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ORIGINAL ARTICLE

Seed dispersal of Madagascar's iconic baobab species, *Adansonia grandidieri*

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Abstract

Certain plant species have traits adapted for seed dispersal by megafauna, which may be absent in their current ranges. Characterizing the dispersal mechanism of such plant species can provide insights about their population dynamics and regeneration. We investigated the effectiveness of the extant fauna as seed dispersers of the Malagasy baobab, *Adansonia grandidieri*, which have megafaunal dispersal traits. We documented the animal species that interact with its fruits and seeds in the canopy and on the ground through direct observations, camera trapping, opportunistic search of feces with seeds, and dispersal experiments. We also estimated seed fate using a model parameterized with data obtained through experiments on seed removal and seed germination under and away from adult *A. grandidieri* trees. Further, we examined the impacts of seed dispersal in mitigating herbivore pressures on *A. grandidieri* seedling through an exclosure experiment. We did not find animals interacting with fruits in the canopy. However, we observed a native rodent species, *Eliurus myoxinus*, handling fruits/seeds on the ground, and found seeds in bush pig feces. Also, while the rates of germination for the dispersed *A. grandidieri* seeds were low, their probability of producing viable seedlings was higher than when the seeds stayed under adult trees. We also found that the seedlings of *A. grandidieri* had a high probability of surviving even when herbivores were present. Overall, our results provide insights into the regeneration of *A. grandidieri* and suggest that some extant local ground-dwelling fauna can provide seed dispersal services to this species.

Abstract in Malagasy is available with online material.

KEYWORDS

large-bodied animals, megafaunal plants, rodents, seedling survival, tropical dry forest

Seheno Andriantsaralaza and O. H. Razafindratsima shared equal contribution.

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1 | INTRODUCTION

As sessile organisms, plants rely on biotic or abiotic vectors to carry their seeds, enabling them to reach and establish locations away from the parent plant (Howe & Smallwood, 1982; Nathan et al., 2008). Seed dispersal is indeed a vital process in a plant life cycle, influencing plant regeneration and species survival (Howe & Miriti, 2004), because it allows seeds and seedlings to escape the density-dependent mortality near parent plants and reduce competition among offspring (Janzen, 1970). For plant communities, seed dispersal sets the stage for certain ecological processes, such as migration and competition, that are critical for community dynamics, species coexistence, and the maintenance of biodiversity (Bascompte & Jordano, 2007; Levin et al., 2003). Thus, elucidating the mechanisms by which seed dispersal operates as well as its outcomes can have significant implications in conservation and restoration efforts.

In tropical tree communities, up to 90% of plant species rely on animals to disperse their seeds (zoochory) (Jordano, 2000), having characteristics that confer rewards for the animals that feed on their fruits and then disperse their seeds (Herrera, 2002). A plant's fruiting characteristics can often indicate a dispersal syndrome, as its fruits are best suited (through their defensive or rewarding traits) to consumption by a particular suite of frugivores. One compelling puzzle in the study of seed dispersal concerns plant species with a given seed dispersal syndrome that exists in ecosystems appearing to lack complementary frugivores. This is, for instance, the case of plant species that have fruit and seed traits adapted for seed dispersal by the largest frugivores (defined here as “megafauna”, weighing between 100 and 1000 kg; Hansen & Galetti, 2009; Moleon et al., 2020). Such traits include overbuilt design (i.e., large fruit mass and size) and fruits with hard epicarp (Guimarães et al., 2008; Hansen et al., 2008; McConkey et al., 2022). Most of megafauna went extinct at the end of the Pleistocene and some of them disappeared around 350 years BP (Galetti et al., 2018; Hansen & Galetti, 2009; Janzen & Martin, 1982). Yet, some plant species with megafaunal seed dispersal traits still persist even though their dispersers are extinct (Bunney, 2014; Cui et al., 2023; McConkey et al., 2022; Puc-Sánchez et al., 2023). This persistence hints at the existence of unidentified dispersal mechanisms that have supported species survival over time. Resolving these mechanisms may help us better understand the factors contributing to species persistence and inform our assessment of future forest health in the face of ongoing global defaunation.

There are generally multiple dispersal mechanisms at play in tropical forest ecosystems, providing complementary or overlapping services to plant communities. Some animals play the role of primary seed dispersers (i.e., removing fruits and seeds from the parent plants), while others, such as ground-dwelling mammals and ants, can act as secondary seed dispersers (i.e., moving fruits/seeds from the ground after primary dispersal or dispersal by gravity) (Vander Wall et al., 2005). For some plant species, both primary

and secondary seed dispersal are needed for reproduction (Culot et al., 2018; Passos & Oliveira, 2002). While plant species with megafaunal syndromes may be mainly dispersed by the largest frugivores, it is likely that a combination of dispersal mechanisms is at play. Seed dispersal by smaller-bodied animals that may be able to move large seeds without ingesting them could also have occurred as complementary or redundant mechanisms along with megafaunal dispersal (McConkey et al., 2018). For example, some native rodents (Jansen et al., 2012; Puc-Sánchez et al., 2023), bird species (Stevenson et al., 2021; Tella et al., 2020), and carnivores (Cui et al., 2023; Muñoz-Concha et al., 2022) were found to be capable of dispersing the seeds of some plant species that were dispersed by extinct megafauna. Introduced species, such as feral pigs and cattle, can also contribute to the dispersal of megafauna-dispersed plant species if they are functionally similar to the extinct seed dispersers (Donatti et al., 2007; Pedrosa et al., 2019). Plant domestication by humans has also allowed for the persistence of certain megafauna-dependent plant species (Spengler, 2020; Van Zonneveld et al., 2018).

The Malagasy baobab, *Adansonia grandidieri* Baillon, is an example of a plant species with megafaunal dispersal syndrome that is still present, although its fruit trait does not appear to match the traits of extant disperser assemblages in Madagascar (Albert-Daviaud et al., 2020; Andriantsaralaza et al., 2010; Baum, 1995). This large deciduous species, which is one of the six endemic baobab species in Madagascar, produces large hard- and thick-husked fleshy fruit pods (up to 120 mm in diameter and 800 g in weight). This species is distributed across Madagascar's southwestern dry forest (Figure 1), can reach up to 25 m in height and 3 m in diameter when mature (Baum, 1995; Wan et al., 2021) and each fruit pod contains an average of 60 seeds (12–14 mm length × 10–12 mm width) enveloped in a white, fibrous, and powdery pulp. According to the categorization of megafaunal fruits by Guimarães et al. (2008), baobab fruits can be classed as megafaunal fruit of Type II, defined as fleshy overbuilt fruits (>100 mm in diameter) with numerous small seeds with <20 mm in diameter. This species is speculated to be dispersed by extinct megafaunal communities, such as giant lemurs (*Archaeolemur majori*), tortoises (*Aldabrachelys grandidieri*), and elephant birds (*Aepyornis* spp.), which occurred within its distribution ranges (Andriantsaralaza et al., 2010; Baum, 1995; Wickens, 2008). These giant species may have been able to break the hard-husked baobab fruits given their large stature (Wickens, 2008). For instance, giant lemurs, such as *Archaeolemur majori*, had thick enamel, large and broad upper incisors, and unique premolars that formed long shearing blades that may have allowed them to open hard-husked fruits (Godfrey et al., 2005). Also, a feeding experiment performed on *Aldabrachelys gigantea*, a species closely related to the extinct Malagasy giant tortoise, demonstrated their ability to break the hard husk of the baobab fruits and then defecate a large proportion of intact and viable seeds (Andriantsaralaza et al., 2014). The consequences of the extinction of these large animals on the survival and recruitment of *A. grandidieri* remain unknown, although previous studies have reported overall low regeneration of this species (Raveloson & Andriafidison, 2014), which currently

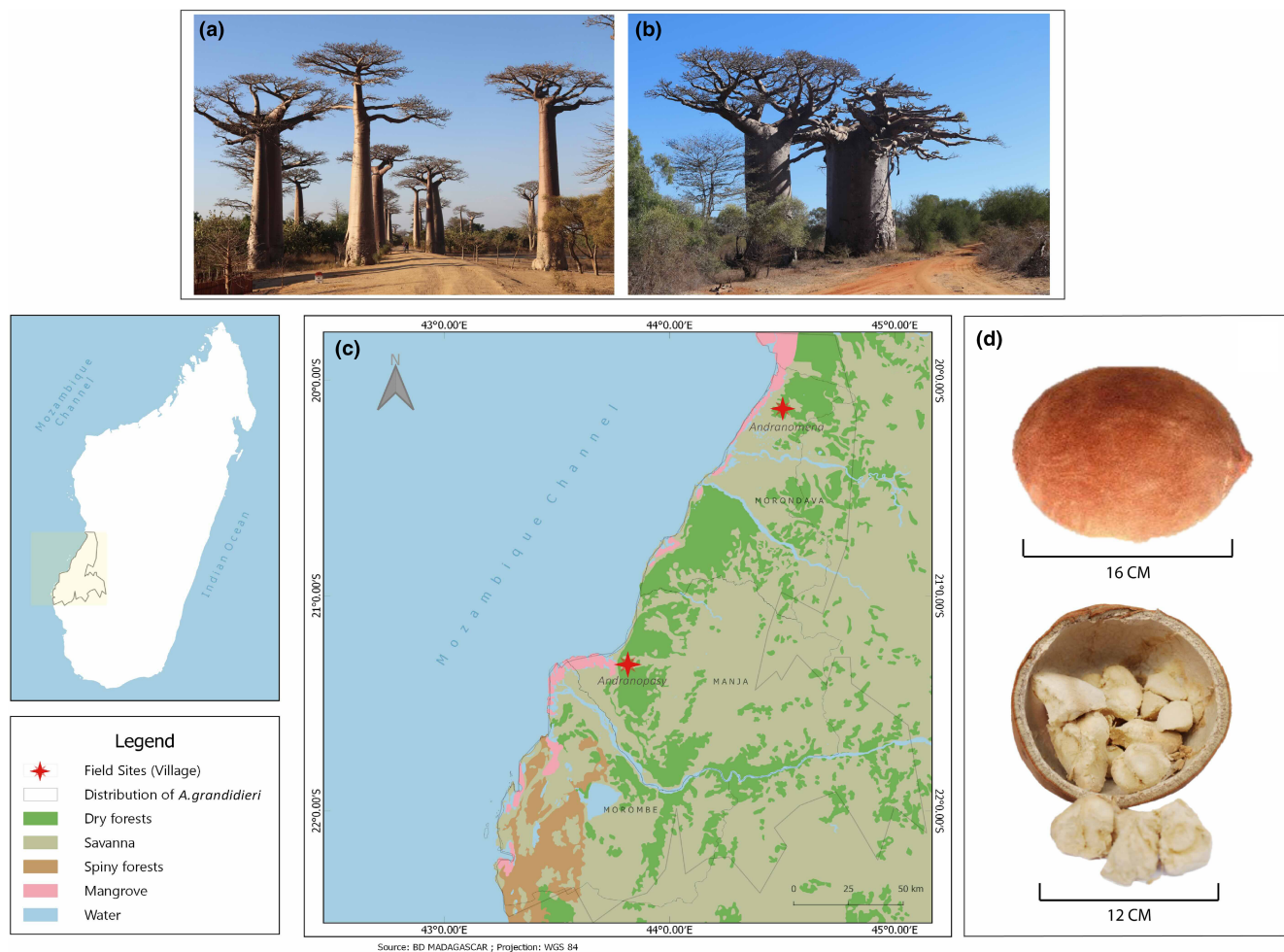


FIGURE 1 (a) The Baobab Avenue in Morondava, showcasing *A. grandidieri* along a main road; (b) *A. grandidieri* in Andranopasy forest; (c) Map of the field sites; (d) *A. grandidieri* fruits and seeds.

places this species in the IUCN Red List as an Endangered species (Ravaomanalina & Razafimanahaka, 2016). In addition to providing shelter and vital resources for animals, such as nectar for bats and insects (Rasoamanana et al., 2015; Razanamaro et al., 2015; Ryckewaert et al., 2011), *A. grandidieri* also has socioeconomic importance to local communities. It is a source of revenue for many households as a tourist attraction, a food source (edible fruits), raw materials for household items (e.g., rope), and beauty products as seeds are used to extract beneficial oil (Andriafidison et al., 2019; Baum, 1995; Marie et al., 2009). There is currently no study that investigated the impact of fruit harvesting on the regeneration of *A. grandidieri*. However, the overexploitation of its fruits and seeds for international trade led to its inscription in the CITES- Appendix II (Ravaomanalina & Razafimanahaka, 2016), which is aimed to control its trade in the international market, ensuring its continued survival. Despite this measure, this species remains at risk because of low natural regeneration in their habitats. One important step in informing recovery efforts may be to assess which dispersal mechanisms, if any, provide viable seed movement.

There are multiple taxa that might act seed dispersers for *A. grandidieri* across its current range. These include native large-sized

lemurs, native rodents, and introduced bush pigs. Previous studies have reported that several lemur species, namely *Eulemur rufifrons*, *Propithecus verreauxi*, *Lepilemur ruficaudatus*, *Phaner furcifer*, and *E. coronatus* were able to break and consume both ripe and unripe fruits of *A. rubrostipa* and *A. suarezensis*, which have similar thick husks as the fruits of *A. grandidieri* (DuPuy, 1996; Ganzhorn et al., 1999; Wickens, 2008). However, there is currently no evidence that any existing lemur species play a role in the seed dispersal of *A. grandidieri*. Native rodents, such as those in the genus *Eliurus* and *Nesomys*, could act as secondary dispersers of large-seeded plants in Madagascar (Razafindratsima, 2017). Although there is currently no evidence of any rodents handling baobab fruits or eating baobab seeds, we suspect these rodents might be attracted to the fleshy pulp surrounding the baobab seeds and then cache seeds in safe locations, which will give them an opportunity to germinate and grow. Also, with their strong upper incisors (Goodman & Soarimalala, 2011), they might be able to make holes in baobab fruit pods and access the seeds. In addition, the introduced African bush pig, *Potamochoerus larvatus*, which occurs in the same range as *A. grandidieri*, could act as a potential seed disperser for this plant species. Previous field observations reported that bush pigs consumed the fruits of *A. grandidieri*

(Wickens & Lowe, 2008) and can disperse certain native and non-native plant species in Madagascar (Ganzhorn et al., 1999) and other tropical systems (Hikel et al., 2023).

In the present study, we aimed to assess the presence and impact of these dispersal mechanisms that may enable the persistence of *Adansonia grandidieri*. We address this by (1) documenting the arboreal and terrestrial animal species that interact with its fruits and seeds in the canopy and on the ground, (2) analyzing their seed dispersal effectiveness in terms of seed germination and seedling survival using a simulation of seed fate model, parameterized with empirical data obtained through germination experiments, and (3) examined the impacts of seed dispersal in mitigating herbivore pressures on *A. grandidieri* seedlings through an enclosure experiment.

2 | METHODS

2.1 | Study period and site characteristics

Adansonia grandidieri usually produces fruits from November to mid-January with a peak in November, based on phenological monitoring of 50 trees for 15 years (Razanamaro, unpubl. data). Therefore, we conducted this study for 4 months from the peak fruiting season in November 2021 to February 2022, which allowed observations of animal interactions with the fruits and an additional period to monitor seed fate.

We collected data in two sites of the dry deciduous forests in the Menabe region in the western part of Madagascar (Figure 1): Andranomena Special Reserve (20°9'57.93"S; 44°30'32.70" E) and Andranopasy Forest (21°19'22.23"S; 43°50'16.12" E). Andranopasy forest is part of the protected area of the Complexe Mangoky Ihotry. Both sites are characterized by a subarid climate with an annual average precipitation of 887 mm and 617 mm and an average daily temperature of 18°C and 30°C, respectively (Goodman et al., 2018).

We conducted an initial survey of the vegetation in two 1-ha (100×100 m) plots per site to describe the vegetation characteristics of the site. We found that *A. grandidieri* represents only 1% of the trees with a Diameter at Breast Height (DBH) >2.5 cm (Table S1). Among the adult trees, *A. grandidieri* trees are the tallest with an average estimated height of 16 m ± 1.26 m (N = 8 adult trees) and 15.5 m ± 0.7 m (N = 7 adult trees) in Andranomena and Andranopasy, respectively (Table S1). We also conducted a survey of the animal community along 10 linear transects and through live-capture using 44 Sherman traps and 11 Tomahawk traps (see Appendix S1 for further details on the survey methodology) and found three small-bodied lemur species (body mass range of 30–600 g; Goodman et al., 2018), three rodent species, one tenrec hedgehog species, and 56 bird species (Tables S2 and S3). The two sites slightly varied, with some bird species being more abundant in one site than the other (Figure S1) and native rodent species were only found in Andranomena (Figure S2). It is important to note that the large-bodied lemur species, *Eulemur rufifrons* (body mass ~2.1 kg; Taylor & Schwitzer, 2012) and fruit bats, *Pteropus rufus* (body size 0.39 kg;

Goodman, 2011) known as important seed dispersers in several ecosystems in Madagascar (Razafindratsima et al., 2022), might be present in these sites given their current geographic distributions (Andriafidison et al., 2006; Goodman, 2011). However, we did not encounter any individual of these species during our surveys. Also, there is currently no record of these species consuming the fruits of *A. grandidieri* (reviews in Steffens, 2020 for lemurs and Aziz et al., 2021 for bats). The now-extinct potential megafaunal seed dispersers that may have occurred in this region were giant lemurs (*Archaeolemur majori*), giant tortoises (*Aldabrachelys grandidieri*), and the Elephant-birds (*Aepyornis* sp) (Goodman & Jungers, 2014).

2.2 | Observations of species interactions

To document the arboreal and terrestrial animal species that interact with the fruits and seeds of *A. grandidieri* in the canopy and on the ground, we conducted direct observations of interactions in the canopy, dispersal experiments on the ground, and opportunistic search of animal feces with *A. grandidieri* seeds.

We observed what animal species interact with fruits in the canopy of 15 fruiting *A. grandidieri* trees: five in Andranomena and 10 in Andranopasy. Sampling size differed because of a lower density of fruiting *A. grandidieri* in Andranomena during our study period. The trees were at least 100 m apart. Following previous studies of plant-frugivore interactions (e.g., Bollen, 2003; Ramos-Robles et al., 2018; Raelinjanakolona et al., 2023), we monitored the vertebrates visiting the fruiting branches of *A. grandidieri* trees from 0600 h to 1100 h and then from 1400 h to 1700 h for 3 days, for a total of 36 nonconsecutive hours per tree. For any animal visitor, we recorded the species and the general behavior of the individuals towards the fruits/seeds. If the individual was observed feeding on the fruits, we noted its fruit-handling behavior to determine its potential ability to disperse seeds—that is, opening the fruit or feeding on an already opened fruit, eating the powdery pulp of the fruit only or eating the seeds with/without the pulp (Bollen, 2003; Raelinjanakolona et al., 2023).

For the dispersal experiments on the ground, we set up marked fruits and seeds on the ground under fruiting trees of *A. grandidieri* and observed the animals that interacted with them using camera traps. We first selected 20 fruiting trees of *A. grandidieri* that were 100 m apart and located outside the vegetation plots in each site to conduct these experiments. We collected 15 ripe fruits on the ground from each tree (300 fruits in total). We used these fruits to set up the following treatments of each selected fruiting tree: (1) “fruits”, in which the entire pods without manipulation (10 fruits); (2) “seeds with pulp”, in which seeds were extracted manually from the fruits, but the pulp left enveloping each seed (10 seeds). This treatment mimics seeds that may fall out of the fruits if they break when hitting the ground, which may be attractive to ground-dwelling animals. Following previous methods (e.g., Forget, 1990; Razafindratsima, 2017; Wenny, 2000), we tied on each propagule (fruit/seed) a 75 cm sewing thread with a piece of flagging tape marked with a unique identification number

at the end. We set these marked fruits and seeds next to each other on the ground under the selected *A. grandidieri* trees. We then monitored them every 2 days for a total of 72 days to get detailed information on fruit/seed removal.

We deployed digital camera traps (Bushnell Trophy 119,876 & 119,837 and Campark T40) in front of 12 trees at a time (one camera trap per tree; six traps per site) and alternated their locations every 7 days to cover all the trees where the marked fruits and seeds were set. We placed them at a height of 40–60 cm above the ground, pointing towards the marked fruits and seeds. We set the camera traps to record a 30-s video when triggered by an animal passing by. In total, the cameras were active for 50 nights/days. We identified the animal species captured in the videos based on their morphological characteristics, as described and pictured in Goodman and Soarimalala (2011). We determined the potential ability of the identified animal species to disperse the seeds of *A. grandidieri* based on their observed behavior in these videos. When a propagule was missing from their initial setup, we searched for it within a 25 m radius by looking for the conspicuous tag (Forget, 1990; Wenny, 2000). We then measured the distance from the initial location to where the propagule was recovered (i.e., dispersal distance) and recorded how it was deposited (buried in the soil, placed on, or under leaf litter). We considered any seed that was moved at >10 cm from its initial location as removed. If a propagule could not be found or was totally destroyed with only a small piece left, we replaced it with another marked and intact propagule, and monitored the new individual independently from the previous propagule in the following surveys.

Finally, we conducted an opportunistic search of animal feces on the ground whenever we went into the forest to conduct any of the activities mentioned above. For each encountered feces, we examined the content to determine the presence of *A. grandidieri* seeds and attempted to identify the animal species based on our knowledge of the fauna in the area.

2.3 | Seed dispersal effectiveness

To assess the potential seed dispersal effectiveness of the available fauna in terms of seed germination and seedling survival, we parameterized a seed fate model using empirical data. We ran the model under two scenarios: (a) seeds dispersed away after falling on the ground (dispersal away from parents) and (b) seeds falling and staying under the parent trees (i.e., not dispersed away from parents). We considered only seeds that had already fallen on the ground in this study because we did not find any animals interacting with the fruits in the canopy (see results). The models followed a simple pathway (Figure 2) and required the following parameters: seed crop size that would fall on the ground to represent the quantitative component of seed dispersal effectiveness, probabilities of seed removal and predation, and probabilities of seed germination and seedling survival.

We calculated seed crop size, defined here as the number of seeds produced per *A. grandidieri* tree, by multiplying the number of fruits produced per tree by the average number of seeds per fruit

(Table S4). To estimate fruit crop production in the field, we selected a total of 78 *A. grandidieri* adult trees (25 in Andranomena and 53 in Andranopasy), then counted the number of ripe fruits in the canopy and on the ground within at least 2 m in radius from the trunk, which corresponds to the surface covered by the tree crown, and the number of seeds inside three ripe fruits per tree.

We determined the probability of seeds being removed or predated on the ground using data from another set of dispersal experiments. We manually extracted seeds from ripe fruits collected on the ground and removed the pulp from the seeds. We focused on seeds without pulp to address this specific question to have the same type of treatment as with the seed germination experiment described below. Similar to the dispersal experiments described above, we marked each seed, put a set of 10 marked seeds next to each other on the ground under each *A. grandidieri* tree in Andranopasy (20 trees), and monitored them every 2 days for a total of 72 days. We also searched for any removed seeds within a 25 m radius around their initial locations. We defined seed predation as any visible sign of consumption, such as partially eaten or totally consumed with pieces remaining. We calculated the probability of seed removal from under the parent tree (p_r) as the average proportion of seeds that were removed relative to the total number of seeds set up under each tree. We also calculated following predation probabilities from the data of this experiment: (1) probability of predation for the seeds that were dispersed away from the parent tree (p_{p1}) as the average proportion of the seeds that were removed from initial location and then found predated relative to the total number of seeds removed; and (2) probability of predation for those that were not dispersed (p_{p2}), calculated as the average proportion of seeds that were predated relative to the total number of seeds that were still present at the initial locations.

We determined the probabilities of seed germination and short-term seedling survival using data from experiments conducted at both sites. We extracted seeds without pulp from 40 ripe fruits collected on the ground under the crown of *A. grandidieri* trees at each site. We set up two experimental plots in each site: (1) at a distance of 50 m away from *A. grandidieri* trees to represent the condition of seeds that are dispersed; and (2) under an *A. grandidieri* tree to represent the state of not being dispersed. We replicated this experimental setup 10 times. We placed a set of 10 seeds next to each other on the ground in each plot for a total of 200 seeds per site (10 seeds $\times$ 2 plots $\times$ 10 replications). We marked each seed the same way as with the dispersal experiment described above. We monitored the plots weekly for 42 days. At this monitoring, we checked each seed for germination (i.e., emergence of a radicle) and each seedling for survival (i.e., leaves and stems remained green). According to Fenner (1987), a seedling comes into being when a seed germinates. Using data from these monitoring, we calculated the following probabilities: (1) probability of seed germination as the proportion of seeds that germinated relative to the initial number of seeds set up in the plots (p_{g1} and p_{g2} for seeds dispersed and not dispersed, respectively); and (2) probability of short-term seedling survival as the proportion of

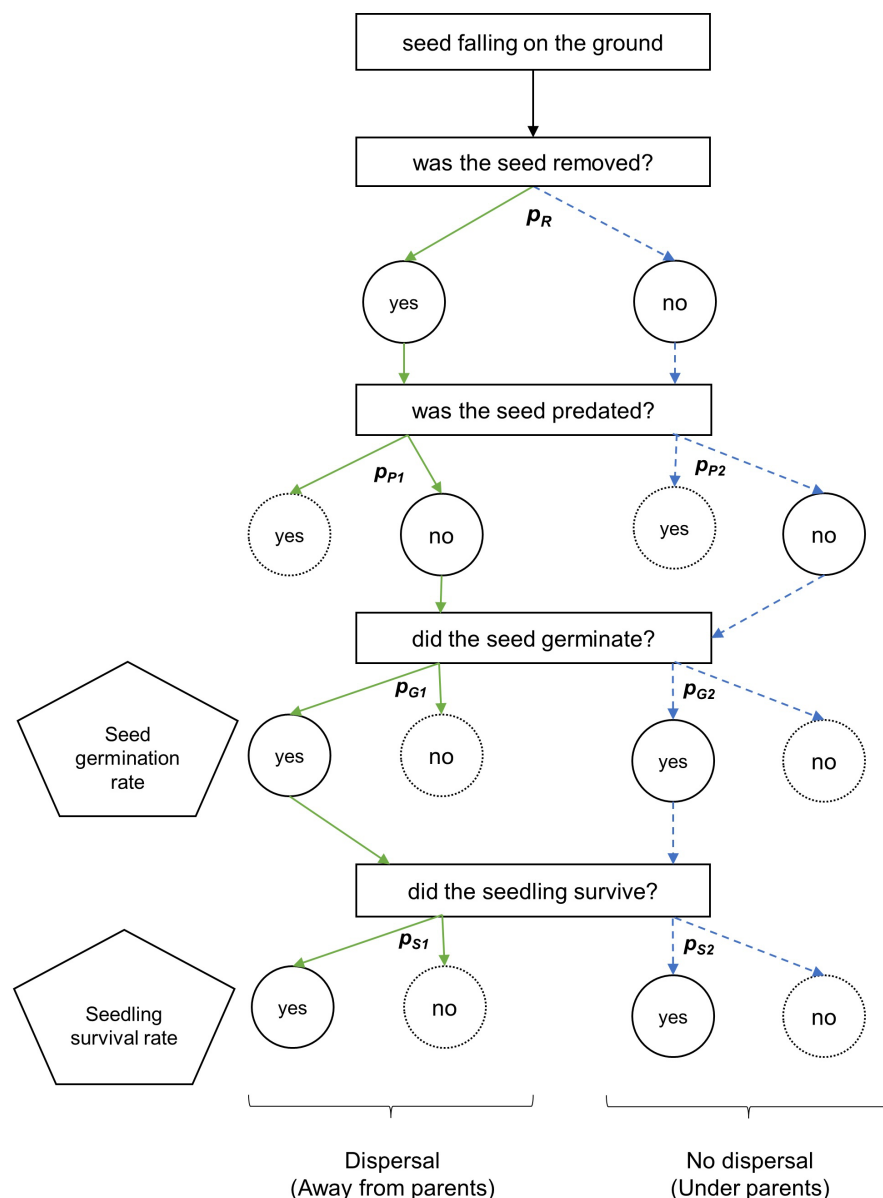


FIGURE 2 Pathway of our seed fate model of *Adansonia grandidieri* with the two scenarios. The green full arrow indicates the steps for the seeds removed from the initial location, while the blue dashed arrow indicates seeds that were not dispersed. p_R , the probability of seed removal; p_P , probabilities of seed predation; p_G , probabilities of seed germination; p_S , probabilities of seedling survival. The outputs are seed germination rates and seedling survival rates.

seedlings that stay alive at the end of the experiment relative to the number of seeds that germinated (p_{s1} and p_{s2}).

We ran the simulation models 1000 times to compute the germination and survival rates under each of the two scenarios (dispersal vs. no dispersal). The rates consisted of the number of seeds that germinated divided by the number of seeds falling on the ground (germination rate; p_g) and the number of seedlings that survived divided by the number of seeds that germinated (survival rate; p_s). We also calculated an overall cumulative survival rate, which represents the probability of the seeds to produce established seedlings (i.e., alive at the end of the experiment) as p_g multiplied by p_s .

2.4 | Exclosure experiments

We examined the potential impacts of herbivores that may feed on seedlings (e.g., caterpillars and folivorous ground-dwelling birds)

on the regeneration of *A. grandidieri* through an exclosure experiment. We set up two experimental plots at least 100m from the open experimental plots that were set up away from *A. grandidieri* trees: invertebrate exclosure and vertebrate exclosure. The exclosures consisted of metal wired cages measuring 40×35×35 cm each, with mesh sizes of 1 mm² and 1 cm² to, respectively, prevent invertebrates and vertebrates from interacting with the seeds on the ground. Compared with the outcomes from the open plots without exclosure described above, these data can inform us of the potential of *A. grandidieri* seedlings to survive in the presence of herbivores to infer the potential impacts on their regeneration. We placed 10 seeds without pulp, marked with a unique identification number, in each exclosure, for a total of 200 seeds per site (10 seeds × 2 exclosure types × 10 replications). We also monitored these plots weekly for 42 days to check for germination and for herbivory signs on seedlings (i.e., whether the seedlings were consumed or not).

2.5 | Statistical analysis

We assessed seed dispersal effectiveness based on the results of the seed fate models, by analyzing how the rates of seed germination, seedling survival, and overall cumulative survival obtained from the seed fate models differ between the two scenarios (dispersal vs. no dispersal). To do so, we performed Generalized Linear Models with the scenario as predictor and the rates as dependent variables. Also, we assessed the impacts of animal species on the regeneration of *A.grandidieri* by comparing the survival rates of seedlings in exclosures and those in open areas at different times throughout the experiments. We first performed a survival analysis to determine the probabilities of seedling survival over time using the R-package "survival" (McNair et al., 2012). We then fitted Cox regression models to assess how these probabilities differ between plots in open areas versus the two types of exclosures. All statistical analyses were conducted in R 4.3.2 (R Development Core Team, 2013).

3 | RESULTS

3.1 | Potential seed dispersers of *Adansonia grandidieri*

We found no fruit-eating animals interacting with the fruits in the canopy of *A.grandidieri*. No fruit removal from the canopy was, therefore, observed. On the ground, camera trap images revealed the native western tuft-tailed rat, *Eliurus myoxinus*, handling fruits in our dispersal experiments (Video S1). We recorded four visits by this species during the 50 nights/days that the cameras were active. Also, we found 13 fruits in Andranopasy with bite marks and some seeds removed (Figure 3), suggesting the ability of extant fauna to open the husk of *A.grandidieri* fruits with their teeth. However, we

are unable to determine the animal species that opened these fruits. Although we did not observe all the interactions with the propagules marked for the dispersal experiments, our data revealed removal of propagules away from their initial locations in both sites, especially for the seeds with pulp (Figure 4). The removed seeds were found on the ground and were not cached. We were able to retrieve 36.36% ($n=11$) and 17.49% ($n=589$) of these removed fruits and seeds, respectively, intact at a very short distance (mean=0.57 m, SD=1.44 m; Figure 4; $n=118$ distances recorded). During the opportunistic observations, we found seven bush pig (*Potamochoerus larvatus*) feces that contained the seeds of *A.grandidieri*. No feces from other animal species were found.

3.2 | Seed dispersal effectiveness

Our seed fate models showed that nondispersed seeds had significantly higher germination rates than seeds that were dispersed ($\beta=.44$, $z=408.345$, $p<.0001$; Figure 5a). Conversely, the seedlings from nondispersed seeds had significantly lower survival rates compared to the seedlings of those that were dispersed ($\beta=.551$, $SE=0.001$, $z=747.978$, $p<.001$; Figure 5b). Further, we found that the probability of the seeds to produce established seedlings is significantly lower for the nondispersed seeds than dispersed seeds ($\beta=-.007$, $SE=0.000$, $z=-183.564$, $p<.001$; Figure 5c).

3.3 | Potential impacts of dispersal in mitigating herbivore pressures on seedlings

We found that the seedlings of *A.grandidieri* had a high probability of surviving when herbivores were present. Seedlings in open plots had higher probabilities than those protected by either type of



FIGURE 3 Photos of *Adansonia grandidieri* fruits with bite marks found in Andranopasy. The four photographs showed different fruits with different bite marks.

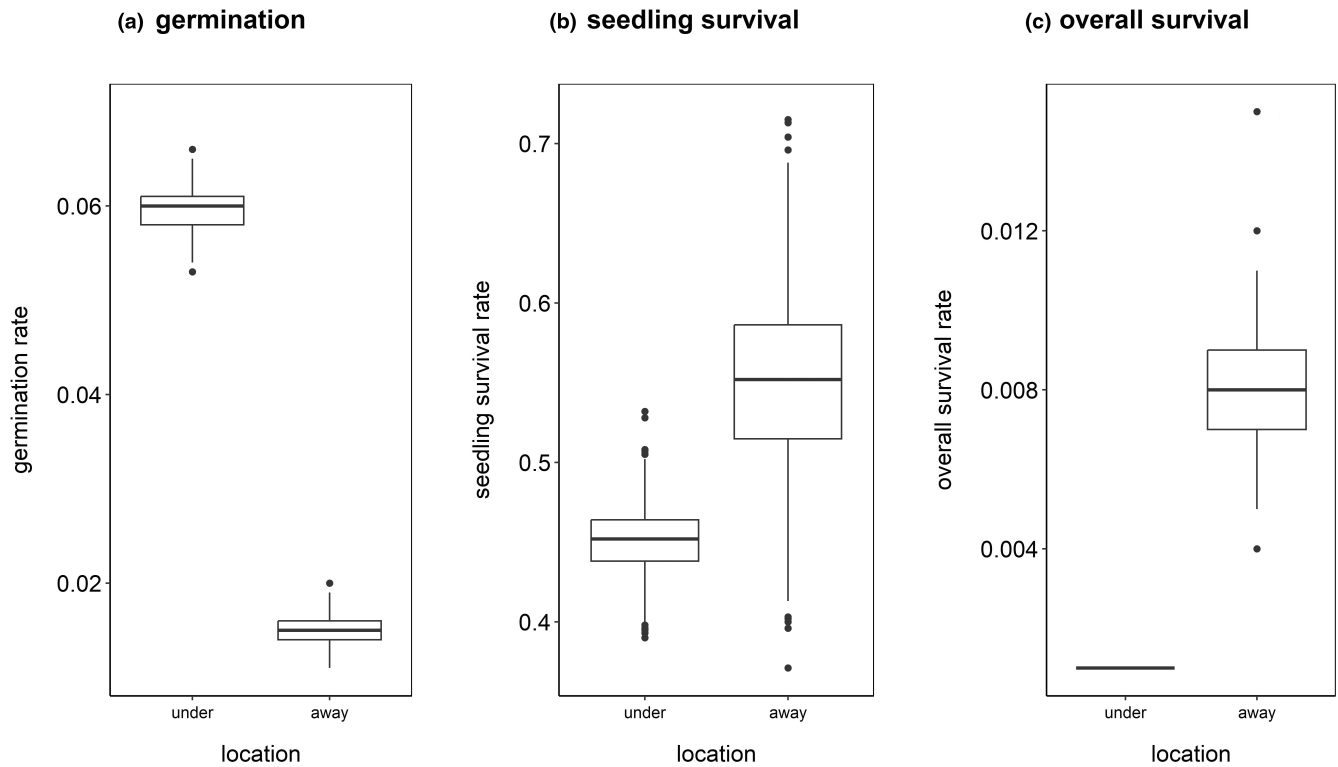


FIGURE 4 Top panel: Removal rates of the different fruits/seeds of *Adansonia grandidieri* in each site. Bottom panel: Dispersal distances of fruits and seeds with pulp removed from the initial locations.

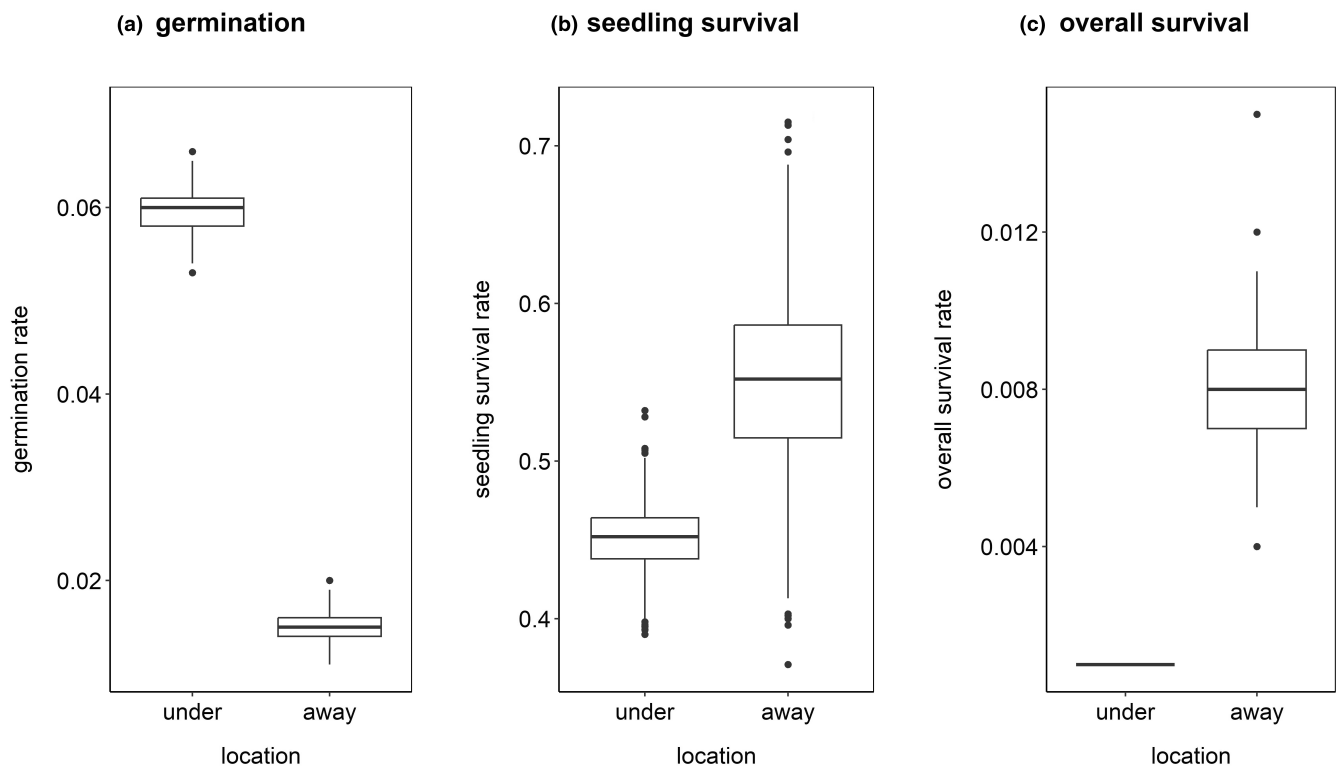


FIGURE 5 Outputs from the seed fate models: Rates of seed germination (a), seedling survival (b), and overall survival (c) for seeds under and away from *Adansonia grandidieri* trees.

exclosures (invertebrate exclosure, $\beta = -1.34$, $p < .001$; vertebrate exclosure: $\beta = -1.68$, $p < .001$; Figure 6).

4 | DISCUSSION

This study adds to the limited knowledge regarding the seed dispersal of Malagasy baobabs, particularly in the case of *A.grandidieri*. This species, along with other plant species with megafaunal dispersal syndromes in Madagascar, is often assumed to have no extant seed dispersers and considered an “orphan” (Albert-Daviaud et al., 2020; Andriantsaralaza et al., 2010; Federman et al., 2016), which may lead to a low regeneration and recruitment of the population and further difficulty in establishing in their habitats (Vieilledent et al., 2013; Wickens, 2008). However, while limited in the duration of baobab-animal observations, the findings of this project present a different story to the dispersal of *A.grandidieri*. The presence of bite marks on *A.grandidieri* fruits, which we speculate as from rodents, and the presence of *A.grandidieri* seeds in the feces of the introduced bush pig species, *P.larvatus*, suggest that some extant animals are capable of opening the hard-husked fruits and disperse the seeds. This species should, therefore, not be considered an orphan.

The observed interaction of the native rodent species, *Eliurus myoxinus*, with the seeds of *A.grandidieri* suggest that this species may be able to disperse the seeds of *A.grandidieri*. However, further study is needed to determine its effectiveness in the seed dispersal of *A.grandidieri*. Another rodent species in the genus *Eliurus* has also been found to participate in the secondary dispersal of seeds in Malagasy forests (Goodman, 1994; Goodman & Sterling, 1996; Razafindratsima, 2017). Although these granivorous rodent species may eat a large proportion of seeds, they may still perform critical seed dispersal functions as they may be able to take seeds to locations that are suitable for their germination and survival (Mittelman et al., 2020; Moore & Vander Wall, 2015). Indeed, if they partially consume the seeds, it can be nonlethal and still allow for successful

germination (Vallejo-Marín et al., 2006). Moreover, like other granivorous rodents, such as agoutis (Mittelman et al., 2020), these rodent species might be attracted by the nutritious pulp inside the baobab fruits. Such an attraction may explain why some fruits have been found with bite marks and seeds taken out from them. Rodents can also disperse seeds over greater distances by caching and re-caching them at different times. This has been demonstrated by Jansen et al. (2012), and it may play an important role in the Malagasy dry forests, although it requires further study.

The dispersal of seeds by the introduced bush pigs, *P.larvatus*, has also been found to have positive outcomes on seed germination in other systems (Hikel et al., 2023). Thus, the presence of *A.grandidieri* seeds in the feces of *P.larvatus* we found in this study suggests newly developed interactions with introduced dispersers could replace the functional gap left by the extinction of the megafauna that may have dispersed *A.grandidieri* in the past. Furthermore, in a simple germination test, we found that the seeds defecated by *P.larvatus* had a similar germination rate as those without pulp (Andriantsaralaza et al., unpubl. data). Domestic and feral pigs have also been recognized as effective seed dispersers of large-seeded plants presumably dispersed by the extinct megafauna in Central American lowland forests (Blanco et al., 2019; Janzen & Martin, 1982) and New Zealand (O'Connor & Kelly, 2012). However, it is worth noting that previous experiments conducted with captive bush pigs in Madagascar showed they extensively chewed and digested 92% of baobab seeds offered to them (Andriantsaralaza, unpubl. data). Finally, while we did not observe any animal interacting with the fruits in the canopy, it is possible that large-bodied arboreal lemur species in this region, such as *E.rufifrons* and *Propithecus verreauxi*, may still be able to disperse the seeds of *A.grandidieri*, if they can open the fruits. Indeed, a recent study in the same region observed one lemur species (*Propithecus verreauxi*) consuming the unripe fruits of *A.rubrostipa* (Ratovonjanahary, comm.pers.).

While we could not fully assess the seed dispersal effectiveness of each observed animal species in this study, our seed fate model

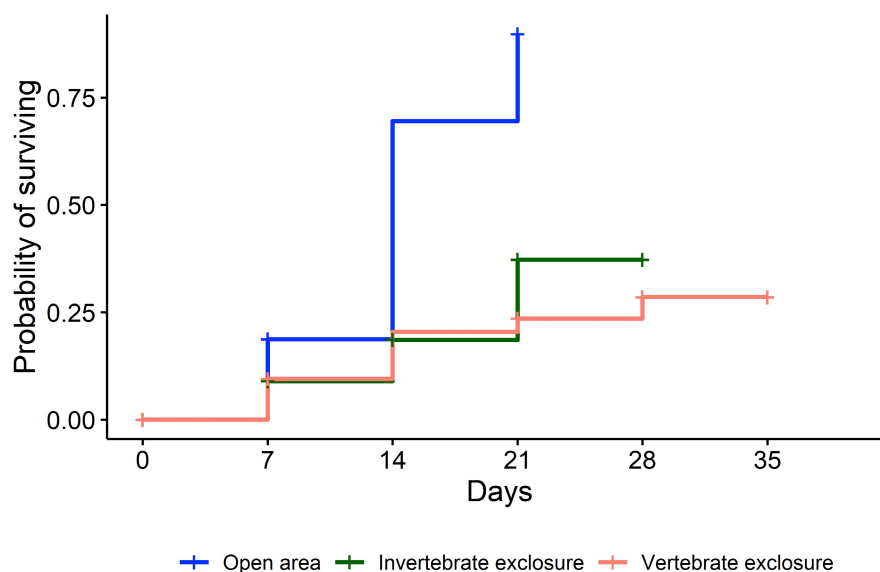


FIGURE 6 Survival probabilities of *A.grandidieri* seedlings through the exclosure experiment: Open areas (blue line), invertebrate exclosure (green line), and vertebrate exclosures (red line).

provides an initial picture of the potential effectiveness of *A. grandidieri* dispersal. The model showed a higher seed germination probability underneath the parent trees than those away from the parents, suggesting that the location under the crown of baobab trees is suitable for seed germination, as suggested by previous studies (DuPuy, 1996). This also suggests that simply being removed from the fruit and the pulp gives chances for seeds to germinate. Indeed, the presence of pulp surrounding seeds has been shown to inhibit germination (Robertson et al., 2006). In the case of *Adansonia grandidieri*, when the pulp is manually extracted from seeds, the germination rate can be up to 80% (Razanameharizaka et al., 2006). However, as the model also showed, being away from the parent trees can lead to an increased probability of seedling recruitment, which corroborates other findings of seed dispersal outcomes (Beckman & Rogers, 2013; Razafindratsima & Dunham, 2015; Wenny, 2001). By being dispersed away, seeds can escape density-dependent mortality near parent plants and reach favorable microsites for establishment (Connell, 1971; Howe & Smallwood, 1982; Janzen, 1970). These advantages of seed dispersal are particularly important for reproductive success and various life stages (Howe & Miriti, 2004). In the case of *A. grandidieri*, seedlings and juvenile stages are exceptionally rare in forests (Andriantsaralaza et al., 2016), which could be attributed to limited seed dispersal. For long-lived trees, such as the baobabs with lifespan of several hundreds of years, low seedling abundance may be typical as has been suggested for *Adansonia digitata* in Africa mainland (Venter & Witkowski, 2013). However, the rarity of animal seed dispersers, combined with habitat loss, and their vulnerability to climate change may affect the regeneration of Malagasy baobab species over time (Tagliari et al., 2021; Vieilledent et al., 2013).

We observed a higher seedling survival rate in open areas compared to both vertebrate and invertebrate exclosures, suggesting a low predation of natural enemies on baobab seedlings. Indeed, herbivorous insects in tropical forests are often attracted by young foliage with nutrient-rich resources (Basset, 1999) such that it might be possible that baobab seedlings with only 42 days of life stage are not attractive for such insect herbivores. Also, because baobab trees grow slowly, their mature leaves appear late during the seedling's growth (Randriamanana et al., 2012). Baobab seedlings might be unpalatable for insect pathogens which may explain the high survival of seedlings in open areas. During the period of our faunal community surveys in the two sites, we found that ground-dwelling vertebrate herbivores were not common, this may also explain the low predation of seedlings. This is in contrast to other ecosystems and baobab species, where herbivores such as elephants and livestock have been shown to heavily predate African baobab seedlings (Venter & Witkowski, 2013). The absence of those large herbivores could explain the high seedling survival rate in open areas. It also might be possible the difference of light that reach the opened versus meshed areas could explain the higher seedling survival of *A. grandidieri* seedlings in the open areas as the mesh may cast additional shade on the seedlings. The need for light availability to increase seedling survival has been reported for other baobab species, such as *A. rubrostipa* (Metcalf et al., 2007).

In summary, our study provides valuable insights into mechanisms enabling the survival of Malagasy baobabs, including interactions with native species and novel interactions with introduced species. It also provides multiple avenues of further research to resolve baobab seed dispersal, the redundancy or complementarity of different baobab seed dispersal mechanisms, and aspects of the habitats that may enable or prevent these interactions. Considering the ongoing habitat loss and defaunation worldwide, understanding the seed dispersal mechanisms of plant species with dispersal syndrome associated with extinct species can contribute to proposing conservation strategies to ensure their persistence.

AUTHOR CONTRIBUTIONS

Seheno Andriantsaralaza was involved in conceptualization, methodology, resources, data curation, validation, visualization, writing—original draft, writing—review and editing, supervision, project administration, and funding acquisition. Onja Razafindratsima was involved in conceptualization, methodology, data curation, validation, formal analysis, visualization, writing—original draft, writing—review and editing, supervision, project administration, and funding acquisition. Onja Razanamaro was involved in conceptualization, methodology, writing—review and editing, supervision, project administration, and funding acquisition. Veronarindra Ramananjato was involved in methodology, data curation, validation, formal analysis, visualization, writing—original draft, writing—review and editing. Finaritra Randimbarison was involved in methodology, investigation, data curation, validation, formal analysis, visualization, writing—review and editing, and supervision. Nancia Raoelinjanakolona was involved in methodology, investigation, data curation, validation, writing—review and editing, and supervision. Tanjoniaina Rabarijaonina and Nirintsoa Raharinomena were involved in methodology, investigation, data curation, validation, formal analysis, writing—original draft, and writing—review and editing. Noelle Hobimalala was involved in methodology, investigation, data curation, and visualization. Rindra Nantenaina was involved in methodology, investigation, data curation, validation, and writing—review and editing. Jadelys Tonos was involved in formal analysis, visualization, and writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare that this research is original and the authors do not have any competing or conflict of interest. In addition, the work was done in the absence of any commercial or financial relationships that could be considered a potential conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository: [10.5061/dryad.mkkwh718k](https://doi.org/10.5061/dryad.mkkwh718k)

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