

Pre-Dispersal Seed Predation by *Cryptorhynchus* sp. Limits Seed Germination in *Adansonia perrieri* Baobab: Implications for Seed Sourcing and Reintroduction Programs

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Abstract

Adansonia perrieri is the only baobab species currently classified as Critically Endangered, and its populations are characterized by limited natural regeneration. Reinforcing remaining populations through reintroduction and ecological restoration requires a reliable supply of high-quality seeds. However, seed availability may be constrained by pre-

dispersal seed predation. This study evaluated variation in seed production and the impact of pre-dispersal seed predation by *Cryptorhynchus* sp. on seed quantity and germination in *A. perrieri* across three regions of northern Madagascar: Loky-Manambato, Plateau d'Ankarana, and Montagne d'Ambre. A total of 351 fruits were collected, and intact and damaged seeds were counted for each fruit. Both seed categories were subsequently subjected to germination tests. Infestation rates were substantially higher in Plateau d'Ankarana and Loky-Manambato, with 83.8 % and 74.4 % of fruits infested, respectively, compared with 4.8 % in Montagne d'Ambre. Damaged seeds failed to germinate, indicating a strong negative effect of insect infestation on seed viability. Furthermore, the proportion of intact seeds decreased to less than 12 % in fruits containing more than five *Cryptorhynchus* sp. individuals. These findings suggest that pre-dispersal seed predation by *Cryptorhynchus* sp. may contribute to reduced reproductive success and limited natural regeneration of *A. perrieri*. Increasing fruit-harvesting efforts in regions with high infestation may help ensure sufficient seed availability while maintaining the geographic and genetic diversity of seed sources for future reintroduction programs.

Keywords: *Adansonia perrieri*, insect, seed predation, threatened plant, Madagascar

Introduction

The success of ecological restoration and plant reintroduction programs for rare and threatened plant species depends largely on the availability of sufficient quantities of high-quality seeds (Kettle et al., 2011; Leger et al., 2024; Merritt & Dixon, n.d.). However, native seed supplies consistently fall short of global restoration demands, a limitation particularly acute for taxa with small, fragmented populations and restricted geographic ranges (Broadhurst et al., 2016; Merritt & Dixon, n.d.; Scariot & Vieira, 2006; Wijdeven & Kuzee, 2000). For long-lived threatened tree species, acquiring adequate seed volumes presents severe challenges, as remaining populations often suffer from low adult density, isolated individuals, and inherently constrained reproductive output (Wambugu et al., 2023).

Among the factors limiting seed availability, pre-dispersal seed predation by insects represents a critical yet frequently overlooked constraint (Zhang et al., 1997). Pre-dispersal predation occurs when insects attack seeds while fruits remain attached to the parent plant (Kolb et al., 2007). By consuming internal food reserves and damaging embryo tissues, seed-feeding larvae destroy seed viability and eliminate germination capacity, severely impairing natural recruitment (Fenner & Thompson, 2005; Downey et al., 2020). These biotic interactions are further modulated by broader

environmental factors; habitat disturbance, fragmentation, and climate change alter the distribution, abundance, and feeding activity of insect seed predators across landscape scales (Schroeder et al., 2021; Downey et al., 2020). Understanding how insect predation intersects with environmental variation to reduce seed quality (Vicky J. Erickson, n.d.) is therefore essential for designing effective conservation and seed-sourcing strategies for threatened tree species.

Adansonia perrieri, a tree endemic to the dry deciduous and humid evergreen forests of northern Madagascar, is the only baobab species currently classified as Critically Endangered, (Baum, 1995; Pettigrew et al., 2012; Karimi et al., 2026). Populations of *A. pierreri* are threatened by severe anthropogenic pressures, including habitat loss, agricultural expansion, altered fire regimes, forest degradation, and climate change (Arboleda et al., 2009; Baum et al., 1998; Vieilledent et al., 2013; Wan et al., 2021). Existing ecological studies indicate that natural regeneration is extremely limited across its range, a problem largely attributed to the historical loss and decline of native pollination agents and seed dispersers (Andriafidison et al., 2006; Andriantsaralaza et al., 2014; Rasoamanana, 2015). However, whether seed-stage mortality through insect predation further exacerbates these recruitment bottlenecks remains unknown.

During field surveys conducted in late 2021, we observed extensive fruit infestation by a seed-feeding beetle belonging to the genus *Cryptorhynchus* (Coleoptera: Curculionidae) across *A. perrieri* populations (Figure 1). Related seed-feeding weevils, such as *Cryptorhynchus mangiferae*, are well-documented seed predators that cause severe internal tissue damage and drastically reduce seed viability and germination success in other woody taxa, including economically important tree species (e.g., *Mangifera indica*) (Mulungu & Mpinga, 2008). Despite the delicate conservation status of *A. perrieri* and the potential severity of insect-mediated seed loss, pre-dispersal seed predation by insects has never been quantified for this or any other endemic Malagasy baobab species.



Figure 1 : Insect *Cryptorhynchus* sp. (Coleoptera: CURCULIONIDAE) identified in the capsule of target baobab fruits

To address this knowledge gap, this study evaluated the impact of *Cryptorhynchus* sp. Infestation on seed availability and quality in *A. pierreri* across three populations in northern Madagascar. Specifically, our objectives were to (i) quantify fruit production and assess the prevalence of *Cryptorhynchus* sp. infestation across geographic populations; (ii) evaluate the effect of insect damage on germination viability; and (iii) examine how insect abundance within fruits influences the yield of intact seeds to inform seed-sourcing strategies for restoration programs. We hypothesized that pre-dispersal seed predation by *Cryptorhynchus* sp. varies geographically, reduces both seed quantity and germination success, and significantly diminishes the supply of healthy viable seeds available for reintroduction programs.

Methods

Study area

This study was conducted across three regions within the natural range of *Adansonia pierreri* in northern Madagascar: Loky-Manambato, Plateau d'Ankarana, and Montagne d'Ambre (Figure 2). These zones encompass two primary vegetation types (Gautier et al. 2018): (i) dry deciduous forest (Loky-Manambato and Plateau d'Ankarana), characterized by a mean annual temperature of 25 °C, annual rainfall of 400 to 1400 mm, and elevations ranging from 0 to 800 m above sea level; and (ii) medium-altitude moist evergreen forest (Montagne d'Ambre) characterized by a mean annual temperature of 15-25 °C, annual rainfall exceeding 1200 mm, and elevations from 800 to 2000 m above sea level.

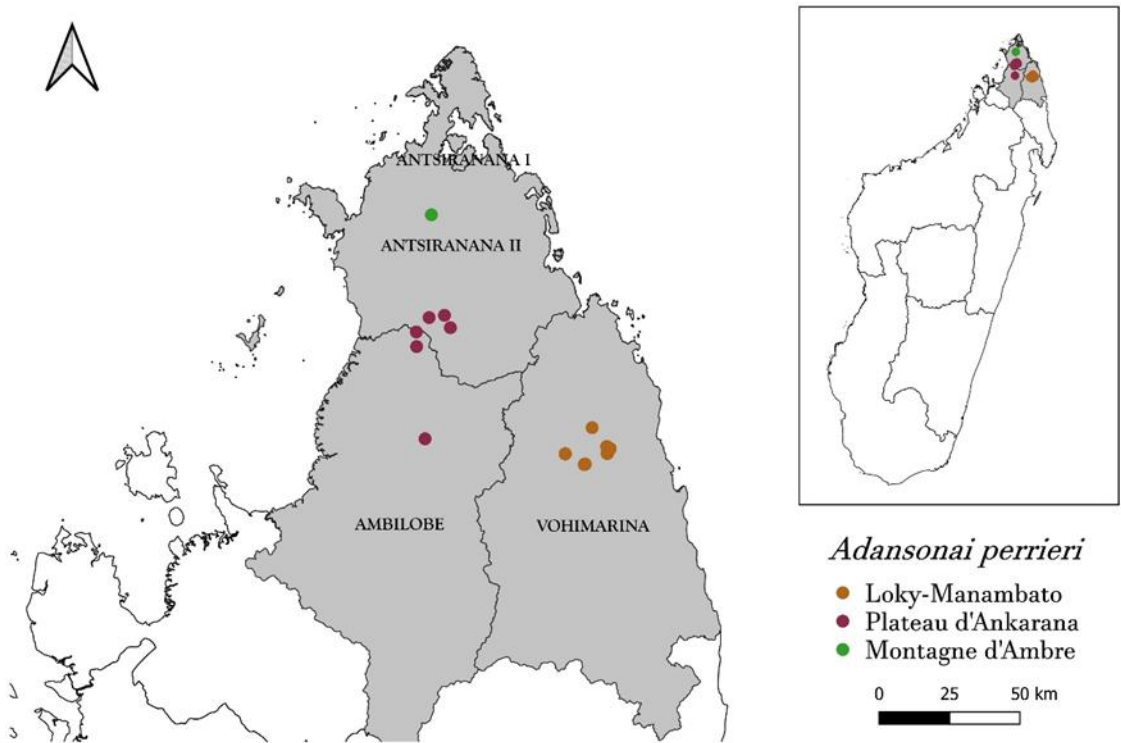


Figure 2 : Study sites of *Adansonia perrieri* species

Fruit collection and infestation assessment

To quantify fruit production per tree, up to 30 mature reproductive individuals were surveyed per site, following Assogbadjo (2011). In sites with fewer than 30 mature trees, all available reproductive individuals were surveyed. For each individual tree, all mature fruits present during the peak fruiting season (November-December 2021) were counted.

To assess insect infestation, up to five fruits per tree (Cornelissen et al., 2003) were harvested directly from the canopy or collected from the ground immediately after drop, depending on availability, yielding a total of 351 collected fruits. Each fruit was opened to record presence and abundance of adult *Cryptorhynchus* sp. beetles. Seeds within each fruit were counted and visually examined for internal damage. Based on the presence of feeding galleries, internal tissue destruction, or exit holes, seeds were classified as either intact (no visible signs of damage or exit holes) or damaged (clear evidence of internal insect feeding).

Germination experiment

To evaluate the impact of *Cryptorhynchus* sp. damage on seed viability, 30 intact seeds and 30 damaged seeds were selected. Seeds within each category were pooled across geographic origins to evaluate the general effect of physical insect damage on germination performance. Both seed groups received identical pre-germination treatments following the protocol established by Razanameharizaka (2006).

Seeds were sown in the same seedbed under uniform environmental conditions, arranged in alternating rows of five seeds per category to facilitate monitoring. Germination was recorded daily for 15 days (Razanameharizaka, 2006), with successful germination defined as the emergence of the radicle.

Statistical analysis

Differences in fruit production per tree among the three regional zones were evaluated using a non-parametric Kruskal–Wallis test due to non-normal data distribution. Post hoc pairwise comparisons were performed using Dunn’s test with Bonferroni correction for multiple comparisons. Geographic differences in the proportions of infested fruits and intact versus damaged seeds were tested using Fisher’s exact test.

To analyse the relationship between *insect* infestation load and intact seed yield, fruits were grouped into insect abundance classes of equal width (intervals of 5 insects: [0–5[, [5–10[, [10–15[, etc.). For each class, the percentage of intact seeds was calculated as the total number of intact seeds divided by the total seed count within that class, multiplied by 100. All statistical analyses were conducted in R version 4.5.3.

Results

Fruit production across geographic zones

A total of 351 fruits were recorded across 79 trees evaluated in the three regional zones. Overall mean fruit production was 6.44 ± 11.5 fruits per tree (median = 0, range = 0–73). Fruit production per tree differed significantly among geographic zones (Kruskal-Wallis test: $H = 11.98$, $df = 2$, $p = 0.002$). Post-hoc pairwise comparisons indicated that fruit production was significantly higher in Plateau d’Ankarana than in Loky-Manambato ($Z = 3.43$, $p = 0.002$). However, no significant differences were detected between Plateau d’Ankarana and Montagne d’Ambre ($Z = 1.22$, $p = 0.663$) or between Loky-Manambato and Montagne d’Ambre ($Z = 1.57$, $p = 0.353$; Figure 2).

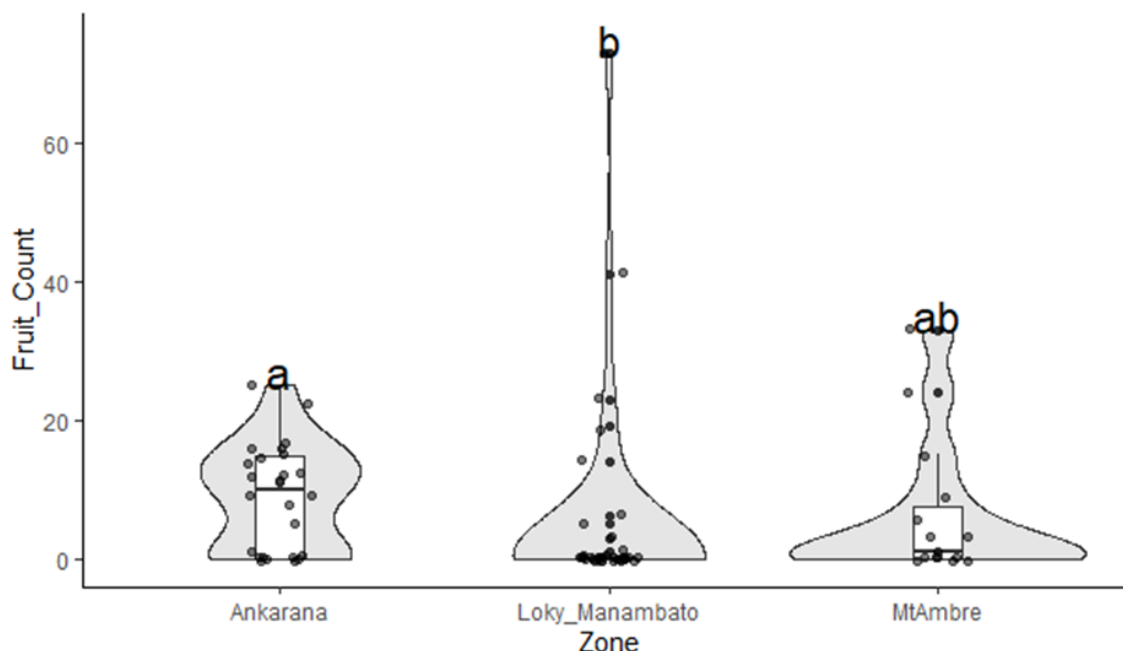


Figure 3 : Variation in fruit production per tree of *Adansonia perrieri* across geographic zones. Different letters indicate significant differences based on Dunn's post hoc test ($p < 0.05$)

Fruit infestation rates and seed damage across zones

Among all collected fruits ($N = 351$), 218 (62.1 %) were infested by *Cryptorhynchus* sp. Infestation rates varied significantly across regional zones (Fisher's exact test, $p < 0.001$; Figure 3). Fruits from Plateau d'Ankarana (83.8 %) and Loky-Manambato (74.4 %) showed substantially higher infestation rates than those from Montagne d'Ambre (4.8 %).

Correspondingly, seed damage showed strong regional differentiation (Table 1). Loky-Manambato and Plateau d'Ankarana recorded the highest mean numbers of damaged seeds per fruit (21.41 ± 32.21 and 13.24 ± 15.96 , respectively), whereas Montagne d'Ambre had the lowest (5.29 ± 15.12 ; Table 3). Conversely, the mean yield of intact seeds per fruit was highest in Montagne d'Ambre (112.88 ± 94.72) compared to Plateau d'Ankarana (39.64 ± 52.23) and Loky-Manambato (9.92 ± 16.24).

Tableau 1: Descriptive statistics of seed quantity, seed damage, and *Cryptorhynchus* sp. abundance in *A. perrieri* fruits across geographic zones.

Geographic zones	Fruits		Intact seeds			Damaged seeds		
	Insect (-)	Insect (+)	Min	Max	Average ($\pm$ SD)	Min	Max	Average ($\pm$ SD)
Plateau Ankarana	16%	84%	1	321	39.64 ± 52.23^{ab}	0	100	13.24 ± 15.96^a
Loky-Manambato	26%	74%	0	112	9.92 ± 16.24^a	0	182	21.41 ± 32.21^a
Montagne d'Ambre	95%	5%	0	488	112.88 ± 94.72^b	0	88	5.29 ± 15.12^b

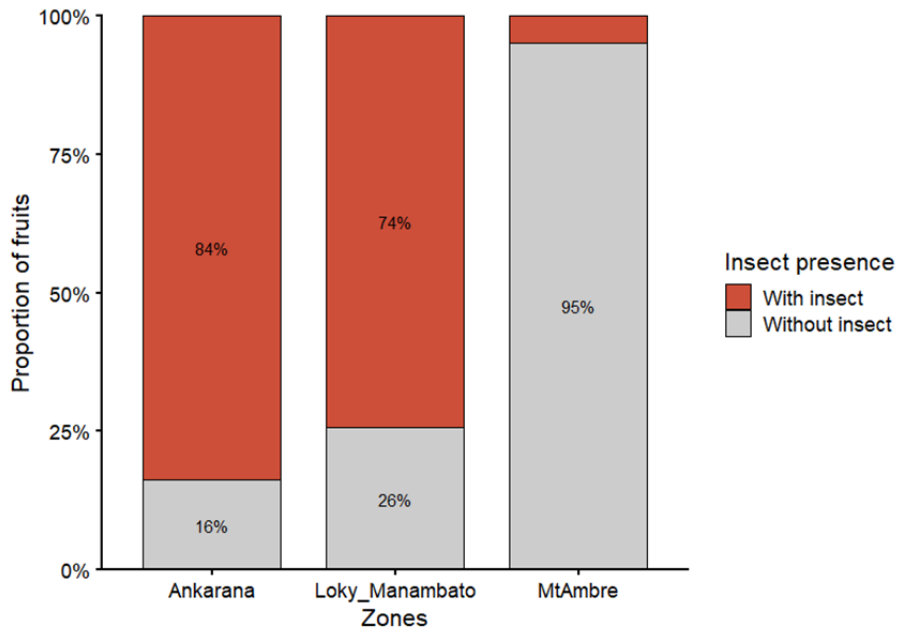


Figure 4 : Proportion of *A. perrieri* fruits with and without *Cryptorhynchus* sp. infestation across the three geographic zones. Bars represent the relative frequency of fruits classified as infested or non-infested within each zone. Differences among zones were assessed using Fisher's exact test ($p < 0.001$).

Impact of *Cryptorhynchus* sp. damage on seed germination

Seed viability was completely lost following insect damage (Figure 5). Over the 15-day monitoring period, no damaged seeds germinated (0%), whereas intact seeds exhibited progressive germination, reaching 33.33% by day 15 (Figure 5). Dissection of damaged seeds confirmed destruction of the seed coat and internal cotyledons caused by *Cryptorhynchus* sp.

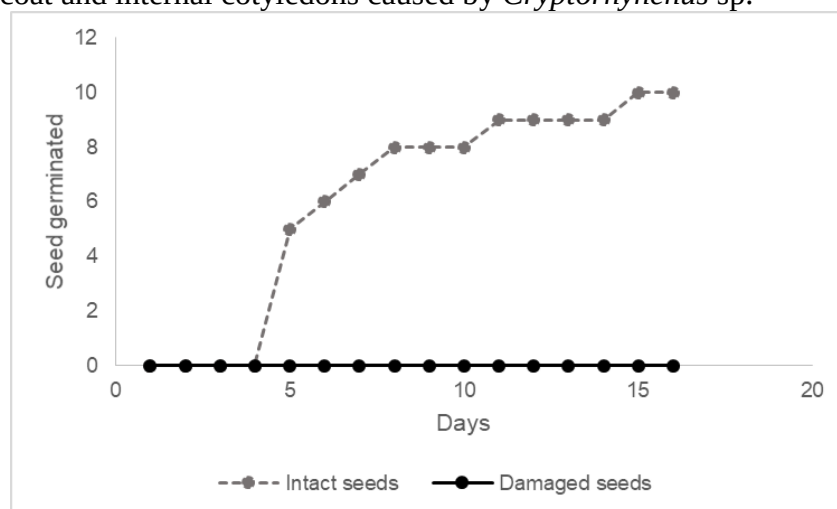


Figure 5 : Germination of intact and damaged *A. perrieri* seeds

Insect abundance and intact seed availability

The proportion of intact seeds within a fruit decreased sharply as *Cryptorhynchus* sp. abundance increased (Table 2; Figure 6). Fruits containing 0–5 insects yielded the highest proportion of intact seeds (73.0 %; Table 2). However, intact seed yields dropped to 12.0 % in fruits with 5–10 insects and to 9.0% in fruits with 10–15 insects. When insect abundance exceeded 30 individuals per fruit, intact seeds represented only 1.0 % of total seed output (Table 2; Figure 6).

Tableau 1 : Proportion of intact seeds per fruit according to the number of *Cryptorhynchus* sp. individuals observed

Nb insects	[0 - 5[	[5 - 10[	[10 - 15[	[15 - 20[	[20 - 25[	[25 - 30[	sup 30
Intact seeds per fruit (%)	73	12	9	1	1	3	1

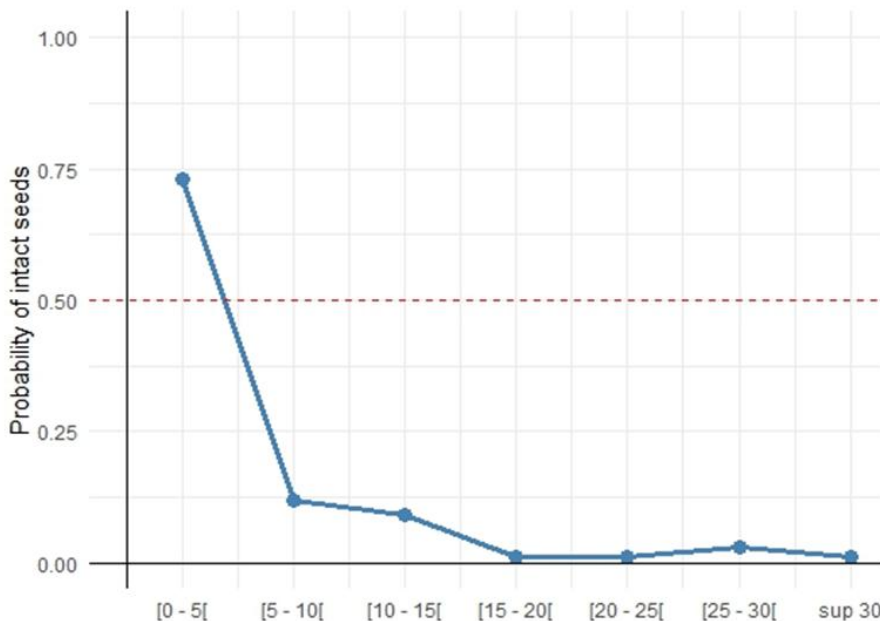


Figure 6 : Probability to find intact seeds according to the number of *Cryptorhynchus* sp. individuals observed within *A. perrieri* fruits

Discussion

Impact of *Cryptorhynchus* sp. on seed viability and regeneration

Our experimental findings demonstrate that pre-dispersal seed predation by *Cryptorhynchus* sp. causes complete seed mortality in *Adansonia perrieri*. Over the 15-day monitoring period, damaged seeds exhibited zero germination, whereas intact seeds successfully germinated. Dissection revealed that larval feeding destroys both the protective seed coat and essential internal nutrient reserves (cotyledons), depriving the embryo of the resources required for development. Consequently, seeds attacked by

Cryptorhynchus sp. cannot contribute to recruitment under any natural or nursery conditions. A similar observation was reported by Baldwin (2002), Beckman & Muller-Landau (2011) and Mulungu & Mpinga (2008), who found that pre-dispersal seed predation by insects reduce plant reproduction.

These results indicate that pre-dispersal insect predation represents a critical, previously unquantified bottleneck in the reproductive cycle of *A. pierreri*. Natural regeneration in this species is already restricted by low adult density, habitat fragmentation, and the historical loss of effective pollinators and seed dispersers (Andriafidison et al., 2006; Razanameharizaka, 2009; Andriantsaralaza et al., 2014; Baum, 2014). Insect-mediated seed destruction acts prior to dispersal, directly reducing the pool of viable propagules before dispersal mechanisms or seedbed conditions can take effect (Statton et al., 2017). While long-term demographic studies are required to determine the exact proportion of recruitment loss attributable to insect predation relative to post-dispersal hazards.

Spatial patterns of infestation and environmental drivers

Fruit production and pre-dispersal seed predation exhibited strong geographic variation across northern Madagascar. Plateau d'Ankarana produced the highest mean fruit yield per tree, whereas Loky-Manambato exhibited the lowest. Similar variation in fruit production has been reported among populations and habitats of other baobab species in Madagascar (Razanameharizaka, 2009), and differences among individual trees may also be associated with reproductive traits and local environmental conditions (Chetty et al., 2021). However, high fruit output did not translate into high seed viability; fruit infestation reached 83.8% Plateau d'Ankarana and 74.4% in Loky-Manambato, resulting in substantial seed loss. Crucially, some fruits that appeared intact externally contained adult beetles and damaged seeds internally. This concealed infestation indicates that visual examination of whole fruits alone cannot reliably detect internal insect damage.

The higher infestation observed in Plateau d'Ankarana and Loky-Manambato may be associated with differences in local environmental conditions. These dry deciduous forest habitats are generally hotter and drier than the medium-altitude moist evergreen forest of Montagne d'Ambre (Ranirison et al., 2010; Gautier et al., 2018). Pre-dispersal seed predation is known to vary across geographic populations in response to climate, habitat characteristics, host phenology, and insect predator dynamics (Beckman & Muller-Landau, 2011; Espelta et al., 2008; Kolb et al., 2007). Although climatic and habitat variables were not directly tested as predictors in this study, spatial differences between dry deciduous and moist evergreen populations suggest that local environmental conditions contribute to variation in *Cryptorhynchus* sp. infestation.

Implications for seed sourcing and restoration

A major practical takeaway from this study is that gross fruit availability does not reliably reflect the supply of viable seeds available for restoration. Because *Cryptorhynchus* sp. infestation rates vary strongly among geographic populations, estimating seed availability based solely on fruit abundance will lead to significant overestimations of viable seed yield in high-infestation regions like Plateau d'Ankarana and Loky-Manambato. Furthermore, our results demonstrate a sharp negative relationship between insect abundance within individual fruits and intact seed yield: fruits containing 0-5 *Cryptorhynchus* sp. individuals yielded 73% intact seeds, whereas yield dropped to 12% in fruits with 5-10 insects and fell to only 1% when insect abundance exceeded 30 individuals. Evaluating insect infestation during seed extraction can therefore serve as a practical field indicator to identify high-yielding fruits and increase the efficiency of seed collection efforts.

From a seed sourcing perspective, Montagne d'Ambre represents the most immediate source for obtaining large quantities of viable seeds due to its low infestation rate and high mean number of intact seeds per fruit. However, relying exclusively on a single population risks reducing genetic diversity in restored populations and losing locally adapted genetic variation present in dry forest environment (McKay et al., 2005; Breed et al., 2013; Thomas et al., 2014). Conversely, inappropriate mixing of strongly differentiated populations could potentially result in outbreeding depression or the disruption of locally adapted traits (Templeton, 1986; Fyfe & Hoffmann, 2024). Preliminary observations of geographic variation in fruit morphology among these populations (Ranaivoandriamanantena et al., unpublished data) may indicate phenotypic differentiation, but such variation cannot by itself be considered evidence of genetic differentiation or local adaptation. Because the genetic differentiation among *A. perrieri* populations remains insufficiently documented, restoration programs should balance three complementary factors: viable seed availability, geographic provenance, and the maintenance of genetic diversity. Therefore, genetic studies are recommended to guide seed sourcing, as demonstrated in other baobab species (Razanamaro et al., 2025). Where feasible, collecting from multiple populations while prioritising fruits with a high probability of containing intact seeds may provide a more balanced approach to seed sourcing.

Conservation implications and future research

The effects of pre-dispersal seed predation should be evaluated within the broader ecological and demographic context of *A. perrieri* conservation. Insect-mediated seed loss may interact with other synergistic

threats affecting this species, including habitat loss and degradation, bushfires, reduced animal-mediated dispersal, climate change, and the decline or scarcity of mature reproductive individuals. During our field surveys, mature *A. perrieri* individuals were scarce or absent at several locations in Loky-Manambato, where high-levels of habitat disturbance and bushfires were also recorded (Ranaivoandriamanantena, personal observation). These field observations highlight the necessity of evaluating insect seed predation alongside other environmental and demographic pressures when developing comprehensive conservation strategies.

Furthermore, insect infestation was noticeable lower in the densely vegetated, moist canopy environment of Montagne d'Ambre than in the more open, disturbed dry forest environments of Plateau d'Ankarana and Loky-Manambato. This variation raises the possibility that surrounding vegetation structure, local plant species diversity, or the density of alternative host plants may influence the occurrence and population dynamics of *Cryptorhynchus* sp. However, because these habitat characteristics were not quantitatively measured or experimentally manipulated in this study, they cannot be interpreted as direct causal drivers. Instead, they represent key hypotheses for future ecological research. Targeted field experiments evaluating canopy structure, microclimate, and host availability across forest fragments are needed to determine the exact mechanisms driving spatial variation in infestation.

The taxonomic status and life history of the *Cryptorhynchus* sp. associated with *A. perrieri* also require further investigation. In particular, establishing whether this insect is taxonomically close or related to *Cryptorhynchus mangiferae*, a well-known seed predator of mango, will clarify its host specificity, evolutionary origin, and potential ecological impacts. Detailed investigations into its life cycle, reproductive timing, host preference, and exact mechanisms of seed tissue damage will be crucial for developing targeted, evidence-based management responses.

Overall, pre-dispersal seed predation represents a critical constraint that must be incorporated into conservation and restoration planning for *A. perrieri*. Integrating systematic infestation assessment into seed harvesting protocols, while concurrently sampling across maintaining multiple provenances, will optimise the yield of viable seeds while preserving the geographic and genetic integrity of restored populations.

Conclusions

Overall, this study identifies pre-dispersal seed predation by *Cryptorhynchus* sp. as a previously overlooked constraint on seed availability for the restoration of *Adansonia perrieri*. The marked regional variation in fruit infestation, with substantially higher rates in dry deciduous

forest populations, highlights the necessity of accounting for geographic differences when assessing seed sources. The complete failure of damaged seeds to germinate further demonstrates that insect predation directly eliminates seed viability, restricting the supply of viable seeds suitable for reintroduction efforts. Consequently, seed sourcing strategies must not rely solely on gross fruit production or collection volume, but must systematically incorporate infestation levels, seed quality, and geographic provenance. Using multiple seed sources where feasible may help balance the need for sufficient viable seeds with the conservation of genetic diversity. These considerations are particularly important for the long-term restoration and conservation of this Critically Endangered baobab species.

Future research should clarify the taxonomy, biology, and ecology of the *Cryptorhynchus* sp. associated with *A. perrieri*, particularly to determine its taxonomic relationship with *Cryptorhynchus mangiferae*, a seed-feeding species reported from mango. Further studies should also investigate the environmental and biological factors influencing infestation intensity across *A. perrieri* populations. Such information would improve seed collection strategies and contribute to more effective conservation and restoration programs for this threatened Malagasy baobab species.

Conflict of Interest: The authors reported no conflict of interest.

Data Availability: All data are included in the content of the paper.

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