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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

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Abstract Reforestation in Madagascar often relies on a few tree species with known properties. Species selection may consider aspects like human use, growth characteristics and animal use. Here, we investigated the use of the kapok tree (*Ceiba pentandra*) as a food source for vertebrates during the dry season in North West Madagascar. We observed 21 native vertebrate species (five lemurs, five bats and 11 birds) feed on or within *C. pentandra* during this period of low food availability, 48% of which are known seed dispersers. As a fast-growing species, *C. pentandra* may therefore be suitable for inclusion in reforestation and forest restoration efforts to facilitate seed dispersal, natural forest regeneration and animal movement between adjacent forest fragments.

Key words: connectivity, food source, neophyte, pamba, seed dispersers.

Millions of hectares of land have been deforested to accommodate the cultivation of crops globally (Pendrill *et al.* 2019). This land conversion process is most profound in the tropics, where approximately 78% of new agricultural areas are derived from the clearing of forests (Lambin & Meyfroidt 2011). Many plants cultivated within these agroecosystems are neophytes that do not occur naturally within the region (Jeschke *et al.* 2014). In many countries, neophytes now have self-sustaining populations and some species have become invasive, causing degradation to the native ecosystems resulting in major declines of biodiversity, ecological integrity and habitat quality (Pimentel *et al.* 2001). However, many other neophytes cause no direct harm to existing ecosystems and may prove to be valuable resources for both local wildlife and human populations (Hettinger 2001).

The kapok tree (*Ceiba pentandra*) is a large, hermaphroditic tree native to Central and South America, the Caribbean and North West Africa (Fig. 1). Due to its many commercial uses, the tree has been introduced to numerous countries throughout Africa and Asia, and it is now widespread throughout the tropics (Dick *et al.* 2007). Like many neophytes, *C. pentandra* is a fast-growing species that can grow in dry conditions and poor-quality soils (Gawali 2014; Gawali *et al.* 2015; Immanuel & Ganapathy 2020). *Ceiba pentandra* (locally known as 'pamba') was first introduced to Madagascar in the early 1900s for cultivation of its seed fibres (Montagnac 1952; Kull *et al.* 2012), and it is now distributed throughout the west of the island, from Sahamalaza-Iles Radama National Park (SIRNP) in the North West to Manja in the south west (Sussman & Tattersall 1976; Jenkins & Racey 2008; Hending pers. comm., 2019). Throughout its range in Madagascar, people use its wood for house and canoe construction, its seed fibre to fill blankets and pillows, and it is believed the trees themselves ward off evil spirits (Randrianarison & Hending pers. comm., 2019). Although *C. pentandra* is a non-native species throughout much of its current range, there is little evidence to suggest that this species is invasive, or a threat to native species assemblages (Kull *et al.* 2012, but see Space *et al.* 2000). Due to the high nectar content of its flowers, *C. pentandra* has been observed as a food source for many nectivorous species of bat, primate, bird and invertebrate within its geographic range (Gribel *et al.* 1999). However, the ecology and role of this introduced species as a food source for native animals has been studied in only a few geographic locations within its current range (Gribel *et al.* 1999; Singaravelan & Marimuthu 2004; Dick *et al.* 2007; Steffens 2020).

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Here, we conducted a short study of how many vertebrate species feed on or within *C. pentandra* in Anabohazo forest (S14°19′, E47°54′, ~250 m a.s.l.), a 1169 ha sub-humid, transitional forest in SIRNP, North West Madagascar. Despite its protected status, SIRNP has undergone widescale deforestation, and tree-felling still occurs within some areas of the national park (Seiler *et al.* 2010; Hending *et al.* 2017), although a reforestation scheme has recently been established within SIRNP.

We selected five *C. pentandra* trees with large visible crowns at which we conducted focal observations of day-active and night-active (Charles-Dominique 1975) animal use twice daily for a 30-min period (10:00–10:30 and 21:00–21:30) over a 15-day period in July 2019. During these observations, we recorded all vertebrate species that we observed to feed within the *C. pentandra* trees. We selected the five survey trees as they were (i) separated from each other by at least 200 m, (ii) spread throughout the entire area of Anabohazo forest, (iii) in good health and visibly flowering and (iv) at least 15 m in height. All trees were situated in the interior of Anabohazo forest itself, which is approximately 3 km away from the nearest villages. Only one tree was surveyed per day ($N = 3$ survey days per tree). Locally, *C. pentandra* flowers May–July and fruits July–September, a period within Madagascar's dry season.

During our observations, we witnessed 21 native vertebrate species (5 lemurs, 11 birds, 5 bats) feed on or within the *C. pentandra* trees (Table 1). For all species, we witnessed multiple individuals visit these

Fig. 1. (a) A *Ceiba pentandra* specimen and (b) its flowers beginning to open in May 2019 in the Anabohazo forest, Sahamalaza-Iles Radama National Park, North West Madagascar.

Table 1. Vertebrate species and their IUCN status (2020), that were observed to feed within five *Ceiba pentandra* trees, surveyed in July 2019 in the Anabohazo forest, Sahamalaza-Iles Radama National Park, North West Madagascar. Species highlighted with an asterisk (*) are known seed dispersers (Razafindratsima 2014; Albert-Daviaud *et al.* 2018; Albert-Daviaud *et al.* 2020; Ramananjato *et al.* 2020; Hending *et al.* pers. comm., 2019)

				Feeding	
	Common Name	Species Name	IUCN Status	Flowers	Invertebrates
Lemurs	Blue-Eyed Black Lemur*	*Eulemur flavifrons*	CR	✓	
	Fat-Tailed Dwarf Lemur*	*Cheirogaleus medius*	VU	✓	✓
	Northern Giant Mouse Lemur*	*Mirza zaza*	EN	✓	✓
	Sahamalaza Sportive Lemur	*Lepilemur sahamalaza*	CR	✓	
	Sambirano Mouse Lemur*	*Microcebus sambiranensis*	EN	✓	✓
Bats	Commerson's Leaf-Nosed Bat	*Macronycteris commersoni*	NT		✓
	Madagascan Fruit Bat*	*Eidolon dupreanum*	VU	✓	
	Madagascan Rousette*	*Rousettus madagascariensis*	VU	✓	
	Madagascar Flying Fox*	*Pteropus rufus*	VU	✓	
	Unidentified Bat Species	-	-	✓	
Birds	Chabert's Vanga*	*Leptopterus chabert*	LC		✓
	Crested Drongo*	*Dicrurus forficatus*	LC		✓
	Long-Billed Bernieria	*Bernieria madagascariensis*	LC		✓
	Madagascan Hoopoe	*Upupa marginata*	LC		✓
	Madagascar Bulbul*	*Hypsipites madagascariensis*	LC		✓
	Madagascar Paradise Flycatcher	*Terpsiphone mutata*	LC		✓
	Madagascar Red Fody	*Foudia Madagascariensis*	LC	✓	✓
	Malagasy Green Sunbird	*Cinnyris notatus*	LC	✓	
	Olive Bee-Eater	*Merops superciliosus*	LC		✓
	Sickle-Billed Vanga	*Falculea palliata*	LC		✓
	Souimanga Sunbird	*Cinnyris sovimanga*	LC	✓	

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trees during the study period. Twelve (12) species visited *C. pentandra* to feed on the flower's nectar or the flowers themselves, whilst 13 species visited *C. pentandra* to feed on invertebrates attracted to the trees by the flower's nectar (Gribel *et al.* 1999). We also observed one *Lepilemur sahamalaza* regularly using a fissure within the trunk of one of the *C. pentandra* trees as a sleeping site.

Our observations suggest that *C. pentandra* is an important food source for many native vertebrates (38% classified as Threatened by the World Conservation Union, IUCN 2020) in SIRNP during Madagascar's dry season. This finding is also supported by observations of species-specific use of *C. pentandra* as a food source in the literature (Sussman & Tattersall 1976; Andriafidison *et al.* 2006; Jenkins & Racey 2008; Gérard *et al.* 2015). The dry season is synonymous with food scarcity in Madagascar's transitional forests (Volampeno *et al.* 2013), and fruit prevalence in SIRNP is at its annual lowest during much of this period (April–August: Volampeno *et al.* 2013; Hending *et al.* unpubl. data, 2019). *Ceiba pentandra* therefore flowers at a time when many other tree species do not harbour fruit (Andriaharimalala *et al.* 2012), and many animals likely rely on *C. pentandra* as a source of food during this period in SIRNP, and the rest of Madagascar's western transitional forests more generally.

Interestingly, 48% of the animals that we observed feeding in the *C. pentandra* trees are known to be important seed dispersers (Razafindratsima 2014; Albert-Daviaud *et al.* 2018; Albert-Daviaud *et al.* 2020; Ramananjato *et al.* 2020; Hending *et al.* pers. comm., 2019). Due to the large number of seed dispersers that this species attracts (e.g. the blue-eyed black lemur, *E. flavifrons*), *C. pentandra* may promote the movement of native seed dispersers between individual food sources (*C. pentandra* trees) within the forest. This would facilitate seed dispersal by these animals and thus contribute to natural regeneration of the forest; seed dispersers would be unlikely to disperse the seeds of *C. pentandra* itself, as the fruits are fibrous, non-fleshy and too large to be swallowed. Considering this, our findings suggest that *C. pentandra* may be a suitable species for inclusion in reforestation and forest restoration projects in Madagascar. This is because *C. pentandra* (i) attracts seed dispersers that can promote forest regeneration, (ii) has a large height and crown (Gribel *et al.* 1999; Dick *et al.* 2007) which would facilitate the movement of animals between adjacent forest trees and may provide sleeping sites and resting opportunities for them, similarly to some other exotic species in Madagascar (e.g. *Eucalyptus*, *Pinus*: Ganzhorn 1987), and (iii) is a fast-growing species that can ameliorate degraded soil (Gawali *et al.* 2015; Immanuel and Ganapthy, 2020). Although the inclusion of *C. pentandra* in reforestation and forest restoration schemes, along with native tree species, may contribute to natural forest regeneration and the restoration of ecological integrity (Ramanamanjato & Ganzhorn 2001; Brancalion *et al.* 2020), this is something that does need to be tested.

Madagascar's natural forest cover decreased by 44% over the period 1953–2014 (Vieilledent *et al.* 2018), and reforestation and forest restoration efforts are now underway in some areas of the country (e.g. Holloway 2004; Pareliussen *et al.* 2006; Vincelette *et al.* 2007; Manjaribe *et al.* 2013) to restore this important habitat type on which 90% of Madagascar's endemic animal species depend (Dufils 2003). It is therefore paramount that these reforestation schemes contain suitable species to achieve both successful forest regeneration and accommodation of native fauna, whilst also providing benefits for local human populations. Our preliminary results suggest that *C. pentandra* may have this potential, but further research is now needed to explore this within a reforestation or forest restoration landscape and, whilst *C. pentandra* is not reported as a potentially invasive species in Madagascar (Kull *et al.* 2012), a formal risk assessment must also be carried out. This is something that we aim to do within SIRNP where a new reforestation project has recently started.

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DISCLOSURE

The authors have no conflict of interest to declare.

AUTHOR CONTRIBUTIONS

Daniel Hending: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Funding acquisition (lead); Investigation (equal); Methodology (equal); Project administration (lead); Resources (lead); Software (lead); Supervision (supporting); Validation (equal); Visualization (equal); Writing-original draft (lead); Writing-review & editing (equal). **Heriniaina Randrianarison:** Conceptualization (supporting); Data curation (supporting); Investigation (equal); Methodology

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(supporting); Validation (equal); Visualization (equal); Writing-original draft (supporting); Writing-review & editing (supporting). **Marc Holderied:** Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (supporting); Project administration (supporting); Software (supporting); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (supporting); Writing-review & editing (equal). **Grainne McCabe:** Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (supporting); Project administration (supporting); Software (supporting); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (supporting); Writing-review & editing (equal). **Sam Cotton:** Conceptualization (supporting); Formal analysis (supporting); Funding acquisition (supporting); Project administration (supporting); Software (supporting); Supervision (equal); Validation (equal); Visualization (equal); Writing-original draft (supporting); Writing-review & editing (equal).

DATA AVAILABILITY STATEMENT

There are no associated data for this submission.

REFERENCES

Albert-Daviaud A., Buerki S., Onjalalaina G. E. *et al.* (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,** 418–26.

Andriafidison D., Andrianaivoarivelo R. A., Ramilijaona O. R. *et al.* (2006) Nectarivory by endemic Malagasy fruit bats during the dry season. *Biotropica* **38,** 85–90.

Andriaharimalala T., Roger E., Rajeriarison C. & Ganzhorn J. U. (2012) Phenology of different vegetation types in the dry forest of Andohahela National Park, southeastern Madagascar. *Malagasy Nat.* **6,** 24–45.

Brancalion P. H. S., Amazonas N. T., Chazdon R. L. *et al.* (2020) Exotic eucalypts: from demonized trees to allies of tropical forest restoration? *J. Appl. Ecol.* **57,** 55–66.

Charles-Dominique P. (1975) Nocturnality and diurnality. In: *Phylogeny of the Primates* (eds W. P. Luckett & F. S. Szalay) pp. 69–88. Springer, Boston.

Dick C. W., Bermingham E., Lemes M. R. & Gribel R. (2007) Extreme long-distance dispersal of the lowland tropical rainforest tree *Ceiba pentandra* L. (Malvaceae) in Africa and the Neotropics. *Mol. Ecol.* **16,** 3039–49.

Dufils J. M. (2003) Remaining forest cover. In: *The Natural History of Madagascar* (eds S. M. Goodman & J. P. Benstead) pp. 88–96. University Press, Chicago.

Ganzhorn J. U. (1987) A possible role of plantations for primate conservation in Madagascar. *Am. J. Primatol.* **12,** 205–15.

Gawali A. (2014) Litterfall and carbon, nutrient returns in stands of *Ceiba pentandra* (L.) Gaertn. sub-humid tropics of Eastern India. *Int. J. For. Crop Improv.* **5,** 1–8.

Gawali A., Puri S. & Swamy S. L. (2015) Evaluation growth and yield of wheat varieties under *Ceiba pentandra* (L) based agrisilviculture system. *Univers.J. Agric. Res.* **3,** 173–81.

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. *Restor. Ecol.* **23,** 768–75.

Gribel R., Gibbs P. E. & Queiroz A. L. (1999) Flowering phenology and pollination biology of *Ceiba pentandra* (Bombacaceae) in Central Amazonia. *J. Trop. Ecol.* **15,** 247–63.

Hending D., McCabe G. & Holderied M. (2017) Sleeping and ranging behavior of the Sambirano Mouse Lemur, *Microcebus sambiranensis*. *Int. J. Primatol.* **38,** 1072–89.

Hettinger N. (2001) Exotic species, naturalisation, and biological nativism. *Environ. Values* **10,** 193–224.

Holloway L. (2004) Ecosystem restoration and rehabilitation in Madagascar. *Ecol. Restor.* **22,** 113–9.

Immanuel R. R. & Ganapthy M. (2020) Restoration of soil microbial biomass using multipurpose trees. *Plant Arch.* **20,** 2641–5.

IUCN. (2020) The IUCN. Red List of Threatened Species. Version 2020-2. https://www.IUCN.redlist.org

Jenkins R. K. & Racey P. A. (2008) Bats as bushmeat in Madagascar. *Madag. Conserv. Dev.* **3,** 22–30.

Jeschke J. M., Bacher S., Blackburn T. M. *et al.* (2014) Defining the impact of non-native species. *Conserv. Biol.* **28,** 1188–94.

Kull C. A., Tassin J., Moreau S., Ramiarantsoa H. R., Blanc-Pamard C. & Carrière S. M. (2012) The introduced flora of Madagascar. *Biol. Invasions* **14,** 875–88.

Lambin E. F. & Meyfroidt P. (2011) Global land use change, economic globalization, and the looming land scarcity. *Proc. Natl Acad. Sci. USA* **108,** 3465–72.

Manjaribe C., Frasier C. L., Rakouth B. & Louis E. E. (2013) Ecological restoration and reforestation of fragmented forests in Kianjavato, Madagascar. *Int. J. Ecol.* **2013,** 726275.

Montagnac R. (1952) Le kapockier. Recherche Agronomie Madagascar CR 68–74.

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. *Restor. Ecol.* **14,** 196–203.

Pendrill F., Persson U. M., Godar J. & Kastner T. (2019) Deforestation displaced: trade in forest-risk commodities and the prospects for a global forest transition. *Environ. Res. Lett.* **14,** e055003.

Pimentel D., McNair S., Janecka J. *et al.* (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agric. Ecosyst. Environ.* **84,** 1–20.

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. *Anim. Conserv.* **4,** 175–83.

Ramananjato V., Rakotomalala Z., Park D. S. *et al.* (2020) The role of nocturnal omnivorous lemurs as seed dispersers in Malagasy rain forests. *Biotropica* **52,** 758–65.

Razafindratsima O. H. (2014) Seed dispersal by vertebrates in Madagascar's forests: review and future directions. *Madag. Conserv. Dev.* **9,** 90–7.

Seiler M., Randriatahina G. H. & Schwitzer C. (2010) Ongoing threats to lemurs and their habitat inside the Sahamalaza-Iles Radama National Park. *Lemur News* **15,** 7–9.

Singaravelan N. & Marimuthu G. (2004) Nectar feeding and pollen carrying from *Ceiba pentandra* by pteropodid bats. *J. Mammal.* **85,** 1–7.

Space J. C., Waterhouse B., Denslow J. S. & Nelson D. (2000) Invasive Plant Species on Rota, Commonwealth of the Northern Mariana Islands. USDA Forest Service, Honolulu, Hawai'i.

Steffens K. J. E. (2020) Lemur food plants as options for forest restoration in Madagascar. *Restor. Ecol.* **28,** 1517–27.

Sussman R. W. & Tattersall I. (1976) Cycles of activity, group composition, and diet of *Lemur mongoz mongoz* Linnaeus 1766 in Madagascar. *Folia Primatol.* **26,** 270–83.

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. *Biol. Conserv.* **222,** 189–97.

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: *Biodiversity, Ecology and Conservation of Littoral Forest Ecosystems in Southeastern Madagascar, Tolagnaro (Fort Dauphin)* (eds J. U. Ganzhorn, S. M. Goodman & M. Vincelette) pp. 337–54. Smithsonian Institution, Washington.

Volampeno M. S. N., Downs C. T. & Randriatahina G. (2013) Structure and composition of Ankarafa Forest, Sahamalaza-Iles Radama National Park, Madagascar: Implications for the frugivorous endemic blue-eyed black lemur (*Eulemur flavifrons*). *S. Afr. J. Wildl. Res.* **43,** 91–102.

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