94. Washington, D.C., Smithsonian Institution.

Rakotondraparany F, Andriambeloson JB (2015). *Étude des lémuriens phares de la Nouvelle Aire Protégée (NAP) Oronjia, Antsiranana II*. Antananarivo, Université d'Antananarivo.

Ramananjato V, Rakotomalala Z, Park DS, DeSisto CMM, Raoelinjanakolona NN, Guthrie NK, et al. (2020). The role of nocturnal omnivorous lemurs as seed dispersers in Malagasy rain forests. *Biotropica* 00:1-8.

Razafindratsima OH (2014). Seed dispersal by vertebrates in Madagascar's forests: Review and future directions. *Madagascar Conservation & Development* 9: 90-97.

Razafindratsima OH, Dunham AE (2015). Assessing the impacts of nonrandom seed dispersal by multiple frugivore partners on plant recruitment. *Ecology* 96: 24-30.

Razafindratsima OH, Jones TA, Dunham AE (2014). Patterns of movement and seed dispersal by three lemur species. *American Journal of Primatology* 76: 84-96.

Razafindratsima OH, Martinez BT (2012). Seed dispersal by red-ruffed lemurs: Seed size, viability, and beneficial effect on seedling growth. *Ecotropica* 18: 15-26.

Razafindratsima OH, Razafimahatratra E (2010). Effect of red ruffed lemur gut passage on the germination of native rainforest plant species. *Lemur News* 15: 39-42.

Richardson DM, Pysek P, Rejmanek M, Barbour MG, Panetta FD, West CJ (2000). Naturalization and invasion of alien plants: Concepts and definitions. *Diversity and Distributions* 6: 93-107.

Samuels IA, Levey DJ (2005). Effects of gut passage on seed germination: Do experiments answer the questions they ask? *Functional Ecology* 19: 365-368.

Sato H (2012). Frugivory and seed dispersal by brown lemurs in a Malagasy tropical dry forest. *Biotropica* 44: 479-488.

Sato H, Santini L, Patel ER, Campera M, Yamashita N, Colquhoun IC, et al. (2016). Dietary flexibility and feeding strategies of *Eulemur*: A comparison with *Propithecus*. *International Journal of Primatology* 37: 109-129.

Schmider E, Ziegler M, Danay E, Beyer L, Bühner M (2010). Is it really robust? Reinvestigating the robustness of ANOVA against violations of the normal distribution assumption. *Methodology* 6: 147-151.

Schupp EW (1993). Quantity, quality and the effectiveness of seed dispersal by animals. In *Frugivory and seed dispersal: Ecological and evolutionary aspects* (Fleming TH, Estrada A, eds.), pp 15-29. Dordrecht, Springer Netherlands.

Schupp EW, Jordano P, Gómez JM (2010). Seed dispersal effectiveness revisited: A conceptual review. *New Phytologist* 188: 333-353.

Soma T (2006). Tradition and novelty: *Lemur catta* feeding strategy on introduced tree species at Berenty Reserve. In *Ringtailed lemur biology: Lemur catta in Madagascar* (Jolly A, Sussman RW, Koyama N, Rasamimanana H, eds.), pp 141-159. New York, Springer Science + Business Media, LLC.

Steffens KJE (2020). Lemur food plants as options for forest restoration in Madagascar. *Restoration Ecology* 28: 1517-1527.

Stevenson PR (2000). Seed dispersal by woolly monkeys (*Lagothrix lagothricha*) at Tinigua National Park, Colombia: Dispersal distance, germination rates, and dispersal quantity. *American Journal of Primatology* 50: 275-289.

Styger E, Rakotoarimanana JEM, Rabevohitra R, Fernandes ECM (1999). Indigenous fruit trees of Madagascar: Potential components of agroforestry systems to improve human nutrition and restore biological diversity. *Agroforestry Systems* 46: 289-310.

Terborgh J, Pitman N, Silman M, Schichter H, P Núñez V (2002). Maintenance of tree diversity in tropical forests. In *Seed dispersal and frugivory: Ecology, evolution and conservation* (Levey DJ, Silva WR, Galetti M, eds.), pp 1-17. Wallingford, CAB International.

Traveset A, Robertson AW, Rodríguez-Pérez J (2007). A review on the role of endozoochory in seed germination. In *Seed dispersal: Theory and its application in a changing world* (Dennis AJ, Schupp EW, Green RJ, Westcott DA, eds.), pp 78-103. Wallingford, CAB International.

Tsuji Y, Su H-H (2018). Macaques as seed dispersal agents in Asian forests: A review. *International Journal of Primatology* 39: 356-376.

Valiente-Banuet A, Aizen MA, Alcántara JM, Arroyo J, Cocucci A, Galetti M, et al. (2015). Beyond species loss: The extinction of ecological interactions in a changing world. *Functional Ecology* 29: 299-307.

Verdú M, Traveset A. (2005). Early emergence enhances plant fitness: A phylogenetically controlled meta-analysis. *Ecology* 86: 1385-1394.

Wang BC, Smith TB (2002). Closing the seed dispersal loop. *Trends in Ecology & Evolution* 17: 379-386.

Weinberg SL, Abramowitz SK (2008). *Statistics using IBM SPSS: an integrative approach* (Third edition). Cambridge, Cambridge University Press.

Wirta H, Viljanen H, Orsini L, Montreuil O, Hanski I (2010). Three parallel radiations of Canthonini dung beetles in Madagascar. *Molecular Phylogenetics and Evolution* 57: 710-727.

Wunderle Jr. JM (1997). The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management* 99: 223-235.

Zuberbühler K, Wittig RM (2011). Field experiments with non-human primates: A tutorial. In *Field and laboratory methods in primatology* Second edition (Setchell JM, Curtis DJ, eds.), pp 207-224. Cambridge, Cambridge University Press.

SUPPLEMENT

Figure S1 Photograph showing the reference collection of seeds, produced by KJES and JS.

Figure S2 Photograph showing the tree nursery of the Missouri Botanical Garden in Oronjia, where the germination experiments of this study were conducted.

Table S1 Characteristics of plant species whose seeds were dispersed and whose entire fruits were swallowed by crowned lemurs in Oronjia, northern Madagascar; and mean lengths of seeds/ fruits (bold). Abbreviations column Distribution (*Catalogue of the Vascular Plants of Madagascar*; Madagascar Catalogue, 2021): ”end”= endemic, “nnend”= native, but not endemic, “natu”= naturalized; column IUCN Red List Status (IUCN, 2021): “ni”= not included, “LC”= Least Concern, “NT”= Near Threatened, “V”= Vulnerable, “En”= Endangered; columns Seed/Fruit size category: “s”= small (<5 mm), “m”= medium (5-10 mm), “l”= large (>10 mm); NA= “not applicable”. Please note that plant species are sorted in descending order, according to the number of seeds dispersed. For *Ficus* sp. 3, seeds were too little and numerous to count.

Plant species	Number of seeds dispersed	Distribution (*Catalogue of the Vascular Plants of Madagascar*)	IUCN Red List Status	Mean seed length (mm); *SD*; *N*	Seed size category	Mean fruit length (mm); *SD*; *N*	Fruit size category
Ficus sp. 3	NA	NA	NA	**1**; SD= 0; N= 20	s	**17.7**; SD= 1.9; N= 20	l
Capuronia benoistii	4583	end	LC	**3.2**; SD= 0.4; N= 20	s	**7.4**; SD= 0.7; N= 20	m
Cissus lanea	3426	end	ni	**2**; SD= 0; N= 20	s	**8.5**; SD= 0.5; N= 20	m
Ampelocissus sphaerophylla	3258	end	ni	**8.2**; SD= 0.8; N= 20	m	**10.1**; SD= 0.6; N= 20	l
Tricalysia ovalifolia	2677	nnend	ni	**4.2**; SD= 0.4; N= 20	s	**5.9**; SD= 0.6; N= 20	m
Flacourtia ramontchi	2499	nnend	ni	**5.5**; SD= 0.6; N= 20	m	**18.1**; SD= 1.8; N= 20	l
Phyllanthus casticum	2099	nnend	LC	**2**; SD= 0; N= 20	s	**7**; SD= 0; N= 20	m
Senna petersiana	1923	natu	LC	**4.6**; SD= 0.6; N= 20	s		
Erythroxylum rignyanum	1416	end	ni	**9.7**; SD= 0.7; N= 20	m	**11.2**; SD= 0.6; N= 20	l
Macphersonia gracilis	790	nnend	LC	**8.7**; SD= 1; N= 19	m		
Diospyros analamerensis	684	end	EN	**13.5**; SD= 0.6; N= 20	l		
Diospyros aculeata	497	end	LC	**14.4**; SD= 0.8; N= 20	l		
Lantana camara	469	natu	ni	**4.9**; SD= 0.5; N= 20	s	**5.2**; SD= 0.7; N= 20	m
Cinnamosma madagascariensis	441	end	LC	**9.7**; SD= 2.8; N= 26	m		
Terminalia mantaly	381	end	LC	**12**; SD= 3.1; N= 20	l	**18**; SD= 3; N= 20	l
Terminalia ankaranensis	376	end	V	**8.6**; SD= 1.1; N= 20	m	**10.8**; SD= 0.6; N= 20	l
Landolphia sp.	333	NA	NA	**16.5**; SD= 0.8; N= 20	l		
Grewia sp. 1	329	NA	NA			**11.3**; SD= 0.6; N= 20	l
Operculicarya sp. 1	300	NA	NA	**7.3**; SD= 0.4; N= 20	m	**9.3**; SD= 0.5; N= 20	m
Pyrostria antsirananensis	268	end	ni	**4**; SD= 0.5; N= 20	s	**4**; SD= 0.2; N= 20	s
Xanthocercis madagascariensis	237	end	LC	**16**; SD= 1.4; N= 20	l		
Capurodendron nodosum	233	end	V	**12.6**; SD= 1.3; N= 20	l		
Berchemia discolor	232	nnend	LC	**14.7**; SD= 0.9; N= 20	l		
Petchia sp.	219	NA	NA	**10.2**; SD= 0.7; N= 20	l	**14.5**; SD= 1.2; N= 20	l
Diospyros perrieri	191	end	NT	**13.2**; SD= 1.5; N= 20	l		
Thilachium panduriforme	171	end	ni	**6.2**; SD= 0.5; N= 20	m		
Grewia lapiazicola	144	end	V	**4.5**; SD= 0.6; N= 20	s	**13**; SD= 1.4; N= 20	l
Salacia madagascariensis	138	other	ni	**18.8**; SD= 1.8; N= 20	l		
Tacca pinnatifida	131	natu	ni	**7.3**; SD= 0.8; N= 20	m		
Unidentified species (I45)	128	NA	NA	**4.7**; SD= 0.7; N= 20	s		
Diospyros sp. 3	123	NA	NA	**10.1**; SD= 0.8; N= 20	l	**15.6**; SD= 1.6; N= 20	l
Strychnos madagascariensis	120	nnend	LC	**16**; SD= 1.2; N= 20	l		
Lythraceae	107	NA	NA	**4.7**; SD= 0.5; N= 20	s		
Diospyros vescoi	105	end	LC	**16.4**; SD= 1.1; N= 20	l		
Carissa sp.	105	NA	NA	**7.2**; SD= 0.7; N= 20	m	**10.1**; SD= 1.6; N= 20	l
Bakerella sp. 1	93	NA	NA				
Verbenaceae 4	92	NA	NA	**4.7**; SD= 0.5; N= 20	s	**6.1**; SD= 0.7; N= 20	m
Operculicarya sp. 2	75	NA	NA	**18.7**; SD= 1; N= 20	l		
Allophylus sp.	71	NA	NA	**6**; SD= 0.7; N= 20	m	**7.5**; SD= 0.5; N= 20	m
Garcinia verrucosa	65	end	LC	**27**; SD= 3.7; N= 20	l		
Rhopalocarpus suarezensis	61	end	V	**15.4**; SD= 1.1; N= 20	l		
Diospyros sp. 7	60	NA	NA	**11.9**; SD= 0.7; N= 20	l	**19.9**; SD= 1.5; N= 20	l
Trilepisium sp.	59	NA	NA	**10.1**; SD= 0.8; N= 20	l	**15**; SD= 0.7; N= 20	l
Bakerella sp. 2	57	NA	NA				
Bremeria sp.	57	NA	NA	**10.9**; SD= 0.8; N= 20	l		
Diospyros cf. *olacinoides*	55	end	LC	**8.8**; SD= 0.6; N= 20	m	**13**; SD= 1.3; N= 20	l
Cissus microdonta	49	nnend	ni	**7.9**; SD= 0.7; N= 20	m	**8.5**; SD= 1; N= 20	m
Azima tetracantha	41	nnend	LC	**5.6**; SD= 0.6; N= 16	m		
Cassia alata	34	natu	LC				
Erythroxylum platyclados	34	other	ni	**5.5**; SD= 0.5; N= 20	m	**6.4**; SD= 0.5; N= 20	m
Olax dissitiflora	27	nnend	LC	**13.2**; SD= 1; N= 20	l	**16.6**; SD= 0.8; N= 20	l
Phoenix reclinata	26	nnend	LC			**14.2**; SD= 0.7; N= 20	l
Cordia lowryana	25	end	LC	**12.4**; SD= 1.5; N= 15	l	**20.2**; SD= 1.2; N= 20	l
Tamarindus indica	24	nnend	LC				
Menispermaceae	24	NA	NA	**14.5**; SD= 1.5; N= 20	l		
Unidentified species (I36)	23	NA	NA	**9.8**; SD= 1; N= 19	m		
Abrahamia suarezensis	22	end	LC	**27.4**; SD= 2.5; N= 19	l		
Mystroxylon aethiopicum	21	nnend	LC	**9.2**; SD= 1.1; N= 18	m	**10.4**; SD= 0.6; N= 20	l
Cordia myxa	20	other	ni	**15**; SD= 2.5; N= 19	l	**23.9**; SD= 2.1; N= 20	l
Ziziphus spina-christi	17	other	LC	**11.6**; SD= 1.6; N= 20	l	**17.4**; SD= 2; N= 20	l
Terminalia calcicola	15	end	LC	**16.3**; SD= 1.2; N= 19	l	**15.7**; SD= 0.5; N= 20	l
Olax capuronii	13	end	V			**6.6**; SD= 0.5; N= 20	m
Rinorea sp. 1	12	NA	NA				
Strychnos panganensis	10	nnend	ni				
Acanthaceae	10	NA	NA				
Annona squamosa	9	other	LC	**14.6**; SD= 1.2; N= 15	l		
Mimusops coriacea	9	nnend	ni			**33.7**; SD= 2.8; N= 20	l
Diospyros pruinosa	8	end	LC				
Rhamnaceae	6	NA	NA				
Sclerocarya birrea	5	nnend	ni			**34.9**; SD= 1.8; N= 20	l
Rinorea sp. 3	5	NA	NA				
Unidentified species (I48)	5	NA	NA				
Erythroxylum pervillei	4	end	ni				
Unidentified species (I49)	4	NA	NA				
Adenia firingalavensis	3	end	ni				
Cissus sp.	2	NA	NA				
Capurodendron greveanum	1	end	LC				
Uvaria antsiranensis	1	end	V				
Rubiaceae	1	NA	NA				
Unidentified species (I50)	1	NA	NA				

Table S2 Comparison of the results of studies on the number of plant species dispersed by different *Eulemur* species. ^{a} From Goodman et al. (2018), ^{b} from Rabenantoandro et al. (2007).

Reference	*Eulemur* species	Study site	Number of plant species dispersed	Number of plant species occurring	Share of dispersed in occurring plant species	Sampling effort (h)	Sampling timing	Sampling method
Razafindratsima et al. (2014), Razafindratsima & Dunham (2015)	*E. rufifrons*	Ranomafana National Park	25	938^{a}	3%	524	Wet + dry season	Habituation, behavioural observation, feces analysis
Razafindratsima et al. (2014), Razafindratsima & Dunham (2015)	*E. rubriventer*	Ranomafana National Park	26	938^{a}	3%	524	Wet + dry season	Habituation, behavioural observation, feces analysis
Sato (2012)	*E. fulvus*	Ankarafantsika National Park	70	520^{a}	13%	1212	Wet + dry season	Habituation, behavioural observation, feces analysis
Birkinshaw (2001)	*E. macaco*	Lokobe National Park	57	363^{a}	16%	1272	Wet + dry season	Habituation, behavioural observation, feces analysis
Bollen et al. (2004)	*E. collaris*	Sainte Luce: Forest fragment S9	100	259^{b}	39%	?	Wet + dry season	Tree watches, opportunistic observations, feces analysis, fruit-trap analysis
This study	*E. coronatus*	Oronjia New Protected Area	80	290^{a}	28%	527	Wet + dry season	Habituation, behavioural observation, feces analysis

Chapter 2 author contributions

I hereby confirm that Kim J. E. Steffens designed the study. He and Justin Sanamo contributed equally to carry out the germination experiments in the field. Jeremi Razafitsalama identified plants and contributed to the germination experiments. Kim J. E. Steffens analyzed the data and wrote the manuscript.

Jörg Ganzhorn

Prof. Dr. Jörg Ganzhorn

CHAPTER 3

Utilization of degraded habitats by a frugivorous primate in northern Madagascar: implications for forest restoration

(submitted to *Animal Conservation*)

Kim J. E. Steffens[a], Justin Sanamo[b], Jeremi Razafitsalama[c], Jörg U. Ganzhorn[a]

[a]Department of Biology, Institute of Zoology, Universität Hamburg, Martin-Luther-King Platz 3, 20146 Hamburg, Germany

[b]Département Sciences de la Nature et de l'Environnement, Facultés des Sciences, Université d'Antsiranana, Antsiranana 201, Madagascar

[c]Missouri Botanical Garden Antsiranana, BP 268, Antsiranana 201, Madagascar

ABSTRACT

Non-human primate species are threatened worldwide. Their population declines go along with the loss of ecological functions such as seed dispersal that plays a crucial role in plant regeneration. Restoring essential habitat structures could thus not only protect primates, but also facilitate forest regeneration. We used classical vegetation description on the ground and a remote sensing analysis to describe habitat use of crowned lemurs (*Eulemur coronatus*), a seed-dispersing primate endemic to northern Madagascar. Our aim was to find vegetation characteristics important for lemurs that might be targeted in a restoration approach. For this we applied both methods in differently degraded forest types. Both classical vegetation description and remote sensing analysis were able to distinguish these forest types. The habitat use of our two study groups was associated consistently with vegetation structures measured on the microhabitat scale such as tree height and density of thick trees. In contrast, vegetation productivity and water content derived from satellite imagery on a larger scale could not consistently explain habitat use of lemurs. Thus, measurements on the ground can identify suitable microhabitats that do not show on the satellite imagery scale. These suitable little patches might be very important conservation tools to create buffer zones and corridors. Further, they might attract seed dispersing species into degraded areas targeted for forest restoration, acting as natural regeneration nuclei. The potential of these patches for conservation would not be recognized when analyses were based solely on landscape analyses on large scales.

Keywords: Point-centred quarter method, Frugivores, Landsat, NDVI, NDWI, EVI, MSAVI, Dispersal

INTRODUCTION

Given the decline of primate populations around the world (Estrada *et al* 2017), an increasing number of studies is addressing the question on how primates deal with degraded habitats and which habitat components might be important to allow the persistence of different primate species in degraded forests (Johns & Skorupa 1987; Chapman *et al* 2000; Isabirye-Basuta & Lwanga 2008; Irwin *et al* 2010; Schwitzer *et al* 2011; Sha *et al* 2018). Knowing essential structures that allow the utilization of degraded habitats is not only important for the persistence of species, but these structures could also be targeted as nuclei where restoration of habitats can be initiated (Corbin & Holl 2012; Gann *et al* 2019). This concept might be most applicable for frugivorous species that disperse seeds and thus contribute to some kind of facilitated restoration (Wunderle Jr. 1997; Farwig & Berens 2012; Charles *et al* 2019).

Primates have been identified as important seed dispersers, because more than half of all primate species does not only exploit fruits, but also disperses their seeds, primates can cover large distances per day and they are able to swallow and defecate larger seeds than birds and bats (Howe 1986; Chapman & Onderdonk 1998; Gómez & Verdú 2012; Heymann *et al* 2017; Andresen, Arroyo-Rodríguez & Ramos-Robles 2018). Frugivorous birds and bats, on the other hand, are much more species-rich and therefore might disperse a larger variety of seed types. This pattern holds for most tropical regions, but not for Madagascar: Most frugivorous species there are lemurs, the endemic group of primates (Fleming, Breitwisch & Whitesides 1987; Albert-Daviaud, Perillo & Stuppy 2018). Further, the majority of Malagasy plant species whose seeds are endozoochorously dispersed is adapted to dispersal by lemurs, implying that loss of lemur populations or species may have detrimental effects on recruitment and thus survival of these plant species (Crowley, Godfrey & Irwin 2011; Federman *et al* 2016; Albert-Daviaud *et al* 2018; Albert-Daviaud *et al* 2020).

Habitat characteristics that could explain lemurs' occurrence or abundance on the microhabitat scale, and that may be altered in degraded forests, are for example food resources and vegetation structures like tree density, diameter and height, and understory density (Ganzhorn 1989; Rendigs *et al* 2002; Andrianasolo *et al* 2006; Schwitzer *et al* 2007; Lahann 2008; Sehen *et al* 2010; Rakotondranary & Ganzhorn 2011; Andriamandimbiarisoa *et al* 2015; Steffens *et al* 2017; Forbanka 2018). Such characteristics can be described through classical vegetation descriptions that are carried out in the field, e.g., the point-centred quarter (PCQ) method conducted in plots or at sampling points (Brower, Zar & von Ende 1990; Andriamaharoa, Birkinshaw & Reza 2010; Ganzhorn, Rakotondranary & Ratovonamana 2011). However, animals from different groups, including primates, apparently select their habitat on different scales, depending on their purpose, such as feeding or travelling (Kotliar & Wiens 1990; Storch 2002; Boyce *et al* 2003; Stickler & Southworth 2008). Thus, there are also cases where it was possible to describe habitat suitability for lemurs on relatively large scales, using habitat characteristics assessed by remote sensing methods (Irwin, Johnson & Wright 2005; Lahoz-Monfort *et al* 2010; Mercado Malabet *et al* 2020; Steffens, Mercado Malabet & Lehman 2020).

To assess habitat suitability, or to predict species' abundance and occurrence using remote sensing, spectral indices derived from satellite images have proven very useful (St-Louis *et al* 2009; Lahoz-Monfort *et al* 2010; Pettorelli *et al* 2011). Various spectral indices have been developed that focus on different characteristics of vegetation and are differently suited in different scenarios. The Normalized Difference Water Index (NDWI) measures liquid water content of the vegetation (Gao 1996). The Normalized Difference Vegetation Index (NDVI) correlates strongly with chlorophyll abundance and energy absorption, and thus growth, net primary production and biomass of plants (Tucker *et al* 1981; Myneni *et al* 1995; Hicke *et al* 2002). The Enhanced Vegetation Index (EVI) is a modification of the NDVI, which in comparison does not become saturated in highly vegetated areas; and is more correlated to structural variations of the canopy, such as canopy type and leaf area index (Gao *et al* 2000; Pettorelli *et al* 2011). The Modified Soil Adjusted Vegetation Index (MSAVI) is a further development of the Soil Adjusted Vegetation Index (SAVI), developed to overcome a weakness of the NDVI, which is its problem to handle bare soil or areas with low vegetation cover (Qi *et al* 1994). Following other authors (e.g., Richardson & Everitt 1992; Wang, Price & Rich 2001; Rahaman, Hassan & Ahmed 2017), in this paper we use the term “productivity” to describe what the NDVI and its derivates, EVI and MSAVI, measure.

Here, we exemplify differences between possible applications of structural information based on classical vegetation descriptions and productivity information derived from satellite images in a study of habitat utilization of crowned lemurs (*Eulemur coronatus*) in a highly degraded forest habitat of northern Madagascar. The two approaches were used to investigate whether it would be possible to identify sites with habitat characteristics important for crowned lemurs. Specific questions are:

1. Can habitat use by *E. coronatus* be linked to structural vegetation characteristics described by PCQ on a small scale?
2. Can habitat use by *E. coronatus* be linked to vegetation productivity and vegetation water content derived from satellite images on a large scale?
3. Is the information from PCQ and remote sensing methods exchangeable?

MATERIALS AND METHODS

Study site

The study was carried out in the southeastern part of the Oronjia New Protected Area in northern Madagascar (between 12°16´17´´ S – 12°16´53´´ S and 49°23´10´´ E – 49°23´53´´ E; WGS84). The western dry deciduous forest that covers the study site (Moat & Smith 2007), is highly degraded due to anthropogenic disturbances in the past: The leaf density reaches its maximum at only 0.2-2 m, most of the trees are no more than 8 m tall, and there are many open areas covered by no or little vegetation (Missouri Botanical Garden 2015). Due to different usage intensity and/or regeneration and succession processes, there are differently degraded areas of the forest. In this study, we differentiate between "intact" and "degraded" forest, which we assessed visually based on tree density, stratification and the presence of open areas. Please note that this definition is only valid within the Oronjia forest. "Intact" forest here is also degraded, but in a better state than the forest classified here as "degraded". Intact western dry deciduous forests of other sites in northern Madagascar reach heights of 11-14 m in Montagne des Français or 8-16 m in Ankarana (Goodman, Raherilalao & Wohlhauser 2018).

Data collection and preparation

Classical vegetation description

To investigate structural characteristics of the vegetation on a small scale we applied the point-centred quarter method (Brower *et al* 1990; Rakotondranary, Ganzhorn & Ratovonamana 2010). This was done at lemur defecation points and at transect points in the intact and degraded forest for comparison.

In March and April 2019, we installed transects of 475 m length each, one in the intact and one in the degraded forest. On each transect we marked 20 points at 25 m intervals, totalling 40 points.

During our lemur behaviour study (Steffens, Sanamo & Razafitsalama accepted), we marked lemur defecation points of two groups of lemurs (“A” and “B”) by use of a handheld GPS (Garmin GPSMAP 64s) and red tissue flags. To ensure independency of data we marked only points with at least 25 m distance. Per season, we marked 20 points per lemur group, totalling 40 points in the dry season (May to October) 2018, and 40 points in the wet season (November to April) 2018/2019 (Missouri Botanical Garden 2015).

At each lemur defecation point and transect point we drew a cross in the ground, dividing the area into 4 squares. In each square, we measured the distance between the centre of the cross and the closest thin and thick tree. Thin trees were defined as trees with a diameter at breast height (DBH) of 5-9.9 cm, thick trees as trees with a DBH ≥ 10 cm. We further measured crown diameter and estimated the height of the trees, and identified the species. In preparation of the analysis, we took the mean of 4 thin/thick trees per point for distance, DBH, crown diameter and height. The mean distance per point was converted to mean tree density in individuals/ha using the formula 10,000/distance^2, following Rakotondranary *et al* (2010). We calculated the total tree density per point as the sum of mean thin and thick tree density. Finally, we calculated the number of different tree species and the number of *Delonix regia* at each point. The former was included as a proxy for plant diversity, the latter because *D. regia* was the most abundant tree species in our analysis and forms the basic structure in large parts of the forest, thus we assume it might have an influence on lemur habitat use.

Remote sensing

To investigate vegetation productivity and water content on a larger scale we downloaded and used satellite imagery to calculate various spectral indices of these characteristics. This was done at the lemur defecation and transect points established above.

We downloaded freely available Landsat 8 Operational Land Imager multispectral images from https://glovis.usgs.gov/, considering two criteria: Date of acquisition and cloud cover above the research site. We selected scenes from months in the middle of each season, to accurately depict possible differences. For the dry season we chose three scenes, acquired in July, August and September 2018; for the wet season, we chose two scenes acquired in February, and one in March 2019 (Table S1). For January 2019 there was no scene available that had no or low cloud coverage, thus we had to choose a second scene acquired in February.

To prepare the data from satellite imagery we used QGIS (3.20.2.) and SAGA GIS (7.8.2). With the Semi-Automatic Classification Plugin (7.8.36; Congedo 2021), we converted the original multispectral bands processed in units of absolute radiance to top of atmosphere (TOA) reflectance, applying atmospheric correction, for each scene separately (USGS & NASA 2019). With the same tool we performed PAN-sharpening applying the Brovey Transform procedure, to improve the resolution of all bands from 30 m to 15 m (Rahaman *et al* 2017). Using the pan-sharpened bands we calculated three spectral indices of vegetation productivity (NDVI, EVI and MSAVI), and one spectral index of vegetation water content (NDWI) for each scene (Fig. 1; Qi *et al* 1994; Gao 1996; Huete *et al* 2002).

$$\mathrm{NDVI} = \frac{\text{Near Infrared } - \text{ Red}}{\text{Near Infrared } + \text{ Red}}$$

$$\mathrm{EVI} = \mathrm{G} * \frac{\text{Near Infrared } - \text{ Red}}{\text{Near Infrared } + \mathrm{C1} * \text{Red} - \mathrm{C2} * \text{Blue} + \mathrm{L}}$$

$$\mathrm{MSAVI} = \frac{2 * \text{Near Infrared} + 1 - \sqrt{(2 * \text{Near Infrared} + 1)^2 - 8 * (\text{Near Infrared} - \text{Red})}}{2}$$

$$\mathrm{NDWI} = \frac{\text{Near Infrared} - \text{Short Wave Infrared}}{\text{Near Infrared} + \text{Short Wave Infrared}}$$

Figure 1 Equations to calculate vegetation productivity and water content-related indices using reflectance values at certain wavelength ranges: Near Infrared= 0.85-0.88 µm, Red=

0.64-0.67 µm, Blue= 0.45-0.51 µm, Short Wave Infrared= 1.57-1.65 µm (USGS & NASA 2019). In EVI equation: G (Gain factor)= 2.5; C1, C2 (coefficients for atmospheric resistance): C1= 6, C2= 7.5; L (canopy background adjustment)= 1. Please note that the equation for MSAVI is labelled as "$MSAVI_2$" in the original work by Qi *et al* (1994). The authors developed two different equations ($MSAVI_1$, $MSAVI_2$), but as they led to very similar results, they concluded the two equations may be used interchangeably to calculate the MSAVI (Qi *et al* 1994).

In preparation of the analysis, we took the mean of the spectral indices per season, i.e. for instance, the $NDVI_{dry}$ calculated as a mean of the NDVI values from the scenes of July, August and September 2018. Finally, we extracted the indices season means at the lemur defecation and transect points.

Analyses

The analyses were carried out using IBM SPSS Statistics (27). To test the variables from PCQ analysis and spectral indices from remote sensing analysis for differences between the forest types or lemur groups (Question 1 + 2), respectively, we carried out ANOVA (global) and Tukey HSD post hoc tests, if homogeneity of variance was given according to Levene's test, or Welch-ANOVA (global) and Games-Howell post hoc tests, if homogeneity of variance was not given. As ANOVA is robust against violations of normal distribution assumptions, we ignored small deviations from normality (Schmider *et al* 2010).

Lemur behaviour might vary seasonally. But the vegetation structures (tree density etc.) described by the PCQ variables should not differ between the seasons. As we did not find significant differences within each lemur group between the seasons, we do not differentiate between the seasons in the PCQ analysis in this paper. In case of the remote sensing analysis the season should have an influence on the vegetation characteristics described by the indices. As there are significant differences with respect to the remote sensing variables within each lemur group between the seasons, we differentiate between the seasons in the remote sensing analysis in this paper.

For correlations between variables from PCQ and spectral indices from remote sensing analysis (Question 3), we carried out a principal component analysis (PCA). To facilitate interpretation, we restricted the analysis to the first two principal components, and applied Varimax rotation with Kaiser normalization (Kaiser 1958).

RESULTS

To facilitate differentiating between results of PCQ and remote sensing analysis, points in plots and variable names in tables are coloured differently: PCQ results in blue, remote sensing results in yellow. Tables contain all results, but plots only significant ones.

Habitat utilization by *E. coronatus* in relation to structural vegetation characteristics (PCQ)

At the global analysis level, there were significant differences between the forest types or lemur groups, respectively, in 7 out of 11 variables analysed (Table 1). Post hoc tests revealed many significant differences between intact and degraded forest, with the former showing larger heights of thin and thick trees, larger crown diameter and density of thick trees, larger number of *D. regia*, but lower number of species than degraded forest (Figs. 2-4). Both lemur groups used microhabitats that are often similar or equal in structure and number of *D. regia* and number of species to the intact forest, except for the crown diameters of thick trees (Fig. 3b). The habitat use of the two lemur groups did not differ significantly between groups in any of the PCQ variables.

Table 1 Vegetation structure described by PCQ variables in forest types and at lemur defecation points with means ± standard deviation; and results of global statistical analysis. N gives number of transect or lemur defecation points; df1= degrees of freedom for groups; df2= degree of freedom for individual points.

Variable	**Intact (N= 20)**	**Degraded (N= 20)**	**Lemur group A (N= 40)**	**Lemur group B (N= 40)**	**Result ANOVA / Welch-ANOVA* (F)**	**p**	**df1**	**df2**
Thin tree DBH (cm)	6.6 ± 0.7	6.5 ± 0.9	6.8 ± 0.7	7.0 ± 0.7	3.182	< 0.05	3	116
Thin tree height (m)	3.4 ± 0.4	2.8 ± 0.2	3.3 ± 0.5	3.2 ± 0.4	10.814	< 0.001	3	116
Thin tree crown diameter (m)	3.3 ± 0.7	3.1 ± 0.6	3 ± 0.6	3 ± 0.7	1.420	0.240	3	116
Thin tree density (ind/ha)	521.5 ± 792.1	503.8 ± 515	682.3 ± 834.8	547.2 ± 480.4	0.470	0.704	3	116
Thick tree DBH (cm)	18.7 ± 5.4	16.9 ± 4.2	18.6 ± 4.8	17.3 ± 4.4	0.965	0.412	3	116
Thick tree height (m)	4.4 ± 0.4	3.5 ± 0.4	4.4 ± 0.7	4.1 ± 0.6	11.410	< 0.001	3	116
Thick tree crown diameter (m)	6.8 ± 1.5	5.2 ± 1.1	5.7 ± 1.4	5.2 ± 1.1	7.310	< 0.001	3	116
Thick tree density (individuals/ha)	186.3 ± 91	73.2 ± 23.9	311.9 ± 323.7	269.8 ± 202.9	26.726*	< 0.001	3	51.913
Total tree density (individuals/ha)	707.8 ± 788.9	577 ± 524.7	994.2 ± 974	817 ± 463	1.639	0.184	3	116
Number of *Delonix regia*	4.1 ± 1.1	0.7 ± 0.8	3.8 ± 2.1	2.8 ± 2.3	51.898*	< 0.001	3	61.360
Number of species	4 ± 0.9	5.7 ± 1.1	4.3 ± 1.6	4.3 ± 1.4	9.975*	< 0.001	3	57.005

Thin trees

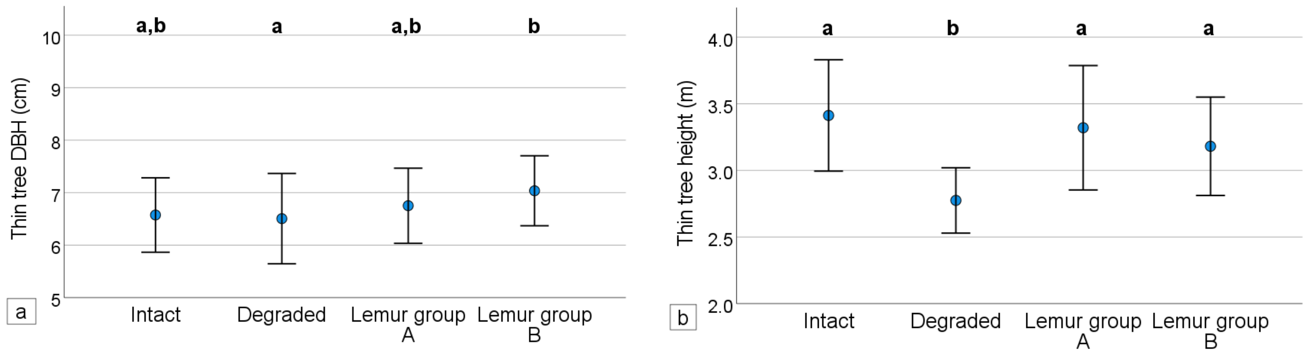

Figure 2 DBH (a) and height (b) of thin trees (DBH of 5-9.9 cm) in forest types and at lemur defecation points with means ± standard deviation. Same letters above the bars mark no significant difference of post hoc tests at α= 0.05 (Table S2).

Thick trees

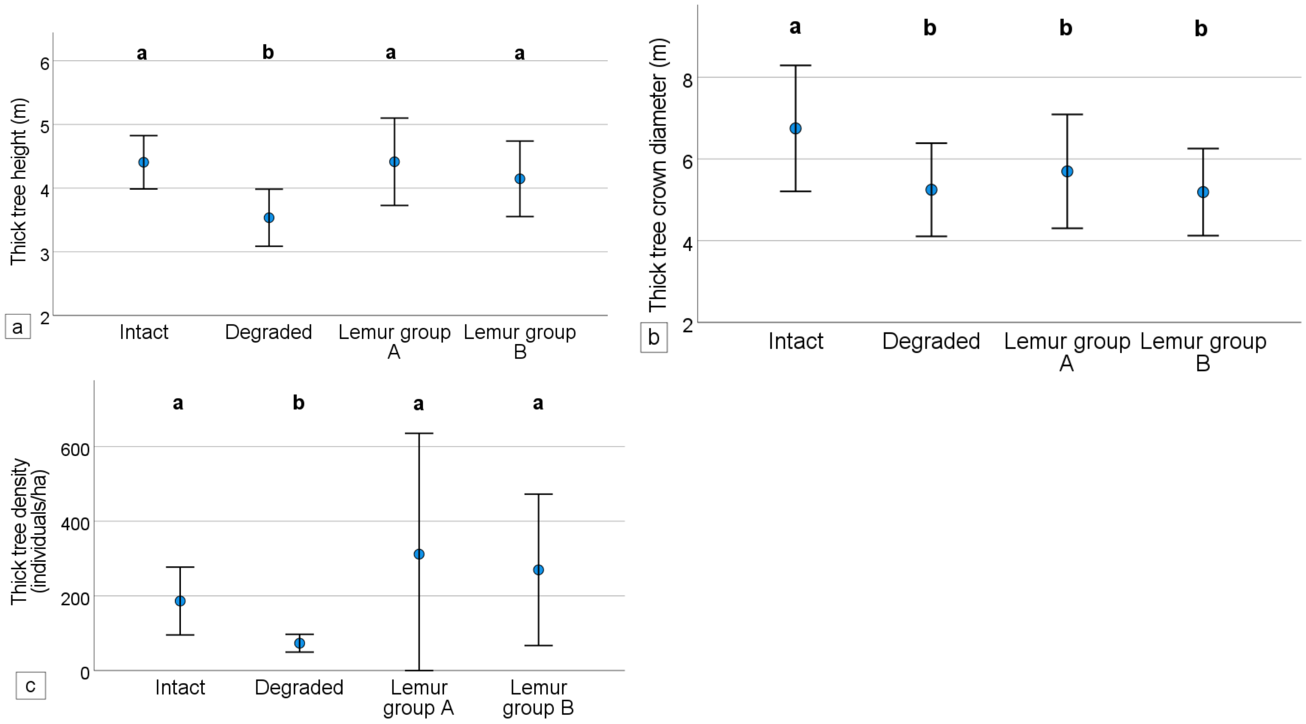

Figure 3 Height (a), crown diameter (b) and density (c) of thick trees (DBH ≥ 10 cm) in forest types and at lemur defecation points with means ± standard deviation. Same letters above the bars mark no significant difference of post hoc tests at α= 0.05 (Table S2). Please note that in Figure 3c, we cut the error bar for the standard deviation of the Lemur group A mean as it extends into the negative range.

Thin and thick trees

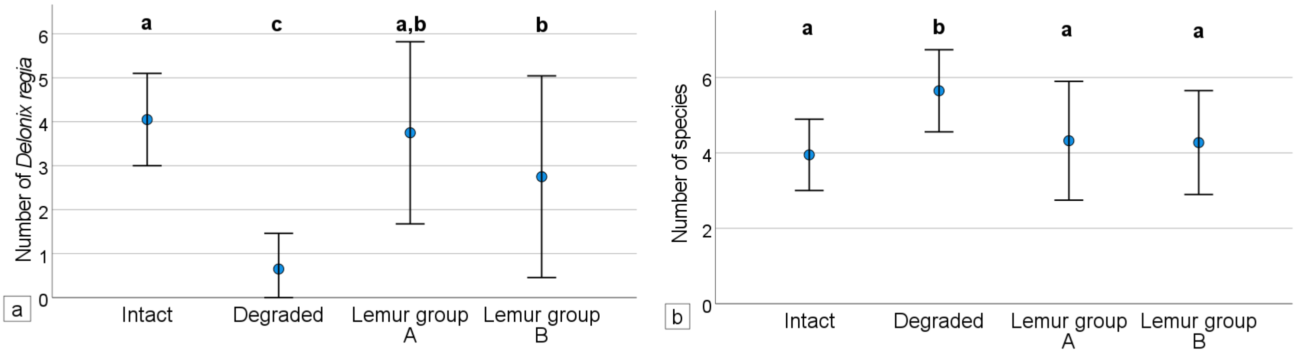

Figure 4 Number of *D. regia* (a) and number of species (b) in forest types and at lemur defecation points with means ± standard deviation. Same letters above the bars mark no significant difference of post hoc tests at α= 0.05 (Table S2). Please note that in Figure 4a, we cut the error bar for the standard deviation of the degraded forest mean as it extends into the negative range.

Habitat utilization by *E. coronatus* in relation to vegetation productivity and water content (remote sensing)

Vegetation characteristics measured at PCQ points

At the global analysis level, there were significant differences between the forest types or lemur groups, respectively, in all spectral indices analysed during both seasons (Tables 2-3). Patterns of vegetation productivity and water content were in general highly congruent in each season (Figs. 5-6). Post hoc tests again revealed significant differences between intact and degraded forest, with the former showing lower vegetation productivity and water content during the dry season, and the opposite during the wet season. The lemur groups differed significantly in almost all comparisons during both seasons. Lemur group A used habitat with vegetation productivity and water content equal to the intact forest, on the other hand, lemur group B used habitat with these characteristics being equal or similar in the degraded forest.

Dry season

Table 2 Vegetation characteristics described by vegetation productivity and water content-related indices during the dry season with means ± standard deviation; and results of global statistical analysis. N gives number of transect or lemur defecation points.

Variable	Intact (N= 20)	Degraded (N= 20)	Lemur group A dry (N= 20)	Lemur group B dry (N= 20)	Result ANOVA / Welch-ANOVA* (F)	p	df1	df2
NDVI dry	0.59 ± 0.02	0.62 ± 0.02	0.58 ± 0.05	0.60 ± 0.05	10.923*	< 0.001	3	39.783
EVI dry	0.36 ± 0.02	0.39 ± 0.02	0.35 ± 0.04	0.40 ± 0.04	12.156	< 0.001	3	76
MSAVI dry	0.31 ± 0.02	0.34 ± 0.02	0.30 ± 0.03	0.34 ± 0.04	12.276	< 0.001	3	76
NDWI dry	0.06 ± 0.04	0.15 ± 0.04	0.07 ± 0.06	0.13 ± 0.06	16.180	< 0.001	3	76

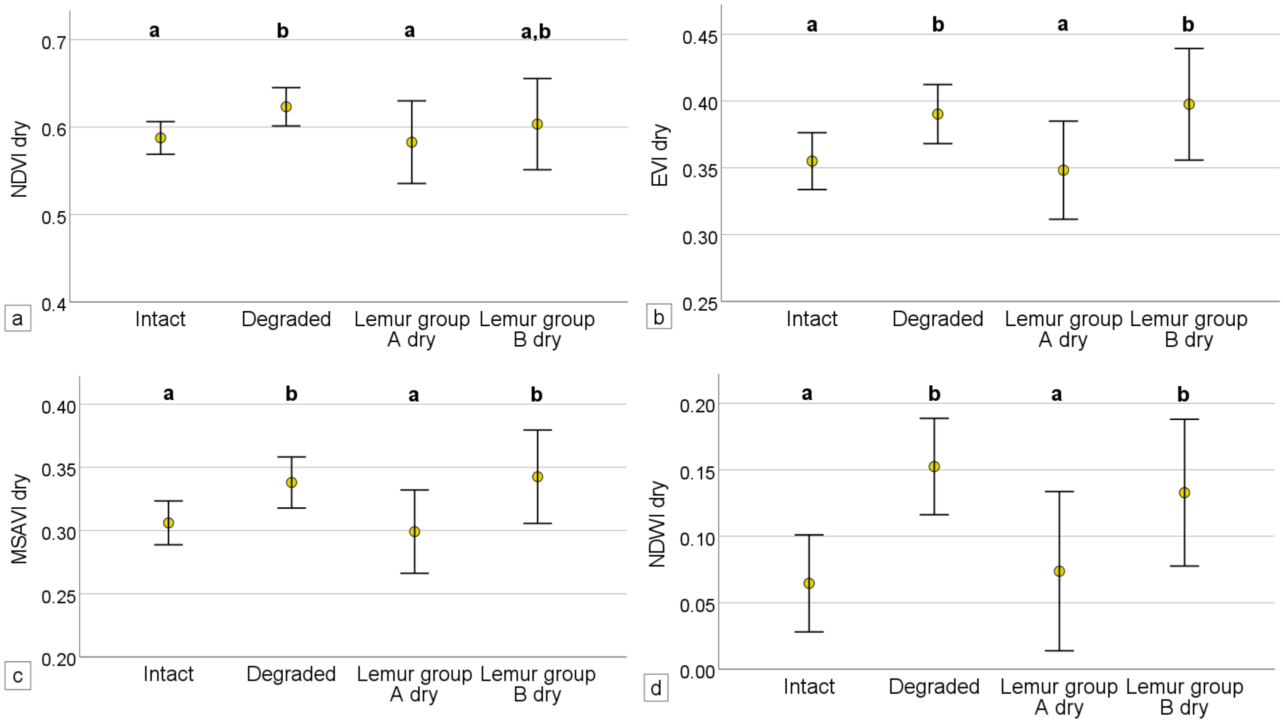

Figure 5 Vegetation productivity (NDVI (a), EVI (b) and MSAVI (c)) and water content (NDWI (d)) in forest types and at lemur defecation points during the dry season with means ± standard deviation. Same letters above the bars mark no significant difference of post hoc tests at α= 0.05 (Table S3).

Wet season

Table 3 Vegetation characteristics described by vegetation productivity and water content-related indices during the wet season with means ± standard deviation; and results of global statistical analysis. N gives number of transect or lemur defecation points.

Variable	Intact (N= 20)	Degraded (N= 20)	Lemur group A wet (N= 20)	Lemur group B wet (N= 20)	Result ANOVA / Welch-ANOVA* (F)	p	df1	df2
NDVI wet	0.87 ± 0.01	0.85 ± 0.01	0.87 ± 0.01	0.80 ± 0.08	13.091*	< 0.001	3	40.563
EVI wet	0.74 ± 0.05	0.70 ± 0.03	0.76 ± 0.03	0.62 ± 0.14	14.774*	< 0.001	3	39.807
MSAVI wet	0.70 ± 0.05	0.66 ± 0.03	0.71 ± 0.03	0.58 ± 0.14	16.110*	< 0.001	3	39.758
NDWI wet	0.49 ± 0.03	0.47 ± 0.02	0.49 ± 0.02	0.43 ± 0.07	10.024*	< 0.001	3	40.712

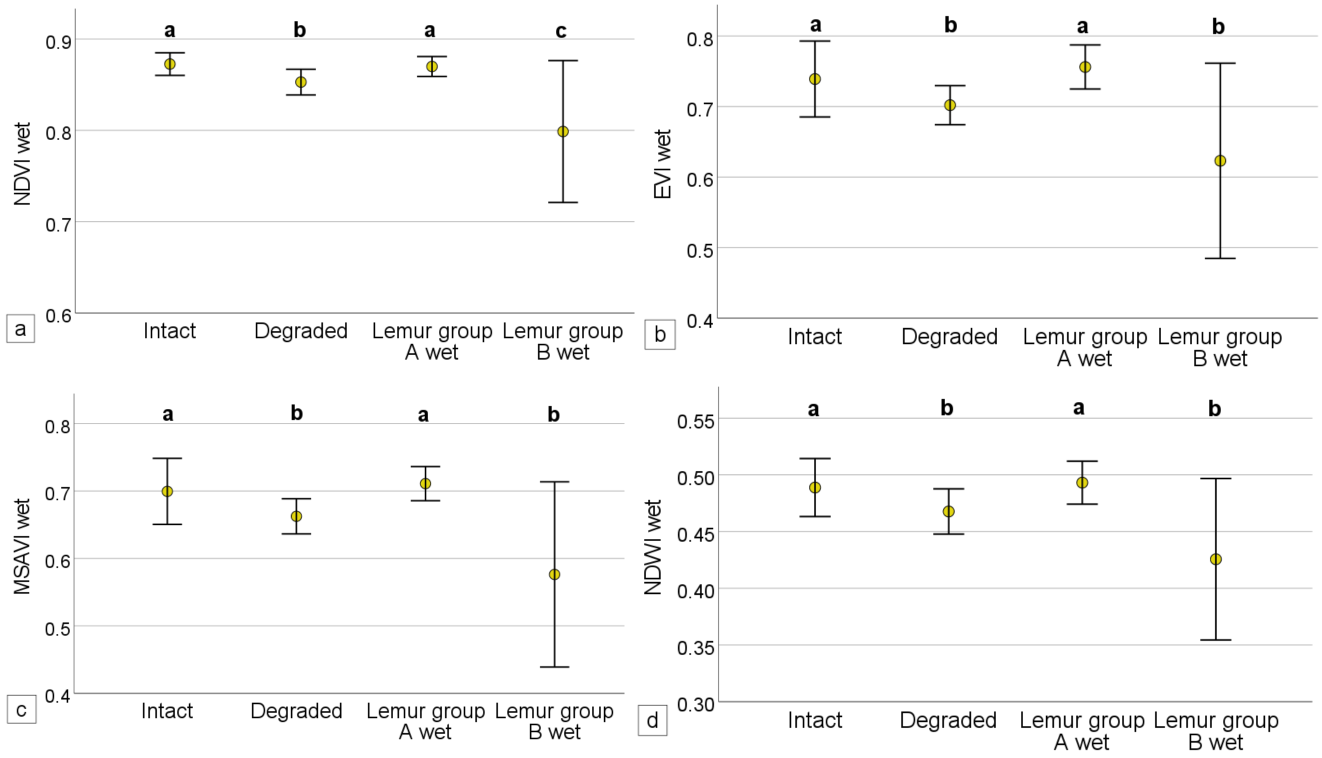

Figure 6 Vegetation productivity (NDVI (a), EVI (b) and MSAVI (c)) and water content (NDWI (d)) in forest types and at lemur defecation points during the wet season with means ± standard deviation. Same letters above the bars mark no significant difference of post hoc tests at α= 0.05 (Table S3).

Vegetation characteristics measured at all lemur occurrence points

In order to verify the differences between lemur groups in vegetation characteristics measured by remote sensing, we re-examined this result in a follow-up analysis. In this analysis, we follow the same methods as described above, but extracted the indices values at all lemur occurrence points that we georeferenced during our behavioural observations (Steffens *et al* accepted). This allowed us to investigate a much larger sample size compared to the first analysis (Lemur group A: N= 4156; Lemur group B: N= 2170).

The second analysis confirmed the results of the first: The habitat used by group A was significantly less productive and had lower water content during the dry season than the habitat used by group B, while the pattern was opposite during the wet season (Fig. 7, Table S4).

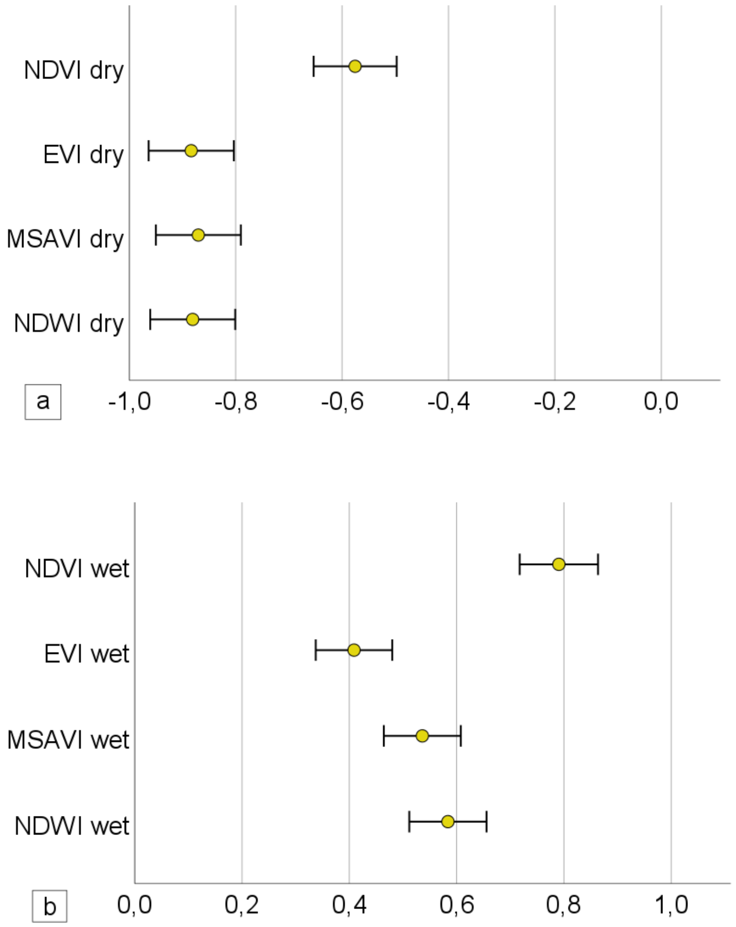

Figure 7 Effect sizes of differences in habitat use between lemur groups during the dry (a) and wet (b) season, described by vegetation productivity and water content-related indices. Plots depict the deviation of group A from group B found by T-tests with Cohen's d (points) and 95%

confidence intervals (whiskers) (Table S4). Please note the sign of the x-axis values, which differs between the two plots (negative/positive).

Complementarity of PCQ and remote sensing information

The PCA clearly separated the structural variables of the PCQ analysis and the productivity and water content-related indices of the remote sensing analysis: Principal component (PC) 1 reflects vegetation information derived from PCQ measures while PC 2 reflects vegetation information derived from satellite images (Fig. 8, Table S5). The latter is separated in the dry and wet season measurements, which are negatively correlated with PCQ variables in case of the dry season spectral indices or uncorrelated in case of the wet season indices. Only the number of tree species is correlated with dry season indices. PC 1 accounts for 22.90% of the variation in the data, PC 2 for 22.88% (rotated solution, Table S6).

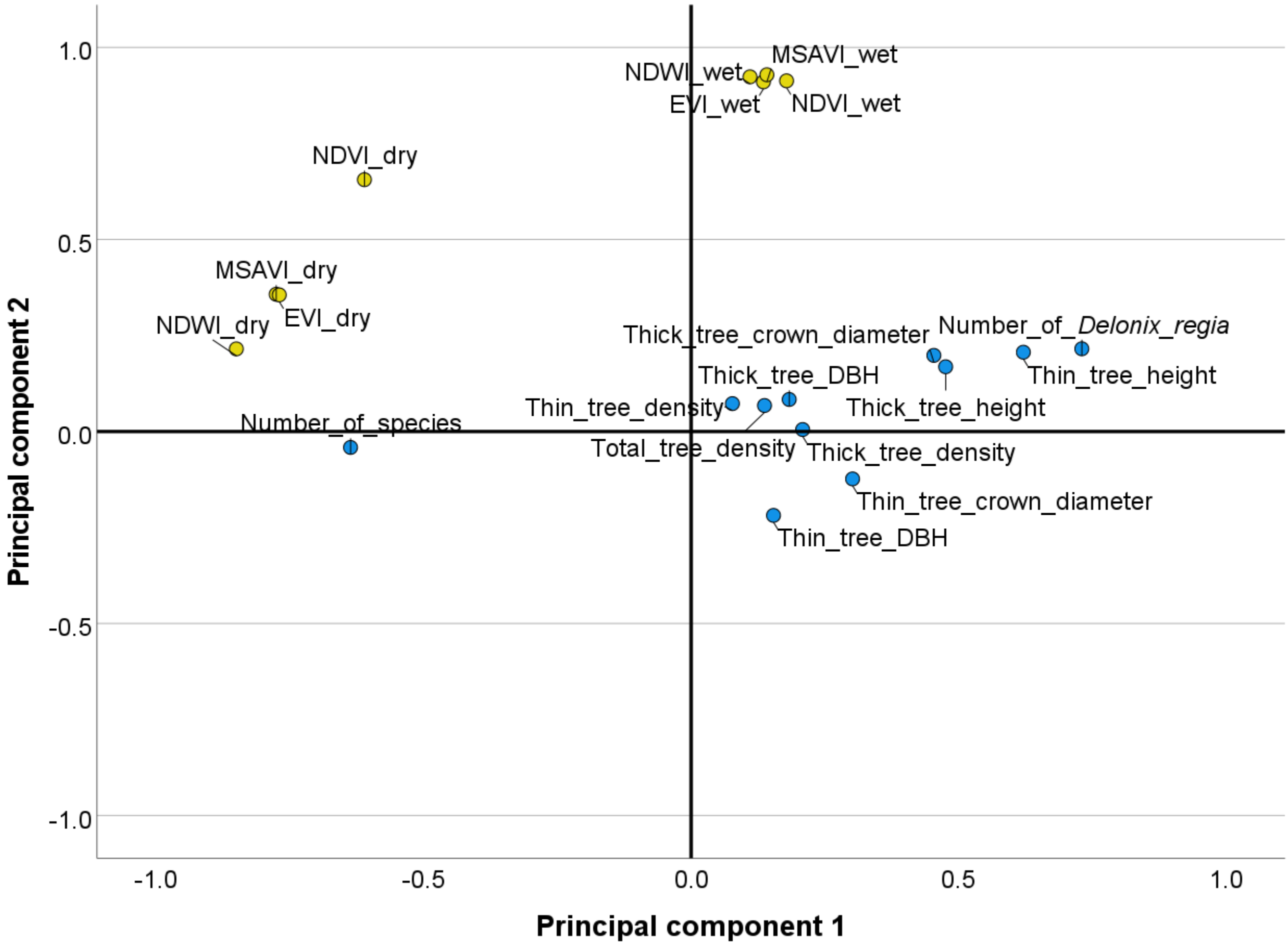

Figure 8 Rotated component plot of principal component analysis. PCQ variables depicted in blue, remote sensing indices in yellow dots.

DISCUSSION

In this paper, we investigated whether simple measures of vegetation characteristics can be used to differentiate between forests of different degrees of degradation and to identify vegetation plots that provide still suitable habitat for crowned lemurs (*Eulemur coronatus*) in northern Madagascar.

For this, we applied classical vegetation descriptions and remote sensing methods. The classical vegetation description describes mostly vegetation structures on the level of trees, while remote sensing indices provide proxies for various aspects of photosynthesis and thus plant productivity integrated over at least 15 x 15 m.

Both methods clearly separate forest of different degrees of degradation. On the small scale, microhabitat structures used by *E. coronatus* were rather stereotypic and could be linked to structural vegetation characteristics described by PCQ methods: there were no differences between the two groups of lemurs, and the structures used by lemurs were similar to the structures characterising intact forest. On the other hand, *E. coronatus* habitat was not associated consistently with vegetation productivity and water content derived by remote sensing methods from satellite images on a large scale. Locations used by group A were similar in productivity and water content to the intact forest, while locations used by group B were similar to the degraded forest in general. The latter result does not come as a surprise because the home range of group B was mostly in the degraded forest type, while the home range of group A was located mostly in the more intact part of the forest. More interestingly and on a smaller scale, *E. coronatus* obviously used microhabitats in the degraded forest type that matched the characteristics of the intact forest. Also, the lemurs used single remnant trees in heavily degraded forest to move to more intact parts of the forest. The stable PCQ characteristics and the variation in spectral indices of habitat used by lemurs indicate that the animals have specific requirements that are reflected by the structures measured by PCQ method. In contrast, once a certain limiting requirement is granted, the properties represented by satellite images seem to be used according to their availability. This limit is reflected by more extreme forms of forest degradation (e.g., Irwin *et al* 2005; Mercado Malabet *et al* 2020). Therefore, large scale degradation does not mean necessarily that the whole area is less or even unsuitable for lemurs. Rather, the question is, how many of these islands of suitable microhabitats are needed to turn an area into a permanently inhabitable habitat for lemurs, or to allow movements between suitable habitats, or to allow colonization of restored habitats.

From a conceptual point of view this brings us back to the old question of scale and graininess in habitat selection, the role of different perception of habitat features by different species (in our case differences between terrestrial, diurnal and visually oriented humans and arboreal, cathemeral and less visually oriented lemurs), the question on how to define the niche of a species, and the relative and possibly seasonally changing importance of structural versus food-related features (Klopfer 1969; Van der Putten, Macel & Visser 2010; Leitão & Santos 2019; Owens *et al* 2020).

These issues are exemplified by many studies where several lemur species occur within a seemingly homogenous vegetation formation but the different species use different microhabitats, such as lemurs of the humid forest of Andasibe (Ganzhorn 1989), the dry forest of Ankarafantsika (Rendigs *et al* 2002; Sehen *et al* 2010) or the humid littoral forests (Lahann 2008). While the structures measured might be important, there are many other components not considered by the PCQ measures, such as water either provided by the plants or by open water sources (e.g., Wilson *et al* 1989; Scholz & Kappeler 2004; Amoroso *et al* 2019). At least larger water sources are easily identified and accounted for by remote sensing techniques (Mercado Malabet *et al* 2020).

Remote sensing tools have certainly proved useful for mapping the area of possible occurrence and for defining categories of habitat suitability in Madagascar (Smith, Horning & Moore 1997; Irwin *et al* 2005; Kremen *et al* 2008; Lahoz-Monfort *et al* 2010; Brown & Yoder 2015) and elsewhere (e.g., Zinner, Peláez & Torkler 2001; Boyce *et al* 2003; Willems, Barton & Hill 2009; Pettorelli *et al* 2011; Farrell *et al* 2013). Though, as our investigation has shown, vegetation information derived from remote sensing methods may not always be able to explain habitat use. Reasons for this might be on the one hand that the characteristics analysed are not ecologically relevant for the study species. In this case this seems unrealistic, however, as crowned lemurs feed on fruits and leaves and are tree dwellers dependent on vegetation. Also, other lemur species' diversity, abundance and habitat use is positively correlated to plant productivity (Hudson 2011; Herrera 2017; Campera *et al* 2020). On the other hand, the results might come about by different temporal or spatial scales of analysis which may or may not reflect the “habitat graininess” perceived by an animal at a given time (compare Lahoz-Monfort *et al* 2010).

A problem encountered with both classical vegetation descriptions and remote sensing methods is that variables can be intercorrelated (Huete *et al* 2002; Verbesselt *et al* 2007; Rakotondranary *et al* 2010), as in this study, complicating to determine which vegetation characteristics are critical for habitat utilization. This may be less of a problem concerning the PCQ variables, as they were not as strongly intercorrelated as remote sensing indices.

While we cannot assess the various confounding factors, the two methods provided different vegetation information that is not exchangeable. This has to be kept in mind when basing conservation decisions on only one or the other technique. Areas classified as unsuitable might still contain elements that can serve as stepping stones for movements between suitable habitats and as nuclei for the restoration of forests. Restoring these microhabitats first could be a target for punctual restoration that could then lead to facilitated restoration through seeds dispersed by lemurs and probably also other animal groups. What remains to be clarified here are the tipping points that define thresholds in the distribution of these structures below which any given species can no longer make use of any given area (Huggett 2005; Betts, Forbes & Diamond 2007; Steffens *et al* 2017).

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REFERENCES

Albert-Daviaud, A., Buerki, S., Onjalalaina, G. E., Perillo, S., Rabarijaona, R., Razafindratsima, O. H., Sato, H., Valenta, K., Wright, P. C., & Stuppy, W. (2020). The ghost fruits of Madagascar: identifying dysfunctional seed dispersal in Madagascar's endemic flora. *Biol. Conserv.* **242**, 108438.

Albert-Daviaud, A., Perillo, S., & Stuppy, W. (2018). Seed dispersal syndromes in the Madagascan flora: the unusual importance of primates. *Oryx* **52**, 418–426.

Amoroso, C. R., Kappeler, P. M., Fichtel, C., & Nunn, C. L. (2019). Fecal contamination, parasite risk, and waterhole use by wild animals in a dry deciduous forest. *Behav. Ecol. Sociobiol.* **73**, 153.

Andresen, E., Arroyo-Rodríguez, V., & Ramos-Robles, M. (2018). Primate seed dispersal: old and new challenges. *Int. J. Primatol.* **39**, 443–465.

Andriamaharoa, H., Birkinshaw, C., & Reza, L. (2010). Day-time feeding ecology of *Eulemur cinereiceps* in the Agnalazaha Forest, Mahabo-Mananivo, Madagascar. *Madagascar Conservation & Development* **5**, 55–63.

Andriamandimbiarisoa, L., Blanthorn, T. S., Ernest, R., Ramanamanjato, J.-B., Randriatafika, F., Ganzhorn, J. U., & Donati, G. (2015). Habitat corridor utilization by the gray mouse lemur, *Microcebus murinus*, in the littoral forest fragments of southeastern Madagascar. *Madagascar Conservation & Development* **10**, 144–150.

Andrianasolo, T. H., Andrianjazalahatra, T. L., Rakotondranary, S. J., Ramarokoto, R. E. A. F., Randria, G., Rüdel, N., Schüller, J., & Ganzhorn, J. U. (2006). Habitat utilisation of nocturnal lemurs in evergreen littoral forests of different degrees of degradation. In *Proceedings of the German-Malagasy Research Cooperation in Life and Earth Sciences*: 151–159. Schwitzer, C., Brandt, S., Ramilijaona, O., Razanahoera, M. R., Ackermand, D., Razakamanana, T. & Ganzhorn, J. U. (Eds.). Berlin: Concept Verlag.

Betts, M. G., Forbes, G. J., & Diamond, A. W. (2007). Thresholds in songbird occurrence in relation to landscape structure. *Conserv. Biol.* **21**, 1046–1058.

Boyce, M. S., Mao, J. S., Merrill, E. H., Fortin, D., Turner, M. G., Fryxell, J., & Turchin, P. (2003). Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Écoscience* **10**, 421–431.

Brower, J. E., Zar, J. H., & von Ende, C. N. (1990). *Field and laboratory methods for general ecology*. Dubuque, Iowa: WCB Publishers.

Brown, J. L., & Yoder, A. D. (2015). Shifting ranges and conservation challenges for lemurs in the face of climate change. *Ecol. Evol.* **5**, 1131–1142.

Campera, M., Santini, L., Balestri, M., Nekaris, K. A. I., & Donati, G. (2020). Elevation gradients of lemur abundance emphasise the importance of Madagascar's lowland rainforest for the conservation of endemic taxa. *Mam. Rev.* **50**, 25–37.

Chapman, C. A., Balcomb, S. R., Gillespie, T. R., Skorupa, J. P., & Struhsaker, T. T. (2000). Long-term effects of logging on African primate communities: a 28-year comparison from Kibale National Park, Uganda. *Conserv. Biol.* **14**, 207–217.

Chapman, C. A., & Onderdonk, D. A. (1998). Forests without primates: primate/plant codependency. *Am. J. Primatol.* **45**, 127–141.

Charles, L. S., Dwyer, J. M., Chapman, H. M., Yadok, B. G., & Mayfield, M. M. (2019). Landscape structure mediates zoochorous-dispersed seed rain under isolated pasture trees across distinct tropical regions. *Landscape Ecol.* **34**, 1347–1362.

Congedo, L. (2021). Semi-Automatic Classification Plugin: a Python tool for the download and processing of remote sensing images in QGIS. *Journal of Open Source Software* **6**, 3172.

Corbin, J. D., & Holl, K. D. (2012). Applied nucleation as a forest restoration strategy. *Forest Ecol. Manag.* **265**, 37–46.

Crowley, B. E., Godfrey, L. R., & Irwin, M. T. (2011). A glance to the past: subfossils, stable isotopes, seed dispersal, and lemur species loss in southern Madagascar. *Am. J. Primatol.* **73**, 25–37.

Estrada, A., Garber, P. A., Rylands, A. B., Roos, C., Fernandez-Duque, E., Di Fiore, A., Nekaris, K. A.-I., Nijman, V., Heymann, E. W., Lambert, J. E., Rovero, F., Barelli, C., Setchell, J. M., Gillespie, T. R., Mittermeier, R. A., Arregoitia, L. V., de Guinea, M., Gouveia, S., Dobrovolski, R., Shanee, S., Shanee, N., Boyle, S. A., Fuentes, A., MacKinnon, K. C., Amato, K. R., Meyer, A. L. S., Wich, S., Sussman, R. W., Pan, R., Kone, I., & Li, B. (2017). Impending extinction crisis of the world's primates: why primates matter. *Sci. Adv.* **3**, e1600946.

Farrell, S. L., Collier, B. A., Skow, K. L., Long, A. M., Campomizzi, A. J., Morrison, M. L., Hays, K. B., & Wilkins, R. N. (2013). Using LiDAR-derived vegetation metrics for high-resolution, species distribution models for conservation planning. *Ecosphere* **4**, 42.

Farwig, N., & Berens, D. G. (2012). Imagine a world without seed dispersers: a review of threats, consequences and future directions. *Basic Appl. Ecol.* **13**, 109–115.

Federman, S., Dornburg, A., Daly, D. C., Downie, A., Perry, G. H., Yoder, A. D., Sargis, E. J., Richard, A. F., Donoghue, M. J., & Baden, A. L. (2016). Implications of lemuriform extinctions for the Malagasy flora. *Proc. Natl. Acad. Sci. USA* **113**, 5041–5046.

Fleming, T. H., Breitwisch, R., & Whitesides, G. H. (1987). Patterns of tropical vertebrate frugivore diversity. *Annu. Rev. Ecol. Syst.* **18**, 91–109.

Forbanka, D. N. (2018). Microhabitat utilization by fork-marked dwarf lemurs (*Phaner* spp.) and needle-clawed galagos (*Euoticus* spp.) in primary and secondary forests. *Am. J. Primatol.* **80**, e22864.

Gann, G. D., McDonald, T., Walder, B., Aronson, J., Nelson, C. R., Jonson, J., Hallett, J. G., Eisenberg, C., Guariguata, M. R., Liu, J., Hua, F., Echeverría, C., Gonzales, E., Shaw, N., Decleer, K., & Dixon, K.

W. (2019). International principles and standards for the practice of ecological restoration. 2nd edn. *Restor. Ecol.* **27**, S1–S46.

Ganzhorn, J. U. (1989). Niche separation of seven lemur species in the eastern rainforest of Madagascar. *Oecologia* **79**, 279–286.

Ganzhorn, J. U., Rakotondranary, S. J., & Ratovonamana, Y. R. (2011). Habitat description and phenology. In *Field and laboratory methods in primatology*: 51–68. Setchell, J. M. & Curtis, D. J. (Eds.). 2nd edn. Cambridge, UK: Cambridge University Press.

Gao, B.-C. (1996). NDWI—a normalized difference water index for remote sensing of vegetation liquid water from space. *Remote Sens. Environ.* **58**, 257–266.

Gao, X., Huete, A. R., Ni, W., & Miura, T. (2000). Optical–biophysical relationships of vegetation spectra without background contamination. *Remote Sens. Environ.* **74**, 609–620.

Gómez, J. M., & Verdú, M. (2012). Mutualism with plants drives primate diversification. *Syst. Biol.* **61**, 567–577.

Goodman, S. M., Raherilalao, M. J., & Wohlhauser, S. (2018). *Les aires protégées terrestres de Madagascar: Leur histoire, description et biote / The terrestrial protected areas of Madagascar: Their history, description, and biota.* Antananarivo, Madagascar: Association Vahatra.

Herrera, J. P. (2017). The effects of biogeography and biotic interactions on lemur community assembly. *Int. J. Primatol.* **38**, 692–716.

Heymann, E. W., Culot, L., Knogge, C., Noriega Piña, T. E., Tirado Herrera, E. R., Klapproth, M., & Zinner, D. (2017). Long-term consistency in spatial patterns of primate seed dispersal. *Ecol. Evol.* **7**, 1435–1441.

Hicke, J. A., Asner, G. P., Randerson, J. T., Tucker, C., Los, S., Birdsey, R., Jenkins, J. C., & Field, C. (2002). Trends in North American net primary productivity derived from satellite observations, 1982-1998. *Global Biogeochem. Cy.* **16**, 1–14.

Howe, H. F. (1986). Seed dispersal by fruit-eating birds and mammals. In *Seed Dispersal*: 123–189. Murray, D. R. (Ed.). New York: Academic Press.

Hudson, M. (2011). *Estimating population trends in elusive species using dynamic occupancy modelling; the Critically Endangered Alaotran gentle lemur.* Master thesis. London, UK: Imperial College London.

Huete, A. R., Didan, K., Miura, T., Rodriguez, E. P., Gao, X., & Ferreira, L. G. (2002). Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sens. Environ.* **83**, 195–213.

Huggett, A. J. (2005). The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biol. Conserv.* **124**, 301–310.

Irwin, M. T., Johnson, S. E., & Wright, P. C. (2005). The state of lemur conservation in south-eastern Madagascar: population and habitat assessments for diurnal and cathemeral lemurs using surveys, satellite imagery and GIS. *Oryx* **39**, 204–218.

Irwin, M. T., Wright, P. C., Birkinshaw, C., Fisher, B. L., Gardner, C. J., Glos, J., Goodman, S. M., Loiselle, P., Rabeson, P., Raharison, J.-L., Raherilalao, M. J., Rakotondravony, D., Raselimanana, A., Ratsimbazafy, J., Sparks, J. S., Wilmé, L., & Ganzhorn, J. U. (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biol. Conserv.* **143**, 2351–2362.

Isabirye-Basuta, G. M., & Lwanga, J. S. (2008). Primate populations and their interactions with changing habitats. *Int. J. Primatol.* **29**, 35–48.

Johns, A. D., & Skorupa, J. P. (1987). Responses of rain-forest primates to habitat disturbance: a review. *Int. J. Primatol.* **8**, 157–191.

Kaiser, H. F. (1958). The varimax criterion for analytic rotation in factor analysis. *Psychometrika* **23**, 187–200.

Klopfer, P. H. (1969). *Habitats and territories: a study of the use of space by animals*. New York: Basic Books.

Kotliar, N. B., & Wiens, J. A. (1990). Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos* **59**, 253.

Kremen, C., Cameron, A., Moilanen, A., Phillips, S. J., Thomas, C. D., Beentje, H., Dransfield, J., Fisher, B. L., Glaw, F., Good, T. C., Harper, G. J., Hijmans, R. J., Lees, D. C., Louis, E., Nussbaum, R. A., Raxworthy, C. J., Razafimpahanana, A., Schatz, G. E., Vences, M., Vieites, D. R., Wright, P. C., & Zjhra, M. L. (2008). Aligning conservation priorities across taxa in Madagascar with high-resolution planning tools. *Science* **320**, 222–226.

Lahann, P. (2008). Habitat utilization of three sympatric cheirogaleid lemur species in a littoral rain forest of southeastern Madagascar. *Int. J. Primatol.* **29**, 117–134.

Lahoz-Monfort, J. J., Guillera-Arroita, G., Milner-Gulland, E. J., Young, R. P., & Nicholson, E. (2010). Satellite imagery as a single source of predictor variables for habitat suitability modelling: how Landsat can inform the conservation of a critically endangered lemur. *J. Appl. Ecol.* **47**, 1094–1102.

Leitão, P. J., & Santos, M. J. (2019). Improving models of species ecological niches: a remote sensing overview. *Front. Ecol. Evol.* **7**, 9.

Mercado Malabet, F., Peacock, H., Razafitsalama, J., Birkinshaw, C., & Colquhoun, I. (2020). Realized distribution patterns of crowned lemurs (*Eulemur coronatus*) within a human-dominated forest fragment in northern Madagascar. *Am. J. Primatol.* **82**, e23125.

Missouri Botanical Garden. (2015). *Plan d'aménagement et de gestion de la Nouvelle Aire Protégée Oronjia.* Antananarivo, Madagascar: Missouri Botanical Garden Madagascar.

Moat, J., & Smith, P. (2007). *Atlas of the vegetation of Madagascar*. Kew, UK: Royal Botanic Gardens.

Myneni, R. B., Hall, F. G., Sellers, P. J., & Marshak, A. L. (1995). The interpretation of spectral vegetation indexes. *IEEE T. Geosci. Remote* **33**, 481–486.

Owens, H. L., Ribeiro, V., Saupe, E. E., Cobos, M. E., Hosner, P. A., Cooper, J. C., Samy, A. M., Barve, V., Barve, N., Muñoz-R., C. J., & Peterson, A. T. (2020). Acknowledging uncertainty in evolutionary reconstructions of ecological niches. *Ecol. Evol.* **10**, 6967–6977.

Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., & Kausrud, K. (2011). The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. *Clim. Res.* **46**, 15–27.

Qi, J., Chehbouni, A., Huete, A. R., Kerr, Y. H., & Sorooshian, S. (1994). A modified soil adjusted vegetation index. *Remote Sens. Environ.* **48**, 119–126.

Rahaman, K., Hassan, Q., & Ahmed, M. (2017). Pan-sharpening of Landsat-8 images and its application in calculating vegetation greenness and canopy water contents. *ISPRS Int. J. Geo-Inf.* **6**, 168.

Rakotondranary, S. J., & Ganzhorn, J. U. (2011). Habitat separation of sympatric *Microcebus* spp. in the dry spiny forest of south-eastern Madagascar. *Folia Primatol.* **82**, 212–223.

Rakotondranary, S. J., Ganzhorn, J. U., & Ratovonamana, Y. R. (2010). Distributions et caractéristiques des microhabitats de *Microcebus griseorufus* (Cheirogaleidae) dans le Parc National de Tsimanampetsotsa (Sud-ouest de Madagascar). *Malagasy Nature* **4**, 55–64.

Rendigs, A., Radespiel, U., Wrogemann, D., & Zimmermann, E. (2002). Relationship between microhabitat structure and distribution of mouse lemurs (*Microcebus* spp.) in northwestern Madagascar. *Int. J. Primatol.* 18.

Richardson, A. J., & Everitt, J. H. (1992). Using spectral vegetation indices to estimate rangeland productivity. *Geocarto Int.* **7**, 63–69.

Schmider, E., Ziegler, M., Danay, E., Beyer, L., & Bühner, M. (2010). Is it really robust? Reinvestigating the robustness of ANOVA against violations of the normal distribution assumption. *Methodology* **6**, 147–151.

Scholz, F., & Kappeler, P. M. (2004). Effects of seasonal water scarcity on the ranging behavior of *Eulemur fulvus rufus*. *Int. J. Primatol.* **25**, 599–613.

Schwitzer, C., Glatt, L., Nekaris, K. A.-I., & Ganzhorn, J. U. (2011). Responses of animals to habitat alteration: an overview focussing on primates. *Endang. Species. Res.* **14**, 31–38.

Schwitzer, N., Randriatahina, G. H., Kaumanns, W., Hoffmeister, D., & Schwitzer, C. (2007). Habitat utilization of blue-eyed black lemurs, *Eulemur macaco flavifrons* (Gray, 1867), in primary and altered forest fragments. *Primate Conserv.* **22**, 79–87.

Sehen, L., Goetze, D., Rajeriarison, C., Roger, E., Thorén, S., & Radespiel, U. (2010). Structural and floristic traits of habitats with differing relative abundance of the lemurs *Microcebus murinus* and *M. ravelobensis* in northwestern Madagascar. *Ecotropica* **16**, 15–30.

Sha, J. C. M., Chua, S. C., Chew, P. T., Ibrahim, H., Lua, H. K., Fung, T. K., & Zhang, P. (2018). Small-scale variability in a mosaic tropical rainforest influences habitat use of long-tailed macaques. *Primates* **59**, 163–171.

Smith, A. P., Horning, N., & Moore, D. (1997). Regional biodiversity planning and lemur conservation with GIS in western Madagascar. *Conservation Biology* **11**, 498–512.

Steffens, K. J. E., Rakotondranary, S. J., Ratovonamana, Y. R., & Ganzhorn, J. U. (2017). Vegetation thresholds for the occurrence and dispersal of *Microcebus griseorufus* in southwestern Madagascar. *Int. J. Primatol.* **38**, 1138–1153.

Steffens, K. J. E., Sanamo, J., & Razafitsalama, J. (accepted). The role of lemur seed dispersal in restoring degraded forest ecosystems in Madagascar. *Folia Primatol*.

Steffens, T. S., Mercado Malabet, F., & Lehman, S. M. (2020). Occurrence of lemurs in landscapes and their species-specific scale responses to habitat loss. *Am. J. Primatol.* **82**, e23110.

Stickler, C. M., & Southworth, J. (2008). Application of multi-scale spatial and spectral analysis for predicting primate occurrence and habitat associations in Kibale National Park, Uganda. *Remote Sens. Environ.* **112**, 2170–2186.

St-Louis, V., Pidgeon, A. M., Clayton, M. K., Locke, B. A., Bash, D., & Radeloff, V. C. (2009). Satellite image texture and a vegetation index predict avian biodiversity in the Chihuahuan Desert of New Mexico. *Ecography* **32**, 468–480.

Storch, I. (2002). On spatial resolution in habitat models: can small-scale forest structure explain capercaillie numbers? *Conserv. Ecol.* **6**, 6.

Tucker, C. J., Holben, B. N., Elgin, J. H., & McMurtrey, J. E. (1981). Remote sensing of total dry-matter accumulation in winter wheat. *Remote Sens. Environ.* **11**, 171–189.

USGS & NASA. (2019). *Landsat 8 (L8) Data users handbook*. Version 5.0. Sioux Falls, South Dakota: Earth Resources Observation and Science Center.

Van der Putten, W. H., Macel, M., & Visser, M. E. (2010). Predicting species distribution and abundance responses to climate change: why it is essential to include biotic interactions across trophic levels. *Phil. Trans. R. Soc. B* **365**, 2025–2034.

Verbesselt, J., Somers, B., Lhermitte, S., Jonckheere, I., van Aardt, J., & Coppin, P. (2007). Monitoring herbaceous fuel moisture content with SPOT VEGETATION time-series for fire risk prediction in savanna ecosystems. *Remote Sens. Environ.* **108**, 357–368.

Wang, J., Price, K. P., & Rich, P. M. (2001). Spatial patterns of NDVI in response to precipitation and temperature in the central Great Plains. *Int. J. Remote Sens.* **22**, 3827–3844.

Willems, E. P., Barton, R. A., & Hill, R. A. (2009). Remotely sensed productivity, regional home range selection, and local range use by an omnivorous primate. *Behav. Ecol.* **20**, 985–992.

Wilson, J. M., Stewart, P. D., Ramangason, G.-S., Denning, A. M., & Hutchings, M. S. (1989). Ecology and conservation of the crowned lemur, *Lemur coronatus*, at Ankarana, N. Madagascar. *Folia Primatol.* **52**, 1–26.

Wunderle Jr., J. M. (1997). The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecol. Manag.* **99**, 223–235.

Zinner, D., Peláez, F., & Torkler, F. (2001). Distribution and habitat associations of baboons (*Papio hamadryas*) in Central Eritrea. *Int. J. Primatol.* **22**, 397–413.

SUPPLEMENT

Table S1 Overview of Landsat scenes covering the Oronjia New Protected Area, selected for the analysis of vegetation characteristics in different seasons.

Landsat Product ID	**Date acquisition**	**Season**
LC08_L1TP_158069_20180718_20180731_01_T1	18.07.2018	dry
LC08_L1TP_158069_20180803_20180814_01_T1	03.08.2018	dry
LC08_L1TP_158069_20180920_20180928_01_T1	20.09.2018	dry
LC08_L1TP_158069_20190211_20190222_01_T1	11.02.2019	wet
LC08_L1TP_159068_20190218_20190222_01_T1	18.02.2019	wet
LC08_L1TP_158069_20190315_20190325_01_T1	15.03.2019	wet

Table S2 Results of post hoc tests for vegetation structure described by PCQ variables. In this table we included only post hoc comparisons for variables that were significant at the global level (Table 1). Intact N= 20, Degraded N= 20, Lemur group A N= 40 and Lemur group B N= 40 for all comparisons.

Variable	**Test type**	**Forest type/ lemur defecation points (a)**	**Forest type/ lemur defecation points (b)**	**Mean difference (a-b)**	**Standard error**	**p**
Thin tree DBH	Tukey-HSD	Intact	Degraded	0.07	0.23	0.990
			Lemur group A	-0.18	0.20	0.809
			Lemur group B	-0.46	0.20	0.098
		Degraded	Intact	-0.07	0.23	0.990
			Lemur group A	-0.25	0.20	0.602
			Lemur group B	-0.53	0.20	0.042
		Lemur group A	Intact	0.18	0.20	0.809
			Degraded	0.25	0.20	0.602
			Lemur group B	-0.28	0.16	0.299

		Lemur group B	Intact	0.46	0.20	0.098
			Degraded	0.53	0.20	0.042
			Lemur group A	0.28	0.16	0.299
Thin tree height	Tukey-HSD	Intact	Degraded	0.64	0.13	0.000
			Lemur group A	0.09	0.11	0.832
			Lemur group B	0.23	0.11	0.150
		Degraded	Intact	-0.64	0.13	0.000
			Lemur group A	-0.55	0.11	0.000
			Lemur group B	-0.41	0.11	0.002
		Lemur group A	Intact	-0.09	0.11	0.832
			Degraded	0.55	0.11	0.000
			Lemur group B	0.14	0.09	0.401
		Lemur group B	Intact	-0.23	0.11	0.150
			Degraded	0.41	0.11	0.002
			Lemur group A	-0.14	0.09	0.401
Thick tree height	Tukey-HSD	Intact	Degraded	0.87	0.18	0.000
			Lemur group A	-0.01	0.16	1.000
			Lemur group B	0.26	0.16	0.367
		Degraded	Intact	0.87	0.18	0.000
			Lemur group A	0.88	0.16	0.000
			Lemur group B	0.61	0.16	0.001
		Lemur group A	Intact	0.01	0.16	1.000
			Degraded	0.88	0.16	0.000
			Lemur group B	0.27	0.13	0.173
		Lemur group B	Intact	-0.26	0.16	0.367
			Degraded	0.61	0.16	0.001
			Lemur group A	-0.27	0.13	0.173
Thick tree crown diameter	Tukey-HSD	Intact	Degraded	1.50	0.40	0.002
			Lemur group A	1.05	0.35	0.017
			Lemur group B	1.56	0.35	0.000
		Degraded	Intact	-1.50	0.40	0.002
			Lemur group A	-0.45	0.35	0.574
			Lemur group B	0.06	0.35	0.998
		Lemur group A	Intact	-1.05	0.35	0.017
			Degraded	0.45	0.35	0.574
			Lemur group B	0.51	0.29	0.292
		Lemur group B	Intact	-1.56	0.35	0.000
			Degraded	-0.06	0.35	0.998
			Lemur group A	-0.51	0.29	0.292
Thick tree density	Games-Howell	Intact	Degraded	113.08	21.04	0.000
			Lemur group A	-125.56	55.09	0.117
			Lemur group B	-83.53	37.99	0.136
		Degraded	Intact	-113.08	21.04	0.000
			Lemur group A	-238.64	51.47	0.000
			Lemur group B	-196.61	32.52	0.000
		Lemur group A	Intact	125.56	55.09	0.117
			Degraded	238.64	51.47	0.000

			Lemur group B	42.03	60.41	0.898
		Lemur group B	Intact	83.53	37.99	0.136
			Degraded	196.61	32.52	0.000
			Lemur group A	-42.03	60.41	0.898
Number of *Delonix regia*	Games-Howell	Intact	Degraded	3.40	0.30	0.000
			Lemur group A	0.30	0.40	0.879
			Lemur group B	1.30	0.43	0.020
		Degraded	Intact	-3.40	0.30	0.000
			Lemur group A	-3.10	0.37	0.000
			Lemur group B	-2.10	0.41	0.000
		Lemur group A	Intact	-0.30	0.40	0.879
			Degraded	3.10	0.37	0.000
			Lemur group B	1.00	0.49	0.181
		Lemur group B	Intact	-1.30	0.43	0.020
			Degraded	2.10	0.41	0.000
			Lemur group A	-1.00	0.49	0.181
Number of species	Games-Howell	Intact	Degraded	-1.70	0.32	0.000
			Lemur group A	-0.38	0.33	0.661
			Lemur group B	-0.33	0.30	0.708
		Degraded	Intact	1.70	0.32	0.000
			Lemur group A	1.33	0.35	0.002
			Lemur group B	1.38	0.33	0.001
		Lemur group A	Intact	0.38	0.33	0.661
			Degraded	-1.33	0.35	0.002
			Lemur group B	0.05	0.33	0.999
		Lemur group B	Intact	0.33	0.30	0.708
			Degraded	-1.38	0.33	0.001
			Lemur group A	-0.05	0.33	0.999

Table S3 Results of post hoc tests for vegetation characteristics described by vegetation productivity and water content-related indices during the dry and wet season. In this table we included only post hoc comparisons for variables that were significant at the global level (Tables 2-3). Intact N= 20, Degraded N= 20, Lemur group A dry N= 20, Lemur group B dry N= 20, Lemur group A wet N= 20 and Lemur group B wet N= 20 for all comparisons.

Variable	Test type	Forest type/ lemur defecation points (a)	Forest type/ lemur defecation points (b)	Mean difference (a-b)	Standard error	p
NDVI dry	Games-Howell	Intact	Degraded	-0.04	0.01	0.000
			Lemur group A dry	0.00	0.01	0.973
			Lemur group B dry	-0.02	0.01	0.589
		Degraded	Intact	0.04	0.01	0.000
			Lemur group A dry	0.04	0.01	0.009
			Lemur group B dry	0.02	0.01	0.414
		Lemur group A dry	Intact	0.00	0.01	0.973

			Degraded	-0.04	0.01	0.009
			Lemur group B dry	-0.02	0.02	0.561
		Lemur group B dry	Intact	0.02	0.01	0.589
			Degraded	-0.02	0.01	0.414
			Lemur group A dry	0.02	0.02	0.561
EVI dry	Tukey-HSD	Intact	Degraded	-0.04	0.01	0.004
			Lemur group A dry	0.01	0.01	0.906
			Lemur group B dry	-0.04	0.01	0.000
		Degraded	Intact	0.04	0.01	0.004
			Lemur group A dry	0.04	0.01	0.000
			Lemur group B dry	-0.01	0.01	0.885
		Lemur group A dry	Intact	-0.01	0.01	0.906
			Degraded	-0.04	0.01	0.000
			Lemur group B dry	-0.05	0.01	0.000
		Lemur group B dry	Intact	0.04	0.01	0.000
			Degraded	0.01	0.01	0.885
			Lemur group A dry	0.05	0.01	0.000
MSAVI dry	Tukey-HSD	Intact	Degraded	-0.03	0.01	0.003
			Lemur group A dry	0.01	0.01	0.863
			Lemur group B dry	-0.04	0.01	0.001
		Degraded	Intact	0.03	0.01	0.003
			Lemur group A dry	0.04	0.01	0.000
			Lemur group B dry	0.00	0.01	0.957
		Lemur group A dry	Intact	-0.01	0.01	0.863
			Degraded	-0.04	0.01	0.000
			Lemur group B dry	-0.04	0.01	0.000
		Lemur group B dry	Intact	0.04	0.01	0.001
			Degraded	0.00	0.01	0.957
			Lemur group A dry	0.04	0.01	0.000
NDWI dry	Tukey-HSD	Intact	Degraded	-0.09	0.02	0.000
			Lemur group A dry	-0.01	0.02	0.932
			Lemur group B dry	-0.07	0.02	0.000
		Degraded	Intact	0.09	0.02	0.000
			Lemur group A dry	0.08	0.02	0.000
			Lemur group B dry	0.02	0.02	0.572
		Lemur group A dry	Intact	0.01	0.02	0.932
			Degraded	-0.08	0.02	0.000
			Lemur group B dry	-0.06	0.02	0.001
		Lemur group B dry	Intact	0.07	0.02	0.000
			Degraded	-0.02	0.02	0.572
			Lemur group A dry	0.06	0.02	0.001
NDVI wet	Games-Howell	Intact	Degraded	0.02	0.00	0.000
			Lemur group A wet	0.00	0.00	0.888
			Lemur group B wet	0.07	0.02	0.002
		Degraded	Intact	-0.02	0.00	0.000

			Lemur group A wet	-0.02	0.00	0.001
			Lemur group B wet	0.05	0.02	0.028
		Lemur group A wet	Intact	0.00	0.00	0.888
			Degraded	0.02	0.00	0.001
			Lemur group B wet	0.07	0.02	0.003
		Lemur group B wet	Intact	-0.07	0.02	0.002
			Degraded	-0.05	0.02	0.028
			Lemur group A wet	-0.07	0.02	0.003
EVI wet	Games-Howell	Intact	Degraded	0.04	0.01	0.048
			Lemur group A wet	-0.02	0.01	0.617
			Lemur group B wet	0.12	0.03	0.009
		Degraded	Intact	-0.04	0.01	0.048
			Lemur group A wet	-0.05	0.01	0.000
			Lemur group B wet	0.08	0.03	0.090
		Lemur group A wet	Intact	0.02	0.01	0.617
			Degraded	0.05	0.01	0.000
			Lemur group B wet	0.13	0.03	0.002
		Lemur group B wet	Intact	-0.12	0.03	0.009
			Degraded	-0.08	0.03	0.090
			Lemur group A wet	-0.13	0.03	0.002
MSAVI wet	Games-Howell	Intact	Degraded	0.04	0.01	0.028
			Lemur group A wet	-0.01	0.01	0.785
			Lemur group B wet	0.12	0.03	0.005
		Degraded	Intact	-0.04	0.01	0.028
			Lemur group A wet	-0.05	0.01	0.000
			Lemur group B wet	0.09	0.03	0.054
		Lemur group A wet	Intact	0.01	0.01	0.785
			Degraded	0.05	0.01	0.000
			Lemur group B wet	0.13	0.03	0.002
		Lemur group B wet	Intact	-0.12	0.03	0.005
			Degraded	-0.09	0.03	0.054
			Lemur group A wet	-0.13	0.03	0.002
NDWI wet	Games-Howell	Intact	Degraded	0.02	0.01	0.030
			Lemur group A wet	0.00	0.01	0.930
			Lemur group B wet	0.06	0.02	0.005
		Degraded	Intact	-0.02	0.01	0.030
			Lemur group A wet	-0.03	0.01	0.001
			Lemur group B wet	0.04	0.02	0.080
		Lemur group A wet	Intact	0.00	0.01	0.930
			Degraded	0.03	0.01	0.001
			Lemur group B wet	0.07	0.02	0.003
		Lemur group B wet	Intact	-0.06	0.02	0.005
			Degraded	-0.04	0.02	0.080
			Lemur group A wet	-0.07	0.02	0.003

Table S4 Results of tests for differences in habitat use between lemur groups during each season, described by vegetation productivity and water content-related indices. Cohen’s d gives effect sizes of the deviation of group A from group B. For these analyses we used all lemur occurrence points (Lemur group A: N= 4156; Lemur group B: N= 2170).

	Levene's test for equality of variances		Independent samples T-test			Cohen's d		
Variable	**F**	**p**	**T**	**df**	**p (2-sided)**	**Point estimate**	**Lower value 95% CI**	**Upper value 95% CI**
NDVI dry	71.66	< 0.001	-13.92	1790.07	< 0.001	-0.58	-0.65	-0.50
EVI dry	47.21	< 0.001	-21.53	1831.70	< 0.001	-0.88	-0.96	-0.80
MSAVI dry	56.29	< 0.001	-21.12	1808.99	< 0.001	-0.87	-0.95	-0.79
NDWI dry	61.75	< 0.001	-21.75	1905.22	< 0.001	-0.88	-0.96	-0.80
NDVI wet	254.04	< 0.001	17.97	1457.15	< 0.001	0.79	0.72	0.86
EVI wet	58.76	< 0.001	10.21	1762.67	< 0.001	0.41	0.34	0.48
MSAVI wet	75.26	< 0.001	13.30	1735.49	< 0.001	0.54	0.46	0.61
NDWI wet	223.51	< 0.001	14.09	1637.83	< 0.001	0.58	0.51	0.66

Table S5 Component loadings of variables used in principal component analysis, rotated solution. PCQ variables in blue, remote sensing variables in yellow.

	Principal Component	
Variable	**1**	**2**
Number of *Delonix regia*	0.73075448	0.21538997
Thin tree height	0.62144679	0.20645671
Thick tree height	0.47609176	0.16858874
Thick tree crown diameter	0.45403517	0.19820352
Thin tree crown diameter	0.30197683	-0.12342231
Thick tree density	0.20861314	0.00519153
Thick tree DBH	0.18347586	0.08344323
NDVI wet	0.17853691	0.91313294
Thin tree DBH	0.15412161	-0.21847014
MSAVI wet	0.14173008	0.928876
Total tree density	0.13726768	0.06772668
EVI wet	0.13527789	0.9104982
NDWI wet	0.11014132	0.92349733
Thin tree density	0.07725064	0.0726542
NDVI dry	-0.61103671	0.65570443
Number of species	-0.63698443	-0.0414397
EVI dry	-0.77027287	0.35572237
MSAVI dry	-0.77606108	0.35731867
NDWI dry	-0.85060199	0.21510567

Table S6 Eigenvalues, percentage of variance accounted for and cumulative percentage of components extracted by the principal component analysis, including the original and rotated solution.

	Initial eigenvalues			**Extraction sums of squared loadings**			**Rotation sums of squared loadings**		
Principal Component	**Total**	**% of variance**	**Cumulative %**	**Total**	**% of variance**	**Cumulative %**	**Total**	**% of variance**	**Cumulative %**
1	4.522	23.80	23.80	4.522	23.80	23.80	4.351	22.90	22.90
2	4.176	21.98	45.78	4.176	21.98	45.78	4.347	22.88	45.78
3	2.180	11.48	57.25						
4	1.821	9.59	66.84						
5	1.620	8.53	75.37						
6	1.167	6.14	81.51						
7	0.855	4.50	86.01						
8	0.702	3.69	89.70						
9	0.497	2.62	92.32						
10	0.437	2.30	94.62						
11	0.344	1.81	96.43						
12	0.290	1.53	97.96						
13	0.188	0.99	98.95						
14	0.092	0.48	99.43						
15	0.077	0.41	99.83						
16	0.028	0.15	99.98						
17	0.003	0.01	99.99						
18	0.001	0.01	100.00						
19	0.000	0.00	100.00						

Chapter 3 author contributions

I hereby confirm that Kim J. E. Steffens designed the study. He and Justin Sanamo contributed equally to carry out behavioral observations of crowned lemurs and the forest structure descriptions in the field. Jeremi Razafitsalama identified plants and contributed to the habitat analyses at the site. Kim J. E. Steffens analyzed the data of these descriptions, and carried out further analyses of satellite imagery. Kim J. E. Steffens and Jörg U. Ganzhorn equally contributed to writing the manuscript.

Jörg Ganzhorn

Prof. Dr. Jörg Ganzhorn

CHAPTER 4

Using utilitarian plants for lemur conservation

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Using Utilitarian Plants for Lemur Conservation

Cathlin Konersmann, et al. ***[full author details at the end of the article]***

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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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Cathlin Konersmann, Fanambinantsoa Noromiarilanto and Yedidya R. Ratovonamana contributed equally to this work.

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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

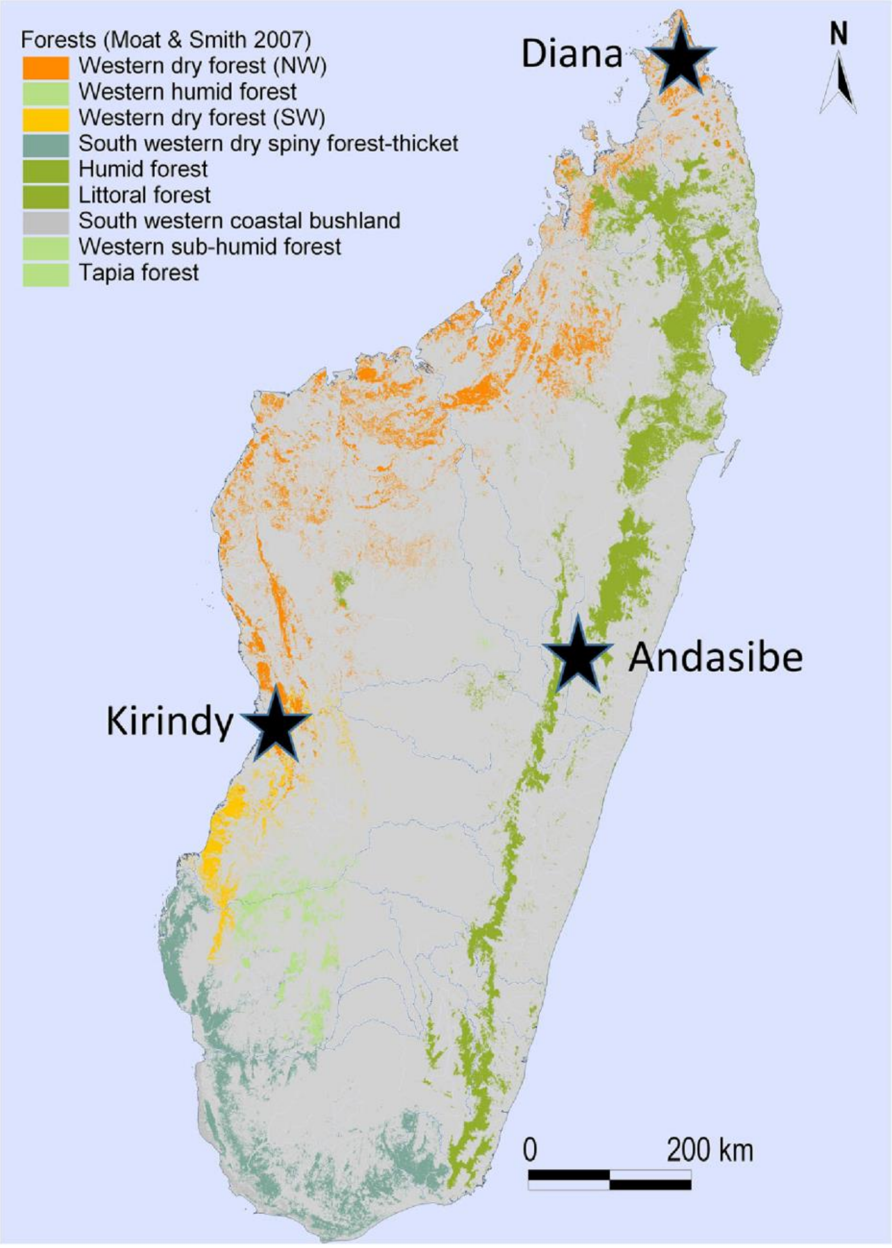

Fig. 1 Location of the selected study regions. Modified from Moat and Smith (2007).

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.

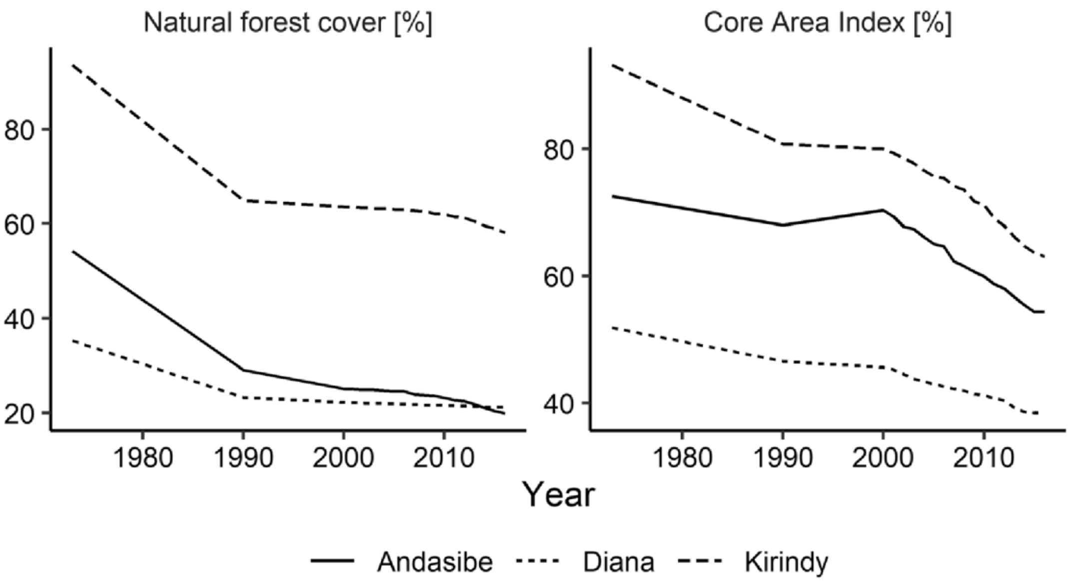

Fig. 2 Development of natural forest cover (left) and forest fragmentation (right) between 1973 and 2016 in three study regions in Madagascar. For 1973–2000, we used forest cover maps from Vieilledent *et al.* (2018). For 2001–2016, we produced annual forest cover maps by combining the forest cover map 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

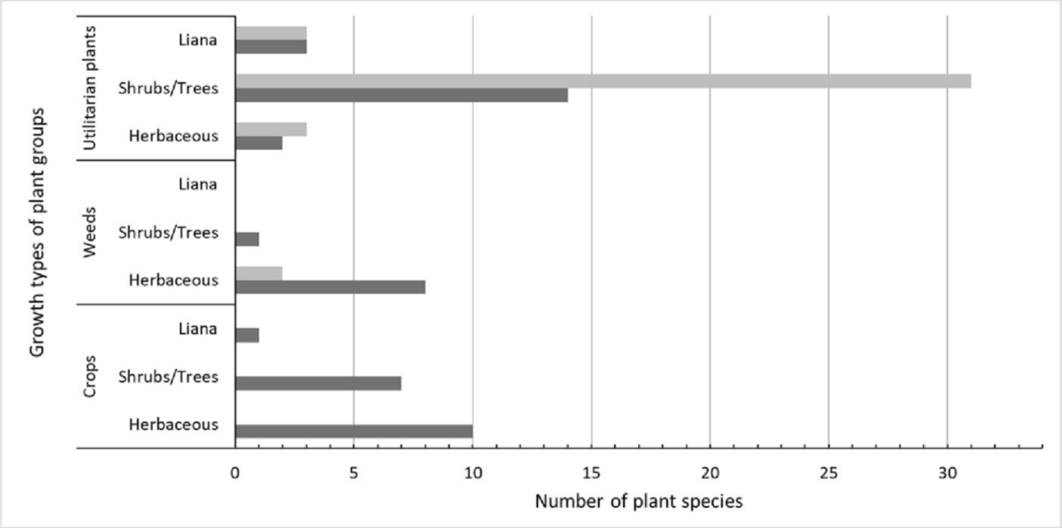

Fig. 3 Number of important plant species for local people and native vertebrates by growth form and plant group (crops, weeds, and utilitarian plants) in three study regions in Madagascar; dark grey = introduced plant species, light grey = native plant species.

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 agroforestry 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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Authors' contributions CN, FN, YRR, KB, SK, DK, KJES and JUG conceived and designed the study. FN, YRR, KB, SK and DK conducted fieldwork. CK, FN and KB compiled the data. CK and KJES analyzed the data. CT, KS and JUG wrote the manuscript; other authors provided editorial advice.

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References

Andriamandimbiarisoa, L., Blanthorn, T., Ernest, R., Ramanamanjato, J.-B., & Randriatafika, F. (2015). Habitat corridor utilisation by the gray mouse lemur, *Microcebus murinus,* in the littoral forest fragments of southeastern Madagascar. *Madagascar Conservation & Development, 10*, 144–150.

Andriamparany, J. N., Brinkmann, K., Jeannoda, V., & Buerkert, A. (2014). Effects of socio-economic household characteristics on traditional knowledge and usage of wild yams and medicinal plants in the Mahafaly region of south-western Madagascar. *Journal of Ethnobiology and Ethnomedicine, 10*, 82.

Bernard, H. R. (2011). *Research methods in anthropology: Qualitative and quantitative approaches*. Lanham: AltaMira Press, Rowman & Littlefield.

Birkinshaw, C., Andrianjafy, M., & Rasolofonirina, J. J. (2009). Survival and growth of seedlings of 19 native tree and shrub species planted in degraded forest as part of a forest restoration project in Madagascar's highlands. *Madagascar Conservation & Development, 4*, 128–131.

Brinkmann, K., Noromiarilanto, F., Ratovonamana, R.-Y., & Buerkert, A. (2014). Deforestation processes in south-western Madagascar over the past 40 years: What can we learn from settlement characteristics? *Agriculture, Ecosystems and Environment, 195*, 231–243.

Brown, K. A., Johnson, S. E., Parks, K. E., Holmes, S. M., Ivoandry, T., et al (2013). Use of provisioning ecosystem services drives loss of functional traits across land use intensification gradients in tropical forests in Madagascar. *Biological Conservation, 161*, 118–127.

Carrière, S. M., Randrianasolo, E., & Hennenfent, J. (2008). Aires protégées et lutte contre les bioninvasions: Des objectifs antagonistes? Le cas de *Psidium cattleianum* Sabine (Myrtaceae) autour du parc national de Ranomafana à Madagascar. *VertigO – La revue en sciences de l'environnement, 8*, 1–14.

Chapman, C. A., Bicca-Marques, J. C., Dunham, A. E., Fan, P., Fashing, P. J., *et al*. (in press). Primates can be a rallying symbol to promote tropical forest restoration. *Folia Primatologica*.

DeSisto, C. M. M., Park, D. S., Davis, C. C., Ramananjato, V., Tonos, J. L., & Razafindratsima, O. H. (2020). An invasive species spread by threatened diurnal lemurs impacts rainforest structure in Madagascar. *Biological Invasions, 22*, 2845–2858.

De Wilde, M., Buisson, E., Ratovoson, F., Randrianaivo, R., Carrière, S. M., & Lowry, P. P. (2012). Vegetation dynamics in a corridor between protected areas after slash-and-burn cultivation in south-eastern Madagascar. *Agriculture, Ecosystems & Environment, 159*, 1–8.

Diemont, S. A. W., Martina, J. F., Levy-Tacher, S. I., Nigh, R. B., Lopez, P. R., & Golicher, J. D. (2006). Lacandon Maya forest management: Restoration of soil fertility using native tree species. *Ecological Engineering, 28*, 205–212.

Donati, G., Campera, M., & Balestri, M. (2020). Life in a fragment: Evolution of foraging strategies of translocated collared brown lemurs, *Eulemur collaris*, over an 18-year period. *American Journal of Primatology, 82*, e23106.

Eco-Services Consulting (2017). *Etude d'inventaire et analyse des plantes mellifères et évaluation de leur potentiel de production dans les zones de production de miel d'Ambanja et de ses environs*. Antananarivo: GIZ, Helvetas.

Ehrensperger, T., Urech, Z. L., Rehnus, M., & Sorg, J. P. (2013). Fire impact on the woody plant components of dry deciduous forest in Central Menabe. *Madagascar. Applied Vegetation Science, 16*, 619–628.

Favre, J.-C. (1990). Evaluations qualitatives et quantitatives des utilisations villageoises des ressources en forêt dense sèche: Etude de cas du village de Marofandilia dans la région de Morondava/Madagascar. *ETH Zürich, Arbeitsberichte Internationale Reihe, 90*, 1–59.

Favre, J.-C. (1996). Traditional utilization of the forest. In J. U. Ganzhorn & J.-P. Sorg (Eds.), *Ecology and economy of a tropical dry forest in Madagascar* (pp. 33–40). Primate Report, 46–1). Göttingen: Erich Goltze.

Fohavelo, A., & Gulley, J. (2000). Les espèces de plantes mellifères des alentours de Marofandilia. *Lemur News, 5*, 14–16.

Fritz-Vietta, N. V. M., Ferguson, H. B., Stoll-Kleemann, S., & Ganzhorn. J. U. (2011). Conservation in a biodiversity hotspot: Insights from cultural and community perspectives in Madagascar. In F. E. Zachos & J. C. Habel (Eds.), *Biodiversity hotspots* (pp. 209–233). Heidelberg: Springer.

Gann, G. D., McDonald, T., Walder, B., et al (2019). *International principles and standards for the practice of ecological restoration. 2nd ed. Restoration Ecology, 27*, 3–46.

Ganzhorn, J. U. (1987). A possible role of plantations for primate conservation in Madagascar. *American Journal of Primatology, 12*, 205–215.

Ganzhorn, J. U., & Abraham, J.-P. (1991). Possible role of plantations for lemur conservation in Madagascar: Food for folivorous species. *Folia Primatologica, 56*, 171–176.

Gardner, C. J., Gabriel, F. U. L., St John, F. A. V., & Davies, Z. G. (2016a). Changing livelihoods and protected area management: A case study of charcoal production in south-west Madagascar. *Oryx, 50*, 495–505.

Gardner, C. J., Jasper, L. D., Eonintsoa, C., Duchene, J. J., & Davies, Z. G. (2016b). The impact of natural resource use on bird and reptile communities within multiple-use protected areas: Evidence from sub-arid Southern Madagascar. *Biodiversity and Conservation, 25*, 1773–1793.

Gardner, T. A., Barlow, J., Sodhi, N. S., & Peres, C. A. (2010). A multi-region assessment of tropical forest biodiversity in a human-modified world. *Biological Conservation, 143*, 2293–2300.

Gay-des-Combes, J. M., Robroek, B. J. M., Herve, D., et al (2017). Slash-and-burn agriculture and tropical cyclone activity in Madagascar: Implication for soil fertility dynamics and corn performance. *Agriculture Ecosystems & Environment, 239*, 207–218.

Genini, M. (1996). Deforestation. In *J. U. Ganzhorn & J.-P. Sorg (Eds.), Ecology and economy of a tropical dry forest in Madagascar (pp. 49–55). Primate Report* (pp. 46–41). Göttingen: Erich Goltze.

Gérard, A., Ganzhorn, J. U., Kull, C. A., & Carrière, S. M. (2015). Possible roles of introduced plants for native vertebrate conservation: The case of Madagascar. *Restoration Ecology, 23*, 768–775.

Gérard, A., Wollni, M., Holscher, D., et al (2017). Oil-palm yields in diversified plantations: Initial results from a biodiversity enrichment experiment in Sumatra. *Indonesia. Agriculture Ecosystems & Environment, 240*, 253–260.

GIZ/GREEN-Mad (2007). Le reboisement villageois individuel: Stratégies. In *techniques et impacts de GREEN-Mad (MEM-GTZ) dans la région d'Antsiranana Madagascar*. Antananarivo: GIZ.

Goodman, S. M., Raherilalao, M. J., & Wohlhauser, S. (2018). *Les aires protégées terrestres de Madagascar: Leur histoire, description et biote / The terrestrial protected areas of Madagascar: Their history, description, and biota*. Antananarivo: Association Vahatra.

Hänke, H., Barkmann, J., Müller, C., & Marggraf, R. (2018). Potential of *Opuntia* seed oil for livelihood improvement in semi-arid Madagascar. *Madagascar Conservation & Development, 13*, 34–44.

Hansen, M. C., Potapov, P. V., Moore, R., et al (2013). High-resolution global maps of 21st-century forest cover change. *Science, 342*, 850–853.

Harper, G. J., Steininger, M. K., Tucker, C. J., Juhn, D., & Hawkins, F. (2007). Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation, 34*, 325–333.

Hending, D., Andrianiaina, A., Rakotomalala, Z., & Cotton, S. (2018). The use of vanilla plantations by lemurs: Encouraging findings for both lemur conservation and sustainable agroforestry in the Sava region. *northeast Madagascar. International Journal of Primatology, 39*, 141–153.

Holloway, L. (2003). Ecosystem restoration and rehabilitation in Madagascar. In S. M. Goodman & J. Benstead (Eds.), *The natural history of Madagascar* (pp. 1444–1451). Chicago: University of Chicago Press.

Hume, D. W. (2006). Swidden agriculture and conservation in eastern Madagascar: stakeholder perspectives and cultural belief systems. *Conservation and Society, 4*, 287–303.

Iehlé, C., Razafitrimo, G., Razainirina, J., et al (2007). Henipavirus and Tioman virus antibodies in pteropodid bats. *Madagascar. Emerging Infectious Diseases, 13*, 159–161.

Irwin, M. T., Wright, P. C., Birkinshaw, C., et al (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation, 143*, 2351–2362.

Joffrin, L., Goodman, S. M., Wilkinson, D. A., et al (2020). Bat coronavirus phylogeography in the Western Indian Ocean. *Scientific Reports, 10*, 6873.

Jolly, A. (2004). *Lords and lemurs*. Boston: Houghton Mifflin Company.

Klanderud, K., Mbolatiana, H. Z. H., Vololomboahangy, M. N., et al (2010). Recovery of plant species richness and composition after slash-and-burn agriculture in a tropical rainforest in Madagascar. *Biodiversity and Conservation, 19*, 187–204.

Kull, C. A., Tassin, J., Moreau, S., Ramiarantsoa, H. R., Blanc-Pamard, C., & Carrière, S. M. (2012). The introduced flora of Madagascar. *Biological Invasions, 14*, 875–888.

Lavialle, J., Carrière, S. M., Miandrimanana, C., Tilahimena, A., Birkinshaw, C. R., & Aronson, J. (2015). Complementarity of native and introduced tree species: Exploring timber supply on the east coast of Madagascar. *Madagascar Conservation & Development, 10*, 137–143.

Leprun, J. C., Grouzis, M., & Randriambanona, H. (2009). Post-cropping change and dynamics in soil and vegetation properties after forest clearing: Example of the semi-arid Mikea Region (southwestern Madagascar). *Comptes Rendus Geoscience, 341*, 526–537.

Manjaribe, C., Frasier, C. L., Rakouth, B., & Louis Jr., E. E. (*2013*). Ecological restoration and reforestation of fragmented forests in Kianjavato, Madagascar. *International Journal of Ecology, 2013*, 726275.

Mansourian, S., Stanturf, J. A., Derkyi, M. A. A., & Engel, V. L. (2017). Forest landscape restoration: Increasing the positive impacts of forest restoration or simply the area under tree cover? *Restoration Ecology, 25*, 178–183.

Marie, C. N., Sibelet, N., Dulcire, M., Rafalimaro, M., Danthu, P., & Carrière, S. M. (2009). Taking into account local practices and indigenous knowledge in an emergency conservation context in Madagascar. *Biodiversity and Conservation, 18*, 2759–2777.

Martin, E. A., Ratsimisetra, L., Laloe, F., & Carrière, S. M. (2009). Conservation value for birds of traditionally managed isolated trees in an agricultural landscape of Madagascar. *Biodiversity and Conservation, 18*, 2719–2742.

Martin, E. A., Viano, M., Ratsimisetra, L., Laloë, F., & Carrière, S. M. (2012). Maintenance of bird functional diversity in a traditional agroecosystem of Madagascar. *Agriculture, Ecosystems & Environment, 149*, 1–9.

Martinez, B. T. (2008). Occurrence of bamboo lemurs, *Hapalemur griseus occidentalis*, in an agricultural landscape on the Masoala Peninsula. *Lemur News, 13*, 11–14.

Martinez, B. T., & Razafindratsima, O. H. (2014). Frugivory and seed dispersal patterns of the red-ruffed lemur, *Varecia rubra*, at a forest restoration site in Masoala National Park. *Madagascar. Folia Primatologica, 85*, 228–243.

McConnell, W. J., Vina, A., Kull, C., & Batko, C. (2015). Forest transition in Madagascar's highlands: Initial evidence and implications. *Land, 4*, 1155–1181.

McGarigal, K., & Marks, B. J. (1995). *FRAGSTATS: Spatial pattern analysis program for quantifying landscape structure*. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Moat, J., & Smith, P. (2007). *Atlas of the vegetation of Madagascar, Atlas de la Végétation de Madagascar*. Kew: Kew Publishing, Royal Botanic Gardens.

Ndriantsoa, S. H., Riemann, J. C., Raminosoa, N., Rodel, M. O., & Glos, J. S. (2017). Amphibian diversity in the matrix of a fragmented landscape around Ranomafana in Madagascar depends on matrix quality. *Tropical Conservation Science, 10*, 1–16.

Rabenantoandro, J., Randriatafika, F., & Lowry II, P. P. (2007). Floristic and structural characteristics of remnant littoral forest sites in the Tolagnaro area. In J. U. Ganzhorn, S. M. Goodman, & M. Vincelette (Eds.), *Biodiversity, ecology and conservation of littoral ecosystems in southeastern Madagascar, Tolagnaro (Fort Dauphin)* (pp. 65–93). Washington, DC: Smithsonian Institution.

Rafidison, V. M., Rakouth, B., Carrière, S. M., Kjellberg, F., & Aumeeruddy-Thomas, Y. (2020). Multiple values of isolated and clusters of *Ficus* tree species protected by Betsileo farmers in rural landscapes in Madagascar: Implications for biodiversity conservation. *Biodiversity and Conservation, 29*, 1027–1058.

Raharimalala, O., Buttler, A., Ramohavelo, C. D., Razanaka, S., Sorg, J. P., & Gobat, J. M. (2010). Soil-vegetation patterns in secondary slash and burn successions in Central Menabe. *Madagascar. Agriculture Ecosystems & Environment, 139*, 150–158.

Rakotoarivelo, N. H., Rakotoarivony, F., Ramarosandratana, A. V., et al (2015). Medicinal plants used to treat the most frequent diseases encountered in Ambalabe rural community. *Eastern Madagascar. Journal of Ethnobiology and Ethnomedicine, 11*, 68.

Ranaivoson, T., Brinkmann, K., Rakouth, B., & Buerkert, A. (2015). Distribution, biomass and local importance of tamarind trees in south-western Madagascar. *Global Ecology and Conservation, 4*, 14–25.

Randriamalala, J. R., Herve, D., Letourmy, P., & Carrière, S. M. (2015). Effects of slash-and-burn practices on soil seed banks in secondary forest successions in Madagascar. *Agriculture Ecosystems & Environment, 199*, 312–319.

Ratsimbazafy, J. H., Ramarosandratana, H. V., & Zaonarivola, R. J. (2002). How do black-and-white ruffed lemurs still survive in a highly disturbed habitat? *Lemur News, 7*, 7–10.

Razafintsalama, V., Ramananantoandro, T., Belloncle, C., Rajoelison, G. L., & Sorg, J.-P. (2014). Utilisations villageoises et potentialités technologiques des bois de forêts secondaires dans le Menabe central, Madagascar. *Bois et Forêts des Tropiques, 3202*, 59–73.

Schatz, G. E. (2001). *Generic tree flora of Madagascar. Kew: Royal Botanic Gardens and St*. Louis: Missouri Botanical Garden.

Schwitzer, C., Glatt, L., Nekaris, K. A.-I., & Ganzhorn, J. U. (2011). Responses of animals to habitat alteration: An overview focussing on primates. *Endangered Species Research, 14*, 31–38.

Schwitzer, C., Mittermeier, R. A., Johnson, S. E., et al (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science, 343*, 842–843.

Sorg, J.-P. (1996). Vernacular and scientific names of plants of the Morondava region. In J. U. Ganzhorn & J. P. Sorg (Eds.), *Ecology and economy of a tropical dry forest in Madagascar* (pp. 339–346). Primate Report, 46–1). Göttingen: Erich Goltze.

Sorg, J.-P., & Rohner, U. (1996). Climate and phenology of the dry deciduous forest at Kirindy. In J. U. Ganzhorn & J.-P. Sorg (Eds.), *Ecology and economy of a tropical dry forest in Madagascar* (pp. 57–80). Primate Report 46–1). Göttingen: Erich Goltze.

Steffens, K. J. E. (2020). Lemur food plants as options for forest restoration in Madagascar. *Restoration Ecology, 28*, 1517–1527.

Styger, E., Rakotondramasy, H. M., Pfeffer, M. J., Fernandes, E. C. M., & Bates, D. M. (2007). Influence of slash-and-burn farming practices on fallow succession and land degradation in the rainforest region of Madagascar. *Agriculture Ecosystems & Environment, 119*, 257–269.

Tassin, J., & Kull, C. A. (2015). Facing the broader dimensions of biological invasions. *Land Use Policy, 42*, 165–169.

Vieilledent, G., Grinand, C., Rakotomalala, F. A., et al (2018). Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biological Conservation, 222*, 189–197.

Waeber, P. O., Wilmé, L., Mercier, J.-R., Camara, C., & Lowry, P. P. I. I. (2016). How effective have thirty years of internationally driven conservation and development efforts been in Madagascar? *PLoS ONE, 11*, e0161115.

Waeber, P. O., Wilmé, L., Ramamonjisoa, B., et al (2015). Dry forests in Madagascar: Neglected and under pressure. *International Forestry Review, 16*, 127–148.

Webber, A. D., Solofondranohatra, J. S., Razafindramoana, S., et al (2020). Lemurs in cacao: Presence and abundance within the shade plantations of northern Madagascar. *Folia Primatologica, 91*, 96–107.

Wielgoss, A., Tscharntke, T., Rumede, A., et al (2014). Interaction complexity matters: Disentangling services and disservices of ant communities driving yield in tropical agroecosystems. *Proceedings of the Royal Society B: Biological Sciences, 281*, 20132144.

Wilmé, L. (2014). *Inventaire ornithologique dans les plantations d'eucalyptus et les terrains incultes de la région Diana, Madagascar*. Antananarivo: Eco Consult.

Wilmé, L., Innes, J. L., Schuurman, D., et al (2020). The elephant in the room: Madagascar's rosewood stocks and stockpiles. *Conservation Letters, 13*, e12714.

Zemp, D. C., Ehbrecht, M., Seidel, D., et al (2019). Mixed-species tree plantings enhance structural complexity in oil palm plantations. *Agriculture Ecosystems & Environment, 283*, 106564.

Zinner, D., Wygoda, C., Razafimanantsoa, L., et al (2014). Analysis of deforestation patterns in the Central Menabe, Madagascar, between 1973 and 2010. *Regional Environmental Change, 14*, 157–166.

Zwartendijk, B. W., van Meerveld, H. J., Ghimire, C. P., Bruijnzeel, L. A., Ravelona, M., & Jones, J. P. G. (2017). Rebuilding soil hydrological functioning after swidden agriculture in eastern Madagascar. *Agriculture Ecosystems & Environment, 239*, 101–111.

Affiliations

Cathlin Konersmann[1] · Fanambinantsoa Noromiarilanto[2] · Yedidya R. Ratovonamana[1,2] · Katja Brinkmann[3] · Kai Jensen[4] · Susanne Kobbe[1] · Michael Köhl[5] · Daniel Kuebler[5] · Petra Lahann[6] · Kim J. E. Steffens[1] · Jörg U. Ganzhorn[1]

✉ Jörg U. Ganzhorn
ganzhorn@uni-hamburg.de

[1] Institute of Zoology, Animal Ecology and Conservation, Universität Hamburg, Hamburg, Germany

[2] Département de Biologie et Ecologie Végétale, Faculté des Sciences, Université d’Antananarivo, Antananarivo, Madagascar

[3] ISOE – Institute for Social-Ecological Research, Frankfurt am Main, Germany

[4] Applied Plant Ecology, Universität Hamburg, Hamburg, Germany

[5] Institute for World Forestry, Universität Hamburg, Hamburg, Germany

[6] Sector Project International Forest Policy, GIZ, Eschborn, Germany

Chapter 4 author contributions

I hereby confirm that Kim J. E. Steffens contributed along with Cathlin Konersmann, Fanambinantsoa Noromiarilanto, Yedidya R. Ratovonamana, Katja Brinkmann, Susanne Kobbe, Daniel Kübler and Jörg U. Ganzhorn to the design of the study. He contributed to analyzing the data, together with Cathlin Konersmann, and writing the manuscript, together with Cathlin Konersmann and Jörg U. Ganzhorn.

Jörg Ganzhorn

Prof. Dr. Jörg Ganzhorn

GENERAL DISCUSSION

In comparison with other restoration efforts in the tropics, projects in Madagascar are relatively small-scale and do not reach their full potential for counteracting some of the main causes of biodiversity loss and contributing to the development of sustainable livelihoods for the local people (Holloway, 2000, 2004). Reasons for this may be a lack of model projects and the scientific base to inform and convince decision-makers to invest in restoration (Birkinshaw et al., 2013; Carrasco et al., 2020). This potential could become relevant at times when the political will for extensive ecosystem restoration seems to exist, such as during the present UN Decade on Ecosystem Restoration that aims “to prevent, halt and reverse the degradation of ecosystems worldwide” (United Nations Environment Programme, 2021, p. 2). In the course of the African Forest Landscape Restoration Initiative (AFR100), the government of Madagascar has committed itself to restore 4 million hectares of land until 2030 (https://afr100.org/).

Even though such commitments sound promising, it has to be questioned what they really mean, apart from whether they are really implemented (Mansourian et al., 2017). The name itself reveals that commitments to the AFR100 are supposed to deal with forest landscape restoration. However, the Malagasy government is aiming to “reforest” around 40.000 ha of land per year, not to “restore” (https://afr100.org/content/madagascar). As outlined in the Introduction, reforestation only refers to the establishment of any sort of tree cover, whereas restoration includes ecological aspects and the recovery of biodiversity (Elliott et al., 2013). Although it might only be a matter of definition or expression, it appears that the ecological aspects inherent in restoration are not necessarily included in Madagascar’s commitment to the AFR100. This is supported by considering the results of a study chaired by the “Ministère de l’Environnement, de l’Écologie, de la Mer et des Forêts” of Madagascar, carried out to prepare the implementation of the AFR100 commitment. The authors prioritized five options for its implementation, two of these being “Afforestation of degraded sites with fast-growing species for timber, construction and service wood” and “Restoration of degraded pine forests (artificial forests) to restore old plantations for industrial purposes” (Lacroix et al., 2016, p. 18). As depicted in the introduction of this dissertation, these forms of tree plantings are incompatible with the ecological aims of restoration, and afforestation with eucalypt and pine trees can even end up in an “ecological disaster” (Fernandes et al., 2016, p. 146).

It is certain that decisions concerning tree plantings made today will have far-reaching impact on biodiversity, the natural heritage of Madagascar, and the future of its people. New approaches and ideas are needed, to unite development for the people with conservation goals. One such approach could be forest restoration with plant species of use for humans and animals, as explored in this dissertation. In this general discussion, I summarize the key insights of Chapter 1 to 4 and place them in the context of other studies, drawing conclusions about our findings and their application throughout.

Lemur food plants as a basis for restoration

Chapter 1 gives the most up-to-date overview of lemur food plants. The last comprehensive overview of this type was published almost 20 years ago, by Birkinshaw and Colquhoun (2003). Since then, more studies on food-related behavior by lemurs have been carried out than in 55 preceding years, proven by the fact that more than half of the data sources considered in Chapter 1 were published after 2001 - the year the youngest data source considered by Birkinshaw and Colquhoun (2003) was published - and less than half from 1945 to 2001. Moreover, a large number of lemur and plant species has been identified since then, and the taxonomic classification of many species has changed. Therefore, the time was ripe to provide an updated database of lemurs feeding on plants.

The analysis in Chapter 1 revealed that out of 101 lemur species currently recognized (Schwitzer et al., 2014), more than half (56; 55%) are represented in the database. In addition, out of all 11,220 plant species occurring in Madagascar according to current estimates (Callmander et al., 2011), lemurs exploit 1026 (9.14%). Even though some lemur species are more intensively studied than others, and others again not at all, and research on primates including lemurs is heavily biased towards study sites (Chapter 1: Figs. 1,2; Bezanson & McNamara, 2019), these numbers illustrate the extensive knowledge already available about this lemur-plant interaction. This great knowledge harbors great potential for its use in restoration activities. As the database is published in an open-access data repository, researchers or decision-makers may freely access and use it, for instance to select plant species for tree plantings. My analysis of the most heavily exploited genera and families of plants may help to get a quick insight into taxa that come into consideration for this purpose.

Searches or queries of lemur or plant species within the database allow a far more detailed access to such information.

Clearly, this should not be the only basis of information upon which plant species are selected for restoration. Other characteristics of plant species also play an important role in this process, such as traits related to performance (e.g., survival and growth) or to ecology of the plant (e.g., adaptations to environmental conditions). These were studied in plant species native to Madagascar for example by Pareliussen et al. (2006), Birkinshaw et al. (2009), and Manjaribe et al. (2013), but more research is needed that includes further species. Information on traits related to performance and ecology could be added to the database by the decision-makers themselves or by future studies. Similarly, I have already added the information about origin, invasive status and life form - i.e., whether it is a tree, a shrub or a liana - of plant species to the database, which is of importance to assess their suitability for a certain restoration purpose. Following this example, more information can be added to allow the sharing of experiences and knowledge among practitioners, something that is missing in Madagascar (Birkinshaw et al., 2013), to improve the use of the database and therewith restoration.

Benefits for lemurs and diversity

By restoring forests through planting species that are used as food or habitat by lemurs, one could contribute to the protection of these animals. Many other animal and plant species would profit likewise, as they directly depend on lemurs as prey, pollinating or seed dispersing species (Heymann, 2011; Razafindratsima, 2014; Goodman & Ganzhorn, in press). For example, crowned lemurs in Oronjia dispersed 80 different plant species, and one fourth of these seem to be dispersed only be lemurs (Chapter 2), exemplifying the direct dependence of other species, in this case plant species, on lemurs. But it is not only species depending directly on lemurs that would benefit from their protection. The protection or restoration of forest habitats of lemurs as “umbrella species” would protect all the diversity of flora and fauna occurring in these habitats (Baden et al., 2019; Ganzhorn, 1999; Ganzhorn et al., 2000).

Facilitated regeneration and conclusions for application

The seed dispersal of lemurs and other dispersers could itself play an important role in such a restoration. The large majority (94%) of seeds dispersed by crowned lemurs were intact, and the germination success and time of the majority of plant species was influenced positively (Chapter 2), findings that are true for some other lemur species as well (Razafindratsima, 2014). An increased and faster germination following seed dispersal can positively impact fitness variables of plants such as survival, growth and fecundity (Verdú & Traveset, 2005), and may thus facilitate regeneration in a restoration scenario.

Apart from primary dispersal and its influence on germination, it has to be considered that not all seeds reaching the forest floor get the chance to germinate. Following primary dispersal, seeds can be secondarily dispersed but also preyed upon, with important consequences for recruitment patterns (Böhning-Gaese et al., 1999; Hubbell, 1980). In Oronjia, the occurrence of seed predators and secondary dispersers seems to be correlated with the condition of the forest: the more intact the habitat, the larger was the proportion of secondarily dispersed and predated seeds, a pattern found also in the rainforest of Ranomafana (Fiedler et al., 2021; Razafindratsima, 2017). Though, as only very few of all seeds examined in Oronjia were secondarily dispersed without being eaten (3 of 1080), the negative influence of seed predation seems to predominate. This influence in turn is lower in the more disturbed areas savanna and degraded forest, which could theoretically lead to a high recruitment there, but it must be considered that there is a large grazing pressure in those areas, due to free-ranging zebu cattle (*Bos indicus*) and goats (*Capra hircus*). On the other hand, these animals themselves may act as secondary seed dispersers, as seen in the example of the tree *Sclerocarya birrea*. This species, dispersed by African elephants (*Loxodonta africana*) in South Africa, is heavily dispersed by zebus in Oronjia (Rakotondraparany & Andriambeloson, 2015). In conclusion, in a comprehensive planning of restoration activities, the influences of different primary and secondary seed dispersers, as well as predators, should be investigated thoroughly, in order to include measures such as cattle or goat exclusion, if necessary.

The question remains whether primary seed dispersers such as crowned lemurs use degraded areas at all - depositing seeds there - or whether they stick to relatively intact forest. Indeed, we observed crowned lemurs also using heavily degraded forest areas almost free from vegetation, as long as there were still trees that could be used to travel along or to feed on.

Hence, structural conditions of the vegetation seem to be more important to crowned lemurs than general productivity or intactness of the forest (Chapter 3). Two other *Eulemur* species used forests in western dry forests with densities of trees similar or much higher than crowned lemurs' habitat (our study: 906 individuals/ha; Sato, 2012: 2313 individuals/ha, *Eulemur fulvus*; Volampeno et al., 2013: 707 individuals/ha, *Eulemur flavifrons*; numbers refer to trees with a diameter at breast height larger than 5 cm), exemplifying that differences in habitat use may occur within the same genus. Likewise, responses to habitat degradation cannot be generalized for all lemurs, as there are species that avoid forest edges and degraded areas, whereas other species frequently use these edges, and degraded or secondary forest (Donati et al., 2011; Irwin et al., 2010; Knoop et al., 2018; Razafindratsima et al., 2021; Schwitzer et al., 2007b). Nevertheless, it seems possible to lure some species into restoration areas, a concept applying not only to lemurs, but also to other dispersers such as birds or bats (Martinez & Razafindratsima, 2014; Ramananjato et al., 2020; Wunderle Jr., 1997). Single planted food trees or bushes, or suitable little habitat patches, might then act as seed centers ("nuclei"), analogous to remnant food trees on forest clearings (Chapter 3). Even though this does not apply to all plant species and environmental conditions, germination and seedling growth, and thus recruitment, were found to be particularly high in open areas found around nuclei or in forest gaps. Therefore, these nuclei can act as starting points for natural forest regeneration (Charles et al., 2019; Corbin & Holl, 2012; Guevara et al., 1986; Holloway, 2000; Jacob et al., 2017; Manjaribe et al., 2013; Razafindratsima & Dunham, 2015; Yarranton & Morrison, 1974).

Previous and future application in restoration projects

To my knowledge, there are only two projects so far that included the approach of planting food plants to attract lemurs for facilitating regeneration, and reported on it in the scientific literature. The first one has been carried out around the Masoala National Park in northeastern Madagascar. There, the Wildlife Conservation Society planted native tree species into degraded and cleared forest areas lying between intact rainforest blocks, to lure frugivorous vertebrates to these areas (Holloway, 2004). Subsequently, the seed dispersal patterns by the red ruffed lemur (*Varecia rubra*) and its effect on regeneration were studied by Razafindratsima & Razafimahatratra (2010), Razafindratsima & Martinez (2012) and

Martinez & Razafindratsima (2014). Their main findings were that lemurs used forest edges, open canopy areas and small vegetation structures to travel and forage. Thereby they dispersed a large number of intact seeds belonging to native and non-native species - 41 species in total - into undisturbed forest and restoration sites, the majority into the former. The lemurs' gut passage had a positive effect on germination, growth and survival of defecated seeds or seedlings, respectively. Another important finding was that red ruffed lemurs fed extensively on *Clidemia hirta*, its seeds were among the four most frequently dispersed taxa. *C. hirta* is a fast-growing nonnative shrub that was not planted by the program, but fruits year-round (Wester & Wood, 1977), therefore playing an important role in luring the lemurs into the regenerating parcels. However, the species is considered invasive in Madagascar (Kull et al., 2012), and there is the risk of dispersal to the natural forest via the lemurs, and its subsequent establishment, as it can thrive in all possible light conditions (Wester & Wood, 1977). How *C. hirta* will affect the forest structure and community of restoration plantings and natural forest in the future cannot be reliably predicted, both positive and negative effects on the regeneration of native plants are possible (Martinez & Razafindratsima, 2014). The conclusions regarding the ecological outcome of the project were generally positive, because a young diverse forest has grown back, with lemurs playing an important role. Further research is still needed to assess the long-term success, and also the effect of the *C. hirta* dispersal (Holloway, 2007; Razafindratsima & Martinez, 2012).

The second project is the "Education Promoting Reforestation Project", carried out in Kianjavato, southeastern Madagascar (Manjaribe et al., 2013). In a community-based effort, a corridor between remaining forest fragments was planted using native and introduced species that are food plants of *Varecia variegata,* or species used by the local people to produce timber, to harvest fruits or essential oils. Manjaribe et al. (2013) studied germination of seeds defecated by lemurs and extracted from fruits, and survival and growth of seedlings 5 and 16 months after planting. For the majority of species, the germination percentage was higher for seeds passed by the lemurs than for seeds extracted from fruits. Therefore, Manjaribe et al. (2013) consider the collection of defecated seeds and raising plants of them as an appropriate measure to optimize and accelerate reforestation efforts. The seedling survival varied greatly among the species, with high and low survival rates both among introduced and native species. While growth rates were generally higher in introduced species, there were also native species with high rates, which is why they are proposed as alternatives to introduced pioneer species by Manjaribe et al. (2013). As by the time of the publication the project was still in the initial phase, no further conclusions concerning the long-term success, for example with regard to regeneration, could be drawn.

As summarizing these projects documents, the approach of planting species to attract seed dispersers such as lemurs is poorly represented so far, both in terms of implementation and of scientific monitoring. Both projects were carried out in the rainforest, none so far in the dry forest. To counteract this, it is necessary to apply the approach and study its successes and problems in further areas. This application would be imaginable not only in the form of Forest Landscape Restoration, but also in reforestation and restoration schemes whose implementation is less complex. For example, mixed-species plantations could be established, or existing monocultures could be enriched with different plant species. Promising results come from experiments on biodiversity enrichment in palm oil plantations. In those experiments, tree islands of different sizes, composed of native species, were planted into conventional plantations. The studies revealed a positive impact of the enrichment on structural complexity and biodiversity, while the yield was maintained (Gérard et al., 2017; Teuscher et al., 2016; Zemp et al., 2019). In Madagascar, these results could be transferred to vanilla or cacao plantations. Depending on the type of management these support different lemur species already, but often cannot be considered real habitat in terms of floral species richness and structural diversity (Hending et al., 2018, 2020; Webber et al., 2020).

In conclusion, though research and application are still largely absent, it would be a gain for nature and its protection to restore forest habitats with lemur food plants. However, it is questionable whether these habitats could last in Madagascar, where anthropogenic disturbance is high, illustrated by the fact that about half of the forest is less than 100 m from the forest edge (Vieilledent et al., 2018). Many years of experience prove that without taking into account the economic and resource needs of the local population, nature conservation is doomed to fail. This seems logical, because the use of resources by humans is often the reason for the need for nature conservation in the first place (Aymoz et al., 2013; Durbin & Ralambo, 1994; Gardner et al., 2013; Mansourian et al., 2017; Marcus, 2001).

Planting species of benefit for animals and humans

One possibility to integrate needs of animals and humans in conservation efforts could be to plant species of mutual benefit. Such species are easy to find, exemplified by the plant species that are exploited most often and by most different lemur species (Table 2, Chapter 1). These are all being used by humans in a variety of ways, for example parts of the plants are used for house building, as food or medicine (Rabearivony et al., 2015; Rakotoarivelo et al., 2014; Styger et al., 1999). To gain access to plants of mutual benefit it is also possible to proceed the other way around, i.e., to examine utilitarian plants of humans with regard to their use by animals. Of 139 plant taxa that are used as food, medicine or to produce charcoal by the people in three different regions of Madagascar, 72 are being used by more than 200 different terrestrial vertebrate species as habitat or food (Chapter 4). These numbers illustrate on the one hand the large knowledge we already have about vertebrate-plant interactions, though definitely not yet at its limit; and the great treasure of knowledge that local people have about plant utilization, of which only a glimpse is known to the scientific world. On the other hand, these numbers illustrate the significance of plants of mutual benefit, and their potential to be used in principle in all kinds of planting efforts.

However, this approach of using plant species of mutual benefit for restoration does not only harbor potential, but also the risk of conflict due to competition and disease transmission, which is introduced in the next paragraphs. Thereafter, the use of introduced plant species is dealt with in a separate paragraph, as they represent both an opportunity and a risk for the purpose of restoration (Carrière & Randriambanona, 2007; Gérard et al., 2015; Manjaribe et al., 2013).

Risk of conflict due to competition and disease transmission

If species are planted in restoration activities that are being used by humans and animals alike, this could lead to competition for resources. There are incidences of crop-raiding by lemurs with a negative impact on food and livelihood security of the local people, and thus human-animal conflicts (LaFleur & Gould, 2009; Loudon et al., 2006; Nadhurou et al., 2017). Competition for fruit trees such as mango or litchi, on the other hand, seems to be less likely, as they produce large quantities of fruits over a short time span and may satisfy both humans' and animals' needs (Gérard et al., 2015; own observation, Oronjia, 2019). In agroforestry systems of cacao and vanilla production even win-win situations are possible, where lemurs benefit from fruit plants different than the cultivar, and farmers from the seed dispersal and positive effect on regeneration, and possibly the contribution of primates to primary productivity (Estrada et al., 2012; Hending et al., 2018, 2020; Webber et al., 2020). On the other hand, there could be relatively close contact between humans and animals in such systems, with the risk of disease or parasite transmission in both directions (Bublitz et al., 2015; Ehlers et al., 2019; Estrada et al., 2012; Ragazzo et al., 2018). Transmission to humans might for example take place via feces, which could be ingested by consuming improperly washed fruit; transmission to lemurs can happen through the consumption of fecal matters (coprophagy) of humans or their domesticated animals (Loudon et al., 2006).

In conclusion, especially crops harbor the risk of human-animal conflict due to resource competition, while this risk seems to be lower in other cultivation systems. Also, there is the real risk of transmission of diseases in both directions, a risk that already appears to be extremely high in Madagascar's forests, where hunting on lemurs is common, and where fragmentation has progressed to the point that about 80% of the forest are less than 1 km away from the forest edge (Borgerson et al., 2021; Harper et al., 2007). Nevertheless, these dangers should not be ignored during restoration planning, and research on and measures for their prevention are needed. One example, how such a measure for the prevention of resource competition could look like, is planting tree species of which different resources are used by humans and animals. The traveller's tree (*Ravenala madagascariensis*) is such a species: its nectar is exploited by a variety of lemur species, which thus contribute to the plant's pollination, and different plant parts are used by humans as food, as construction material, and to produce tools and utensils (Andriamaharoa et al., 2010; Birkinshaw & Colquhoun, 1998; Kress et al., 1994; Rabearivony et al., 2015; Rakotoarivelo et al., 2014).

Introduced species: opportunity and risk

Introduced plant species can offer resources such as habitat structures or food to the Malagasy fauna. This becomes especially important in times of food scarcity due to the natural phenological cycle of the native plants, or due to natural disasters such as cyclones, or in early phases of colonizing or recolonizing habitats (Donati et al., 2020; Eppley et al., 2015; Hending et al., 2021; Ratsimbazafy et al., 2002). In addition to their significance for the fauna, these plant species offer several important ecosystem services to humans, such as the provision with food or timber that is usually the reason for introducing them in the first place (Gérard et al., 2015; Kull et al., 2012). However, this potential for exploitation is offset by the risk of invasion of native species communities, which can have diverse serious consequences both ecologically, e.g., through preventing regeneration of native plants or degrading soils (Binggeli, 2003; Bosshard and Mermod, 1996, as cited in Kull et al., 2015), and economically, e.g., through reducing agricultural productivity or blocking waterways (Kull et al., 2015).

Chapter 1 revealed that lemurs exploit 7.40% (102) of all plant species that have been introduced to Madagascar (1379), and 33.33% (34) of these are considered invasive according to Kull et al. (2012). These numbers are similar for endemic vertebrates in general (Gérard et al., 2015). Within the individual lemur genera, there are large differences in the use of introduced and invasive plant species, ranging from more than 40% of all feeding observations made on introduced species in *Daubentonia*, to 0% in *Indri* (Figure 5, Chapter 1). Of all species exploited by crowned lemurs in Oronjia about 8% are introduced, and 4% are invasive (Chapter 2). Thus, they are not far from the average in *Eulemur*, with about 12% introduced and 3% invasive (Chapter 1). These numbers reveal that exploitation and spread of invasive plant species through lemurs is likely, which is not due to their preference for these species, but simply because they are often available in the anthropogenically disturbed habitats of Madagascar (Gérard et al., 2015). Availability may also explain the large differences in use of introduced plant species between the lemur genera. *Daubentonia*, for example, was often studied in cultivated areas, and *Indri* in natural forests, which obviously differ in the occurrence of introduced plant species.

As a conclusion for restoration activities and especially for including lemurs in these activities, measures for the prevention and fight against the spread of invasive species should be implemented from the beginning. The database of Chapter 1 may play a role in this, because it can serve to find out which species of plants are exploited and potentially dispersed by lemurs, and also whether these plants are considered invasive. However, it has to be kept in mind that even if certain species are more likely to become invasive than others due to their characteristics, species are not invasive per se. The consequences rather depend on the environment where plants are introduced, with disturbed habitats being prone to invasion (DeSisto et al., 2020; Kull et al., 2015; Richardson et al., 2000). Furthermore, the invasive status of species or populations may change over time, and even widely spread populations of introduced species may be outcompeted by regenerating native plants in the long term (Kull et al., 2015). Thus, if ecosystems or ecosystem restorations are kept more natural, where niches are occupied by native species or will so in the future, there should also be fewer problems with species' invasions, and one could tackle their causes rather than their consequences.

Conclusions and outlook

This dissertation has shown that seed dispersal by lemurs may positively influence regeneration and diversity of Madagascar's degraded forests. With this, it seems reasonable to integrate these animals into restoration activities, and the results of our research can facilitate to do so. The approach to plant species to attract lemurs, and in the best case also to benefit humans, is extendable and replicable in all parts of Madagascar. Even though crowned lemurs seem to be a key disperser species, *Eulemur* species are in general flexible (except that they heavily rely on fruits in their diet: Sato et al., 2016) and spread over the whole country except the far southwest, thus they may play an important role in the approach (Donati et al., 2011; Mittermeier et al., 2010; Sato et al., 2014, 2016; Schwitzer et al., 2007a). But even formerly overlooked and omnivorous genera or species, such as *Microcebus* spp., can have an important influence on forest regeneration and diversity through seed dispersal (Génin & Rambeloarivony, 2018; Ramananjato et al., 2020), making clear that this ecological interaction is not restricted to certain genera or their dietary classification. Except for *Microcebus* and other genera with small body sizes, lemurs generally disperse relatively large seeds, while birds and bat disperse smaller seeds (Razafindratsima, 2014). This does not implicate though, that seed dispersal of bats and birds should be neglected, but rather that they complementarily disperse other plant species and may likewise play a role in regeneration of diverse forests in the process of restoration.

To bring forward the rehabilitation of Madagascar's forests, it seems neither promising to condemn plantations per se, nor to overestimate restoration (Ganzhorn, 1987; Lavialle et al., 2015). It would rather be desirable to include more ecological aspects into reforestation and to support restoration wherever possible, in order to integrate the aspects of biodiversity conservation and human development. While our approach of planting species of mutual benefit is a step in this direction, it is surely not a solution to all problems, and further measures to generate alternative and sustainable sources of income should be pursued.

Importantly, the mutual use of plant species only works in the long run if resources are used sustainably by humans, rather than being overexploited. Returning to the example of *Ravenala madagascariensis*, this is not yet the case, strategies for its sustainable use are lacking (Rakotoarivelo et al., 2014). Therefore, research in this direction should be carried out. A positive example of such research refers to yam (*Dioscorea* spp.), an important food plant of people from many different regions of Madagascar, which is usually collected in the wild with often devastating impact on its regeneration (Jeannoda et al., 2003). Randriamboavonjy et al. (2013) determined the importance as a food source and the degree of exploitation of different yam species, and successfully established a cultivation system of *Dioscorea alata*, reducing the pressure on wild yams. Another example is “samata” (*Euphorbia stenoclada*), a native tree that is the most important fodder plant for cattle during the dry season in southwestern Madagascar. Overexploitation and unsustainable techniques of utilization have led to its degradation, but measures how to efficiently reproduce and sustainably use this plant were found and promoted (Goetter, 2017; Goetter et al., 2015).

Overall, more research and especially applications need to be done concerning the approach of restoration discussed in this dissertation. By doing so, it will be possible to assess the chance of successfully rehabilitating Madagascar’s diverse forests. There are also risks, for instance in terms of possible competition between animals and humans. However, from a pragmatic point of view, it is better to have a forest to fight over than to have no forest at all.

References

Andriamaharoa, H., Birkinshaw, C., & Reza, L. (2010). Day-time feeding ecology of *Eulemur cinereiceps* in the Agnalazaha Forest, Mahabo-Mananivo, Madagascar. *Madagascar Conservation & Development*, *5*, 55–63. http://dx.doi.org/10.4314/mcd.v5i1.57341

Aymoz, B. G. P., Randrianjafy, V. R., Randrianjafy, Z. J. N., & Khasa, D. P. (2013). Community management of natural resources: a case study from Ankarafantsika National Park, Madagascar. *AMBIO*, *42*(6), 767–775. https://doi.org/10.1007/s13280-013-0391-9

Baden, A. L., Mancini, A. N., Federman, S., Holmes, S. M., Johnson, S. E., Kamilar, J., Louis, E. E., & Bradley, B. J. (2019). Anthropogenic pressures drive population genetic structuring across a Critically Endangered lemur species range. *Scientific Reports*, *9*(1), 16276. https://doi.org/10.1038/s41598-019-52689-2

Bezanson, M., & McNamara, A. (2019). The what and where of primate field research may be failing primate conservation. *Evolutionary Anthropology: Issues, News, and Reviews*, *28*(4), 166–178. https://doi.org/10.1002/evan.21790

Binggeli, P. (2003). Introduced and invasive plants. In S. M. Goodman & J. P. Benstead (Eds.), *The Natural History of Madagascar* (pp. 257–268). Chicago: The University of Chicago Press.

Birkinshaw, C., Andrianjafy, M., & Rasolofonirina, J.-J. (2009). Survival and growth of seedlings of 19 native tree and shrub species planted in degraded forest as part of a forest restoration project in Madagascar’s highlands. *Madagascar Conservation & Development*, *4*(2), 128–131. https://doi.org/10.4314/mcd.v4i2.48653

Birkinshaw, C., & Colquhoun, I. C. (1998). Pollination of *Ravenala madagascariensis* and *Parkia madagascariensis* by *Eulemur macaco* in Madagascar. *Folia Primatologica*, *69*, 252–259. https://doi.org/10.1159/000021634

Birkinshaw, C., & Colquhoun, I. C. (2003). Lemur food plants. In S. M. Goodman & J. P. Benstead (Eds.), *The Natural History of Madagascar* (pp. 1207–1220). Chicago: The University of Chicago Press.

Birkinshaw, C., Lowry II, P. P., Raharimampionona, J., & Aronson, J. (2013). Supporting target 4 of the global strategy for plant conservation by integrating ecological restoration into the Missouri Botanical Garden’s conservation program in Madagascar. *Annals of the Missouri Botanical Garden*, *99*(2), 139–146. https://doi.org/10.3417/2012002

Böhning-Gaese, K., Gaese, B. H., & Rabemanantsoa, S. B. (1999). Importance of primary and secondary seed dispersal in the Malagasy tree *Commiphora guillaumini*. *Ecology*, *80*(3), 821–832. https://doi.org/10.2307/177020

Borgerson, C., Johnson, S. E., Hall, E., Brown, K. A., Narváez-Torres, P. R., Rasolofoniaina, B. J. R., Razafindrapaoly, B. N., Merson, S. D., Thompson, K. E. T., Holmes, S. M., Louis, E. E., & Golden,

C. D. (2021). A national-level assessment of lemur hunting pressure in Madagascar. *International Journal of Primatology*. https://doi.org/10.1007/s10764-021-00215-5

Bublitz, D. C., Wright, P. C., Rasambainarivo, F. T., Arrigo-Nelson, S. J., Bodager, J. R., & Gillespie, T. R. (2015). Pathogenic enterobacteria in lemurs associated with anthropogenic disturbance. *American Journal of Primatology*, *77*(3), 330–337. https://doi.org/10.1002/ajp.22348

Callmander, M. W., Phillipson, P. B., Schatz, G. E., Andriambololonera, S., Rabarimanarivo, M., Rakotonirina, N., Raharimampionona, J., Chatelain, C., Gautier, L., & Lowry II, P. P. (2011). The endemic and non-endemic vascular flora of Madagascar updated. *Plant Ecology and Evolution*, *144*(2), 121–125. https://doi.org/10.5091/plecevo.2011.513

Carrasco, J., Price, V., Tulloch, V., & Mills, M. (2020). Selecting priority areas for the conservation of endemic trees species and their ecosystems in Madagascar considering both conservation value and vulnerability to human pressure. *Biodiversity and Conservation*, *29*(6), 1841–1854. https://doi.org/10.1007/s10531-020-01947-1

Carrière, S. M., & Randriambanona, H. (2007). Biodiversité introduite et autochtone: Antagonisme ou complémentarité? Le cas de l'eucalyptus à Madagascar. *Bois et forêt des Tropiques*, *292*(2), 5–21.

Charles, L. S., Dwyer, J. M., Chapman, H. M., Yadok, B. G., & Mayfield, M. M. (2019). Landscape structure mediates zoochorous-dispersed seed rain under isolated pasture trees across distinct tropical regions. *Landscape Ecology*, *34*(6), 1347–1362. https://doi.org/10.1007/s10980-019-00846-3

Corbin, J. D., & Holl, K. D. (2012). Applied nucleation as a forest restoration strategy. *Forest Ecology and Management*, *265*, 37–46. https://doi.org/10.1016/j.foreco.2011.10.013

DeSisto, C. M. M., Park, D. S., Davis, C. C., Ramananjato, V., Tonos, J. L., & Razafindratsima, O. H. (2020). An invasive species spread by threatened diurnal lemurs impacts rainforest structure in Madagascar. *Biological Invasions*, *22*(9), 2845–2858. https://doi.org/10.1007/s10530-020-02293-7

Donati, G., Campera, M., Balestri, M., Barresi, M., Kesch, K., Ndremifidy, K., Rabenantoandro, J., Racevska, E., Randriatafika, F., Ravaolahy, M., Ravoahangy, A. M., Roma, M., Rowe, F., Santini, L., Serra, V., Zander, S. L., Tsagnangara, C., Vincelette, M., & Ramanamanjato, J. (2020). Life in a fragment: evolution of foraging strategies of translocated collared brown lemurs, *Eulemur collaris*, over an 18-year period. *American Journal of Primatology*, *82*(4), e23106. https://doi.org/10.1002/ajp.23106

Donati, G., Kesch, K., Ndremifidy, K., Schmidt, S. L., Borgognini-Tarli, S. M., & Ganzhorn, J. U. (2011). Better few than hungry: flexible feeding ecology of collared lemurs *Eulemur collaris* in littoral forest fragments. *PLoS ONE*, *6*, e19807. https://doi.org/10.1371/journal.pone.0019807

Durbin, J. C., & Ralambo, J. A. (1994). The role of local people in the successful maintenance of protected areas in Madagascar. *Environmental Conservation*, *21*(2), 115–120. https://doi.org/10.1017/S037689290002453X

Ehlers, J., Poppert, S., Ratovonamana, R. Y., Ganzhorn, J. U., Tappe, D., & Krüger, A. (2019). Ectoparasites of endemic and domestic animals in southwest Madagascar. *Acta Tropica*, *196*, 83–92. https://doi.org/10.1016/j.actatropica.2019.05.008

Elliott, S., Blakesley, D., & Hardwick, K. (2013). *Restoring Tropical Forests: A Practical Guide*. Kew: Royal Botanic Gardens.

Eppley, T. M., Donati, G., Ramanamanjato, J.-B., Randriatafika, F., Andriamandimbiarisoa, L. N., Rabehevitra, D., Ravelomanantsoa, R., & Ganzhorn, J. U. (2015). The use of an invasive species habitat by a small folivorous primate: implications for lemur conservation in Madagascar. *PLoS ONE*, *10*(11), e0140981. https://doi.org/10.1371/journal.pone.0140981

Estrada, A., Raboy, B. E., & Oliveira, L. C. (2012). Agroecosystems and primate conservation in the tropics: a review. *American Journal of Primatology*, *74*(8), 696–711. https://doi.org/10.1002/ajp.22033

Fernandes, G. W., Coelho, M. S., Machado, R. B., Ferreira, M. E., Aguiar, L. M. de S., Dirzo, R., Scariot, A., & Lopes, C. R. (2016). Afforestation of savannas: an impending ecological disaster. *Natureza & Conservação*, *14*(2), 146–151. https://doi.org/10.1016/j.ncon.2016.08.002

Fiedler, P. M. A., De Lapparent, A., Razafitsalama, J., Sanamo, J., Steffens, K. J. E., & Ganzhorn, J. U. (2021). Secondary seed removal in a degraded forest habitat in Madagascar. *Scientific Reports*, *11*, 16823. https://doi.org/10.1038/s41598-021-96306-7

Ganzhorn, J. U. (1987). A possible role of plantations for primate conservation in Madagascar. *American Journal of Primatology*, *12*, 205–215. https://doi.org/10.1002/ajp.1350120208

Ganzhorn, J. U. (1999). Lemurs as indicators for assessing biodiversity in forest ecosystems of Madagascar: why it does not work. In A. Kratochwil (Ed.), *Biodiversity in ecosystems: principles and case studies of different complexity levels* (pp. 163–174). Dordrecht: Kluwer Academic Publishers. https://doi.org/10.1007/978-94-011-4677-7_10

Ganzhorn, J. U., Goodman, S. M., Ramanamanjato, J.-B., Ralison, J., Rakotondravony, D., & Rakotosamimanana, B. (2000). Effects of fragmentation and assessing minimum viable populations of lemurs in Madagascar. In G. Rheinwald (Ed.), *Isolated Vertebrate Communities in the Tropics* (pp. 265–272). Bonn: Zoologisches Forschungsinstitut und Museum A. König.

Gardner, C. J., Nicoll, M. E., Mbohoahy, T., Oleson, K. L. L., Ratsifandrihamanana, A. N., Ratsirarson, J., René de Roland, L.-A., Virah-Sawmy, M., Zafindrasilivonona, B., & Davies, Z. G. (2013). Protected areas for conservation and poverty alleviation: experiences from Madagascar. *Journal of Applied Ecology*, *50*(6), 1289–1294. https://doi.org/10.1111/1365-2664.12164

Génin, F., & Rambeloarivony, H. (2018). Mouse lemurs (Primates: Cheirogaleidae) cultivate green fruit gardens. *Biological Journal of the Linnean Society*, *124*, 607–620. https://doi.org/10.1093/biolinnean/bly087

Gérard, A., Ganzhorn, J. U., Kull, C. A., & Carrière, S. M. (2015). Possible roles of introduced plants for native vertebrate conservation: the case of Madagascar. *Restoration Ecology*, *23*(6), 768–775. https://doi.org/10.1111/rec.12246

Gérard, A., Wollni, M., Hölscher, D., Irawan, B., Sundawati, L., Teuscher, M., & Kreft, H. (2017). Oil-palm yields in diversified plantations: initial results from a biodiversity enrichment experiment in Sumatra, Indonesia. *Agriculture, Ecosystems & Environment*, *240*, 253–260. https://doi.org/10.1016/j.agee.2017.02.026

Goetter, J. (2017). Sustainable propagation of the fodder tree *Euphorbia stenoclada* ("samata") using cuttings (WOCAT-Technology). In H. Liniger, R. M. Studer, P. Moll, & U. Zander (Eds.), *Making sense of research for sustainable land management* (pp. 227–230). Leipzig: Centre for Development and Environment (CDE), University of Bern, Switzerland and Helmholtz-Centre for Environmental Research GmbH – UFZ.

Goetter, J., Rabemirinra, H. A., Antsonantenainarivony, G. O., Tahirindraza, H. S., Feldt, T., Ahlers, F., Müller, C., Ratovonamana, Y., & Weiss, D. (2015). Utilisation de l'arbre fourragère samata (*Euphorbia stenoclada*), le problème de sa dégénération, et l'approche pour l'atténuation: Résultats du projet SuLaMa. In S. Kobbe, E. Verjans, J. Nopper, J. C. Riemann, L. Prill, T. Andrianasolo, S. J. Rakotondranary, D. Fraust, R. Ratsimbarison, & D. Kübler (Eds.), *Recherche participative pour le soutien de la gestion durable des terres du Plateau Mahafaly dans le sud-ouest de Madagascar: Conclusions préliminaires* (pp. 32–36). Hamburg: Universität Hamburg.

Goodman, S. M., & Ganzhorn, J. U. (in press). Predation on lemurs. In S. M. Goodman (Ed.), *The New Natural History of Madagascar*. Princeton: Princeton University Press.

Guevara, S., Purata, S. E., & Van der Maarel, E. (1986). The role of remnant forest trees in tropical secondary succession. *Vegetatio*, *66*, 77–84. https://doi.org/10.1007/BF00045497

Harper, G. J., Steininger, M. K., Tucker, C. J., Juhn, D., & Hawkins, F. (2007). Fifty years of deforestation and forest fragmentation in Madagascar. *Environmental Conservation*, *34*(4), 325–333. https://doi.org/10.1017/S0376892907004262

Hending, D., Andrianiaina, A., Maxfield, P., Rakotomalala, Z., & Cotton, S. (2020). Floral species richness, structural diversity and conservation value of vanilla agroecosystems in Madagascar. *African Journal of Ecology*, *58*(1), 100–111. https://doi.org/10.1111/aje.12682

Hending, D., Andrianiaina, A., Rakotomalala, Z., & Cotton, S. (2018). The use of vanilla plantations by lemurs: encouraging findings for both lemur conservation and sustainable agroforestry in the

Sava region, northeast Madagascar. *International Journal of Primatology*, *39*(1), 141–153. https://doi.org/10.1007/s10764-018-0022-1

Hending, D., Randrianarison, H., Holderied, M., McCabe, G., & Cotton, S. (2021). The kapok tree (*Ceiba pentandra* (L.) Gaertn, Malvaceae) as a food source for native vertebrate species during times of resource scarcity and its potential for reforestation in Madagascar. *Austral Ecology*, *46*(8), 1440-1444. https://doi.org/10.1111/aec.13076

Heymann, E. W. (2011). Florivory, nectarivory, and pollination - a review of primate-flower interactions. *Ecotropica*, *17*, 41–52.

Holloway, L. (2000). Catalysing rainforest restoration in Madagascar. In W. R. Lourenço & S. M. Goodman (Eds.), *Diversité et endémisme à Madagascar - Diversity and endemism in Madagascar* (pp. 115–124). Paris: Mémoires de la Société de Biogéographie.

Holloway, L. (2004). Ecosystem restoration and rehabilitation in Madagascar. *Ecological Restoration*, *22*(2), 113–119. https://doi.org/10.3368/er.22.2.113

Holloway, L. (2007). Targeting sustainable options for restoring natural capital in Madagascar. In J. Aronson, S. J. Milton, & J. N. Blignaut (Eds.), *Restoring Natural Capital: Science, Business, and Practice* (pp. 64–75). Washington: Island Press.

Hubbell, S. P. (1980). Seed predation and the coexistence of tree species in tropical forests. *Oikos*, *35*(2), 214–229. https://doi.org/10.2307/3544429

Irwin, M. T., Wright, P. C., Birkinshaw, C., Fisher, B. L., Gardner, C. J., Glos, J., Goodman, S. M., Loiselle, P., Rabeson, P., Raharison, J.-L., Raherilalao, M. J., Rakotondravony, D., Raselimanana, A., Ratsimbazafy, J., Sparks, J. S., Wilmé, L., & Ganzhorn, J. U. (2010). Patterns of species change in anthropogenically disturbed forests of Madagascar. *Biological Conservation*, *143*(10), 2351–2362. https://doi.org/10.1016/j.biocon.2010.01.023

Jacob, A. L., Lechowicz, M. J., & Chapman, C. A. (2017). Non-native fruit trees facilitate colonization of native forest on abandoned farmland. *Restoration Ecology*, *25*(2), 211–219. https://doi.org/10.1111/rec.12414

Jeannoda, V.-H., Jeannoda, V., Hladik, A., & Hladik, C. M. (2003). Les ignames de Madagascar. Diversité, utilisations et perceptions. *Hommes et Plantes*, *47*, 10–23.

Knoop, S., Chikhi, L., & Salmona, J. (2018). Mouse lemurs' use of degraded habitat. *Lemur News*, *21*, 20–31.

Kress, W. J., Schatz, G. E., Andrianifahanana, M., & Morland, H. S. (1994). Pollination of *Ravenala madagascariensis* (Strelitziaceae) by lemurs in Madagascar: evidence for an archaic coevolutionary system? *American Journal of Botany*, *81*, 542–551. https://doi.org/10.1002/j.1537-2197.1994.tb15483.x

Kull, C. A., Tassin, J., & Carrière, S. M. (2015). Approaching invasive species in Madagascar. *Madagascar Conservation & Development*, *9*(2), 60–70. https://doi.org/10.4314/mcd.v9i2.2

Kull, C. A., Tassin, J., Moreau, S., Ramiarantsoa, H. R., Blanc-Pamard, C., & Carrière, S. M. (2012). The introduced flora of Madagascar. *Biological Invasions*, *14*(4), 875–888. https://doi.org/10.1007/s10530-011-0124-6

Lacroix, E., Carodenuto, S., Richter, F., Pistorius, T., & Tennigkeit, T. (2016). *Restauration des Paysages Forestiers. Evaluation des potentialités dans le contexte des engagements de Bonn 2.0 et de la Déclaration de New York sur les forêts. Méthodologie et résultats pour Madagascar.* Freiburg: UNIQUE forestry and land use GmbH.

LaFleur, M., & Gould, L. (2009). Feeding outside the forest: the importance of crop raiding and an invasive weed in the diet of gallery forest ring-tailed lemurs (*Lemur catta*) following a cyclone at the Beza Mahafaly Special Reserve, Madagascar. *Folia Primatologica*, *80*, 233–246. https://doi.org/10.1159/000240968

Lavialle, J., Carrière, S. M., Miandrimanana, C., Tilahimena, A., Birkinshaw, C., & Aronson, J. (2015). Complementarity of native and introduced tree species: exploring timber supply on the east coast of Madagascar. *Madagascar Conservation & Development*, *10*, 137–143. https://doi.org/10.4314/mcd.v10i3.6

Loudon, J. E., Sauther, M. L., Fish, K. D., Hunter-Ishikawa, M., & Ibrahim, Y. J. (2006). One reserve, three primates: applying a holistic approach to understand the interconnections among ring-tailed lemurs (*Lemur catta*), Verreaux's sifaka (*Propithecus verreauxi*), and humans (*Homo sapiens*) at Beza Mahafaly Special Reserve, Madagascar. *Ecological and Environmental Anthropology*, *2*(2), 54–74.

Manjaribe, C., Frasier, C. L., Rakouth, B., & Louis Jr., E. E. (2013). Ecological restoration and reforestation of fragmented forests in Kianjavato, Madagascar. *International Journal of Ecology*, *2013*, 726275. https://doi.org/10.1155/2013/726275

Mansourian, S., Stanturf, J. A., Derkyi, M. A. A., & Engel, V. L. (2017). Forest Landscape Restoration: increasing the positive impacts of forest restoration or simply the area under tree cover? *Restoration Ecology*, *25*(2), 178–183. https://doi.org/10.1111/rec.12489

Marcus, R. R. (2001). Seeing the forest for the trees: integrated conservation and development projects and local perceptions of conservation in Madagascar. *Human Ecology*, *29*(4), 381–397. https://doi.org/10.1023/A:1013189720278

Martinez, B. T., & Razafindratsima, O. H. (2014). Frugivory and seed dispersal patterns of the red-ruffed lemur, *Varecia rubra*, at a forest restoration site in Masoala National Park, Madagascar. *Folia Primatologica*, *85*, 228–243. https://doi.org/10.1159/000363408

Mittermeier, R. A., Louis Jr., E. E., Richardson, M., Schwitzer, C., Langrand, O., Rylands, A. B., Hawkins, F., Rajaobelina, S., Ratsimbazafy, J., Rasoloarison, R., Roos, C., Kappeler, P. M., & Mackinnon, J. (2010). *Lemurs of Madagascar*, 3rd edition. Bogotá: Conservation International.

Nadhurou, B., Righini, R., Gamba, M., Laiolo, P., Ouledi, A., & Giacoma, C. (2017). Effects of human disturbance on the mongoose lemur *Eulemur mongoz* in Comoros: implications and potential for the conservation of a Critically Endangered species. *Oryx*, *51*(1), 60–67. https://doi.org/10.1017/S0030605315000897

Pareliussen, I., Olsson, E. G. A., & Armbruster, W. S. (2006). Factors limiting the survival of native tree seedlings used in conservation efforts at the edges of forest fragments in upland Madagascar. *Restoration Ecology*, *14*(2), 196–203. https://doi.org/10.1111/j.1526-100X.2006.00121.x

Rabearivony, A. D., Kuhlman, A. R., Razafiariso, Z. L., Raharimalala, F., Rakotoarivony, F., Randrianarivony, T., Rakotoarivelo, N., Randrianasolo, A., & Bussmann, R. W. (2015). Ethnobotanical study of the medicinal plants known by men in Ambalabe, Madagascar. *Ethnobotany Research and Applications*, *14*, 123–138. https://doi.org/10.17348/era.14.0.123-138

Ragazzo, L. J., Zohdy, S., Velonabison, M., Herrera, J., Wright, P. C., & Gillespie, T. R. (2018). *Entamoeba histolytica* infection in wild lemurs associated with proximity to humans. *Veterinary Parasitology*, *249*, 98–101. https://doi.org/10.1016/j.vetpar.2017.12.002

Rakotoarivelo, N., Razanatsima, A., Rakotoarivony, F., Rasoaviety, L., Ramarosandratana, A., Jeannoda, V., Kuhlman, A. R., Randrianasolo, A., & Bussmann, R. W. (2014). Ethnobotanical and economic value of *Ravenala madagascariensis* Sonn. in eastern Madagascar. *Journal of Ethnobiology and Ethnomedicine*, *10*, 57. https://doi.org/10.1186/1746-4269-10-57

Rakotondraparany, F., & Andriambeloson, J. B. (2015). *Étude des lémuriens phares de la Nouvelle Aire Protégée (NAP) Oronjia, Antsiranana II*. Antananarivo: Université d'Antananarivo.

Ramananjato, V., Rakotomalala, Z., Park, D. S., DeSisto, C. M. M., Raoelinjanakolona, N. N., Guthrie, N. K., Fenosoa, Z. E. S., Johnson, S. E., & Razafindratsima, O. H. (2020). The role of nocturnal omnivorous lemurs as seed dispersers in Malagasy rain forests. *Biotropica*, 00:1-8. https://doi.org/10.1111/btp.12789

Randriamboavonjy, T., Wilkin, P., Rajaovelona, L., & Cable, S. (2013). Utilisation et conservation durable des ignames du corridor forestier Ambositra-Vondrozo, Madagascar. *Scripta Botanica Belgica*, *50*, 341–348.

Ratsimbazafy, J., Ramarosandratana, H. V., & Zaonarivelo, R. J. (2002). How do black-and-white ruffed lemurs still survive in a highly disturbed habitat? *Lemur News*, *7*, 7–10.

Razafindratsima, O. H. (2014). Seed dispersal by vertebrates in Madagascar's forests: review and future directions. *Madagascar Conservation & Development*, *9*(2), 90–97. https://doi.org/10.4314/mcd.v9i2.5

Razafindratsima, O. H. (2017). Post-dispersal seed removal by rodents in Ranomafana rain forest, Madagascar. *Journal of Tropical Ecology*, *33*(3), 232–236. https://doi.org/10.1017/S0266467417000104

Razafindratsima, O. H., & Dunham, A. E. (2015). Assessing the impacts of nonrandom seed dispersal by multiple frugivore partners on plant recruitment. *Ecology*, *96*(1), 24–30. https://doi.org/10.1890/14-0684.1

Razafindratsima, O. H., & Martinez, B. T. (2012). Seed dispersal by red-ruffed lemurs: seed size, viability, and beneficial effect on seedling growth. *Ecotropica*, *18*, 15–26.

Razafindratsima, O. H., Raoelinjanakolona, N. N., Heriniaina, R. R., Nantenaina, R. H., Ratolojanahary, T. H., & Dunham, A. E. (2021). Simplified communities of seed-dispersers limit the composition and flow of seeds in edge habitats. *Frontiers in Ecology and Evolution*, *9*, 655441. https://doi.org/10.3389/fevo.2021.655441

Razafindratsima, O. H., & Razafimahatratra, E. (2010). Effect of red ruffed lemur gut passage on the germination of native rainforest plant species. *Lemur News*, *15*, 39–42.

Richardson, D. M., Pysek, P., Rejmanek, M., Barbour, M. G., Panetta, F. D., & West, C. J. (2000). Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions*, *6*(2), 93–107. https://doi.org/10.1046/j.1472-4642.2000.00083.x

Sato, H. (2012). Frugivory and seed dispersal by brown lemurs in a Malagasy tropical dry forest. *Biotropica*, *44*(4), 479–488. https://doi.org/10.1111/j.1744-7429.2011.00838.x

Sato, H., Ichino, S., & Hanya, G. (2014). Dietary modification by common brown lemurs (*Eulemur fulvus*) during seasonal drought conditions in western Madagascar. *Primates*, *55*, 219–230. https://doi.org/10.1007/s10329-013-0392-0

Sato, H., Santini, L., Patel, E. R., Campera, M., Yamashita, N., Colquhoun, I. C., & Donati, G. (2016). Dietary flexibility and feeding strategies of *Eulemur*: a comparison with *Propithecus*. *International Journal of Primatology*, *37*(1), 109–129. https://doi.org/10.1007/s10764-015-9877-6

Schwitzer, C., Mittermeier, R. A., Johnson, S. E., Donati, G., Irwin, M., Peacock, H., Ratsimbazafy, J., Razafindramanana, J., Louis, E. E., Chikhi, L., Colquhoun, I. C., Tinsman, J., Dolch, R., LaFleur, M., Nash, S., Patel, E., Randrianambinina, B., Rasolofoharivelo, T., & Wright, P. C. (2014). Averting lemur extinctions amid Madagascar's political crisis. *Science*, *343*(6173), 842–843. https://doi.org/10.1126/science.1245783

Schwitzer, N., Kaumanns, W., Seitz, P. C., & Schwitzer, C. (2007). Cathemeral activity patterns of the blue-eyed black lemur *Eulemur macaco flavifrons* in intact and degraded forest fragments. *Endangered Species Research*, *3*, 239–247. https://doi.org/10.3354/esr00045

Schwitzer, N., Randriatahina, G. H., Kaumanns, W., Hoffmeister, D., & Schwitzer, C. (2007). Habitat utilization of blue-eyed black lemurs, *Eulemur macaco flavifrons* (Gray, 1867), in primary and altered forest fragments. *Primate Conservation*, *22*(1), 79–87. https://doi.org/10.1896/052.022.0106

Styger, E., Rakotoarimanana, J. E. M., Rabevohitra, R., & Fernandes, E. C. M. (1999). Indigenous fruit trees of Madagascar: potential components of agroforestry systems to improve human nutrition and restore biological diversity. *Agroforestry Systems*, *46*, 289–310. https://doi.org/10.1023/A:1006295530509

Teuscher, M., Gérard, A., Brose, U., Buchori, D., Clough, Y., Ehbrecht, M., Hölscher, D., Irawan, B., Sundawati, L., Wollni, M., & Kreft, H. (2016). Experimental biodiversity enrichment in oil-palm-dominated landscapes in Indonesia. *Frontiers in Plant Science*, *7*, 1538. https://doi.org/10.3389/fpls.2016.01538

United Nations Environment Programme (2021). *Becoming #GenerationRestoration: Ecosystem restoration for people, nature and climate*. Nairobi: United Nations Environment Programme (UNEP) and UN Environment Programme World Conservation Monitoring Centre (UNEP-WCMC).

Verdú, M., & Traveset, A. (2005). Early emergence enhances plant fitness: a phylogenetically controlled meta-analysis. *Ecology*, *86*(6), 1385–1394. https://doi.org/10.1890/04-1647

Vieilledent, G., Grinand, C., Rakotomalala, F. A., Ranaivosoa, R., Rakotoarijaona, J.-R., Allnutt, T. F., & Achard, F. (2018). Combining global tree cover loss data with historical national forest cover maps to look at six decades of deforestation and forest fragmentation in Madagascar. *Biological Conservation*, *222*, 189–197. https://doi.org/10.1016/j.biocon.2018.04.008

Volampeno, M. S. N., Randriatahina, G., & Downs, C. T. (2013). Structure and composition of Ankarafa Forest, Sahamalaza-Iles Radama National Park, Madagascar: implications for the frugivorous endemic blue-eyed black lemur (*Eulemur flavifrons*). *South African Journal of Wildlife Research*, *43*(2), 91–102. https://doi.org/10.3957/056.043.0205

Webber, A. D., Solofondranohatra, J. S., Razafindramoana, S., Fernández, D., Parker, C. A., Steer, M., Abrahams, M., & Allainguillaume, J. (2020). Lemurs in cacao: presence and abundance within the shade plantations of northern Madagascar. *Folia Primatologica*, *91*, 96–107. https://doi.org/10.1159/000501987

Wester, L. L., & Wood, H. B. (1977). Koster's curse (*Clidemia hirta*), a weed pest in Hawaiian forests. *Environmental Conservation*, *4*(1), 35–41. https://doi.org/10.1017/S0376892900024991

Wunderle Jr., J. M. (1997). The role of animal seed dispersal in accelerating native forest regeneration on degraded tropical lands. *Forest Ecology and Management*, *99*, 223–235. https://doi.org/10.1016/S0378-1127(97)00208-9

Yarranton, G. A., & Morrison, R. G. (1974). Spatial dynamics of a primary succession: nucleation. *The Journal of Ecology*, *62*(2), 417. https://doi.org/10.2307/2258988

Zemp, D. C., Ehbrecht, M., Seidel, D., Ammer, C., Craven, D., Erkelenz, J., Irawan, B., Sundawati, L., Hölscher, D., & Kreft, H. (2019). Mixed-species tree plantings enhance structural complexity in oil palm plantations. *Agriculture, Ecosystems & Environment*, *283*, 106564. https://doi.org/10.1016/j.agee.2019.06.003

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Photo credit: Kim Steffens

EIDESSTATTLICHE VERSICHERUNG

Hiermit erkläre ich an Eides statt, dass ich die vorliegende Dissertationsschrift selbst verfasst und keine anderen als die angegebenen Quellen und Hilfsmittel benutzt habe.

Kim Steffens