Seed dispersal and regeneration in a Tanzanian rainforest

BY

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DISSERTATION
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This dissertation is dedicated to my all of my teachers and mentors, from elementary school to graduate school, both formal and informal. I would not be where I am today without you. You inspire me.

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LIST OF ABBREVIATIONS

AIC	Akaike Information Criterion
ANR	Amani Nature Reserve
ATD	Africa Tree Database
CI	Confidence Intervals
dAIC	delta Akaike Information Criterion
EUM	East Usambara Mountains
GLM(s)	Generalized Linear Model(s)
GLMM(s)	Generalized Linear Mixed Model(s)
NODF	Nestedness metric based on Overlap and Decreasing Fill
NTFP(s)	Non-Timber Forest Product(s)

SUMMARY

Afrotropical forests host a diversity of fauna and flora. In particular, the Eastern Arc Mountains of Tanzania and Kenya are biodiversity hotspots with numerous species of plants and animals that occur nowhere else. Many of the plants rely on birds, bats, primates, rodents, or other mammals to disperse their seeds. One of the best-studied areas in Eastern Arc Mountains is the East Usambara Mountains in northeastern Tanzania. The Amani Nature Reserve protects the largest amount of submontane rainforest in the East Usambaras. Over the last century, more than half of the forest cover has been cleared for timber, tea plantations, and small-scale farms. The forest that remains is a patchwork of large forest blocks surrounded by tea fields and agriculture with small forest fragments scattered throughout. Thousands of people live in close proximity to the Nature Reserve and surrounding fragments, many of whom rely directly on the forest for firewood or other ecosystem services, including prohibited activities such as hunting, seed collection, pole cutting, and gold mining. These activities can alter the processes in the forest.

All five chapters are united by the themes of plant-animal interactions and the ways in which human activity can alter the interactions. The first four chapters examine seed dispersal in and around the Amani Nature Reserve. Chapters 1 and 4 deal with seed dispersal by fruit bats in the family Pteropodidae. The first chapter draws attention to the importance of bats as seed dispersers by using observations from Amani and other published observations to point out the general neglect of bats as seed dispersers in Africa. The fourth chapter quantifies seed rain from bats in the context of comparisons between continuous forest and forest fragments. Chapters 2 and 3 examine how seed harvest by humans of a rodent-dispersed endemic canopy tree may

affect dispersal and fate of the remaining seeds, and if enrichment planting of seeds could be a useful management tool. The last chapter takes a continental perspective on seed dispersal and frugivory in Africa by using thousands of published observations in an attempt to reveal patterns that may be more difficult to see at the local scale. These broad-scale patterns have potential to reveal trends in plant-animal coevolution, and may allow us to predict the ramifications of local extinction for other plant and animal groups.

1 SEED DISPERSAL IN THE DARK: SHEDDING LIGHT ON THE ROLE OF FRUIT BATS IN AFRICA

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1.1 Abstract

Seed dispersal affects early regeneration and ultimately plant diversity, but many tropical plant-disperser relationships remain unknown, especially for African fruit bats and their associated flora. Studying fruit and seed remains beneath 480 bat feeding roosts in the East Usambara Mountains of Tanzania revealed 49 species dispersed by fruit bats: 28 species, 18 genera, and one family are novel reports of bat dispersal in Africa. Approximately 20 percent of the submontane tree flora of the East Usambaras are bat-dispersed, which is a higher proportion of seed dispersal by bats than has been found in French Guiana where fruit bats are already recognized as important. Nineteen percent of minimum seed dispersal distances (n= 127) reveal that bats frequently carry diaspores >100 m before feeding. Measured by research effort on Web of Science, (1) bats are among the least studied frugivores and seed dispersers in Africa, and (2) Paleotropical fruit bats overall are less studied than their Neotropical counterparts. Documenting additional bat-plant interactions from under bat feeding roosts can be done alongside studies of diurnal dispersers to increase our understanding of seed dispersal and forest regeneration. Fruit bats are likely important seed dispersers in other Afrotropical forests, as bats elsewhere in Africa are known to consume 20 genera and 16 species of plants reported here. Until we better

understand the role that bats play in seed dispersal, it is difficult to predict the impact of habitat loss or bushmeat hunting (for bats and non-bats) on Afrotropical plant communities.

1.2 Introduction

Animals that disperse seeds are important drivers of forest regeneration, shaping community composition, structure, and functional dynamics. Animals are estimated to disperse >95 percent of seeds in tropical forests (Terborgh *et al.* 2002), where species with fruits adapted for vertebrate seed dispersal comprise 75 - 92 percent of the flora (Jordano 2000). Among dispersers, some taxonomic groups are relatively well-studied, with some vertebrates dispersing scores if not hundreds of species. These dispersers include: African elephants *(Loxodonta africana*, 350+ species, Campos-Arceiz & Blake 2011), primates such as Asian gibbons (*Hylobates mulleri* x *agilis*, 160 species, McConkey 2000), Neotropical howler monkeys (*Alouatta seniculus*, 137 species, Andresen 2002), tamarins (*Saguinus mystax* and *S. fuscicollis*, 166 species, Culot *et al.* 2011), and eight African hornbill species (*Bycanistes* spp. and *Ceratogymna* spp., 163 species, Kitamura *et al.* 2008). These examples result from extensive research on charismatic animals. While vertebrates broadcast seeds of numerous plant species, our knowledge and understanding of the contribution to seed dispersal and recruitment processes by different vertebrate taxa is both geographically and taxonomically limited.

Here we highlight the role of fruit bats as seed dispersers in Africa using new data and literature records. We focus on fruit bats for several reasons: (1) they are small-bodied, but capable of carrying large diaspores or fruits up to 25 - 250 percent of their body weight over 100 m (van der

Pijl 1957); (2) they are important for secondary forest regeneration (Swaine & Hall 1983, Muscarella & Fleming 2007); (3) they have received less research effort than primates, birds and large mammals; and (4) despite their nocturnal habits, making it hard to directly observe and quantify seed dispersal, sampling below feeding roosts can expand our knowledge of plant-bat interactions (Voigt *et al.* 2011). We suggest that the paucity of research on African fruit bats underestimates their role in seed dispersal, and seek to catalyze more interest in this important disperser guild.

Throughout the tropics, fruit bats disperse several hundred species of plants (Fujita & Tuttle 1991, Mickleburgh *et al.* 1992, Lobova *et al.* 2009) and facilitate forest regeneration (Banack 1998, Muscarella & Fleming 2007). Phyllostomid fruit bats of the Neotropics are incredibly diverse (approximately 142 species are at least partially frugivorous), dispersing at least 549 plant species in 191 genera from 62 families (Lobova *et al.* 2009). The 170 species of much larger pteropodid bats of Africa, Asia, southern Europe, Australia, and islands in the Indian and Pacific Oceans (Wilson & Reeder 2005) disperse seeds of at least 145 different plant genera (Marshall 1985), with long-distance seed dispersal estimated at 1- 20 km for ingested seeds (Tsoar *et al.* 2010). Many studies of seed dispersal in Africa have been limited to daylight observations of frugivore behavior (*e.g.* Cordeiro *et al.* 2004, Gross-Camp *et al.* 2009), thus missing potential dispersal by fruit bats.

As an alternative to observing bats directly, fruit bats leave behind abundant evidence of their foraging behavior. Conspicuous and characteristic collections of seeds and fruit remains drop directly below locations where they hang to process fruits. We can study the remains below

where fruit bats eat ("feeding roosts," Voigt *et al.* 2011) to document diet and seed dispersal. The plant material under feeding roosts tends to be scattered in a small radius of ~1-2 m. While processing fruits, the flesh is eaten away from large seeds and the seed is dropped or spit out, sometimes without fruit pulp or with partially or fully masticated fruit pulp. Numerous terms used to describe these plant remains under bat feeding roosts, including ejecta (*e.g.* Nyhagen *et al.* 2005), bolus (*e.g.* Goveas *et al.* 2006), wads (*e.g.* Corlett 1998), wadges (*e.g.* Duncan & Chapman 1999), or spats (*e.g.* Dumont 2003), all are essentially synonymous.

Feeding roosts may be far from the food source. African fruit bats typically process fruits and seeds at feeding roosts within 100 m from fruiting trees (*e.g.* Kankam & Oduro 2009), similar to many fruit bats from other regions (Thomas *et al.* 1988, Melo *et al.* 2009). The fruits they carry can be quite heavy, enabling the dispersal of large seeds. Pteropodid bats, for example, can carry fruits weighing as much as 25 percent (Bonaccorso *et al.* 1980) to 68 percent (Marshall 1983) of their body mass, and in some cases, fruits 250 percent of their body mass can be carried up to 200 m (van der Pijl 1957). Through their feeding behavior, African fruit bats have the potential to move even large seeds between forest, fragments, and farms to facilitate gene flow and colonization for plants.

The goals are to draw attention to bat frugivory and seed dispersal in Africa, suggest that fruit bats may be understudied relative to their contribution to seed dispersal, and ultimately encourage more research in Africa. We place our results on bat frugivory and seed dispersal from one African forest into a broader context, and use Web of Science search results to compare research effort on frugivory and seed dispersal across continents and taxa.

1.3 Methods

1.3.1 Study site

Bat feeding roosts were studied in and around the Amani Nature Reserve in the East Usambara Mountains (EUM) of Tanzania (5° 06' 00" S, 38° 38' 00" E), in the submontane forest from 700-1200 m above sea level. The EUM are part of the Eastern Arc mountain chain that stretches from southeastern Kenya to southern Tanzania. The EUM receive ~ 1900 mm of rain/yr with two rainy seasons and two mild dry seasons (Rodgers & Homewood 1982). Historically, the EUM supported more than 900 km^2 of forest, but today only 263 km^2 of forest cover remains (Burgess *et al.* 2007). Amani Nature Reserve protects ~84 km^2 of lowland, submontane, and plantation forest in the southern region of these mountains (Doody *et al.* 2001). Non-forested lands are mainly tea plantations and subsistence farms. More than 150 native tree species (diameter at breast height $\geq$10 cm) are found in the submontane forest of the EUM (Hamilton & Bensted-Smith 1989, Schulman *et al.* 1998). A preliminary study suggests that approximately 87 percent of submontane tree species have diaspores adapted for animal dispersal (Cordeiro *et al.* 2005). Many of these tree species are endemic or near endemic to the Eastern Arc Mountains (Lovett *et al.* 2006, Burgess *et al.* 2007) although several of the genera are widespread.

1.3.2 Fruit Bats of the East Usambaras

Seven species of fruit bats are found in the EUM (nomenclature follows Nesi *et al*. (2012)): *Rousettus aegyptiacus* (100-166 g), *Stenonycteris lanosus* (120-165 g)*, Myonycteris angolensis* (65-91 g), *Eidolon helvum* (250-311 g), *Myonycteris relicta* (30+ g)*, Epomophorus wahlbergi* (54-120 g), and *E. labiatus* (38-70 g) (Kingdon 1974, Bergmans 1980, Rodgers & Homewood 1982, Doggart *et al.* 1999, Doody *et al.* 2001). All of these species are recorded to primarily eat

fruit, although most also visit flowers (Nowak 1994). In almost all cases the genus or species of bat using the feeding roost was not observed so most observations of frugivory and seed dispersal recorded herein are not attributed to a particular species of bat (except as noted in Appendix 1C).

1.3.3 Plant sampling below bat feeding roosts

Fruits and seeds were identified from under bat feeding roosts, which were identified by freshly dropped fruit, ejecta, or aggregations of large diaspores on the ground (see Appendix 1D for photographs and additional explanation). In African forests, seeds left by fruit bats can easily be distinguished from those defecated by Two-spotted palm civets (*Nandinia binotata*) and large forest hornbills (*Bycanistes* spp.). Palm civets defecate in conspicuous latrines and hornbills drop seeds at the base of mature trees in which they nest or spread seeds out over a wide area when in large communal roosts and rarely have diaspores larger than 3-4 cm in length (NJC & HJN, unpublished data). Bat handling was confirmed by the presence of ejecta or fruit parts with teeth and/or claw marks. Identification of common or distinctive plant species was done by visual or olfactory inspection. Specimens that could not be identified in the field were assigned a morphospecies code and collected for a reference collection and/or germination. When possible, voucher specimens were collected for species identification of unknowns.

A total of 480 observations below feeding roosts at 35 different sites were made between February 2000 and October 2011. Each observation includes all of the plant species found in a discrete area below a feeding roost. Of these, 401 observations (80%) were from the ground below feeding roosts encountered in the forest during other field work. The remaining 79 observations were from eight 1 x 1 m^2 seed traps placed below feeding roosts on farms where the

daily records were pooled by month to equal one observation. One month is approximately the period of time that seeds are observable under feeding roosts without seed traps (C.E. Seltzer, pers. obs). To assess the completeness of our sampling, we plotted cumulative species richness on the number of observation areas below feeding roosts. Species rarefaction curves were generated using 500 randomizations of the sequence of observations added using EstimateS, version 8.2.0 (Colwell 2009).

1.3.4 Seed Sizes

Plant species were grouped according to length of longest seed dimension as small, medium, or large (Appendix 1C). Small seeds can be swallowed by fruit bats, but medium and large sized seeds cannot, based on a maximum ingestible size of 5 mm for *Pteropus conspicillatus* (Australia, 400-1000 g) (Richards 1990).

1.3.5 Minimum dispersal distances

Distance to the nearest mature conspecific tree (possible parent) from the feeding roost remains was measured in as many instances as possible. Lianas and vines were excluded from searches. We searched up to 50 m for the nearest adult conspecific in the forest and up to 325 m in farmland where there are many fewer trees. Observations of species for which the nearest adult could not be located are not included in the minimum dispersal distances. Additionally, plant remains found under a conspecific crown were considered as undispersed, and therefore not included in the calculations for minimum dispersal distances. The distance to the trunk was measured in the field, then the average crown radius for each species (or the average of all species for unmeasured species crowns) was subtracted to calculate the distance of dispersal beyond the crown edge.

1.3.6 Web of Science Searches

Keyword searches about seed dispersal and frugivory were performed in Web of Science for two comparisons: one on fruit bats among geographic areas, and another on different vertebrate taxa in Africa. Details of the keywords used and criteria for article inclusion can be found in Appendix 1A.

1.4 Results

1.4.1 Plant species found below feeding roosts

Thirty-seven genera and 44 different species of trees, lianas, and vines dispersed by bats were identified to species, and two identified to genus only. Three morphospecies remain unidentified (Table S2). Four different species of *Ficus* were identified, and other *Ficus* specimens that could not be identified were lumped as *Ficus* spp. (included in the "two identified to genus only"), which likely contains more than one additional species (at least four other *Ficus* spp. occur in the area). A species rarefaction curve shows that nearly 75 percent of bat-dispersed species were recorded after 150 observations, but new species continued to be added and, even by 480 observations, had not yet leveled off (Figure 1.1).

We searched extensively for previous records of bat dispersal for all plant species reported in this study and found that 20 genera and 16 species are recorded from elsewhere in Africa (Appendix 1C). We identified 18 other genera not previously known to be dispersed by African bat species and/or in Africa and nearby islands (Table S2, Appendix 1C). Including the newly reported species from previously reported genera, this study adds 28 more species dispersed by bats. Six of the bat-dispersed species are non-native (Table S2). Thirty-six species are trees (DBH $\geq$10

cm), six are lianas (woody vines), one is a non-woody vine, and the life form is unknown for five species. Twenty-four and 22 species have also been observed to be dispersed by large birds and primates, respectively (Appendix 1C).

1.4.2 Seed Sizes

Twelve species had small, ingestible seeds (length <5 mm), 31 had medium-sized seeds (5< length < 30 mm), and six had large seeds (length >30 mm) (Table S2). Fruit types, colors, and seed dimensions can be found online (Appendix 1C).

1.4.3 Dispersal distances

Minimum dispersal distances were measured from below feeding roosts to 127 mature trees of 18 different species; the mean minimum dispersal distance was 55.7 m (median= 30.2, range 0.2 - 320.5 m). The median distances for six tree species with at least 7 minimum dispersal distance measures are displayed in Figure 1.2. Species for which we searched unsuccessfully for the nearest adult tree are not included in the calculations. The longest recorded distance was 320.5 m for *Cephalosphaera usambarensis* (Myristicaceae) in a farmland setting.

1.4.4 Web of Science

There are more than ten times as many articles about seed dispersal and frugivory by bats in the Neotropics than in Africa (Figure 1.3A). Worldwide, there are 170 frugivorous pteropodid bat species and 142 frugivorous phyllostomid bat species, but many fewer articles about pteropodids overall. A comparable search on vertebrate dispersers in Africa revealed that primates and birds are most frequently studied, while there are successively fewer articles published on frugivory

and seed dispersal by elephants, rodents, bats, ungulates, and carnivores, respectively (Figure 1.3B).

1.5 Discussion

Evidence from a single area of Tanzania revealed 49 bat-dispersed plant species, of which 28 species, 18 genera, and one family are novel reports of bat dispersal in Africa. This comprises about 20 percent of the submontane tree flora in the East Usambara Mountains (Ruffo *et al.* 1989, Lovett *et al.* 2006), which is notably more than the 6 percent of bat-dispersed tree flora found in central French Guiana (Lobova et al. 2009) where fruit bats are more widely recognized for their role as seed dispersers in the Neotropics (Figure 1.3A). Furthermore, bat dispersal of 16 species and 20 genera is confirmed in other parts of tropical Africa, underscoring the widespread contribution of fruit bats to seed dispersal and regeneration across the continent.

Not only do bats disperse seeds of several plant species in and around the Amani Nature Reserve, they disperse species with a wide range of seed sizes. Seed size has been shown to be an important influence on how seeds are handled and dispersed (Wheelwright 1985). Because bats can swallow small seeds while ingesting fleshy pulp (Utzurrum & Heideman 1991), it is likely that our estimates of the number of small-seeded species are conservative since small seeds could be defecated in flight, hidden by leaf litter, or rot quickly. Many species of bats, especially in the Paleotropics, are known to disperse seeds much larger than they are capable of ingesting (Muscarella & Fleming 2007). It is noteworthy that most plant species recorded in our study (37 of 49) have seeds that are too large to be swallowed by bats. Consequently, fruit bats process and disperse many seeds too large to be ingested by most extant vertebrates in the EUM. Even when these seeds are deposited in high densities, they frequently germinate below bat

feeding roosts (C.E. Seltzer, pers. obs.; Appendix 1D). Bats appear to play an important role in the dispersal of large-seeded species, and in many instances, these non-ingested seeds are often dispersed far from the nearest possible parent.

Dispersal of seeds away from parent trees enables plants to colonize new areas and can be an important mechanism for gene flow (Daïnou *et al.* 2010) and for structuring tree diversity (Terborgh *et al.* 2002). In our study, distances to the nearest possible parent ranged from 0.2 to 320.5 m (median=30.2, mean=55.7), and distances of >100 m were not uncommon (20.5 percent of 127), especially for bat roosts in farmland (Figure 1.2). Three reasons suggest these are conservative estimates of dispersal distances: (1) these represent the minimum possible dispersal distances in each case, since the nearest conspecific is not necessarily (or even likely) the original source (Hardesty *et al.* 2006); (2) in several instances, the nearest conspecific was not located, so no distance was recorded (distances searched ranged from 50-325 m from feeding roosts); and (3) all distances are from spit out fruit or seeds, but defecation of ingested, small-seeded species likely occurs over larger distances (such as those modeled by Tsoar *et al.* 2010). For these reasons, we suspect the actual dispersal distances are more right-skewed than recorded here (Figure 1.2). African fruit bats are certainly capable of dispersing several large-seeded species hundreds of meters. In the fragmented landscape surrounding the Amani Nature Reserve, movement of bats between small patches of forest, isolated trees, or low-density stands in farmland facilitates the transport and deposition of seeds to distant sites.

How representative is the bat-dispersed flora of the EUM for other places in Africa? We suspect that other moist forests may have similar proportions of bat-dispersed species because 1) fruit

bats are found throughout African forests, and 2) several plant species and genera in this study are widely distributed. Frugivory and seed dispersal by bats for 16 species and 20 genera was corroborated by literature records from all over the continent (Appendix 1C). The wide distribution of fruit bats and some of their favored plants suggests that the EUM are not anomalous, but rather that Africa has many more bat-dispersed species than have been published to date. Of African studies (including Madagascar and offshore islands), the most extensive sampling has been on islands such as Pemba (Entwistle & Corp 1997), Madagascar (Bollen 2007, Picot *et al.* 2007, Racey *et al.* 2009), and Mauritius (Nyhagen *et al.* 2005), except for one very detailed but unpublished dissertation from Ivory Coast (Thomas 1982). Studies in Zambia (Richter & Cumming 2006) and Benin (Djossa *et al.* 2008) that used remains below feeding roosts to record bat diets (combined with direct observation or fecal samples, respectively) found only six species each under feeding roosts; we suggest that these low numbers may not be representative of African forests. Richter & Cumming (2006) limited their observations to the season of *Eidolon helvum* migration and to *E. helvum* diets, so we predict that sampling for more bat species and in all seasons would greatly increase the number of bat-dispersed species. Djossa *et al.* (2008) carried out their study in an area that was more savannah than forest, with correspondingly lower tree diversity than evergreen African forests. With a more intensified approach to studying bat feeding roosts elsewhere in Africa, we predict similar proportion of bat-dispersed trees in other Afrotropical forests.

If we examine research effort for seed dispersal and frugivory within Africa, birds and primates are clearly the best studied, whereas rodents and elephants have received less attention (Figure 1.3B). Articles on bats, ungulates, and carnivores in Web of Science searches have the fewest

articles. We suspect that this method has missed more articles about ungulates and carnivores than about bats because animals in these groups may be less likely to be referred to using these terms, whereas "bat" effectively captures all bats (see Appendix 1A). Researchers interested in other vertebrate seed dispersers, such as primates and birds, should consider the possibility of bat dispersal in their African study systems. With an appropriate search image (see photographs in Appendix 1D), remains below bat feeding roosts can easily be found during the day, when research on most other dispersers is conducted.

The role of fruit bats as seed dispersers is less studied in Africa than other parts of the tropics, especially the Neotropics. Searches on the Web of Science of bats as frugivores and/or dispersers compared to frugivorous bat species richness illustrates that there is a greater discrepancy in the proportionate number of articles about bat species in the Paleotropics compared to the Neotropics (Figure 1.3A). Considering the large land area and high biodiversity in Asia, it is peculiar that so few articles turned up. We suspect that, because Asia is so large, keywords are more likely to refer to a country or region rather than the continent, and at least a dozen studies from Asia were captured only with the Paleotropic* and "Old World" keywords. Although geographical biases in research limit what we know, a better understanding the role of African fruit bats in seed dispersal can inform tropical forest conservation.

Local extinction of frugivores can have negative consequences for the dispersal and recruitment of animal-dispersed plant species (Wright *et al.* 2007, Terborgh *et al.* 2008). We suspect that there is considerable overlap in the dietary preferences of fruit bats and other animals, since 45 percent and 49 percent of bat-dispersed species in the EUM have been observed to also be

consumed by primates or large birds (Appendix 1C). Given the diffuse relationship between plants and their animal dispersers (a single species may be dispersed by more than one taxon), fruit bats may act as effective dispersers in fragmented or heavily degraded habitats after primates and other larger vertebrates disappear (but see Vanthomme *et al.* 2010). Predicting which seed dispersers continue to function in altered landscapes requires an analysis of fruits consumed and seeds dispersed not only by bats (*e.g.* Geiselman *et al.* 2002 for the Neotropics) but all major vertebrate dispersers in Africa, as well as the differential contributions of animal species to patterns of seed dispersal (Jordano *et al.* 2007, Nathan *et al.* 2008). African fruit bats clearly disperse seeds, but studies quantifying the seeds dispersed and following seed fates are needed to measure their effectiveness and relative importance as dispersers for different plant species.

Although bats are seldom hunted in East Africa (with the exception of Pemba Island), hunting large fruit bats such as *Eidolon helvum* is much more widespread in central and west Africa (Mickleburgh *et al.* 2009). Degradation and habitat loss is, however, a growing issue for Afrotropical forests, and no studies to date have evaluated how African fruit bats are impacted by these activities. In any event, loss of fruit bats, as found in Pacific islands, limits recruitment of late successional, large-seeded species in native forests, (McConkey & Drake 2006), and impacts bat-dispersed species of high economic and agroforestry value, such as the Shea nut *Vitelleria paradoxa* of western Africa (Djossa *et al.* 2008). Perhaps earlier statements such as "*frugivorous bats are much less important in Africa than in the Neotropics*" (Gautier-Hion *et al.* 1985) may have hindered research on African bats as agents of seed dispersal. Given how poorly bats in Africa have been studied as seed dispersers compared to other animals, we may be missing the

ability to make important links between their loss or persistence and potential effects on forest regeneration. It is necessary to understand the role that bats play in seed dispersal in order to predict the impact of habitat loss or bushmeat hunting on the plant communities in Africa.

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1.8 Figures

Figure 1.1 Plant species rarefaction curve of bat-dispersed species

Plant species rarefaction curve (bold line) and 95% CI (thin lines) of bat-dispersed species with respect to the number of feeding roosts observed. Curves were smoothed by 500 random reorderings.

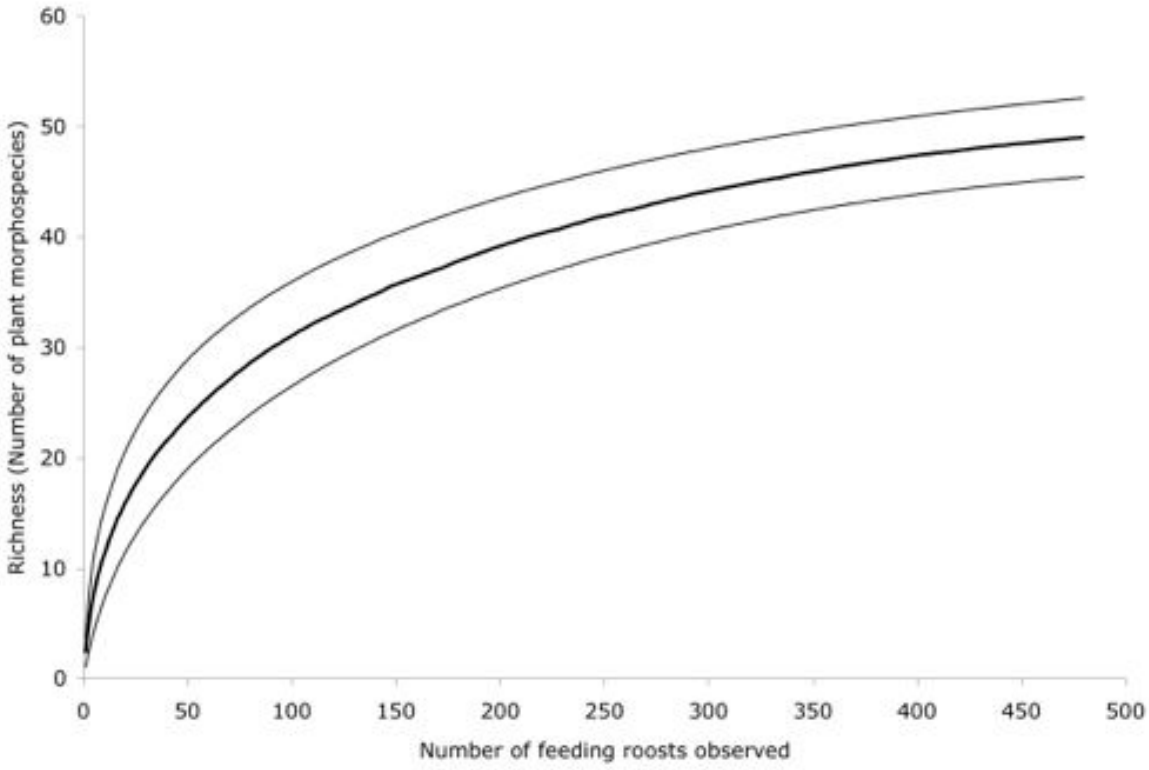


Figure 1.2. Minimum dispersal distances for some bat-dispersed species

Minimum dispersal distances beyond nearest conspecific tree canopy for bat-dispersed species in the East Usambara Mts. (A) Box plots display the minimum dispersal distances for six tree species with n ≥ 7. (B) Histogram of minimum dispersal distances for all species together (n= 127).

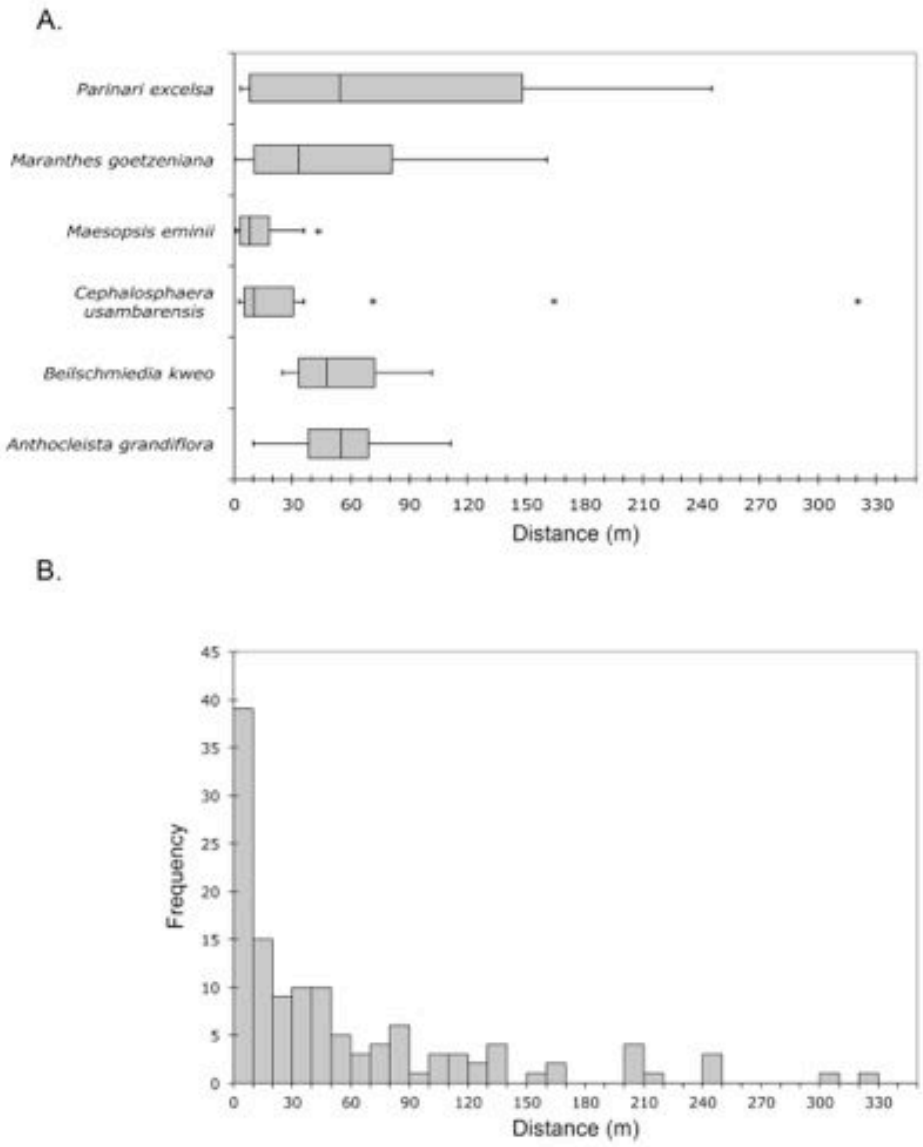
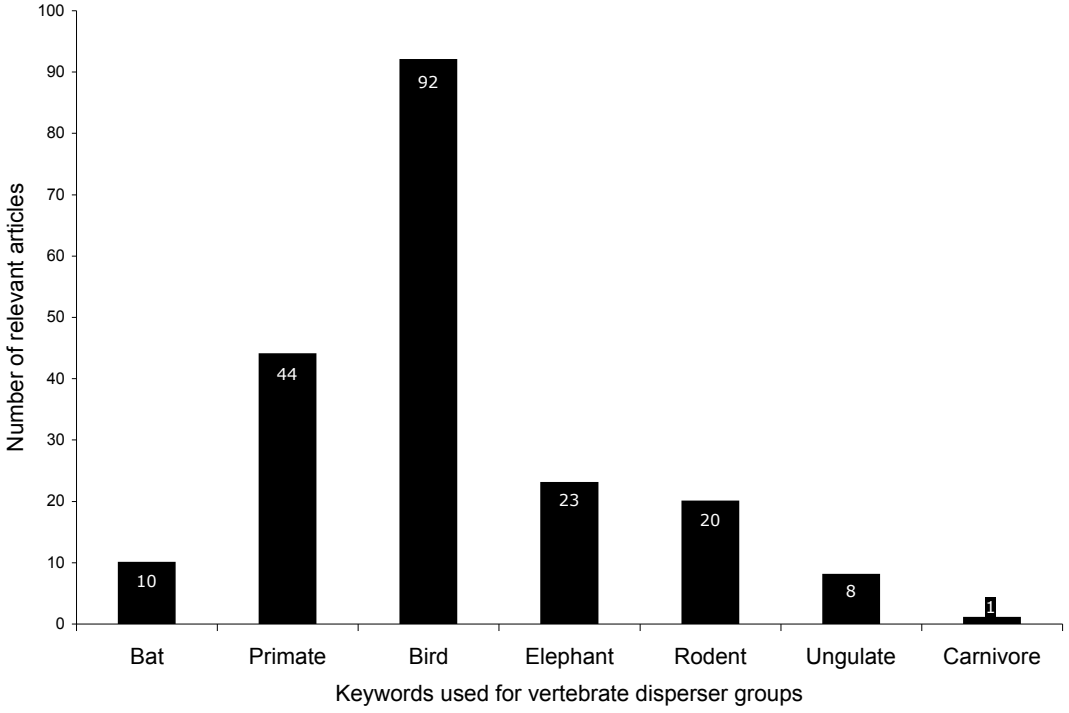
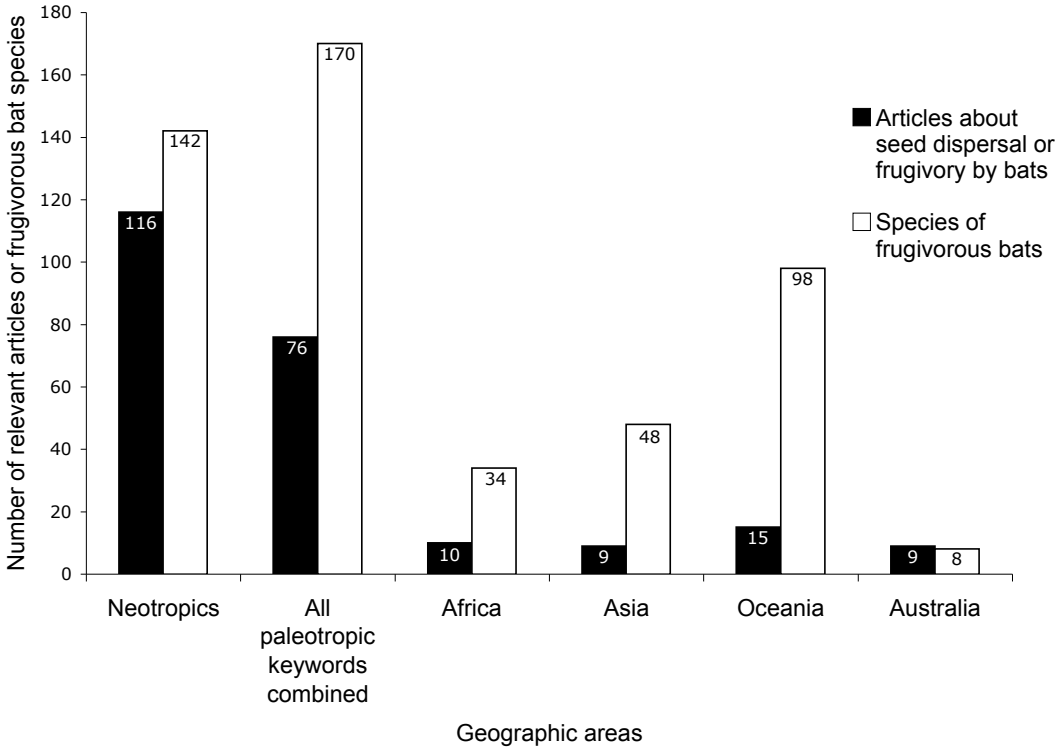


Figure 1.3. Relevant results from Web of Science searches

Relevant results from Web of Science searches. (A) Seed dispersal and frugivory by bats (keywords: seed dispers* or frugivor* and bat) with respect to geographic area (keywords: Neotropic*, "New World", America*, Paleotropic*, "Old World", Africa*, Asia*, Oceani*, Pacific*, and Australia*) (black bars). The number of frugivorous bat species found in each geographic area is also displayed (white bars). The Paleotropics were broken down in to four geographic areas: Africa, Asia, Oceania, and Australia. The articles do not add up to "all Paleotropic keywords combined" because many articles had only "Paleotropic*" or "Old World" keywords rather than continental keywords. All methods for quantifying fruit-eating bat species and literature can be found in Appendix 1A. (B) Seed dispersal and frugivory in Africa (keywords: seed dispers* or frugivor* and Africa*), as a function of animal groupings displayed above on the x-axis (methods in Appendix 1A).


Number of relevant articles
100
90
80
70
60
50
40
30
20
10
0
10
44
92
23
20
8
1
Bat
Primate
Bird
Elephant
Rodent
Ungulate
Carnivore
Keywords used for vertebrate disperser groups


Number of relevant articles or frugivorous bat species
180
160
140
120
100
80
60
40
20
0
116
142
76
170
10
34
9
48
15
98
9
8
Articles about seed dispersal or frugivory by bats
Species of frugivorous bats
Neotropics
All paleotropic keywords combined
Africa
Asia
Oceania
Australia
Geographic areas

Appendix 1A Methods for Web of Science and geographic assignment of bat species

Methods for Web of Science search results and geographic assignment of bat species.

Web of Science literature survey

To compare the volume of research on seed dispersal by bats in Africa to different geographic areas, keyword searches on Web of Science were done on November 29, 2011, using the topic keywords seed dispers* OR frugivor* AND bats with additional geographic keywords (Table 1A.1). We searched SCI-EXPANDED, SSCI, A&HCI for all years with lemmatization on (finds alternative spellings and plurals). Since some of the search results were clearly not relevant, all articles were scored (0 or 1) for inclusion in figure B2.1 based on three criteria: taxon, geographic location, and topic. Articles had to be about the taxon of interest (bats), in the proper geographic location, and broadly related to diet, foraging, seed dispersal, distribution, or community structure. Several articles turned up in the results of more than one search string, and the total number of unique search results was 262 (Table 1A.1). Article lists, scoring, and associated R script are available from the authors upon request.

The number of frugivorous bat species in each geographic area was calculated by using geographic information from each species from Wilson & Reeder (2005). Wallace's Line was used to separate Oceania from Asia. Australia was considered separate from Oceania. Some Pteropodid species occur in more than one geographic area. A species was considered frugivorous if any species in the same genus was recorded to eat fruit, which includes several species of Phyllostomids which are primarily insectivorous but were also recorded eating fruit. Genera for which no diet information was available are counted as frugivorous if "fruit" was in

the common name. Frugivory was determined using Geiselman *et al*. (2002) for Phyllostomid bats and Mickleburgh *et al*. (1992) for Pteropodid bats. Gaps were filled using observations noted in Nowak (1994) and York (2008).

The following geographic areas were considered to be part of Oceania: Sulawesi, Talaud Islands, Lombok, Sumbawa, Flores, Alor Isl, Sumba, Timor, Moyo, Sangeang, Komodo, Adonara, Lembata, Pantar, Wetar Isls, Muna Togian Isls, Sula Isls, Waigeo, Yapen, Batanta, and Misool Isls through New Guinea, Louisiade Arch., D'Entrecasteaux Isls, and Trobriand Isls, Bismarck Archipelago, Solomon Islands, Karakelang, Halmahera, Ambon, Buru, Seram, and small islands east of Seram, Samao Isl, Dyampea Isl, Bonerato Isl, Saleyer Isl, Paternoster Isls, Pelang Isl, Sulawesi, Banda Isls (Indonesia), and Boigu Isl.

The following geographic areas were considered to be part of Asia: Philippines, Borneo, Java, Sumatra, Pelang, Bali, Sipora, Siberut, Mentawai Isls, Riau Arch, Nicobar and Andaman Isls, Engano Isl and Nias Isl (Indonesia), Christmas Isl, and Mentawai Isls.

To compare the volume of research on seed dispersal in Africa by different animal groups, keyword searches on Web of Science were done on November 28, 2011 using the topic keywords frugivor*OR seed dispers* AND Africa* combined with animal keywords (Table 1A.2). We included those groups of animal dispersers most likely to overlap with fruit bats, since that is the main focus of the paper. We acknowledge that we have omitted other disperser guilds such as fish, ants, and other insects such as dung beetles. The same search criteria and scoring methods were used as in the geographic searches explained above. We suspect the carnivor* and ungulate keywords failed to capture many articles about seed dispersal in those taxa. For

example, articles about bat-eared foxes appeared with the keyword bat but not carnivor*. More specific family or genus keywords are probably used in carnivore studies. Similarly, ungulates might be identified using the keyword herbivore, or more taxonomically specific keywords. Many articles were in the results for more than one search string, and the total number of unique results was 264 (Table 1A.2).

Table 1A.1 Search strings used in Web of Science for geographic areas

Search strings used in the advanced search on Web of Science on November 29, 2011, the number of articles matched by Web of Science, and the number of those articles determined to be relevant to seed dispersal. 262 unique search results were reviewed for relevance. Of these 262, 184 unique articles were deemed relevant for one or more geographic areas.

Search string	Articles matched by WoS	Relevant articles from WoS search
TS=(frugivor* OR seed dispers*) AND TS=(america* OR neotropic* OR "new world") AND TS=(bat)	183	116
TS=(frugivor* OR seed dispers*) AND TS=(paleotropic* OR palaeotropic* OR "old world" OR asia* OR africa* OR australia* OR oceani* OR pacific*) AND TS=(bat)	115	76
TS=(frugivor* OR seed dispers*) AND TS=(paleotropic* OR palaeotropic* OR "old world") AND TS=(bat)	47	39
TS=(frugivor* OR seed dispers*) AND TS=(africa*) AND TS=(bat)	27	10
TS=(frugivor* OR seed dispers*) AND TS=(asia*) AND TS=(bat)	15	9
TS=(frugivor* OR seed dispers*) AND TS=(oceani* OR pacific*) AND TS=(bat)	22	15
TS=(frugivor* OR seed dispers*) AND TS=(australia*) AND TS=(bat)	22	9

Table 1A.2 Search strings used in Web of Science for animal groups

Search strings used in the advanced search on Web of Science on November 28, 2011, the number of articles matched by Web of Science, and the number of those articles determined to be relevant to seed dispersal. 264 unique search results were reviewed for relevance. Of these 264, 173 unique articles were relevant to one or more animal group.

Search string	**Articles matched by WoS**	**Relevant articles from WoS search**
TS=(frugivor* OR seed dispers*) AND TS=(africa*) AND TS=(bat)	27	10
TS=(frugivor* OR seed dispers*) AND TS=(africa*) AND TS=(primate)	75	44
TS=(frugivor* OR seed dispers*) AND TS=(africa*) AND TS=(bird)	133	92
TS=(frugivor* OR seed dispers*) AND TS=(africa*) AND TS=(elephant)	36	23
TS=(frugivor* OR seed dispers*) AND TS=(africa*) AND TS=(rodent)	29	20
TS=(frugivor* OR seed dispers*) AND TS=(africa*) AND TS=(ungulate)	13	8
TS=(frugivor* OR seed dispers*) AND TS=(africa*) AND TS=(carnivor*)	10	1

Appendix 1B

Table 1B.1 Plant species found below bat feeding roosts grouped by seed size

Plant species found below bat feeding roosts, grouped by seed size and alphabetized by family. Medium and large seeds cannot be ingested by fruit bats. Species and genera names were verified by the Taxonomic Name Resolution Service (iPlant Collaborative 2011), except for Odyendea zimmermannii (see Clayton et al. 2007). Asterisks indicate first record of bat dispersal for that **genus or *species; new families are indicated by bold font. Plus sign (+) indicates a non-native species. Additional information on seed size, fruit color, fruit type, other disperser guilds, and other reports of bat dispersal can be found online in Appendix 1C.

Species (Family)
Large-seeded species (length >30 mm)
Magnistipula butayei De Wild. (Chrysobalanceae)
Maranthes goetzeniana (Engl.) Prance (Chrysobalanceae) **
Parinari excelsa Sabine (Chrysobalanceae)
Beilschmiedia kweo (Mildbr.) Robyns & R. Wilczek (Lauraceae) *
Cephalosphaera usambarensis (Warb.) Warb. (Myristicaceae) **
Pouteria adolfi-friedericii (Engl.) A. Meeuse (Sapotaceae) **

Medium-seeded species (30 mm> length >5 mm)
Sorindeia madagascariensis Thouars ex DC. (Anacardiaceae) **
Anisophyllea obtusifolia Engl. & Brehmer (Anisophyllaceae) **
Annickia kummeriae Setten & Maas (Annonaceae) **
Greenwayodendron suaveolens (Engl. & Diels) Verdc. (Annonaceae) **
Uvaria dependens Engl. & Diels (Annonaceae) *
Xylopia aethiopica (Dunal) A. Rich. (Annonaceae) **
Landolphia buchanani (Hallier f.) Stapf (Apocynaceae) *
Rauvolfia caffra Sond. (Apocynaceae)
Elaeis guineensis Jacq. (Arecaceae)+
Salacia elegans Welw. ex Oliv. (Celastraceae) **
Rourea minor (Gaertn.) Alston (Connaraceae) **
Drypetes gerrardii Hutch. (Euphorbiaceae) **
Alsodeiopsis schumannii (Engl.) Engl. (Icacinaceae) **
Strychnos sp. (Loganiaceae)
Xymalos monospora (Harv.) Baill. ex Warb. (Monimiaceae) **

Antiaris toxicaria Lesch. (Moraceae)
Trilepisium madagascariense DC. (Moraceae) **
Syzygium cordatum Hochst. (Myrtaceae)
Syzygium guineense (Willd.) DC. (Myrtaceae)
Syzygium jambos (L.) Alston (Myrtaceae)+
Strombosia scheffleri Engl. (Olacaceae) *
Maesopsis eminii Engl. (Rhamnaceae)+
Gambeya gorungosana (Engl.) Liben (Sapotaceae)
Gambeya perpulchra (Mildbr. ex Hutch. & Dalziel) Aubrév. & Pellegr. (Sapotaceae) *
Synsepalum cerasiferum (Welw.) T.D. Penn. (Sapotaceae) **
Synsepalum msolo (Engl.) T.D. Penn. (Sapotaceae) **
Odyendea zimmermannii Engl. (Simaroubaceae) **
Eriobotrya japonica (Thunb.) Lindl. (Rosaceae)+
Unknown species (3 species could not be identified to genus or family)

Small-seeded species (length <5 mm)
Coccinia mildbraedii Harms (Cucurbitaceae) **
Anthocleista grandiflora Gilg (Gentianaceae) *
Ficus cyathistipula Warb. (Moraceae) *
Ficus mucuso Welw. ex Ficalho (Moraceae)
Ficus natalensis Hochst. (Moraceae)
Ficus spp. (Moraceae)
Ficus sur Forssk. (Moraceae)
Milicia excelsa (Welw.) C.C. Berg (Moraceae)
Psidium guajava L. (Myrtaceae)+
Adenia lobata subsp. *rumicifolia* (Engl.) Lye (Passifloraceae) *
Passiflora edulis Sims (Passifloraceae)+
Aoranthe penduliflora (K. Schum.) Somers (Rubiaceae) **

Appendix 1C

Table 1C.1. Additional information about plant species from Table 1B.1, notes, and associated references.

Table 1C.1. Plant species[1] found beneath bat feeding roosts in and around the Amani Nature Reserve, East Usambara Mountains, Tanzania. Plant nomenclature follows the Taxonomic Name Resolution Service (iPlant Collaborative 2011), except for *Odyendea zimmermannii* (see Clayton et al. 2007). Fruit bat nomenclature follows Nesi et al. (2012). Seed/diaspore measurements include the hard endocarp surrounding seeds in some species (e.g. Sorindeia and Parinari). Unless otherwise noted, seed/diaspore lengths represent the longest dimensions measured (± 1SD) from the study area (CES, HJN, NJC). Fruit colours and types are categorised according to Lovett et al. (2006), Flora of Tropical East Africa (Beentje et al. 1952-2010), or observations by all authors: A = arillate, B = berry, D= drupe, M = monocarp, S = syconium or fig, U = unknown. Life forms are categorised by author observations: T= tree, L= liana, V= vine, U= unknown. Frugivores are listed by animal group (Ba = fruit bats, B = birds, Bu = bushpigs, C = Palm civet Nandinia binotata, G = Giant rat Cricetomys gambianus, P = primates, U = unknown) based on foraging observations, faecal investigations, and seed caching (in the case of the giant rat) by NJC between 1998 and 2011 in the study area. Brackets [ ] indicate the unconfirmed possibility of the animal group eating fruits of the plant species. The list of potential dispersers should not be considered exhaustive and seed dispersal effectiveness of any of these animal groups should not be assumed based on these listings.

Species	Total no.	Seed/diaspore length (mm ± SD) or fruit size	Seed size source	Fruit color	Fruit type	Life form	Frugivore grouping	Bat species	Country	Reference(s)
Anacardiaceae										
Sorindeia madagascariensis Thouars ex DC.	10	20.6 ± 3.0 (n = 40)		Yellow/orange	D	T	B, Ba, P			
Anisophylleaceae										
Anisophyllea obtusifolia Engl. & Brehmer	4	19.3 ± 3.2 (n = 62)		Red	D	T	B, Ba, P			
Annonaceae										
Annickia kummeriae (Engl. & Diels) Setten & Maas	2	21.6 ± 3.1 (n = 20)		Black/purple	M	T	B, Ba, P			
Greenwayodendron suaveolens (Engl. & Diels) Verdc.	4	11.4 ± 0.9 (n = 45)		Black	M	T	Ba, B			
Uvaria dependens Engl. & Diels	1	12.3 ± 0.3 (n = 5)		Orange	M	L	Ba			
Xylopia aethiopica (Dunal) A. Rich.	2	6.4 (n = 1)		Green/red	M	T	Ba, [B]			
Apocynaceae										
Landolphia buchananii (Hallier f.) Stapf	4	19 (n = 1)		Green	B	L	Ba, P			
Rauvolfia caffra Sond.	3	13.1 (n = 1)		Dark red	D	T	B, Ba	*Epomophorus gambianus, Epomophorus wahlbergi*	Ghana, South Africa	Lieberman & Lieberman (1986), Taylor (2000)

Arecaceae										
Elaeis guineensis Jacq.	8	22.3 ± 10.8 (n = 12)		Orange/red/black	D	T	B, Ba, P	*Eidolon helvum*	Unspecified	Micklburgh *et al.* (1992)
Celastraceae										
Salacia elegans Welw. ex Oliv.	3	12.7 (n = 2)		Orange	L	L	Ba			
Chrysobalanaceae										
Magnistipula butayei De Wild.	3	39.9 ± 8.0 (n = 13)		NR	D	T	Ba	*Eidolon helvum*	Zambia	Richter & Cumming (2006)
Maranthes goetzeniana (Engl.) Prance [4]	172	32.3 ± 2.6 (n = 20)		Black	D	T	B, Ba, G, [P]			
Parinari excelsa Sabine [4]	64	36.6 ± 5.8 (n = 40)		Brown-grey	D	T	B, Ba, G, P	*Eidolon helvum,* Unspecified	Uganda	Osmaston (1965), Chapman & Chapman (1996)
Connaraceae										
Rourea minor (Gaertn.) Alston	13	12.3 ± 1.4 (n = 8)		Red	A	L	Ba			
Cucurbitaceae										
Coccinia mildbraedii Harms	13	4.5 (n = 1)		Red	B	V	Ba			
Euphorbiaceae										

Drypetes gerrardii Hutch.	29	12.3 ± 1.0 (n = 32)		Yellow/brown	D	T	B, Ba, P			
Gentianaceae										
Anthocleista grandiflora Gilg [2, 4]	46	2.5 ± 0.3 (n = 6)		Green	B	T	Ba			
Icacinaceae										
Alsodeiopsis schumannii (Engl.) Engl.	2	19.6 ± 1.7 (n = 6)		Orange	D	T	B, Ba			
Lauraceae										
Beilschmiedia kweo (Mildr.) Robyns & R. Wilczek [5]	43	50.7 ± 4.0 (n = 53)		Dark red	B	T	Ba	Unspecified	Tanzania	Cordeiro *et al.* (2005)
Loganiaceae										
Strychnos sp.	1	12 (n = 1)		Yellow	B	U	Ba	Unspecified	Unspecified	Marshall (1985)
Monimiaceae										
Xymalos monospora (Harv.) Warb.	2	9.6 ± 0.2 (n = 120)	Lehouck *et al*. (2009)	Orange/red	D	T	B, Ba			
Moraceae										

Antiaris toxicaria Lesch.	2	12.49 ± 0.2 (n = 19)		Red	D	T	B, Ba, P, C	*Eidolon helvum,* unspecified	Ghana, Uganda, Kenya	Kankam & Oduro (2009), Osmaston (1965), Florchinger *et al.* (2010)
Ficus cyathistipula Warb.	3	<1		Green	S	T	Ba, P			
Ficus mucuso Welw. ex Ficalho	5	<1		Red/brown	S	T	Ba, P	*Rousettus aegyptiacus, unspecified*	Uganda, Nigeria	Baranga (1978), Okon (1974)
Ficus natalensis Hochst.	3	<1		Red/orange/yellow	S	T	B, Ba	*Eidolon helvum, Epomophorus labiatus, Epomophorus wahlbergi*	Ivory Coast, South Africa	Thomas (1982), Taylor (2000)
Ficus spp.	34	<1		Various	S	U	B, Ba, P			

Ficus sur Forssk.	11	<1		Red/orange	S	T	B, Ba, P	*Pteropus voeltzkowi, Rousettus aegyptiacus,* unspecified	Tanzania (Pemba), South Africa, Kenya	Entwistle & Corp (1997), Barclay *et al.* (2006), Flörchinger *et al.* (2010)
Milicia excelsa (Welw.) C. C. Berg	3	2.3 ± 0.1 (n = 12)		Green	D	T	Ba	*Eidolon helvum*, *Epomops buettifoferi, Hypsignathus monstrosus, Myonycteris angolensis, Micronycteris pusillus*	Ghana, Ivory Coast, Nigeria, Uganda	Taylor (1960), Osmaston (1965), Okon (1974), Thomas (1982), Taylor (2005)
Trilepisium madagascariense Thouars ex DC.	2	15.0 ± 2.4 (n = 22)		Purple/red	D	T	B, Ba, [P]			
Myristicaceae										
Cephalosphaera usambarensis (Warb.) Warb. [4, 5]	139	49.2 ± 4.8 (n = 38)		Cream	A	T	Ba, G	Unspecified	Tanzania	Cordeiro *et al.* (2005)
Myrtaceae										

Psidium guajava L.	31	3.0 (n= 2)	Pizo (2002)	Green	B	T	B, Ba, P	*Eidolon helvum, Micropteropus pusillus, Nanonycteris veldkampi, Epomophorus gambianus, Pteropus niger*	Ghana, Mauritius	Ayensu (1974), Nyhagen *et al.* (2005)
Syzygium cordatum Hochst.	1	7 (n = ?)	Wilson & Downs (2012)	Purple	B	T	B, Ba, [P]	*Epomophorus wahlbergi*	South Africa	Taylor (2000)
Syzygium guineense (Willd .) D.C.	2	13.0 $\pm$ 1.4 (n = 10)		Purple	B	T	B, Ba, P	*Eidolon helvum*	Zambia	Richter & Cumming (2006)
Syzygium jambos L. (Alston) [3]	13	10-16 (n = ?)	Orwa *et al*. (2009)	White	B	T	Ba	*Pteropus niger*	Mauritius	Nyhagen *et al.* (2005)
Olacaceae										
Strombosia scheffleri Engl.	16	22.7 $\pm$ 2.2 (n = 22)		Black	D	T	B, Ba, P			
Passifloraceae										
Adenia lobata subsp. *rumicifolia* (Engl.) Lye [2]	7	4.1 $\pm$ 0.2 (n = 30)		Green	B	L	Ba			
Passiflora edulis Sims	1	4 (n = 1)		Yellow	B	L	Ba			

Rhamnaceae										
Maesopsis eminii Engl. [3]	181	21.0 ± 1.4 (n = 17)		Black/purple	D	T	B, Ba, Bu, C, G, P	*Eidolon helvum*	Unspecified	Micklburgh *et al.* (1992)
Rosaceae										
Eriobotrya japonica (Thunb.) Lindl.	2	10- 20 (n = ?)	Orwa *et al*. (2009)	Orange	B	T	Ba	*Rousettus aegyptiacus*	Israel	Izhaki *et al.* (1995)
Rubiaceae										
Aoranthe penduliflora (K. Schum.) Somers	3	< 2		Orange	B	T	Ba			
Sapotaceae										
Gambeya gorungosana (Engl.) Liben	1	21 (n = ?)	Dominy & Duncan (2005)	Red-brown	B	T	Ba, C, P	Unspecified	Uganda	Duncan & Chapman (1999)
Gambeya perpulchra (Mildbr. ex Hutch. & Dalziel) Aubrév. & Pellegr.	174	26.9 ± 9.0 (n = 41)		Red-brown	B	T	Ba, C, P			
Pouteria adolfi-friedericii (Engl.) Meeuse	26	32.0 ± 3.8 (n = 40)		Green	B	T	Ba, P			
Synsepalum cerasiferum (Welw.) T. D. Penn.	12	16.9 ± 2.3 (n = 20)		Red	B	T	B, Ba, P			
Synsepalum msolo (Engl.) T. D. Penn.	3	20.1 ± 0.8 (n = 20)		Red	B	T	B, Ba, P			
Simaroubaceae										
Odyendea zimmermanni Engl.	9	27.2 ± 8.3 (n = 85)		Purple-black	D	T	B, Ba, G, P			

Unknown										
Unk4	1	13.3 (n = 1)		Unknown	U	U	Ba			
Unk7	1	12.1 (n = 1)		Unknown	U	U	Ba			
Unk10	1	13.3 (n = 1)		Unknown	U	U	Ba			

Additional notes

[1] Species for which only immature fruits were found (such as jackfruit and avocado) were not included in Appendix 2 and 3 since bats were not observed to disperse mature seeds or fruits.

[2] *Myonycteris angolensis* was observed defaecating *Anthocleista grandiflora* and *Adenia lobata* subsp. *rumicifolia* seeds after capture in a mist net by CES.

[3] *Myonycteris angolensis* was observed dropping *Syzygium jambos* and *Maesopsis eminii* fruits by CES.

[4] *Epomophorus* sp. was captured with a fruit of *Anthocleista grandiflora* in its mouth by NJC, at the same fresh bat roost with seeds of *Cephalosphaera usambarensis*, *Parinari excelsa* and *Maranthes goetzeniana*.

[5] Species previously reported as bat-dispersed in a conference proceedings volume by NJC and HJN (Cordeiro *et al.* 2005) but we have included it in the tally of new bat-dispersed species because the data are presented here.

Table 1C.2. Selected published observations of bat-fruit interactions in Africa.

All plant species are in the same genera (or family) as species reported in Table 1B.1 and Table 1C.1, but they were not included in Table 1C.1 because the plant species are different. Genus and species names are as reported by the original authors.

Plant Family & Species	**Bat Species**	**Country**	**Reference**
Annonaceae			
Uvaria leptocladon	*Pteropus voeltzkowi*	Tanzania (Pemba Is.)	Mickleburgh *et al.* (1992)
Cucurbitaceae			
Momordica spp. ?	*Epomops buettikoferi*	Ivory Coast	Thomas (1982)
Apocynaceae			
Landolphia kirkii	*Pteropus voeltzkowi*	Tanzania (Pemba Is.)	Entwistle & Corp (1997)
Gentianaceae			
Anthocleista longifolia	*Pteropus rufus*	Madagascar	Bollen (2007)
Anthocleista madagascariensis	*Pteropus rufus*	Madagascar	Bollen (2007)
Anthocleista nobilis	*Epomops buettikoferi, Eidolon helvum, Hypsignathus monstrosus, Myonycteris angolensis*	Ivory Coast	Thomas (1982)
Lauraceae			
Beilschmiedia madagascarensis	*Pteropus rufus*	Madagascar	Bollen (2007)
Monimiaceae			
Tambourissa purpea	*Pteropus rufus*	Madagascar	Bollen (2007)
Myristicaceae			
Pycnanthus angolensis	*Eidolon helvum*	Unspecified	Mickleburgh *et al.* (1992)
Olacaceae			
Strombosia glaucescens	Unspecified	Ivory Coast	Alexandre (1978)

Plant Family & Species	Bat Species	Country	Reference
Passifloraceae			
Adenia cissampeloides	*Epomops buettikoferi, Eidolon helvum, Hypsignathus monstrosus, Lissonycteris angolensis, Myonycteris torquata*	Ivory Coast	Thomas (1982)
Adenia meigei	*Epomops buettikoferi, Eidolon helvum, Myonycteris torquata*	Ivory Coast	Thomas (1982)
Passiflora quadrangularis	*Pteropus voeltzkowi*	Tanzania (Pemba Is.)	Entwistle & Corp (1997)

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Appendix 1D How to identify areas below bat feeding roosts.

Figure 1D.1 A photo of fruit and seed remains below a bat feeding roost

Fruit and seed remains below a bat feeding roost indicated by colored arrows: *Cephalosphaera usambarensis* seeds (yellow), *C. usambarensis* aril spats (orange), *Maesopsis eminii* diaspore (teal), and *Coccinea mildbraedii* fruit spats (white).

Figure 1D.2 Another photo of fruit and seed remains below a bat feeding roost

Pouteria adolfi-friedericii seeds (pink arrow) and fruit spats (blue arrow) below a bat feeding roost. Unripe *Parinari excelsa* fruit (green arrow) has no clear evidence of bat dispersal.

Figure 1D.3 A third photo of fruit and seed remains below a bat feeding roost

Fruit and seed remains below a bat feeding roost indicated by colored arrows: *Cephalosphaera usambarensis* seed (yellow), *Maranthes goetzeniana* diaspore (red), *Maesopsis eminii* diaspore (teal), and *Coccinea mildbraedii* fruit spats (white).

Figure 1D.4 Photo of seedlings that germinated below a bat feeding roost

Seedlings that germinated below a bat feeding roost in bamboo at the forest edge. We do not know for sure that these were all bat-dispersed since we did not examine the diaspores. *Cephalosphaera usambarensis* seedling (yellow arrow), *Pouteria adolfi-friedericii* seedling (purple arrow), *Maesopsis eminii* seedling (teal arrow), *Gambeya perpulchra* seedling (black arrow), and *Strombosia scheffleri* seedling (gray arrow).

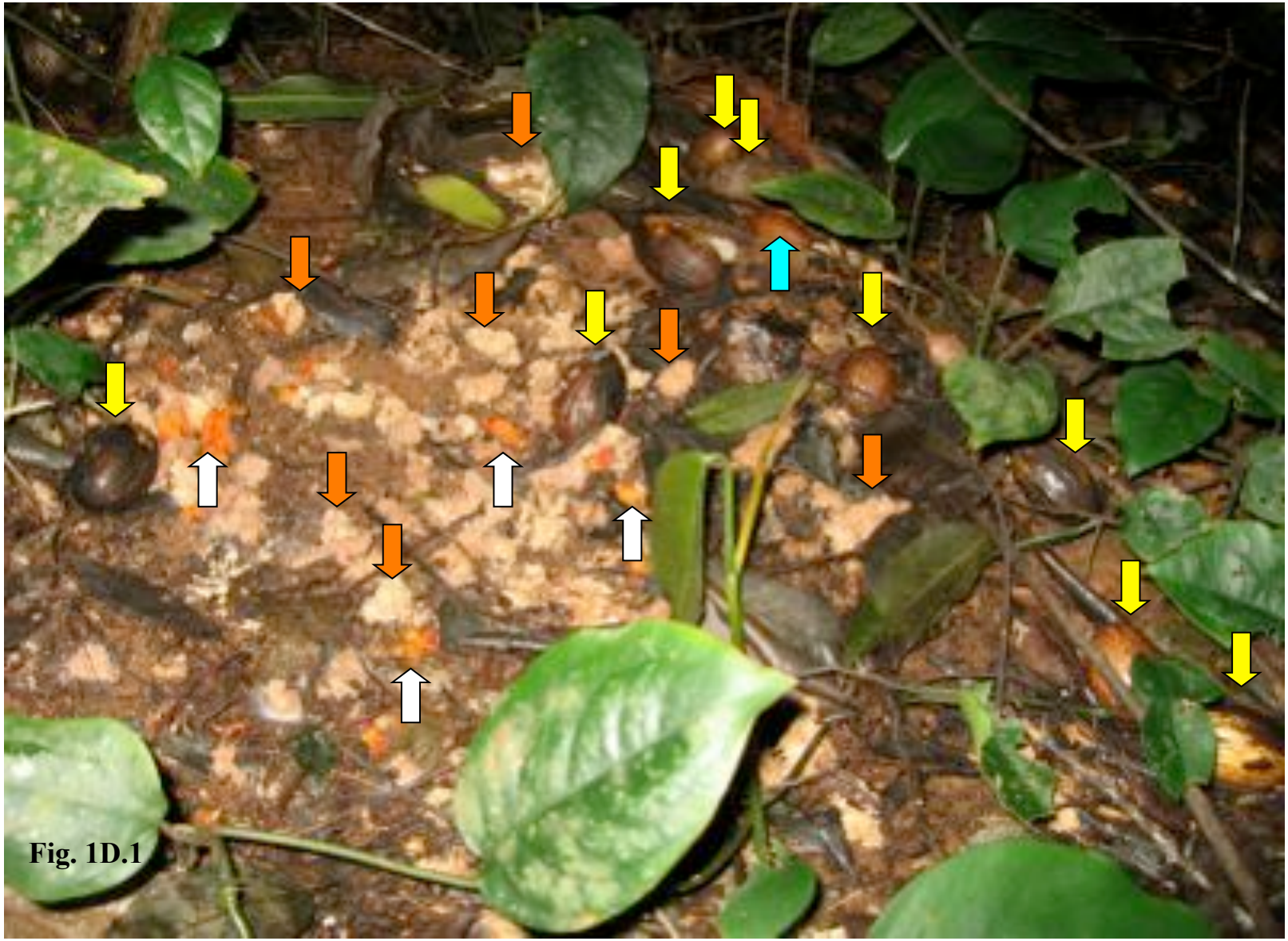

Fig. 1D.1

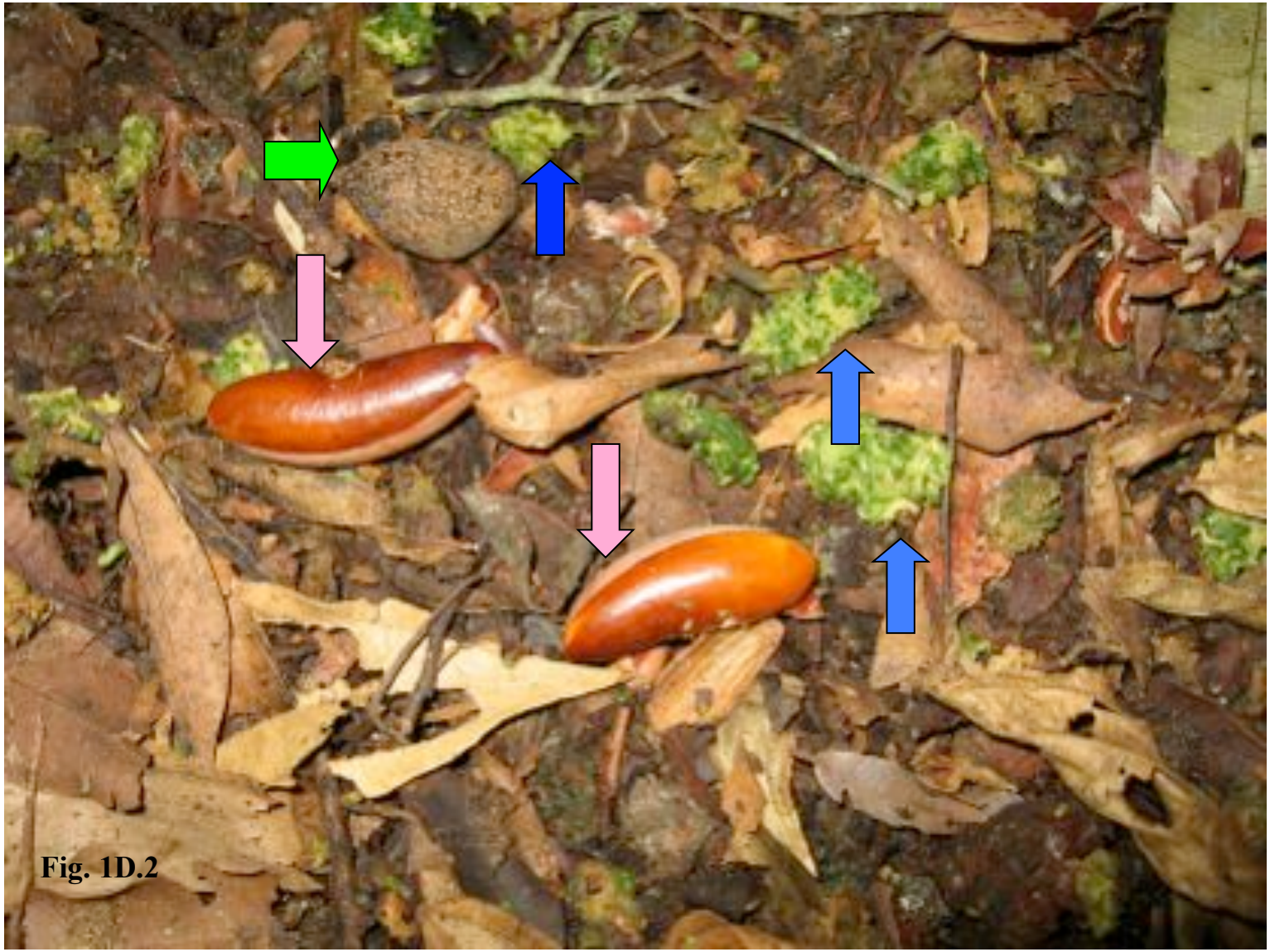

Fig. 1D.2

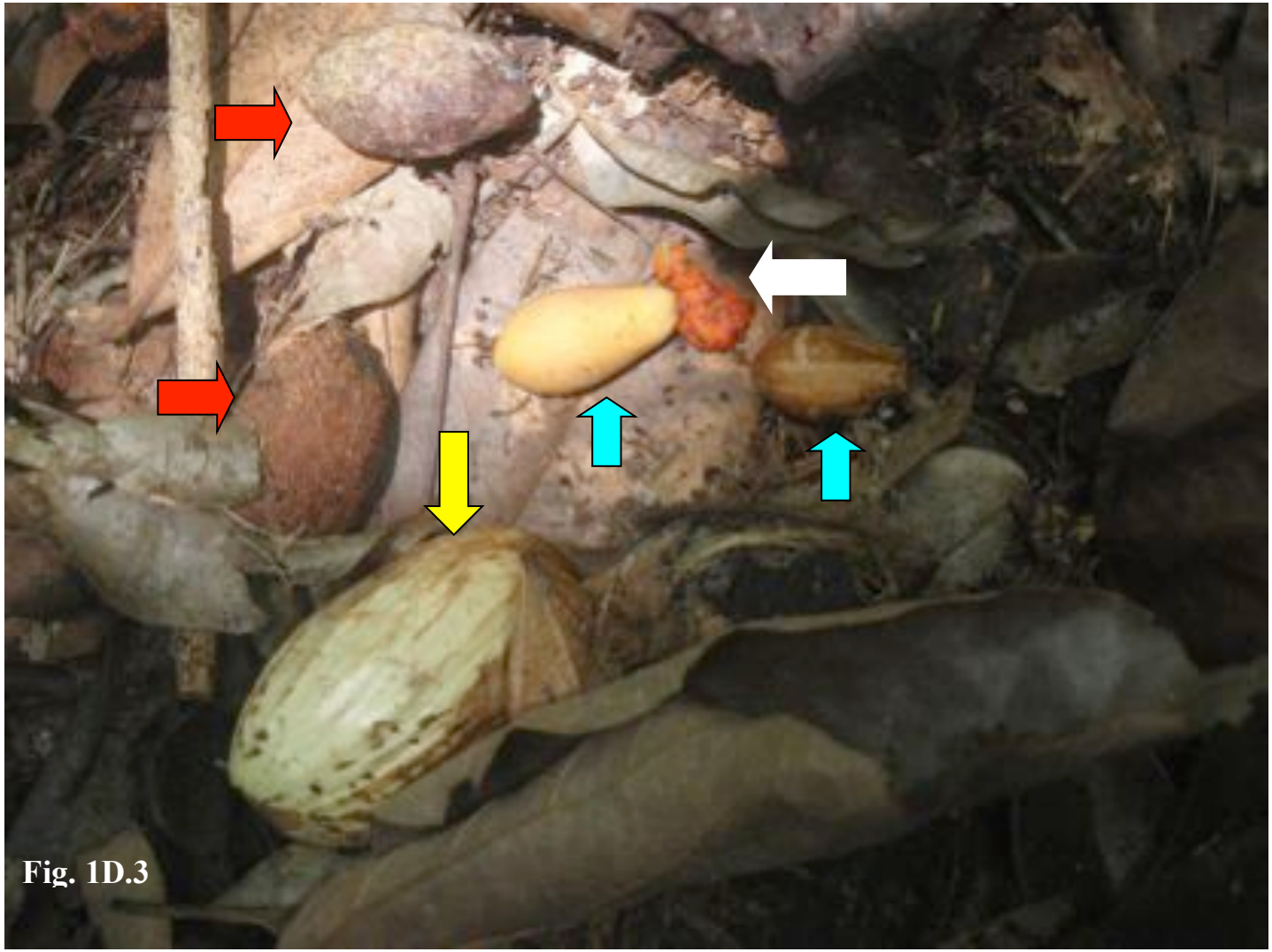

Fig. 1D.3

Fig. 1D.4

2 SEED HARVESTING OF A GLOBALLY THREATENED AFRICAN TREE DISPERSED BY RODENTS: IS ENRICHMENT PLANTING A SOLUTION?

2.1 Abstract

High harvest levels of non-timber forest products such as seeds can alter recruitment of the harvested species. This study tested the potential for enrichment planting of *Allanblackia stuhlmannii* (Clusiaceae), a canopy tree species with seeds harvested and pressed for vegetable oil. I planted 960 seeds in twelve different 50 x 50 m plots within the Amani Nature Reserve (Tanzania) with varying levels of background seed abundance and rodent activity. Seed presence and condition was recorded for 10-11 months after planting. After that time, 9.0% of seeds remained in the original planting location; 1.7% had germinated and an additional 2.2% had established. The fate of seeds that went missing is unknown, but it is possible that some of those seeds germinated in rodent caches, as all seed removal was attributed to rodents. Generalized Linear Mixed Models were used to examine the relationship between seed persistence over specific time intervals and the covariates of background seed abundance and rodent activity. There was no clear effect of seed abundance and rodent activity over the long term, but both covariates decreased the probability of seed persistence over the first 12 days. Assuming 1 in 45 planted seeds would establish, it would cost approximately US$0.14 per seedling in the value of planted seeds in 2012 seed prices. Enrichment planting with seeds could be a cost-effective strategy for increasing *A. stuhlmannii* recruitment.

2.2 Introduction

Non-timber forest products (NTFPs) such as fruits, seeds, sap, or leaves offer income sources from forests without cutting down trees. For example, Brazil nuts (*Bertholletia excelsa*), hearts of palm (*Euterpe edulis*), and açaí berries (*Euterpe oleracea*) are commonly collected from forests rather than grown on plantations. Although NTFP harvest is less damaging than timber extraction or clearing forests for agriculture or pasture, it may still have ecological impacts (Peters 1994, Ticktin 2004, Ticktin and Shackleton 2011). These include direct negative demographic effects on harvested species, as well as altering their relationships with other species. Examples from three different systems illustrate these effects: frankincense resin harvest can reduce seed production (Rijkers et al. 2006), selective collection of the largest herbs (leaving only the smallest to reproduce) can reduce their size over time (Law and Salick 2005), and intensive açaí berry harvest can reduce frugivorous bird diversity (Moegenburg and Levey 2002). Tree populations may be able to sustain harvest of 92-93% of a seed crop (Zuidema and Boot 2002, Emanuel et al. 2005), but sustainable harvest levels depend on details of species' life history traits (Zuidema et al. 2007). There is potential to alter the recruitment of a NTFP species by removing massive amounts of seed from the wild.

The impact of NTFP harvesting in the wild can be managed or mitigated in two main ways: spatial and/or temporal limitations on harvest, and strategies such as enrichment planting of seeds or seedlings to facilitate recruitment (Peters 1994). Each approach has its challenges. Harvest limitations ensure some seed is left to be naturally dispersed, but enforcing these restrictions may be difficult in remote areas or where there are more pressing conservation

threats (Duchelle et al. 2012). Enrichment planting of seeds or seedlings can increase recruitment (e.g. Makana and C Thomas 2004), but requires the investment of time and resources. Most enrichment planting in tropical forests has been studied in the context of reforestation after logging, where researchers compared survival of various species in gaps (e.g. Schulze 2008), skidding trails (e.g. d'Oliveira and Ribas 2011), plantations (e.g. Cole et al. 2011), and secondary forest (e.g. Ådjers et al. 1995). There is some informal and experimental record of enrichment planting with NTFP species, particularly for Brazil nuts (*Bertholletia excelsa*). Traditional strategies of enrichment planting are known from the Amazon estuary where residents have long planted and managed açaí berries (*Euterpe oleracea*) and other desirable NTFP species (Anderson et al. 1995). Experimentally, Peña-Claros et al. (2002) compared Brazil nut seedling growth in lines cleared to different widths, and as a result recommend that enrichment planting should not be done in deep forest with low light levels but that the species is suitable for enrichment planting in more open areas, similar to results from Kainer et al. (1998). Enrichment planting may be done with seeds or seedlings. Seedlings may be more likely to succeed than seeds but require additional time, investment, infrastructure, and care. In contrast, seeds are easier to transport, store, and plant. Studies that have compared the outcomes and quantified the cost of planting both seeds and seeds found that enrichment planting with seeds can be much less expensive (Schulze 2008, Cole et al. 2011). This may make them a better choice for enrichment planting, even though a greater number of seeds need to be planted to achieve the same goal. Determining which management methods to employ depends in part on studying the practical and ecological factors, as well as seed characteristics, influencing the survival, germination, and establishment of planted seeds.

Many oil-rich seeds that are desirable to humans as NTFP's are also preferred food sources of rodents. Scatterhoarding rodents are conditional mutualists, acting as both seed predators and seed dispersers, depending on the relative abundance of food resources and rodents (Theimer 2004). Although many seeds are eaten and destroyed by rodents, some seeds cached by rodents are forgotten and germinate (reviewed by Theimer 2004). Altered seed availability due to NTFP harvest may shift the position of rodents in this ecological interaction. Well-documented examples of rodent-NTFP interactions include agoutis (*Dasyprocta leporina*) and acouchies (*Myoprocta acouchy*) in central and south America with Brazil nuts (e.g. Tuck Haugaasen et al. 2011) and *Carapa* spp. (e.g. Jansen et al. 2004). Spatial distribution of Brazil nut trees influences agouti distribution; agoutis are found in higher densities and have smaller home ranges in areas with Brazil nut trees compared to areas without (Jorge and Peres 2005). d'Oliveira et al. (2011) noted that rodent predation can even be a problem for Brazil nut seedlings that are several months old, but only near adult conspecific trees. Negative demographic effects of NTFP seed harvest may be compounded through promoting increased seed predation. African giant pouched rats (*Cricetomys* spp.) act similarly to agoutis in seed predation and dispersal (Guedje et al. 2003, Nyiramana et al. 2011) but less is known about how their behavior affects NTFP dispersal and regeneration. The ability of scatterhoarding rodents to locate cached seeds also raises the possibility that reduced seed availability might decrease the efficacy of enrichment planting of seeds.

I am interested in the sustainability of seed harvest in Africa, and the management practices that might enable it. Nine species of trees from the genus *Allanblackia* (Clusiaceae) are found in moist forests across tropical Africa. They bear large fruits with lipid-rich seeds traditionally

pressed for cooking oil. Unilever, a multinational corporation with many uses for vegetable oils, is working with The World Agroforestry Centre (ICRAF), The World Conservation Union (IUCN), Netherlands Development Organization (SNV), and several other organizations in a partnership called Novella Africa Initiative. Novella partners are working in Tanzania, Nigeria, and Ghana to develop a sustainable supply chain for three species, *Allanblackia stuhlmannii, A. floribunda*, and *A. parviflora* (Jamnadass et al. 2010). Presently they are encouraging research on *Allanblackia* harvest, propagation, and commercial uses for the oil. Wild populations of *Allanblackia* cannot meet the expected demand for seeds, so the partnership is actively cultivating varieties that are high-yielding and faster to mature. *Allanblackia* is being promoted as a component of mixed agroforestry, but there are several characteristics of *Allanblackia* species that delay its ability to meet demand through farms alone (explained nicely by Pye-Smith (2009)). As a result, much harvesting currently comes (and will continue to come) from wild populations. Some of these populations may be locally managed reserves that permit seed collection, but harvest is also happening in protected areas such as the Amani Nature Reserve in the East Usambara Mountains of Tanzania.

All Novella Initiative partners have stated interest in the long-term sustainability of *Allanblackia* seed harvest. Harvesters are instructed to "encourage the regeneration" (Pye-Smith 2009), "avoid eroding the gene pool by selective harvesting or over-harvesting" and "work with nature by promoting natural regeneration and encouraging dispersers" (Amanor et al. 2003). How exactly can these recommendations be translated into effective instructions?

The objective was to test the effectiveness of seed enrichment planting of *A. stuhlmannii*. Can seed planting result in germination and establishment? The study was conducted under different levels of fruit availability, which could mimic different levels of harvesting since harvest reduces the amount of seeds in an area. How do different levels of background fruit abundance and rodent activity affect seed persistence? How much would enrichment planting cost and who would pay? These are important questions that must be answered to provide land managers and stakeholders with the information they need to ensure sustainable *Allanblackia* seed harvests.

2.3 Methods

2.3.1 Study site

The Amani Nature Reserve (ANR) (S 5° 6', E 38° 38') protects 8380 ha of lowland and submontane rainforest in the East Usambara Mountains in northeastern Tanzania (Tanga region). The East Usambara Mountains (EUM) are part of the Eastern Arc Mountains, which are a discontinuous string of moist submontane and montane massifs separated by drier lowland areas stretching from southwest Tanzania into southeastern Kenya. Up until the 1960s, the East Usambaras were mostly forested (Hamilton and Bensted-Smith 1989); today only 24% remains in forest cover (Burgess et al. 2007). Most forest clearing has been for tea plantations, non-native timber plantations, and small-scale multicrop farming. The EUM receive 1700-2300 mm of rain throughout the year but the heaviest rains are in the short rainy season (October-November) and the long rainy season (late March-May) (Hamilton and Bensted-Smith 1989).

2.3.2 Study species

Allanblackia stuhlmannii Engl. (Clusiaceae) is a rainforest canopy tree endemic to the Eastern Arc Mountains of Tanzania. *A. stuhlmannii* is dioecious (separate male and female trees) and approximately one-third of the mature trees in the forest appear to be reproductive females (Mathew et al. 2009). It is one of the most common canopy tree species in ANR. Both male and female trees produce large, conspicuous, white and pink flowers concurrent with fruiting. Large insects, birds, and bats are possible pollinators (Mathew et al. 2009). Each female tree typically produces 3-160 fruits per year, varying considerably among years and individual trees (NJC & HJN unpub. data). Fruits mature over the course of about one year into large (2-5 kg), brown, drupes that fall to the ground when ripe. Each fruit contains approximately 36 ± 2 (SE) oil-rich seeds, each seed weighing 11.24 ± 0.08 g (Mathew et al. 2009). Seeds are 62-67% fat, and high in stearic and oleic oils, which have the commercially desirable quality of being solid at room temperature and melting at 40-46 °C (Eckey 1954).

2.3.3 Plot selection

To capture natural variation in background fruit abundance in the forest, I established twelve separate 50 x 50 m plots in four different blocks (three plots per block) within ANR. Each plot was at least 200 m from the forest edge. Plot locations were randomly discovered (see appendix 2A for additional details) and each plot included canopies of at least four *Allanblackia* trees with fruit. All *Allanblackia* trees inside the plot were measured (DBH) and the presence of fruit and flowers recorded. Plots within a block were separated by at least 150 m, and blocks were at least 1200 m apart (Figure 2.1).

2.3.4 Seed collection & experimental planting

In total, I planted 960 *Allanblackia* seeds (8 seeds were excluded from analysis because they were planted 4 days late). More than 600 seeds were collected from four different farmland sites. Seeds were washed to remove fruit pulp and air dried. Two plantings of 40 seeds each were directly planted in each plot. Ten seeds were randomly selected from each seed source and the planting sequence was randomized. The weight and source of each seed was recorded immediately before planting using a digital pocket scale (American Weigh AMW-100 Silver Precision Digital Pocket Scale 100 x 0.01 g, Norcross, Georgia, USA). Seeds were planted 2 m apart in U-shaped transects (to keep them inside the boundary of the plot), partially buried 75-90% under soil or humus and then covered with surrounding leaf litter. The depth was chosen to facilitate our ability to census the seeds and is similar to typical caching behavior of large rodents (pers. obs.). A white plastic planting label (~1.9 x 10.2 cm) was placed consistently on one side of the transect approximately 15 cm away from the seed.

2.3.5 Censusing plots

Seeds were experimentally planted twice, once in late February/early March 2011 (referred to as planting 1) and again in late March/early April 2011 (planting 2) to increase the sample size. Each block was censused 4, 8, 12, and 28 or 30 days after setup. Planting 1 seeds were also censused at 28, 32, 36, 40, and 58 days (corresponding with planting 2 setup and 4, 8, 12, and 30 day checks). After late April, each block was visited once per month until September 2011, then seeds were revisited in November 2011 and January 2012 (327 days after beginning the experiment).

During each census, the presence and condition of each planted seed was checked by briefly examining the buried seed while wearing a nitrile glove. Seeds were recorded as either present or missing. Present seeds were classified based on their condition as intact, eaten, germinated, established, or rotten (the latter based on visible signs of dessication, fungus, or insect infestation).

2.3.6 Background fruit abundance

Plots were surveyed for freshly fallen fruits on each census until the end of the fruiting season in 2011. Newly fallen fruits were categorized as available to rodents (either intact or already opened by rodents) or harvested by humans. Fruits with seeds harvested by people and fruits with seeds removed by rodents are easily distinguished. When people harvest seeds, they almost always leave behind the heavy fruit pulp bearing conspicuous machete marks. To prevent re-counting, fruits were marked with a piece of biodegradable flagging tape. Additional details provided in Appendix 2A.

2.3.7 Rodent activity

Camera traps were used to monitor tagged seeds for a parallel experiment (Chapter 3), which was established and visited on the same schedule as the planting experiment. Tagged seeds were placed in three stations within each plot. One randomly selected seed station in each plot received a camera trap. We used photos from ten Bushnell Trophy Cameras (Bushnell Corporation, Overland, Kansas, USA) that recorded animal motion in front of each camera. Two plots were excluded from analyses due to extremely low numbers of photographs that I do not think was representative of activity in the plots. Photos of large rodents (giant rats or squirrels) were tallied for each observation interval. These intervals consisted of the length of time between

subsequent censuses, adjusted for instances when batteries died. Estimates of average daily rodent activity for each plot and census interval were then obtained by dividing the total number of rodent photos by the duration of the interval. See Appendix 2A for specifics on camera settings and photo management.

2.3.8 Analyses

First I addressed questions regarding which factors influence the likelihood that seeds will remain untouched where they were planted. At any given census, seeds were classified as either present (intact, eaten, germinated, established) or absent. Generalized linear mixed models (GLMMs) allowed me to model how the probability of seed persistence over a fixed time interval changes with underlying covariates including seed weight and rodent activity. Nested random effects of plot within block were included to account for the potential lack of independence between observations imposed by the experimental design employed. GLMMs enabled me to model binary data (with a binomial distribution) as a linear function of covariates (by way of a logit link function). These models were used to understand seed persistence over both short time intervals at the beginning of the experiment and across the duration of the entire experiment.

We used the GLMM approach instead of Cox proportional hazards models to facilitate the incorporation of nested random effects. Both modeling approaches can provide insight into how covariates affect survival probabilities over time. Cox proportional hazards models can, within a single model, uncover temporal variation in the effects of covariates on survival, which requires fitting multiple GLMMs over subsequent time intervals. However, it is much more straightforward to implement random effects in GLMMs and this study focuses primarily on

long-term survival outcomes and management implications, rather than fine scale temporal variation in effects.

A model-comparison approach based on Akaike information criteria (AIC) was used to compare and select the best GLMMs based on parsimony and likelihood estimates, as the estimation of reliable p-values for this class of models is contentious (Bolker et al. 2009).

The set of candidate models subjected to model comparison was assembled based on our hypotheses along with the relevant nested models, enabling me to isolate and test the importance of specific effects (Hilborn and Mangel 1997, Burnham and Anderson 2002, Bolker 2008). All GLMMs treated block and plot as nested random effects. The null model included only these random effects. Planting was included in all other models as a fixed effect as it had only two levels, making it difficult to model appropriately as a random effect. Additional models included seed mass (standardized), rodent activity over a specific time interval, and interactions of these variables. Standardized variables were calculated by subtracting the mean and dividing by the standard deviation. All analyses were done in R 2.15.1 (R Core Team 2012) using packages bbmle (Bolker and Team 2012) and lme4 (Bates et al. 2012).

Straightforward comparisons of means and variance used t-tests and F-tests, respectively. We used a Chi-square test to compare the proportions of seeds germinating and persisting from different sources. Confidence intervals for proportions were calculated using the exact method in the R package binom (Dorai-Raj 2009).

2.4 Results

2.4.1 Seed persistence and fate

First I will look at the long-term (final census) fate of the experimentally planted seeds across all plots and both plantings. At the last census in January 2012, 10-11 months after planting, 9.0% of seeds (86 out of 952, 7.3-11.0% (all ranges indicate 95% confidence intervals)) were still in the location where they were planted. Throughout the experiment, germination was observed in 4.8% of seeds (46, 3.6-6.4%) across all censuses, but 0.9% (9, 0.4-1.8%) of seeds that had germinated were no longer present at the last census, meaning they were removed by rodents sometime after germinating. Of seeds that remained at the last observation, 5.1% had no signs of germination (49, 3.8-6.7%), 1.7% (16, 1.0-2.7%) still had only a radicle (germinated but not established), and 2.2% (21, 1.4-3.4%) were established with a shoot visible above ground (Figure 2.2). All remaining seeds still appeared to be viable with no signs of rot or desiccation.

2.4.2 Fruit abundance and rodent activity

The mean number of fruits added to a plot between censuses during the fruiting season varied from 0-5.25 (mean= 0.76, median= 0.50). The cumulative total number of fruits available to rodents in plots over the course of the experiment ranged from 22 to 175 (mean=64.75, median= 46.5). Plots varied considerably in proportion of fruit harvested by humans, from 0-43%; the proportion across all plots combined was 17%.

All seed removal was attributed to rodents. Giant pouched rats and squirrels were photographed on the camera traps near tagged seeds on the soil surface (from a parallel experiment). Of photos with these large rodents, giant pouched rats were in 80.4% of photos. All giant pouched rats in ANR are a single species, *Cricetomys gambianus*. Squirrel photos were all *Paraxerus* spp.

2.4.3 Long-term and short-term effects

Contrary to expectations, average daily rodent activity over the first 40 days did not clearly explain seed persistence until the last observation, nor did background fruit abundance (see Table 2.3 and Appendix 2B). However, incremental processes over shorter timescales result in the seed fates observed at the final census, so it can be illuminating to investigate some of these noteworthy events. For example, most of the seeds that were removed over the course of the entire experiment disappeared in the first 30 days (Figure 2.3). In each planting, seed persistence over the first 12 days decreased with increasing rodent activity and fruit abundance (see GLMM reported in Tables 1 and 2). There was also support for an important positive interaction between rodent activity and fruit abundance. As the value of both covariates increases, the interaction term moderates the negative main effects of both rodent activity and fruit abundance. We visualized the modeled relationship between seed persistence, rodent activity, and fruit abundance (Figure 2.4) using the covariates and intercepts from table 2. Thus, while I found no long-term effects of these biotic interactions on seed persistence, it appears they were operating during a period shortly after planting.

Five to six months after planting (between days 148 and 183), there was a second precipitous drop in the number of seeds present (Figure 2.3). Unfortunately, seeds were only being censused once per month and the cameras were no longer in the field, so we do not have finer-scale censuses or rodent activity during that time. If we did, it may be possible to more precisely identify the timing of predation (e.g. whether it was over days or weeks) to understand what may have prompted it. We do know this second major removal event greatly reduced the mean number of seeds remaining in each plot-planting ($t=3.0041$, $df=46$, $p=0.0043$) and the variance

among plot-plantings (F=2.5259, df=23, p=0.03071) (Figure 2.5) The reduction in variance limits our ability to detect effects of fruit abundance on persistence, since fruit abundance is measured at the plot level and the variation among plots decreases over time. This could either be because the effect sizes become small, or in the extreme because they are cancelled out entirely. This helps explain in part the discrepancy between what I observed in GLMMs with fruit abundance and rodent activity in the long term (no effect) and the short term (biotic effects).

2.4.4 Germination

Germination occurred slowly over several months. Most germination was observed 5-9 months after planting (Figure 2.3), varying from 30 to 327 days. The average time until germination was observed differed between the two plantings, with seeds in planting 1 germinating more slowly (mean= 247 days, or ~8.2 months) than in planting 2 (mean= 176 days, or ~5.8 months) (t= 4.1829, df=44, p<0.001). About 50% more seeds germinated in planting 2 (n=28) as compared to planting 1 (n=18), although more seeds persisted to the final census from planting 1 (n=47) than planting 2 (n=39).

2.4.5 Effects of seed characteristics

Characteristics of the seeds such as mass and source population were potential sources of variation in seed fate. Seed source did not have a significant effect on either seed persistence until the last observation (χ^2 = 4.3256, df=3, p= 0.2284) or germination (χ^2 = 1.1304, df=3, p= 0.7697). Seeds that germinated during the observation period (even if they later disappeared) were significantly heavier (mean= 13.00 g) than seeds that had not yet germinated or had disappeared (mean= 11.78 g) (Figure 2.6) (t= 2.321, df=950, p= 0.010). However, seed mass did not differ between seeds that did and did not persist until the last census (t= -0.3088, df= 950, p=

0.6212), or between seeds that were intact versus germinated or established at the last census (t= -2.0093, df = 84, p= 0.9761). This is consistent with results from the GLMMs that showed little effect of seed mass on probability of seed persistence (Table 2.1 and Table 2.3).

2.5 Discussion

The results of this long-term study are ecologically interesting, with important, applicable findings for conservation. First I review and interpret our main results, then compare them to other research and suggest related avenues of investigation. Finally, I offer specific information for managers and stakeholders about the possible implementation and cost of seed enrichment planting.

The experiment shows that nearly 1 in 10 planted seeds (9.0%, 95% CI 7.3-11.0%) may escape detection by rodents for several months. Based on data from a parallel experiment with tagged *Allanblackia* seeds, about two-thirds of seeds removed by rodents were scatterhoarded (CES, unpub. data). A similar proportion of experimentally planted seeds may have been cached by rodents. Of those, some are likely forgotten and germinate unobserved. Many more seeds still have the potential to establish since *Allanblackia* seeds can have long dormancy and may take up to 3 years to germinate in a screen house (*A. parviflora*, Ofori et al. (2011)). Therefore, our observation of a 2.2% establishment rate is very conservative. The parallel experiment with tagged seeds had only 0.3% establishment after the same time period (CES, unpub. data). This suggests that directly planting seeds can lead to higher rates of establishment compared to what could be expected from seeds left on the surface because rodents are less likely to find and remove them.

I found that seed size did not differ between seeds that were removed and seeds that persisted until the last census, suggesting that there was not a difference in detectability based on seed size (or any difference was too minor to detect). This is different than most other studies examining the effect of seed size on removal by scatterhoarders (Table 9 in Jansen et al. 2004), where most found higher removal for larger seeds. More recently, Wang and Chen (2009) used artificial seeds with controlled nutrient and tannin content to find that rodents were more likely to remove larger seeds even if they had no nutritional value. Since our planted seeds were untagged, we cannot know how seed size influenced the fate of seeds once they were found by rodents, but it is possible that the seeds were moved to areas of lower conspecific tree (and hence seed) density, as demonstrated by agoutis in Panama (Hirsch et al. 2012). Furthermore, cache theft (i.e. removal of a seed from a cache by a different animal than the one that placed it there) can dramatically increase dispersal distance beyond the initial cache distance (Jansen et al. 2012), and we know that *C. gambianus* are capable of cache theft because our experimentally planted seeds were essentially seeds cached by humans.

Forty-five percent of seeds disappeared in the first 12 days after planting, after which removal rates declined dramatically. Unsurprisingly, plots with higher average rodent activity had lower seed persistence during those first 12 days (modeled in Figure 2.4). The second noticeable decline in seed persistence that occurred in August 5-6 months after planting may correspond to a period of low food abundance for rodents in the forest. August is the middle of the cool dry season (Hamilton and Bensted-Smith 1989). Giant rats are known to eat a wide variety of food items and are by no means *Allanblackia* specialists since they occur in many places in Africa where *Allanblackia* does not. That said, *Allanblackia* seeds are highly palatable to rodents in

Amani; rodent trapping censuses found it to be as preferable as coconut (NJC et al., unpub. data). Perhaps after depleting their own stores during a lean time, rodents were more likely to go cache-thieving. Local studies of rodent food preferences and phenology could be used in combination to test this hypothesis, but presently the dietary details of rodents are poorly known in the Eastern Arc Forests.

Future studies of enrichment planting may want to investigate the effect of varying levels of planting depth and seed cleaning on seed persistence to provide species-specific recommendations. The depth at which I planted seeds is similar to what could be expected of someone without a specific digging tool instructed to plant seeds (i.e. a seed harvester). Increasing planting depth decreases the odor at the surface and has also been shown to decrease seed removal (summarized in Vander Wall 1993). Perhaps declining odor from the seeds over time makes them more difficult to detect in the weeks or months after planting. In Panama, experimentally cached palm (*Astrocaryum standleyanum*) seeds that were de-fleshed persisted in greater numbers than palm seeds that were not de-fleshed (Jansen et al. 2010). This is consistent with earlier research that more odoriferous seeds are easier for naïve rodents to find (Stapanian and Smith 1984). Fresh *Allanblackia* seeds have a distinctive odor that people can detect, so it is easy to understand how *C. gambianus* finds seeds that have been planted (or cached by other rodents). Indeed, *C. gambianus* have a keen sense of smell and can be trained to detect land mines (Poling et al. 2011) and tuberculosis (Mgode et al. 2012). The extent to which fruit pulp is removed from seeds influences its odor. In our experiment, *Allanblackia* seeds were washed manually with water to remove all fruit pulp. Since informal planting schemes may not allow for this level of seed processing, it would be wise to test unwashed seeds.

In our experimental plots, the overall seed harvest rate by people was approximately 17% (range 0-43% across plots). If *Allanblackia* is demographically similar to *Sclerocarya birrea* subsp. *caffra* (Emanuel et al. 2005) or Brazil nuts (Zuidema and Boot 2002), then the level is no cause for concern since over 90% of seeds could be harvested without jeopardizing future recruitment. We suspect that harvest rates within ANR near edges and close to human settlement are higher than what I observed since all plots were located at least 200 m from forest edges or major roads through the forest to minimize interference from harvesters. Harvest rates may also rise if increasing *Allanblackia* oil demand raises prices. Research on *Allanblackia* demography along with broader surveys of harvester behavior are sorely needed to assess the sustainability of wild harvest as it is currently practiced.

The sustainability of harvesting has been questioned for many other types of NTFPs. In some East African protected areas, NTFP harvest has significantly reduced pole density even in areas where it is prohibited (Ndangalasi et al. 2007). Meanwhile, some Tanzanian village forest reserves in the East Usambaras, which were created explicitly to allow access to forest resources, in practice, have highly restrictive local enforcement that ends up shifting local use to other forest or farm areas (Rantala et al. 2012). Village forest reserves might be ideal targets for implementation of an informal enrichment planting scheme, since one of the indirect benefits quantified from the reserves was *Allanblackia* seed collection.

Phenology data collected in Amani over several years (NJC and HJN, unpub. data) illustrates that the crop size within trees varies much more year to year than the number of fruiting trees (i.e. most female trees have at least some fruit every year, but some years most trees have a lot of

fruit), resulting in highly variable interannual fruit production. We did not find a clear effect of background fruit abundance on long-term seed persistence. This suggests that, within the ranges I observed, it is equally worthwhile to plant seeds in low- and high-density areas. It is also worth noting that the year of the experiment (2011) was a relatively low year for *Allanblackia* fruit production in Amani (CES, pers. obs.). As a result, the levels of fruit abundance observed in plots were probably at the low end of the possible range. Repeating the same experiment in other years in the same plots is likely to encompass a much different distribution of fruit abundance. However, it is notable that even in a year with low seed availability, some planted seeds escaped detection by rodents, which is promising for the potential for successful enrichment planting.

The enrichment planting strategy I tested could be carried out in two main ways: organized or informal. In an organized strategy, land managers (e.g. private landholders or village leaders) could coordinate the planting of seeds all at once over a defined area. This could be especially useful in areas without *Allanblackia* or in historically over-harvested areas that may need mitigation in the form of planting despite enforced harvest limitations. Alternatively, an informal planting scheme could take the form of guidelines for collectors such as planting one seed in the ground for each fruit they harvest. This informal approach would be consistent with the current vague recommendations to collectors about sustainability (see introduction). It is important that seeds be planted singly, since two or more seeds planted together are more likely to be detected by rodents (Vander Wall 1993), and, even if undetected, would be in clear competition with each other.

Allanblackia seeds provide an important source of supplemental income to households since typical wages in the area are only $1.50/day (Bullock et al. 2011) and many seed collectors are women who are less likely to be wage-earners (Pye-Smith 2009). It is crucial to consider the potential social impact of an informal enrichment planting scheme based on the cost to collectors. The price for selling *Allanblackia* seeds was US$0.288 per kg in 2012 (M. Mpanda, pers. comm.). If we assume an average seed weighs 11.24 g, then there are approximately 89 seeds per kg. Approximately one seed in 45 reaches establishment (952/21), which makes the cost per seedling approximately US$0.145. If harvesters themselves were asked to plant a seed from each fruit, this would represent a missed opportunity cost of about 1/36 of what they collect, or about 2.8% of their potential harvest. Based on data of household income from *Allanblackia* seed collection in 2009 (Bullock et al. 2011), this would represent an average household reduction of US$1.15 per year if all of the seeds were collected from wild sources rather than farms. The approach of planting one seed per fruit would also be consistent with recommendations to ensure that the wild stock is not degraded over time by selectively harvesting from the most preferable trees while leaving seeds from those with less desirable traits (Peters 1994). Considering that *Allanblackia* seed collection is positively associated with participation in conservation behaviors such as planting trees and preserving forest on private land (Morgan-Brown et al. 2010), it seems that harvesters would be amenable to sustainable practices. It is up to managers and stakeholders to decide if enrichment planting of seeds is a worthwhile pursuit.

We tested seed enrichment planting as a management strategy and calculated the approximate cost in terms of the value of weight in seeds needed to produce one seedling. Enrichment

planting using seeds could be effective, but the costs should be considered. While species interactions/ecological dynamics could alter the contexts in which seed enrichment planting is effective, the variables I examined yielded no strong evidence of these effects over the long term. These variables did affect seed persistence over the short term; I suspect long-term effects are weakened or negated by unobserved and intriguing biotic interactions long after the initial planting. Improved measures of rodent abundance or activity, along with knowledge of the scale at which these under-studied rodents make foraging decisions, would be useful for future studies. Estimates of germination and establishment rates from this study, along with additional demographic data for later life stages, can and should be used to make demographic projections critical for understanding the sustainability of the NTFP harvest of *Allanblackia*. Enrichment planting using seeds may also be an affordable and viable option for other wild-harvested seed crops such as Brazil nuts and *Carapa* spp. An experimental approach is important to implement before widespread adoption of enrichment planting, especially in more degraded forest fragments that may not have adult trees as a natural seed source since research with agoutis and acouchies and Brazil nuts have shown that seeds are more predated and dispersed shorter distances in fragments compared to continuous forest (Jorge and Howe 2009). Furthermore, future investigations should examine the potential consequences of seed harvesting for shifting rodent diets to other non-target plant species. Even for NTFPs, it is important to understand the ways in which harvest can alter biotic interactions and use that information to inform management decisions.

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2.8 Figures and Tables

Figure 2.1 Diagram of the experimental setup for *Allanblackia* seed planting

Diagram of the experimental setup for *Allanblackia* seed planting.

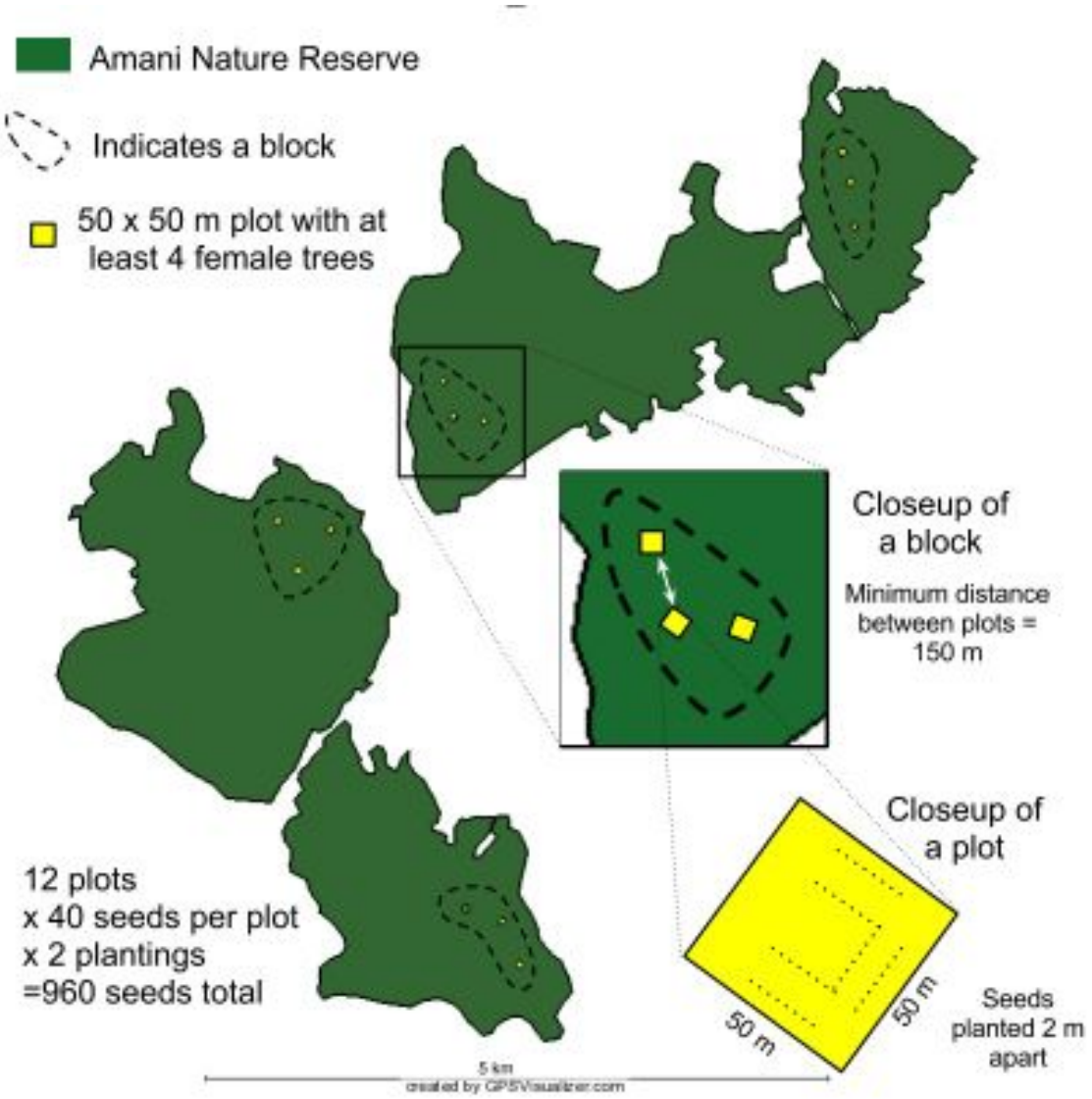

Figure 2.2 Bar chart showing the fate of seeds as of the last census

Bar chart showing the fate of seeds as of the last census in January 2012, 10-11 months after planting. Removed seeds were 89.9% of the total and are not represented in the figure.

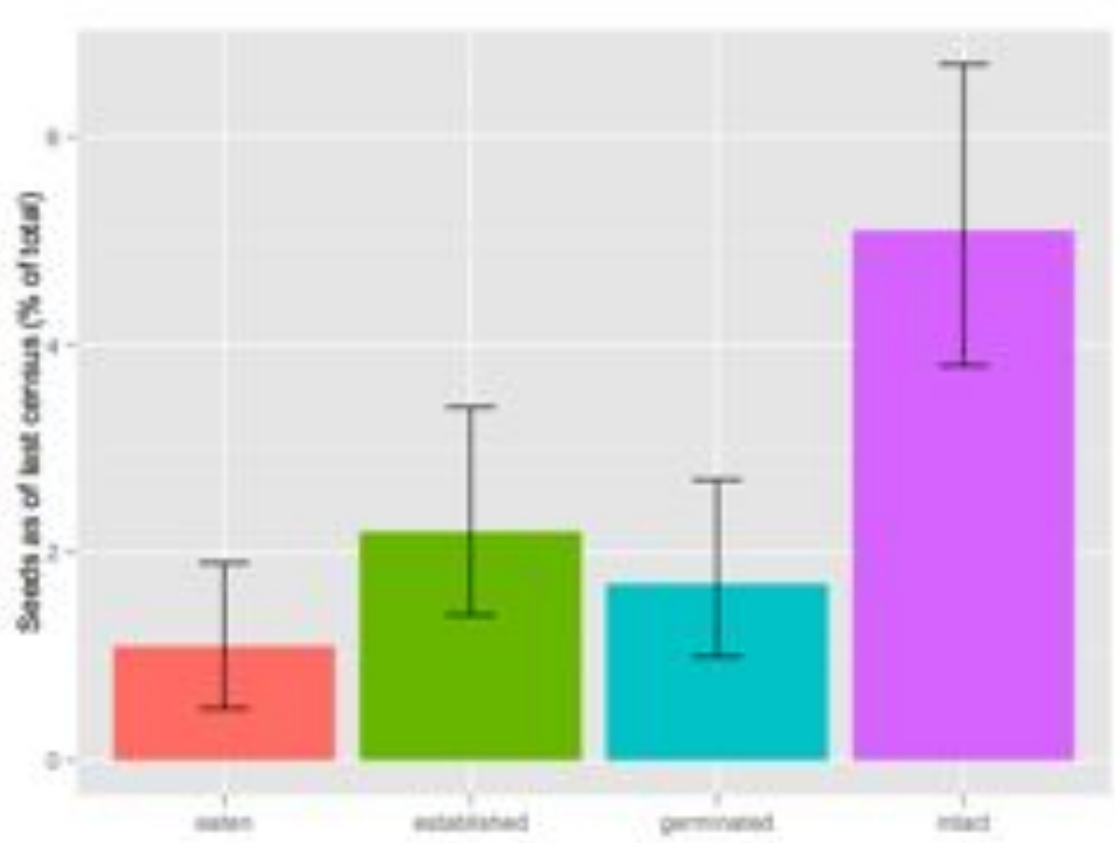

Figure 2.3 Stacked bar graphs showing seed fate over time for the two plantings

Stacked bar graphs showing seed fate over time (all plots pooled) for the two plantings (1 below, 2 above). Red, blue, and green are all conditions where the seed remains present and viable in the original location. Seeds that were recorded as eaten or missing remain in those categories over subsequent censuses.

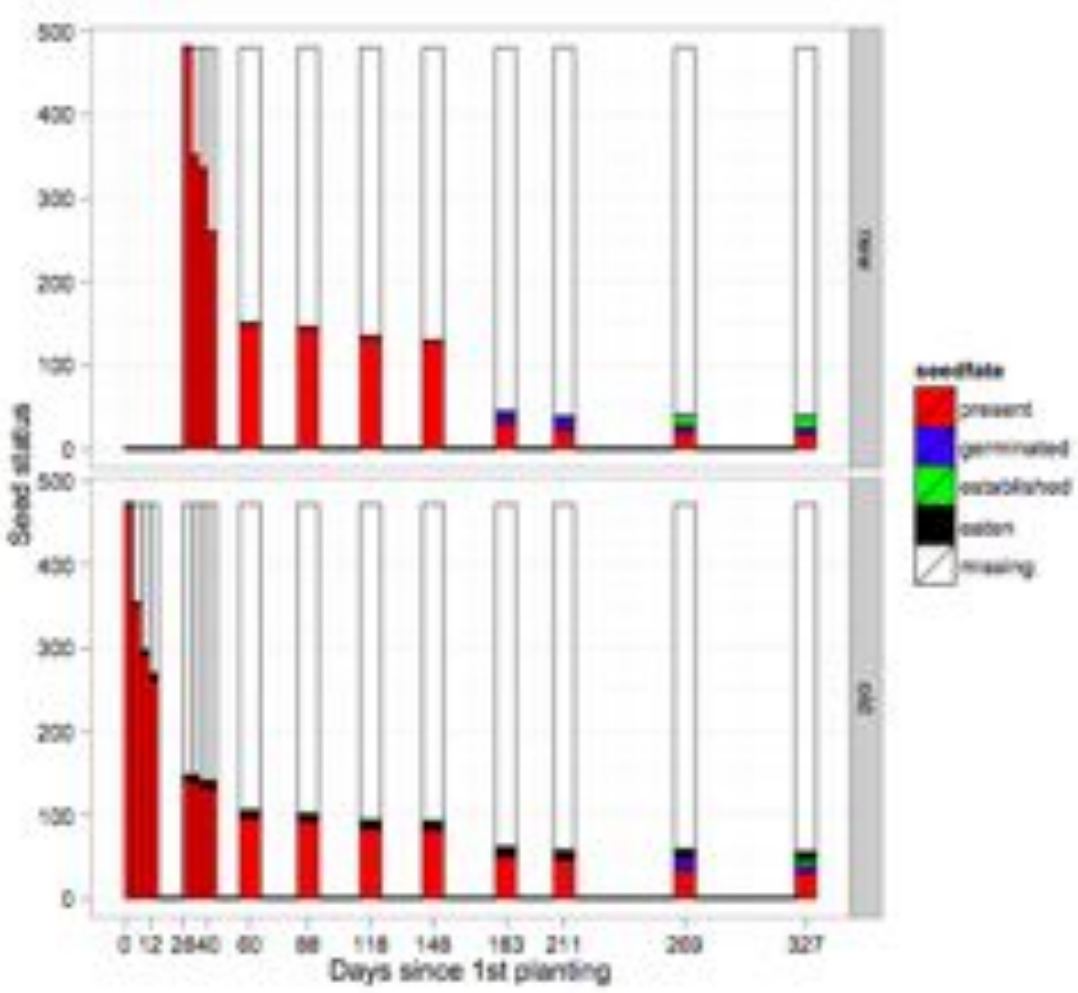

Figure 2.4 Visualization of the coefficient estimates from the model in table 2.2

Visualization of the coefficient estimates from the model in table 2.2 for rodent activity and fruit abundance on seed persistence over the first 12 days after planting. Rodent activity is the mean number of large rodent images captured per day over the first 12 days of each round. Fruit abundance is the mean number of ripe fruits in a plot that were available to rodents over the first 12 days of each planting. The lines indicate the expected proportion of seeds persisting under the combination of rodent activity and fruit abundance conditions.

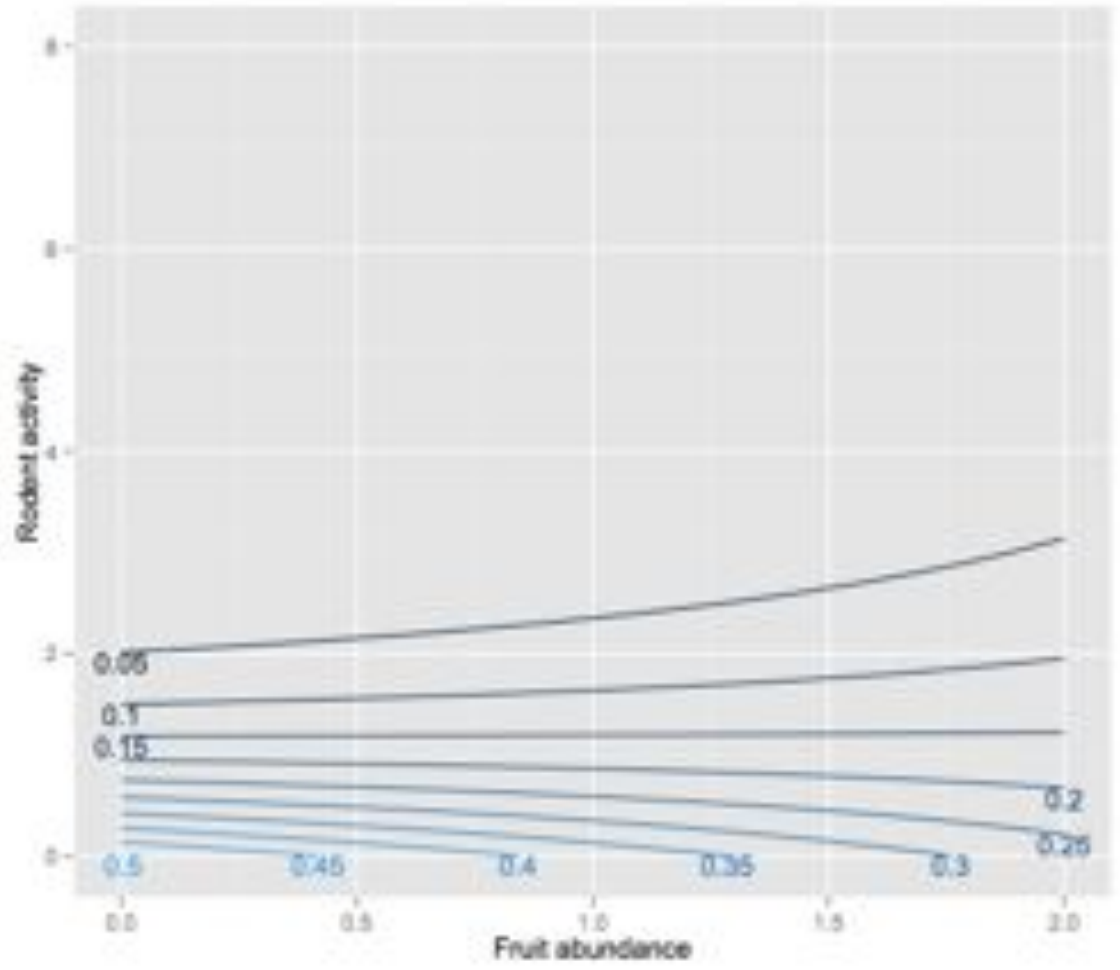

Figure 2.5 Box plot showing the range of counts for the number of seeds present by plot

Box plot showing the range of counts for the number of seeds present from a particular planting and plot (n=24) at days 148 and 183. Boxes show the second quartile, median, and third quartile. Whiskers indicate highest and lowest values within 1.5 times the interquartile range. Asterisks indicate the means.

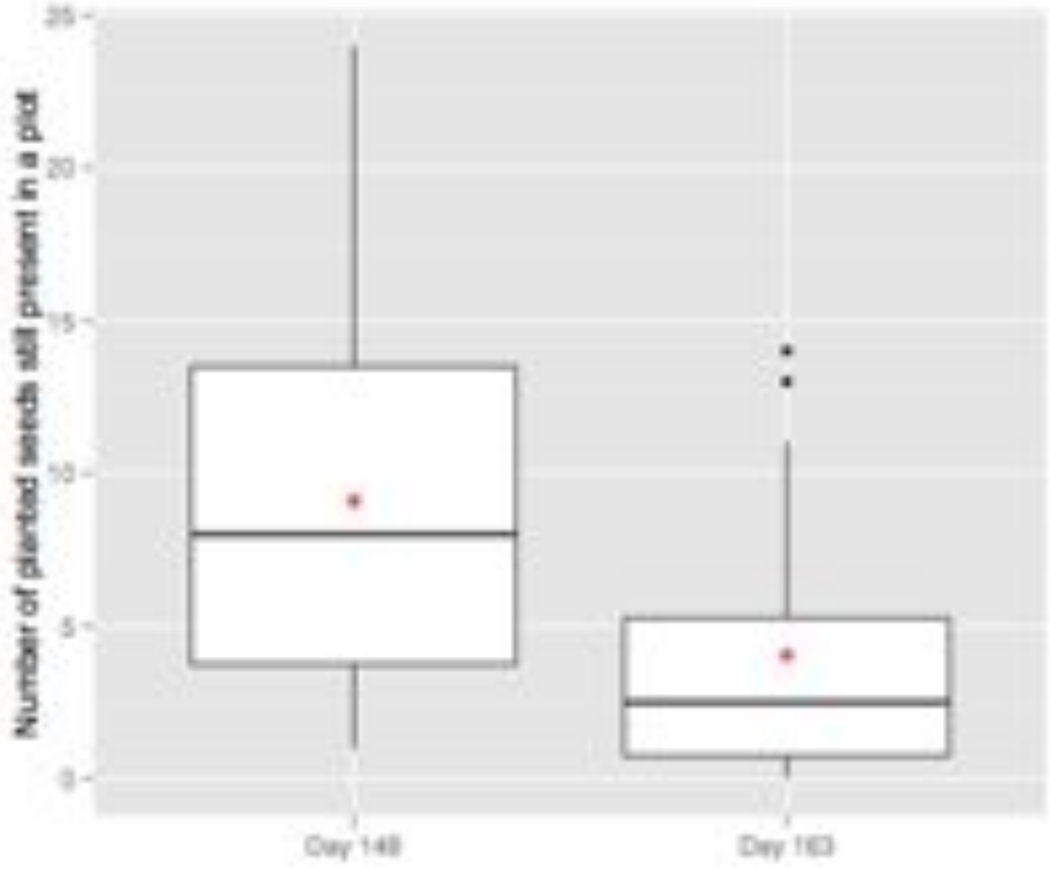

Figure 2.6 Box plot comparing the masses of germinated and non-germinated seeds

Box plot comparing the masses of germinated (G) and non-germinated (NG) seeds. Non-germinated seeds include those that were removed as well as those that were not removed but had not yet germinated. Boxes show the second quartile, median, and third quartile. Whiskers indicate highest and lowest values within 1.5 times the interquartile range. Outliers are values outside 1.5 times the inter-quartile range plus the third quartile or minus the first quartile. Asterisks indicate the means, which are significantly different (t= 2.321, df=950, p= 0.010).

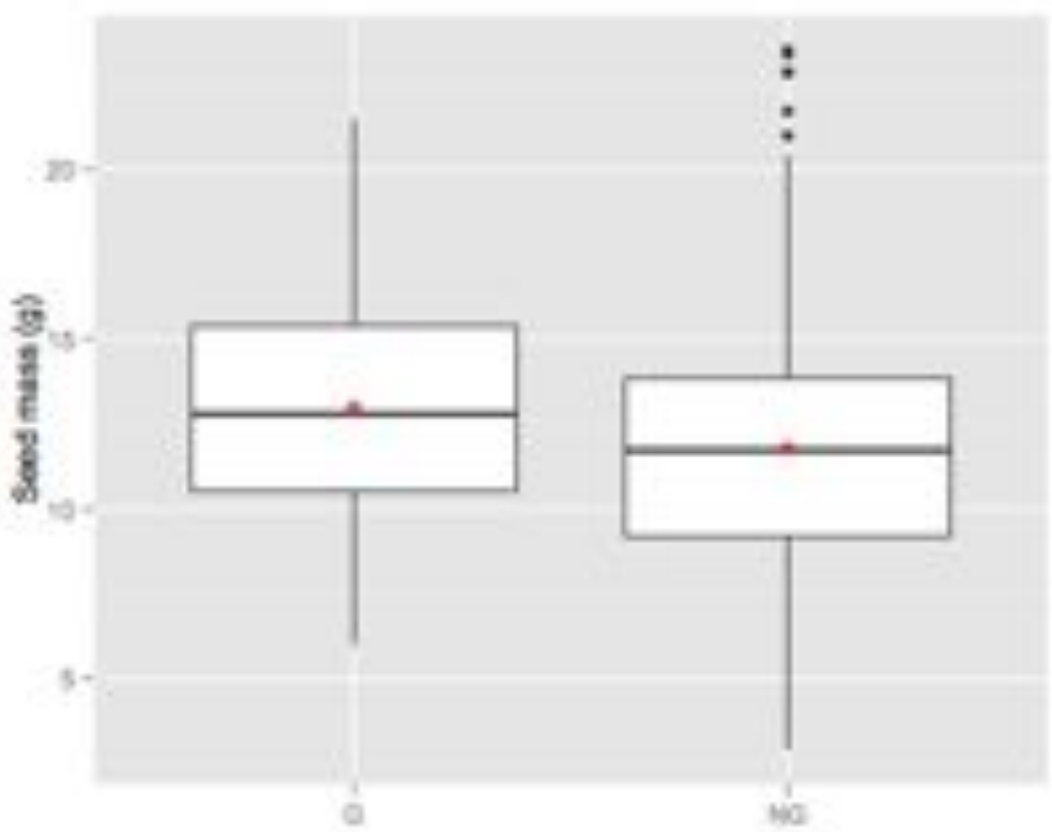

Table 2.1 GLMM model comparison results for seed persistence from planting day 12

GLMM model comparison results for seed persistence from planting until 12 days later. All models contain random effects of plot nested within block (or in lme4 syntax 1|Block/Plot). The null model contains only random effects and an intercept. Delta AIC values (or dAIC) are obtained by calculating the difference between the AIC value of the best fit model (that with the lowest AIC) and the AIC values of each of the remaining models (Burnham and Anderson, 2010). df indicates the degrees of freedom for each model. In the model covariates, seed.mass is standardized seed mass, rodent.activity is the average large rodent activity (photos) per day in a plot over the first 12 days of a round, and fruit.abund is the average daily number of ripe *Allanblackia* fruits that were available to rodents in a plot over the first 12 days of a round. The best fitting model includes rodent activity and fruit abundance.

Model covariates	**dAIC**	**df**
Round + fruit.abund * rodent.activity	0	7
Round + rodent.activity	2.7	5
Round + fruit.abund + rodent.activity	3	6
Round + rodent.activity + seed.mass	3.7	6
Round + seed.mass + fruit.abund + rodent.activity	4.2	7
Round + rodent.activity * seed.mass	4.3	7
Null	6.9	3
Round	8.3	4
Round + seed.mass	8.9	5
Round + fruit.abund	9.7	5
Round + seed.mass + fruit.abund	10.4	6
Round + seed.mass * fruit.abund	12.3	7

Table 2.2 Estimates of coefficients and standard errors from GLMM with the best fit

Estimates of coefficients and standard errors for fixed and random effects from GLMM with the best fit (lowest dAIC) in table 1. There was only one model with dAIC $\leq$2.

Model	
Fixed effects	
	Estimate (S.E.)
Intercept	2.1762 (0.7112)
Round	-0.5952 (0.2125)
fruit.abund	-1.4666 (0.5783)
rodent.activity	-0.4817 (0.1383)
fruit.abund:rodent.activity	0.4173 (0.1792)
Random Effects	
	Variance (S.D.)
Block	3.8847e-12 (1.9710e-06)
Plot:Block	1.4393 (1.1997)
Model fit	
Log Likelihood	-458.5
Df	7

Table 2.3 GLMM model comparison results for seed persistence from planting until the last observation

GLMM model comparison results for seed persistence from planting until the last observation. All models contain random effects, as explained for Table 2.1. In the model covariates, seed.mass is standardized seed mass, std.rodent.activity is the standardized average large rodent activity (photos) per day in a plot over the first 40 days of the experiment, and cml.fruit is the cumulative total number of ripe *Allanblackia* fruits that were available to rodents in a plot over the course of the 2011 fruiting season. Seed mass does not appear in most of the best models, but fruit abundance and rodent activity appear in two and three of the best five models, respectively. The coefficients associated with the best models can be found in Appendix 2B.

Model	Model covariates	dAIC	Df
2	Round + cml.fruit	0	5
00	Null	0.9	3
0	Round	1.3	4
6	Round + cml.fruit + std.rodent.activity	1.3	6
1	Round + std.rodent.activity	1.5	5
5	Round + seed.mass + cml.fruit	1.9	6
3	Round + seed.mass	3.1	5
9	Round + seed.mass * cml.fruit	3.2	7
7	Round + seed.mass + cml.fruit + std.rodent.activity	3.2	7
10	Round + cml.fruit * std.rodent.activity	3.2	7
4	Round + std.rodent.activity + seed.mass	3.3	6
8	Round + std.rodent.activity * seed.mass	5.3	7

Appendix 2A- Additional methods

Plot selection

Using Google Earth imagery to identify the forest edges, a boundary 200 m from the edge was defined for each block using the buffer tool in ArcGIS 9.3.1 (ESRI, Redlands, California, USA). Inside the 200 m boundary, I walked on random compass bearings until I found an area with at least four fruiting *Allanblackia* trees. This approach ensured that there would be natural fruit fall within each plot since randomly placed plots may not have contained fruiting trees. Therefore, the densities of *Allanblackia* trees within the plots are higher than a randomly placed plot in the forest, but I randomized discovery of these high-density areas.

Fruit Abundance

In the field, freshly fallen fruits were categorized as unripe, ripe and intact, ripe and broken, ripe and already opened by rodents, or ripe and harvested by humans. Only seeds available to rodents (ripe and intact, ripe and broken, and ripe and already opened by rodents) were used to calculate the measures of fruit abundance used in analyses.

The original design of the experiment was to have a high, low, and control level of fruit abundance in a plot in each block. Plot treatments were randomly assigned within each block. At each visit, all intact *Allanblackia* fruits from the "low" plot were counted and moved to the "high" plot in the same block. Fruit abundance in control plots was recorded without manipulation. Since the attempted manipulation was overwhelmed by natural variation, the counts of ripe fruits were used instead to distinguish among levels of fruit availability. When calculating fruit abundance, fruits removed from "low" plots were counted in averages of fruit availability for the preceding period, but not in the cumulative totals for a plot. The opposite is

true for “high” plots, where fruits moved into a plot by researchers were counted in the average fruit availability for the next census interval and the cumulative total, but not the preceding period. Essentially, this assumes that the moved fruits were available to rodents in their “low” plot before I moved them, and available to rodents in the “high” plot after I moved them. Even in a “low” plot, fruits with the seeds already removed (either by rodents or humans) were enumerated but not moved to the “high” plot.

Camera settings

Ten Bushnell Trophy Cameras (Bushnell Corporation, Overland, Kansas, USA) and two Buckeye Apollo Cameras (ATSI, Athens, Ohio, USA) recorded animal motion in front of the camera. Camera settings for the Bushnells were 5 megapixels, normal sensitivity, 3 photos per trigger, and 10 sec between trigger events. Buckeye Apollo settings were as close to the Bushnell as possible (high sensitivity, 1.3 megapixels, 3 photos per trigger, and 10 sec between trigger events). For analyses of rodent activity, the plots with Buckeye cameras were excluded due to the extremely low levels of rodent activity captured on camera that I do not think is representative of the plots due to the smaller field of view of those cameras due to their chance location on steep slopes.

Mice were excluded from estimates of rodent activity since *Allanblackia* seeds are so large relative to their size, making mice unlikely to be involved in the excavation and removal of planted seeds.

Photo management

Digital photographs of animals were tagged with the species using Picasa (Version 3.8.9.390 for Mac). For hard-to-see photos, the "I'm feeling lucky" feature in Picasa was used to automatically adjust color and contrast. A script in R that accesses the Terminal (command line Mac OS X 10.6.8) extracted tags and image times from photo metadata. The script it available upon request from the authors and could be adapted for use on other Macs.

Appendix 2B Additional GLMM outputs

Table 2B.1 Estimates of coefficients and standard errors for fixed and random effects from GLMMs in table 2.3 with dAIC ≤2

Estimates of coefficients and standard errors for fixed and random effects from GLMMs in table 2.3 with dAIC ≤2.

Model	Gfit2	Gfit00	Gfit0	Gfit6	Gfit1	Gfit5
Fixed effects						
	Estimate (S.E.)	Estimate (S.E.)	Estimate (S.E.)	Estimate (S.E.)	Estimate (S.E.)	Estimate (S.E.)
Intercept	-3.581375 (0.535519)	-2.5878 (0.3632)	-2.7594 (0.3919)	-3.342957 (0.542028)	-2.6726 (0.3109	-3.598155 (0.539100)
Round	0.322301 (0.257877)	-	0.3241 (0.2571)	0.322210 (0.258162)	0.3239 (0.2578)	0.352531 (0.273133)
ripeAdj.cm	0.016268 (0.008066)	-	-	0.012730 (0.008299)	-	0.016204 (0.008096)
stot.rod.avg	-	-	-	-0.234946 (0.273753)	-0.4261 (0.2777)	-
sWeight		-	-	-	-	0.044045 (0.132479)
Random Effects						
	Variance (S.D.)	Variance (S.D.)	Variance (S.D.)	Variance (S.D.)	Variance (S.D.)	Variance (S.D.)
Block	0.059481 (0.24389)	0.24327 (0.49322)	0.24583 (0.49581)	2.4120e-10 (1.5531e-05)	3.3008e-10 (1.8168e-05)	0.062681 (0.25036)
Plot:Block	0.368215 (0.60681)	0.48365 (0.69545)	0.48617 (0.69726)	3.9061e-01 (6.2499e-01)	5.3733e-01 (7.3303e-01)	0.366651 (0.60552)
Model fit						
Log Likelihood	-224.7	-227.1	-226.3	-224.4	-225.4	-224.7
Df	5	3	4	6	5	6

3 SEED DISPERSAL AND FATE OF TAGGED SEEDS OF AN ECONOMICALLY IMPORTANT, RODENT-DISPERSED TREE

3.1 Abstract

The seeds of many tree species are dispersed by scatterhoarding animals that act as both seed predators and dispersers. Previous research has shown that the relative abundance of seeds and scatterhoarders, as well as characteristics of individual seeds such as seed size, influence seed fate. I examined how these three factors of interest influenced seed dispersal and fate of *Allanblackia stuhlmannii* (Clusiaceae), a tree with seeds harvested by people for vegetable oil. There is concern that seed harvest could be unsustainable by removing large amounts of seed and affecting the fate of remaining seeds. I tagged 1152 seeds in the Amani Nature Reserve, Tanzania, in twelve different plots with varying background seed abundance. A subset of tagged seeds were monitored by heat-motion sensitive cameras to record dispersers and quantify rodent activity. By censusing tagged seeds at regular intervals, I recorded time until seed removal, post-removal seed fate, and dispersal distance of scatterhoarded seeds. The statistical analyses used for each of the aforementioned measures of dispersal and fate were Cox proportional hazard regressions, multinomial logistic regression, and multiple linear regression, respectively. Cox regressions revealed that the time until seed removal varied with background seed abundance and rodent activity, and that the relationship changed over time. Post-removal seed fate was not well explained by seed abundance, rodent activity, or seed size. A handful of seeds (eight) persisted in primary seed caches until the final observation, but the ultimate fate of most seeds was unknown. For seeds that were scatterhoarded, there was a slight decrease in dispersal distance as background seed abundance increased. *A. stuhlmannii* seed production was relatively

low in the experimental year (2011), which may have considerably reduced the observed variation in fruit abundance. Most earlier studies have used a simpler, categorical distinction of high and low seed production years rather than quantify seed abundance on a local level, which distinguishes this study. Repeating the study in future years could allow for a comparison of inter- and intra-annual variation in the effect of seed abundance on removal, fate, and dispersal to address the possible consequences of seed harvest by humans.

3.2 Introduction

Scatterhoarding animals are important seed dispersers, as well as seed predators, of many different plant species. Some plants have evolved a synchronized, highly variable seed production between years (masting) to cope with seed predation in their dispersers (Silvertown 2008, Vander Wall 2010). By producing excessive amounts of seed during only some years, seeds in masting years are more likely to escape predation and establish (e.g. Jansen et al. 2004). Therefore, the overall effect of scatterhoarders for seedling establishment may be detrimental in non-mast years or beneficial in mast years (Theimer 2004, Zwolak and Crone 2011). The balance depends on both the amount of seed available and the abundance of scatterhoarders.

Humans have the ability to shift this balance by reducing the amount of seed available (e.g. by harvesting) or the abundance of animals (e.g. by hunting). For example, across-site studies of Brazil nuts found that heavily harvested areas had fewer young trees than less intensively harvested sites (Peres et al. 2003). Several studies of seed dispersal in defaunated areas have shown reduced seed dispersal as well as reduced seed predation (reviewed by Stoner et al. (2007)). It is even possible that the effects of seed harvest and hunting combined exacerbate

recruitment limitation (Forget and Jansen 2007). Compared to the neotropics, there have been relatively few studies of seed dispersal by rodents in Africa (Seufert and Fischer 2010, Nyiramana et al. 2011). *Allanblackia stuhlmannii* (Clusiaceae) is an Afrotropical tree with large seeds dispersed by rodents and harvested by people. Basic research is still needed to better understand the relationship between *Allanblackia* and the rodents that scatterhoard and disperse its seeds. How would depressed seed abundance as a result of harvesting affect dispersal and survival of the remaining seeds?

The goal was to follow the fate of experimentally tagged *Allanblackia* seeds under a range of background seed abundance conditions to investigate the role of seed abundance, as well as seed size and rodent activity, affect seed dispersal and fate.

3.2.1 Hypotheses

Many earlier studies in the tropics as well as the temperate zone inform current understanding of the relationships between scatterhoarding animals and plants (Vander Wall 2010). My approach was modeled after Jansen et al. (2004), which studied the importance of seed size and seed abundance for seed dispersal and fate by agoutis and acouchies in French Guiana. My *a priori* hypotheses about the effect of fruit abundance and seed size largely follow theirs (Table 3.1). Additionally, I wanted to examine the possible effects of seed tagging on time until removal since the presence of tags could artificially delay seed removal compared to untagged seeds (Xiao et al. 2006). I predicted that increasing background fruit abundance (which is proportional to local seed abundance and easier to quantify for *Allanblackia*) would result in longer times until discovery by rodents of experimental seed stations (Jansen et al. 2004), since under high

levels of fruit abundance rodents would not need to forage extensively. Seed mass becomes a relevant factor for hypotheses related to individual seeds.

Three stages in the dispersal process are important for individual seeds: how long it takes a disperser to remove them, their immediate fate after removal (i.e. eaten or cached), and how far they are dispersed if they are cached. I tracked this sequence of events by experimentally marking seeds so I could observe their initial removal, disappearance or deposit in caches, and subsequent removal from caches (Table 3.1).

In particular, I expected that increasing fruit abundance would increase time until the initial removal of seeds from stations (Li and Zhang 2007), while increasing seed mass would have the opposite effect, decreasing time until removal (Waite and Reeve 1995). After initial seed removal, I expected increasing fruit abundance would favor increases in caching rates relative to predation rates (Zhang et al. 2008). In contrast, Jansen et al. (2004) predicted that higher seed abundance would result in less caching. However, they did not find support for this hypothesis and acknowledged that previous research is unclear (Theimer 2001, Hoshizaki and Hulme 2002). Some confusion may arise given the potential differences between fruit abundance effects on absolute and relative rates. While I expect that absolute removal rates may be lower overall under high fruit abundance, I predict an increase in the relative rate of caching and consumption *given that an individual seed is removed*. If a rodent removes a seed when there is plenty of food to eat, caching seems more likely. Additionally, I predicted that increasing seed mass would increase a seed's chance of being cached relative to being eaten, as Jansen et al. (2002) found that larger seeds are preferentially cached. With respect to cache distance, I predicted that seeds

would be cached at shorter distances under higher fruit abundance (Stapanian and Smith 1978, Jansen et al. 2004, Ouden et al. 2005, but see Li and Zhang 2007), with heavier seeds being moved farther (Jansen et al. 2004, Wang and Chen 2009). These same hypotheses regarding initial seed removal and fate apply to subsequent cache removal and re-caching events (Table 3.1).

The specific *a priori* hypotheses involved only fruit abundance and seed mass. However, rodent behavior, activity, and abundance relative to seed resources are important as well (Theimer 2004). For this reason, after starting to examine the seed fate data, I also incorporated estimates of rodent activity based on pictures from camera traps (initially used only for calculating time until station discovery). It is important to note that rodent activity is not a measure of rodent abundance, since individuals cannot be distinguished. These post-hoc hypotheses are listed separately (Table 3.2), since I did not explicitly design the experiment with the intention of using rodent activity in the analyses. I expected that higher rodent activity would correspond to faster discovery and removal of experimental seeds and further dispersal of cached seeds (Li and Zhang 2007). The potential influences of rodent activity on the probability of seeds being cached versus eaten were less obvious. I suspected that greater rodent activity might correlate with greater rodent abundance, in which case seeds would be increasingly likely to be eaten versus cached. However, Donatti et al. (2009) found that while seed predation increased with agouti abundance, higher rates of caching overshadowed the increase in predation.

I am especially interested in these hypotheses with respect to the interpretation for how increasing seed harvest by humans decreases seed abundance and what that means for the fate of remaining seeds.

3.3 Methods

Many of the methods (study site, study species, plot selection, background fruit abundance, and portions of seed collection, censusing plots, and rodent activity) overlap with planting experiment methods (Chapter 2). For the reader's convenience, they are duplicated here.

3.3.1 Study site

The Amani Nature Reserve (ANR) (S 5° 6', E 38° 38') protects 8380 ha of lowland and submontane rainforest in the East Usambara Mountains in northeastern Tanzania (Tanga region). The East Usambara Mountains (EUM) are part of the Eastern Arc Mountains, which are a discontinuous string of moist submontane and montane massifs separated by drier lowland areas stretching from southwest Tanzania into southeastern Kenya. Up until the 1960s, the East Usambaras were mostly forested (Hamilton and Bensted-Smith 1989); today only 24% remains in forest cover (Burgess et al. 2007). Most forest clearing has been for tea plantations, non-native timber plantations, and small-scale multicrop farming. The EUM receive 1700-2300 mm of rain throughout the year but the heaviest rains are in the short rainy season (October-November) and the long rainy season (late March-May) (Hamilton and Bensted-Smith 1989).

3.3.2 Study species

Allanblackia stuhlmannii Engl. (Clusiaceae) is a rainforest canopy tree endemic to the Eastern Arc Mountains of Tanzania. *A. stuhlmannii* is dioecious (separate male and female trees) and approximately one-third of the mature trees in the forest appear to be reproductive females (Mathew et al. 2009). It is one of the most common canopy tree species in ANR. Both male and female trees produce large, conspicuous, white and pink flowers concurrent with fruiting. Large insects, birds, and bats are possible pollinators (Mathew et al. 2009). Each female tree typically produces 3-160 fruits per year, varying considerably among years and individual trees (NJC & HJN unpub. data). Fruits mature over the course of about one year into large (2-5 kg), brown, drupes that fall to the ground when ripe. Each fruit contains approximately 36 ± 2 (SE) oil-rich seeds, each seed weighing 11.24 ± 0.08 g (Mathew et al. 2009). Seeds are 62-67% fat, and high in stearic and oleic oils, which have the commercially desirable quality of being solid at room temperature and melting at 40-46 °C (Eckey 1954). Hereafter, unless otherwise noted, *Allanblackia* refers to *Allanblackia stuhlmannii*.

3.3.3 Plot selection

To capture natural variation in background fruit abundance in the forest, I established twelve separate 50 x 50 m plots in four different blocks (three plots per block) within ANR. Each plot was at least 200 m from the forest edge. Plot locations were randomly discovered (see Chapter 2, appendix 2A for additional details) and each plot included canopies of at least four *Allanblackia* trees with fruit. All *Allanblackia* trees inside the plot were measured (DBH) and the presence of fruit and flowers recorded. Plots within a block were separated by at least 150 m, and blocks were at least 1200 m apart (Figure 3.1).

3.3.4 Seed tagging & setup

In total, I tagged 1152 *Allanblackia* seeds in February and March 2011 and followed their fates as long as possible, or until January 2012.

3.3.5 Seed collection & Seed tagging

I tagged seeds with a combination of wire, Tyvec ® labels, and thread (Figure 3.2a). More than 600 seeds were collected from four different farmland sites. Seeds were washed to remove fruit pulp and air-dried. A hole not greater than .9 mm in diameter was drilled by hand in the end or side of each seed, taking care to avoid the embryo if possible. A 40 cm length of ~0.25 mm diameter stainless steel wire was folded in half, passed through the hole, and secured to the seed by being twisted back on itself. The mass (measured with a digital pocket scale, American Weigh AMW-100 Silver Precision Digital Pocket Scale 100 x 0.01 g, Norcross, Georgia, USA) and source for each seed was recorded on a Tyvec ® label (Wristband Express, Brookfield, WI, USA) affixed ~1 cm from the end of the wire opposite the seed. Then a nylon 63/10 thread bobbin (Imperial Threads, Northbrook, IL, USA) was attached to each wire. Bobbins were encased in 6 cm of 1.9 cm diameter polyolefin heat shrink tubing (Electro Insulation Corp., Arlington Heights, IL, USA) with the thread able to pull out freely through an opening on one end.

3.3.6 Seed stations

Three seed stations of 16 seeds each were established in each plot (48 seeds per plot simultaneously) ~16.7 m from the edges and ~16.7 m from each other (Figure 3.1). The "corners" used for each plot were randomly selected. Each seed station contained 4 randomly selected seeds from each seed source. Seeds were placed 20 cm apart in a 4 x 4 seed array

(Figure 3.2b). Thread bobbins were buried in the ground below the seed. Each Tyvek ® label had a number for the seed station and an individual seed number. Numbered plastic planting labels (~1.9 x 10.2 cm) were used to mark the original location of each seed in the station, then moved to mark the new location of cached seeds to help find it again in future censuses. I marked 1,152 seeds in total.

3.3.7 Censusing plots & recording seed fate

The experiment was conducted in late February/early March (round 1) and repeated in late March/early April (round 2) to increase the sample size because I was limited in the number of seeds I could start at once by the number of thread bobbins available. During round 1, each block was censused 4, 8, 12, and 28 days after setup. Round 1 seeds that had not been removed from the seed station area after 28 days (when round 2 was initiated) were eliminated from the experiment. Round 2 seeds were censused 4, 8, 12, and 30 days after setup, which corresponds with 32, 36, 40, and 58 days for Round 1 seeds. After late April, each block was visited once per month until September 2011, and then seeds were revisited in November 2011 and January 2012 (327 days after beginning round 1).

During censuses, the presence and condition of each seed was checked by returning to the last location where it was recorded. For seeds that were moved, I measured the distance from the previous location with a measuring tape. The condition of seeds that were not recovered, either because the tags were not found or because the tag was found without the seed, was recorded as unknown. Observable seeds were classified based on their condition as intact, eaten, germinated, established, or rotten (the latter based on visible signs of dessication, fungus, or insect infestation).

3.3.8 Background fruit abundance

At each census until the end of the fruiting season in 2011, the field team surveyed plots for freshly fallen fruits and categorized them as available to rodents (either intact or already opened by rodents) or harvested by humans. Fruits with seeds harvested by people and fruits with seeds removed by rodents are easily distinguished because humans almost always leave behind the heavy fruit pulp bearing conspicuous machete marks. To prevent re-counting, fruits were marked with a piece of biodegradable flagging tape. Additional details are provided in Chapter 2, Appendix 2A. For most analyses, I used the total number of new fruits that were available to rodents in a plot divided by the number of days since the last census, giving a time-varying measure of fruit abundance in each plot.

3.3.9 Effect of tagging on seed removal

I tested effects of seed tagging on seed removal in February 2011 by conducting an experiment with tagged and untagged seeds. Half the seeds in each of four seed stations of 25 seed arrays (5x5) were tagged (as described above) and the others were untagged. I randomized the arrangement of tagged and untagged seeds within each station. A camera trap (Bushnell Trophy Camera, Bushnell Corporation, Overland, Kansas, USA) recorded animal dispersers at each station. Stations were revisited after 3, 4, 7, 13, and 20 days to record seed locations and conditions. Seed locations and conditions were recorded as above for tagged seeds; untagged seeds were recorded as present or removed.

3.3.10 Rodent Activity

A camera trap was installed at one randomly selected seed station in each plot. Ten Bushnell Trophy Cameras (Bushnell Corporation, Overland, Kansas, USA) and two Buckeye Apollo

Cameras (ATSI, Athens, Ohio, USA) recorded animal motion in front of the camera. Camera settings for the Bushnells were 5 megapixels, normal sensitivity, 3 photos per trigger, and 10 sec between trigger events. Buckeye Apollo settings were as close to the Bushnell as possible (high sensitivity, 1.3 megapixels, 3 photos per trigger, and 10 sec between trigger events). Giant pouched rats (*Cricetomys gambianus,* 1,390-2,800 g (Cooper 2008)) and squirrels (*Paraxerus* spp. 670-700 g and *Heliosciurus undulatus* 250-403 g*,* (Kingdon 1988)) are the two main types of rodents that have been observed interacting with *Allanblackia* seeds based on earlier camera trapping (unpub. data). It is also possible for smaller rodents to eat or disperse *Allanblackia* seeds, but due to their smaller size, they are expected to be less important as seed predators (less likely to eat an entire seed) and seed dispersers (less able to move seeds). Therefore, I considered photos of giant rats and squirrels but not smaller rodents in the quantification of rodent activity.

3.3.11 Analyses

Overall, the approach to analysis mirrors Jansen et al. (2004). Table 3.1 summarizes the different statistical approaches used to address different questions and hypotheses. All data analyses were performed in R version 2.15.2 (R Core Team 2012), with additional packages noted for more specific analyses.

3.3.11.1 Removal experiment

Two different methods were used to compare removal time between tagged and untagged seeds: 1) time (in days) from the start of the experiment until a seed was observed to be missing during a census, and 2) time (in minutes) between when a seed station was discovered by a large rodent and when a seed was removed (based on camera images). Both measures of time were used to compare removal times of tagged and untagged seeds with Mann Whitney U tests.

3.3.11.2 Station Discovery Time

Similar to estimates of removal times in the removal experiment, I measured the time until a seed station was discovered by a rodent in two ways: 1) time elapsed between the start of the experiment and when I observed that at least one seed at the station was removed or eaten, or 2) time until a large rodent was first observed on camera for the subset of seed stations that were monitored with cameras. I analyzed the effect of fruit abundance on both measures of time until discovery using Generalized Linear Models with a gamma family distribution and an inverse link function.

3.3.11.3 Time until removal (Cox model)

Techniques from survival analysis can be used to understand the persistence of seeds in a given state until an event of interest occurs. In this case, the events of interest are removal and, for cached seeds, cache recovery. I used Cox proportional hazards regressions (hereafter Cox regressions) to analyze the relationship between covariates of interest (background fruit abundance, seed mass, and rodent activity) and time until removal from a seed station or cache. Cox regression is a semi-parametric method from survival analysis that focuses on estimating how covariates of interest cause proportional increases or decreases in hazard (Cox 1972, Therneau and Grambsch 2000, Fox 2002). Hazard, $h(t)$, is defined as the probability of failure (in this case, being removed from a state) at time t relative to the probability of having survived in the state of interest up until time t. The method is semi-parametric because, given the key assumption that covariates alter hazards proportionally, it is not necessary to directly estimate the baseline form of $h(t)$ through time in order to estimate how factors such as fruit abundance influence the relative hazard faced by seeds in different environments. This ‘proportional

hazards' assumption essentially requires, for example, that if a unit increase in fruit abundance increases a seed's hazard by 10% when the baseline hazard is h_1 it must also increase hazard by 10% for any other value of the baseline hazard, h_2 and so on. Another way to say it is that a unit change in a covariate must have the same relative magnitude of effect across all times.

When fitting a Cox regression model, there are diagnostic methods for checking whether the proportional hazards assumption holds. There are two key ways in which it may fail: 1) if the effect of a covariate on hazard varies through time, or 2) if seeds from different groups/environments do not share the same baseline hazard. These issues can respectively be resolved by: 1) explicitly modeling a covariate's effect as a function of time (Bellera et al. 2010), and 2) stratifying the way data are handled in the Cox regression to allow underlying baseline hazard functions to differ between groups, while the proportional hazards assumption holds within groups. Both techniques were required to appropriately model seed persistence in the data. In general, I used Cox regressions to examine the effects of background fruit abundance and rodent activity on seed persistence, while treating seed source and round as stratifying factors. I verified that the data met the proportional hazards assumption, checked that no single point exerted undue influence, and that there was no evidence of non-linear effects of the covariates.

The vast majority of removals from seed stations occurred within the first 60 days; I censored the few removals occurring after this time in the Cox regressions to avoid introducing potential bias caused by small numbers of influential points. I also censored round 1 seeds that were eliminated at the start of round 2 because they had not been removed from the station. One advantage of

Cox regressions is that the censored seeds are not excluded completely from analysis; rather, it incorporates the known information that a seed was not removed up until the censoring date. I used the average number of fruits available in a plot during the census interval preceding removal observations as the measure of background fruit abundance. Average rodent activity was the number of photographs taken of large rodents over the first 40 days of the experiment (during which the cameras were deployed) divided by the total time a camera was active. This measure does not capture variation in activity over shorter time intervals but is rather a long-term, plot-level average.

I examined Cox regressions that included seed mass as a covariate; however, the effects of seed mass and round are potentially conflated. Mean seed mass differed significantly between rounds, with seeds in round 2 being approximately 2 g heavier (t-test with unequal variance, $t= 15.76$, p-value<0.001). This occurred due to chance, as seeds were collected from the same sites and processed identically. Seed mass was not a significant covariate in Cox regressions when round was also included, whether treated as a stratifying variable, an interaction term, or used to split the data and perform separate analyses. Thus, I chose to retain round as a factor over seed mass, because round captures additional unmeasured variation.

All Cox regression modeling was performed with the 'survival' package (Therneau and Grambsch 2000, Therneau 2013) in R.

3.3.11.4 Post-removal and post-cache recovery seed fates

Immediately after seeds were removed from stations, they experienced one of three possible fates: cached, eaten, or unknown. Since many tags were found without seeds or evidence of the

seed being eaten, I conservatively assumed that the fates of the associated seeds were unknowable, rather than assuming they were eaten. To determine what factors (fruit abundance, rodent activity, seed mass) might influence the fate of removed seeds I used multinomial logistic regression with the 'mlogit' package (Croissant 2011) in R. Seed fates after removal from primary caches were analyzed similarly.

3.3.11.5 Dispersal distances

I used multiple linear regression to examine the relationship between the distance from seed stations to primary caches and several covariates: seed mass, round, and the average fruit abundance within a plot during the time the seed was cached. I used the same approach for investigating the distance between primary and secondary caches. All distances were log transformed.

3.4 Results

3.4.1 Removal experiment

Tagged seeds provided a fair representation of what would happen to untagged seeds. Time until observed removal did not differ between tagged and untagged seeds in either the observed removal times (Mann Whitney U test, $W = 962.5$, p-value = 0.644) or more precise removal times based on camera images (Mann Whitney U test, $W = 316$, $p = 0.157$).

3.4.2 Station Discovery Time

The two different measures of time until station discovery (direct observation during censuses and times based on photo timestamps) were poorly correlated (Spearman's rank correlation, S = 2082.195, p-value = 0.434). Observed station discovery times were much faster in round 2 than round 1 (Wilcoxon signed rank test with continuity correction, V = 116.5, p-value = 0.010), consistent with round 2 seed stations sharing the same locations as stations in round 1. For this reason, I used station discovery times from round 1 only to examine the relationship between fruit abundance and station discovery. Fruit abundance did not affect time until station discovery for either measure of discovery time (observed times: GLM gamma family inverse link, slope= -0.0005, p-value= 0.693; camera times: slope=-0.0039, p-value= 0.223), in contrast to the hypothesis.

3.4.3 Time until seed removal from stations and caches

Overall, seeds were quickly removed from seed stations. More than half of the seeds were removed by day 8 in both rounds (Figure 3.3). Figure 3.3 shows the overall probability of a seed persisting until a certain day. Seeds had less than a 20% probability of persisting at a seed station beyond 30 days. The stair-step pattern is a result of the temporal scale of the censuses; if I censused more often, the pattern would likely be much smoother.

The Cox regression model can explain a modest amount of the observed variation in time until seed removal (Likelihood ratio test= 402.4 on 6 df, $p<0.0001$, Cox & Snell pseudo-R^2= 0.136, Table 3.5). Fruit abundance and rodent activity both had significant effects on hazard, and these effects were found to vary through time. The hazard of removal increases relative to the baseline hazard with increasing rodent activity, but the magnitude of this effect decreases over time until

about day 35, after which it slowly rises again (Figure 3.4a). For fruit abundance, the hazard of removal is initially higher with higher fruit abundance (i.e. seed removal is *more* likely if there are other fruits around). Over time, the opposite becomes true: seed removal is less likely when there are more fruits available (Figure 3.4b). After day 30, removal is once again associated with increasing fruit abundance. The ability to estimate these effects at any given time point is constrained by: 1) the available variation in a covariate, and 2) the number of seeds remaining, and experiencing removal. Towards the end of the 60 day period studied here there is a decline in both of these factors that may drive some of the predictions of this model (Figure 3.4c, d). For example, I believe that the unrealistically sharp upward trend in the effect of fruit abundance on hazard that is predicted by the model past day 40 is in part due to decreasing variation in, and ultimately the absence of, fruits by day 60. At this point, if fruit abundance is zero, the effect of fruit abundance on hazard is zero by default, regardless of the estimated coefficients. Additionally, the present state of technology requires the use of linear statistical models; it is quite possible that, if technology permitted, a non-linear response of fruit abundance effects over time would be preferred to the quadratic model. The quadratic model's most salient and reliable feature may be its ability to capture a decline (and reversal) of the effect of fruit abundance on hazard during the initial stages of the experiment, when both sufficient variation in fruit abundance and large enough sample sizes occurred.

Seed removal from primary caches showed a similarly fast decline, where most seeds were quickly recovered from caches (Figure 3.5). More seeds from round 2 than round 1 were cached (155 versus 128 seeds) and they generally remained cached for longer. Time until removal from caches was not well explained by Cox models incorporating average rodent activity over the first

40 days, the total number of fruits that were available in a plot, seed mass, or interactions between these covariates. Stratifying these removal times by round was necessary, indicating significant differences in the underlying baseline hazard function experienced by seeds in different rounds.

3.4.4 Post-Removal Seed Fate

The fate of seeds after removal from seed stations was poorly explained by multinomial logistic regression models that incorporated fruit abundance, rodent activity, seed mass, and/or round, in combination or alone. Even the most complex model, which also included time of observed removal and seed source, explained less than 10% of the observed variation. I found no support for the hypothesis that heavier seeds were more likely to be cached than eaten after removal or that seeds are more likely to be cached under higher fruit abundance.

Of the 290 seeds that were observed in primary caches, only 31 were observed in secondary caches. The fate of seeds after removal from a cache was not well explained by any multinomial logistic regression models including the same covariates as for the post-removal seed fate models (above), so the hypotheses related to post-cache seed fate were not supported.

In sum, over the course of all censuses, 133 seeds were eaten, 128 seeds were eliminated (from the first round to make way for the second), and one seed rotted. The ultimate fate of the remaining 882 seeds is unknown for various reasons (though some have known intermediate fates). Most were broken off at some point during the study, leaving just the tag behind without a seed. I did not assume these were necessarily eaten, because 597 seeds had their tags broken off

before the first census. Other reasons for unknown seed fate include seeds & tags disappearing high into trees, into burrows, or if the thread broke and the tag was never recovered.

At the last census, eight tagged seeds remained. All eight seeds were left in primary caches. Three of the seeds germinated, and two of those had established.

3.4.5 Primary and secondary caching distances

Distances between seed stations and primary caches ranged from 0.6 to 95.4 m (Figure 3.7a). A modest amount of the variation in distances was explained by fruit abundance, seed mass, the interaction between fruit abundance and seed mass, and round (multiple regression, $F(4,285)= 8.48$, p-value < 0.001, $R^2 = 0.106$; Table 3.4). Seed mass alone was not significant (p-value=0.586) or in the interaction with fruit abundance (p-value=0.07). There was a slight decrease in dispersal distance as fruit abundance increased (p-value=0.01, which is consistent with the hypothesis for fruit abundance.

The distances between primary and secondary caches ranged from 0.7 m to 33.8 m (Figure 3.7b). In some cases, I did not know the distance between primary and secondary caches because the seed was temporarily missing before being recovered, so the sample size is only a subset of re-cached seeds. There was no measurable effect of fruit abundance, seed mass, or round on the distances seeds were moved to secondary caches.

3.5 Discussion

3.5.1 Tagging effects

The tagging experiment appears to fairly represent seed dispersal by large rodents in Africa. I found no effect of tagging on seed removal, contrary to other studies that reported slower removal (Xiao et al. 2006). It might be due in part to the fact that most seed removal at my site occurs at night when the fluorescent yellow flags are difficult to distinguish. This suggests that the results about the fate of tagged seeds can be generalized to non-experimental seeds.

3.5.2 Station Discovery Times

Background fruit abundance and time until station discovery were unrelated, possibly because of rapid discovery times. The first visit occurred on day 4, but it is possible that most stations were discovered before day 4 and thus significant differences in discovery time were missed. Various factors could explain the poor correlation between time until station discovery as measured by the camera times and the direct observation times. First, some photo evidence suggests that smaller rodents such as mice could have removed tagged seeds, but I only counted photos of giant rats and squirrels. Second, camera misalignment resulted in missing some visits of large rodents to seed stations.

3.5.3 Time until seed removal

The relationship between fruit abundance and time until removal was unexpectedly complex. The initial relationship between time until removal and fruit abundance suggests that rodents preferentially forage in areas with higher fruit abundance. This is consistent with observations that palms that produced more fruit had higher proportions of damaged seeds (Grenha et al. 2010). Interestingly, that relationship changed over time so that seeds were *less* likely to be

removed in areas with high fruit abundance. The model predicted an unreasonably high increase in hazard after day 40, but I suspect there was insufficient fruit abundance and not enough seeds remaining to inform removal rates at the later observation dates to realistically describe what was happening in the field (explained in the results, section 3.3.3).

It is possible that removal from caches is related to fruit abundance, but the census intervals led to coarse temporal resolution in the data. Theimer (2001) found that seeds were removed from caches more quickly in non-mast years when there is lower fruit abundance. The year of the experiment was a relatively low fruit year for *Allanblackia* in ANR (pers. obs.), so it may not be possible to distinguish any variation in residence times that may exist across the range of fruit abundance in the plots. Furthermore, if cache residence times were shorter than the census intervals, then they were effectively unobservable. Repeating this study over multiple years or effectively manipulating the fruit density in experimental plots would capture a wider range of fruit availability and potentially reveal relationships between fruit abundance and cache residence time.

3.5.4 Seed fate (post-removal, post-caching, and in general)

Variation in post-removal and post-caching seed fates were not well explained by fruit abundance, seed mass, or rodent activity. In part, it may have been difficult to distinguish among effects due to the high proportion of seeds with unknown fates (Figure 3.6). In the future, camera trap monitoring of cached seeds may be able to provide a better indication of whether some seeds were broken off the wire to potentially be re-cached or whether they were eaten on the spot. The decision to cache or eat seeds may depend also on the future availability of resources relative to the current availability (seasonality) (Jorge et al. 2011), which is something that is not well

known for rodents in the Eastern Arc Forests. Better data are needed on both the diets of rodents and the phenology of their foodstuffs to address variability in seasonal food abundance and how it may in turn influence caching decisions.

3.5.5 Dispersal distances

High fruit abundance tended to reduce dispersal distances, which is consistent with other studies (Jansen et al. 2004, Xiao et al. 2005a, Moore and Swihart 2007) but differs from Li and Zhang (2007) who found higher dispersal distances in mast years compared to non-mast years. Like Donatti et al. (2009), I found no relationship between rodent activity and dispersal distance. Similar to Theimer (2003) but in contrast to many other studies (Jansen et al. 2002, Xiao et al. 2005b, e.g. Wang et al. 2012), I did not find an effect of seed size on dispersal distance. Wang et al. (2012) found that dispersal distance increased with artificial seed size up until seeds that were larger than those naturally available at their study site, at which point it leveled off. Over a large enough range of seed masses, the relationships between seed mass and proportion of seeds removed and cached and the dispersal distance are all best described by non-linear models (quadratic or segmented plateau models) (Wang et al. 2012). The range of available seed sizes in an experiment will influence the nature and detection of a relationship.

Seed size discrimination behavior could vary between species with cheek pouches (giant rats) and without (squirrels). Vander Wall (2003) noted that the ability of pouched species (such as the yellow pine chipmunks in his study) to carry numerous seeds at once suggests they are less discriminating between seed sizes. Vander Wall's chipmunks tended to cache several seeds together, whereas most seeds I found were cached singly, even when it was obvious from parallel thread trails that two or more seeds had been carried together on the same trip. Squirrels

at the site could only carry seeds one at a time; thus the distances of seeds dispersed by squirrels could show a pattern of size selection and dispersal distance even if giant rat-dispersed seeds did not. However, it is also worth noting that it is not known where squirrels (*Paraxerus* spp.) typically cache seeds. I suspect that most of the seeds deposited in trees were taken by squirrels, but do not know if they also cache seeds on the ground. Future studies with more intensive camera use at seed stations could answer this question of where *Paraxerus* cache seeds and whether or not they exhibit more seed size selectivity than *Cricetomys gambianus*.

3.5.6 Comparison to results from Jansen et al. (2004)

Most of the a priori hypotheses were not supported by the data, and thus did not agree with results found by Jansen et al. (2004). Several important methodological differences between our studies and systems may account for these disparate results. I used continuously variable measures of fruit abundance, whereas Jansen et al. (2004) compared seed-rich and seed-poor years, which is by far the most common approach to comparing seed abundance in studies of scatterhoarders. The comparison within sites across years represents a landscape-level study where the seed abundance is assumed to be fairly consistent across space within a given year, whereas my study examined variation at a smaller spatial scale of only 50x50 m. Spatial scale is important: in a study with Brazil nuts at smaller spatial scales, there was no distance effect on seed removal, but inside and outside Brazil nut clusters there was a significant difference in the proportion of seeds removed, where more seeds were removed within a grove compared to >300 m away from a grove (Peres et al. 1997). The relationship between food abundance and resource depletion can vary across scales. For example, Morgan et al. (1997) compared the foraging behavior of North American fox squirrels (*Sciurus niger*) at experimental food patches where

resources were distributed at foraging, intermediate, and landscape scales. They found that although the proportion of seeds removed had a positive relationship with seed abundance at the foraging scale, the effect was opposite at the landscape scale, and there was no relationship at the intermediate scale. My plots were between the foraging and intermediate scale plots of Morgan et al. (1997), and the finding of a weak effect of seed abundance on removal time is consistent with their findings. Perhaps repeating the study across years would eventually yield results similar to Jansen et al. (2004), since *A. stuhlmannii* is indeed a masting tree with high interannual variation in fruit production. An attempt was made to manipulate fruit abundance to achieve high, medium and low levels within the plots (detailed in Chapter 2, Appendix 2A), but natural variation within plots overwhelmed my attempt (I accounted for the attempted manipulation in calculations of fruit abundance). Therefore, I used the continuously variable measure of fruit abundance instead of a simpler categorical one.

3.5.7 Implications for effects of seed harvest by humans

The effects of background seed abundance on seed fate are not clear at the scale at which I measured seed/fruit abundance, but it is possible that seed harvest could diminish the magnitude of differences in fruit abundance between mast years and non-mast years. Fewer mast years or smaller magnitude of difference in seed production could result in fewer seeds escaping predation. It will be important to further study how rodent abundance- especially giant rats- influences seed fate in concert with changing *Allanblackia* seed abundance. Giant rats are hunted as bushmeat in ANR (pers. obs.), though no studies to date have investigated the intensity or impact of hunting. Although most of the null hypotheses could not be rejected, this research will greatly inform future studies that can incorporate additional measures of rodent activity or

abundance and compare background fruit abundance within as well as across seasons. This study represents an important step in beginning to understand the way in which *Allanblackia* seed harvest may affect the fate of remaining seeds.

3.6 Cited Literature

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3.7 Figures and Tables

Figure 3.1 Diagram of the spatial organization of the experimental setup for tagged seeds

Diagram of the spatial organization of the experimental setup for tagged seeds.

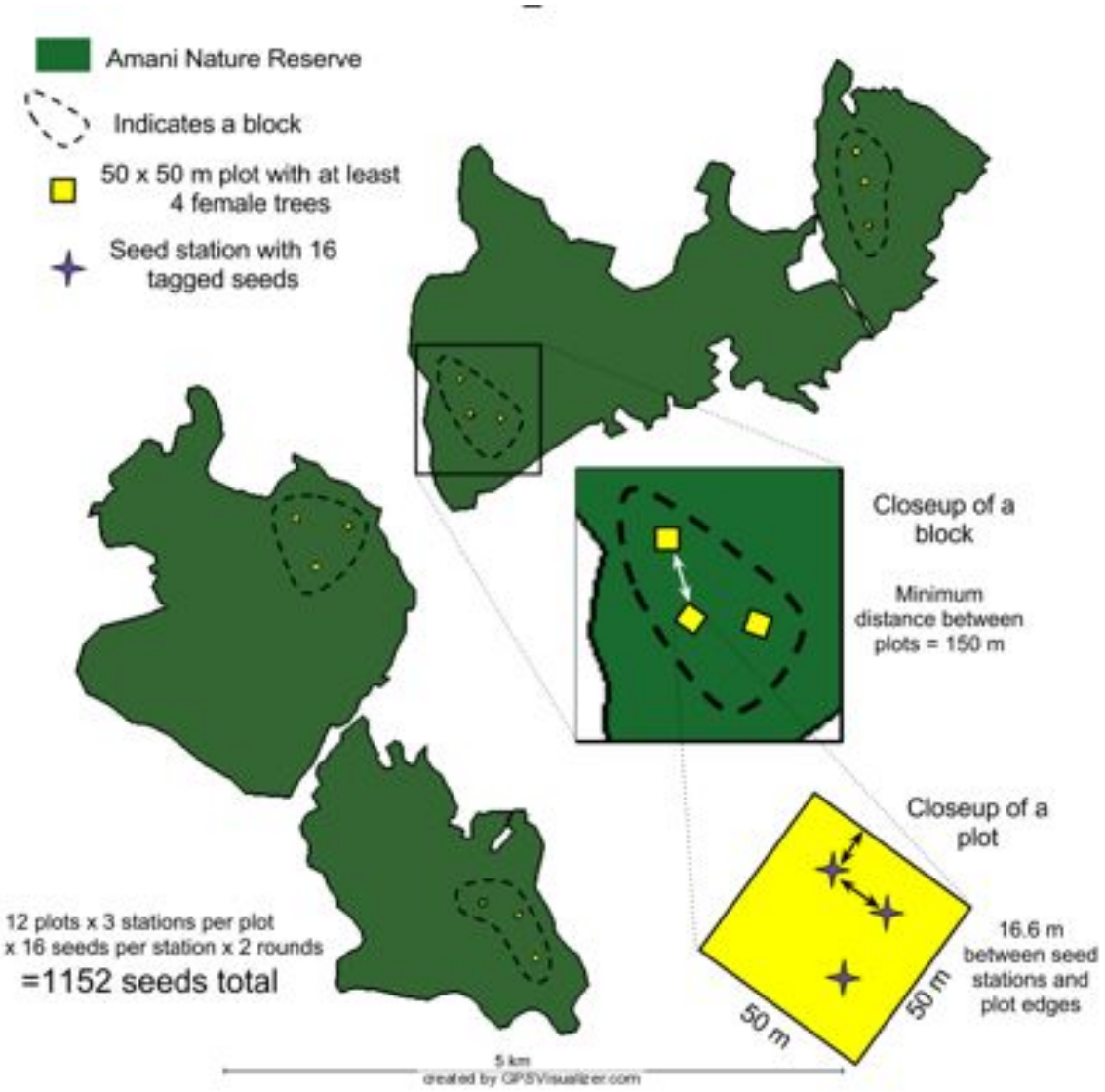

Figure 3.2 Photographs of a tagged seed and seed station

Photographs of a) seed tagged with wire, Tyvec ® label, and thread. b) tagged seeds arranged in a 4x4 array in a seed station.

Figure 3.3 Probability of persisting at a seed station over time

Probability of persisting at a seed station over time (averaged across all stations, rounds combined). The dashed lines indicate 95% point-wise confidence intervals.

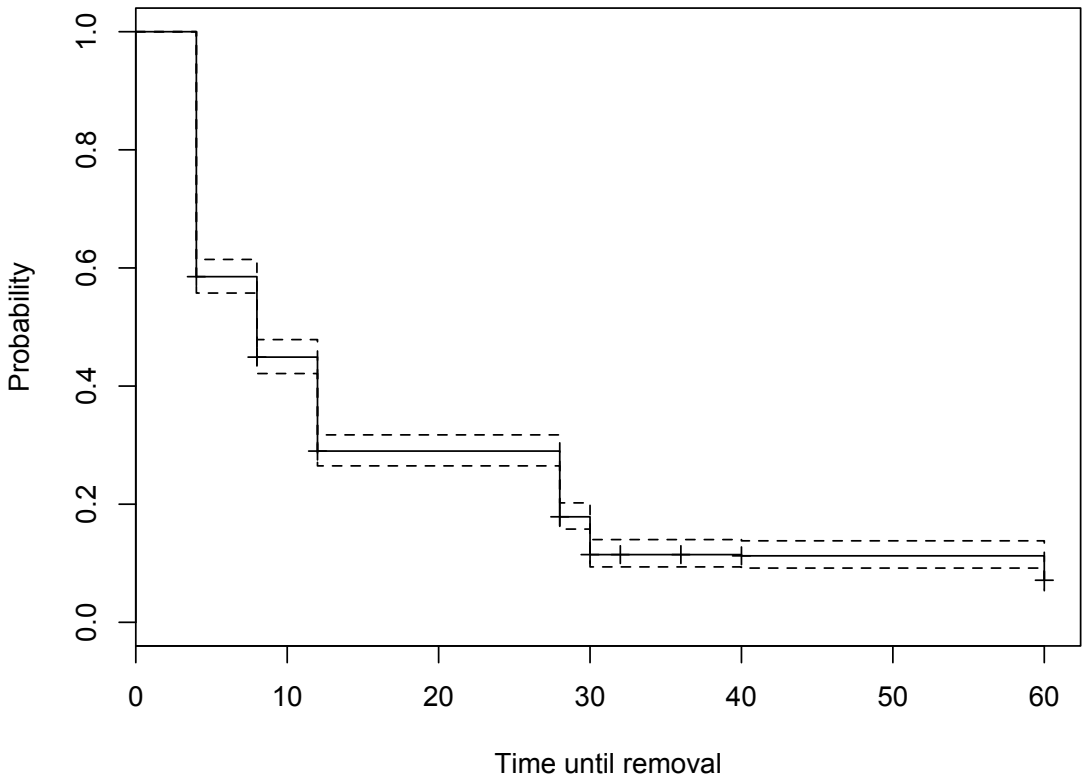

Figure 3.4 Visualizing the time-varying effects of rodent activity and fruit abundance

Visualizing the time-varying effects of a) rodent activity and b) fruit abundance on the proportional hazards of seed removal. The dashed lines are at 1, where the covariate would have no effect on the baseline hazard. Values below one (i.e. for fruit abundance) indicate that the removal hazard decreased (with respect to the baseline) with increasing fruit abundance over that time interval. Hazard scaling curves assume covariates not shown are held at 0 (i.e., fruit abundance = 0 or rodent activity = 0, respectively). For the lower plots, bars indicate range of values of c) rodent activity and d) fruit abundance. Dots indicate means.

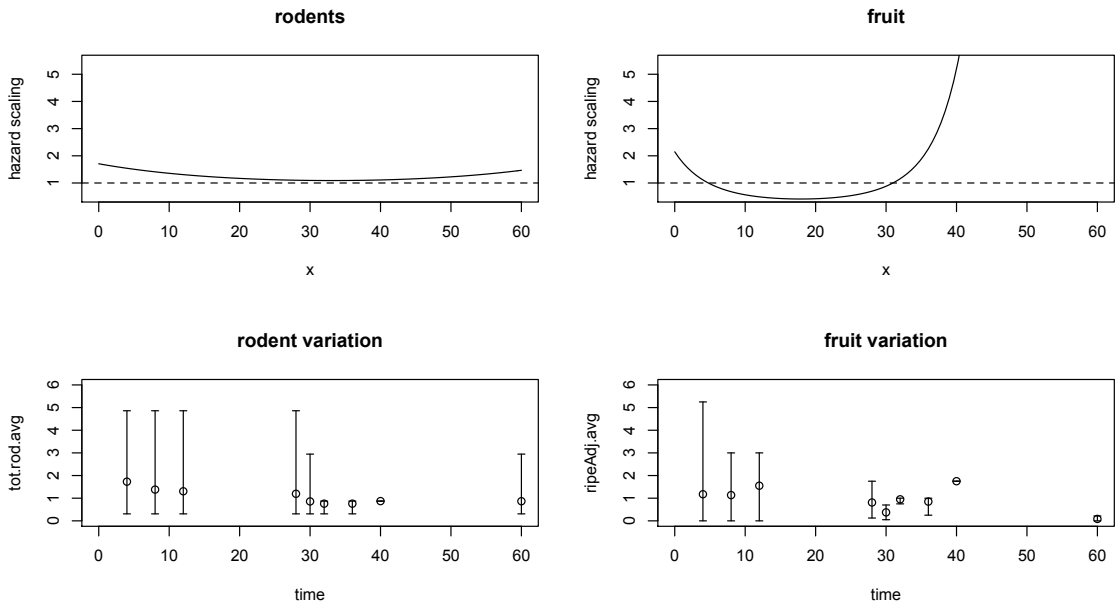

Figure 3.5 Persistence of cached seeds in primary caches over time

Persistence of cached seeds in primary caches over time, separated by round. Dashed lines show 95% point-wise confidence intervals.

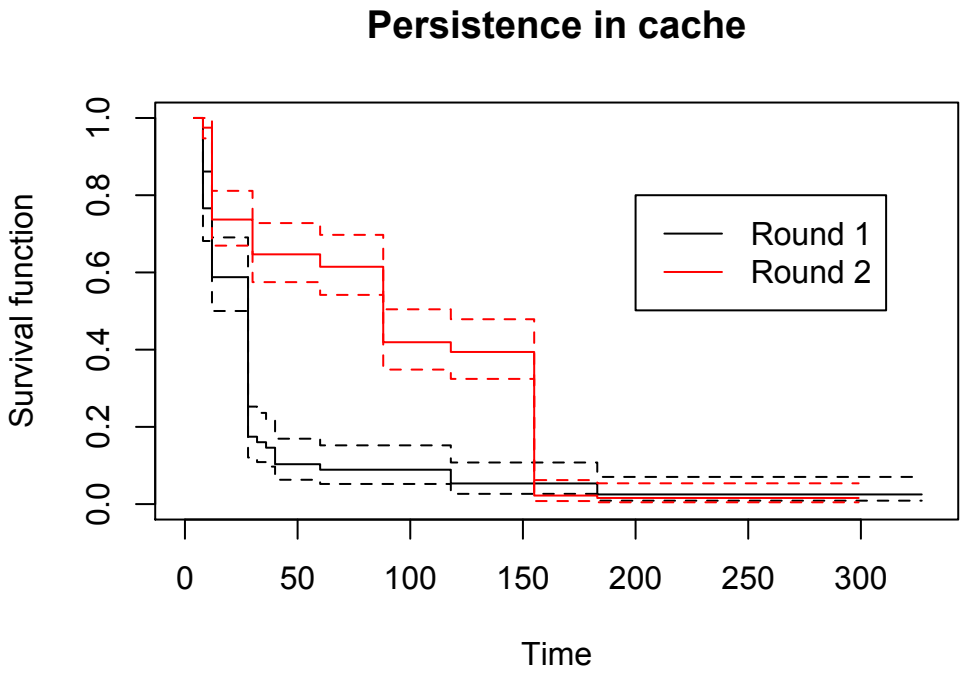

Figure 3.6 Diagram of the different possible seed fates

Diagram of the different possible seed fates and how many seeds reached each fate. Of seeds with unknown fates, 15 seeds were hoarded in burrows and 25 seeds went up trees.

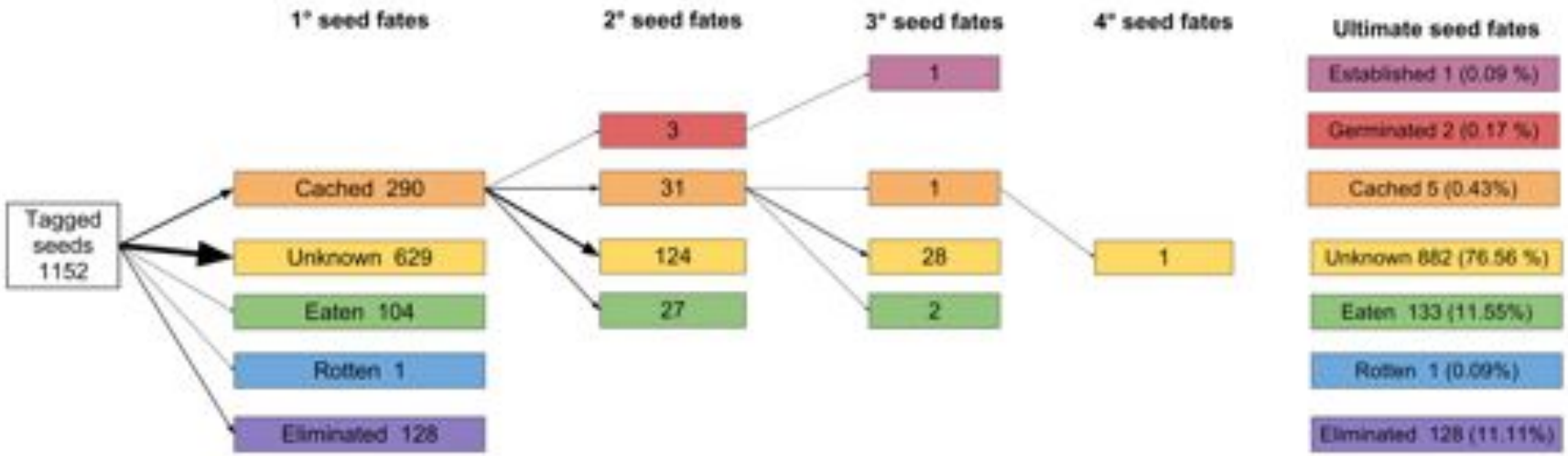

Figure 3.7 Histograms showing the distances seeds were moved to primary and secondary caches

Histograms showing the distances seeds were moved from a) seed stations to primary caches or b) primary caches to secondary caches.

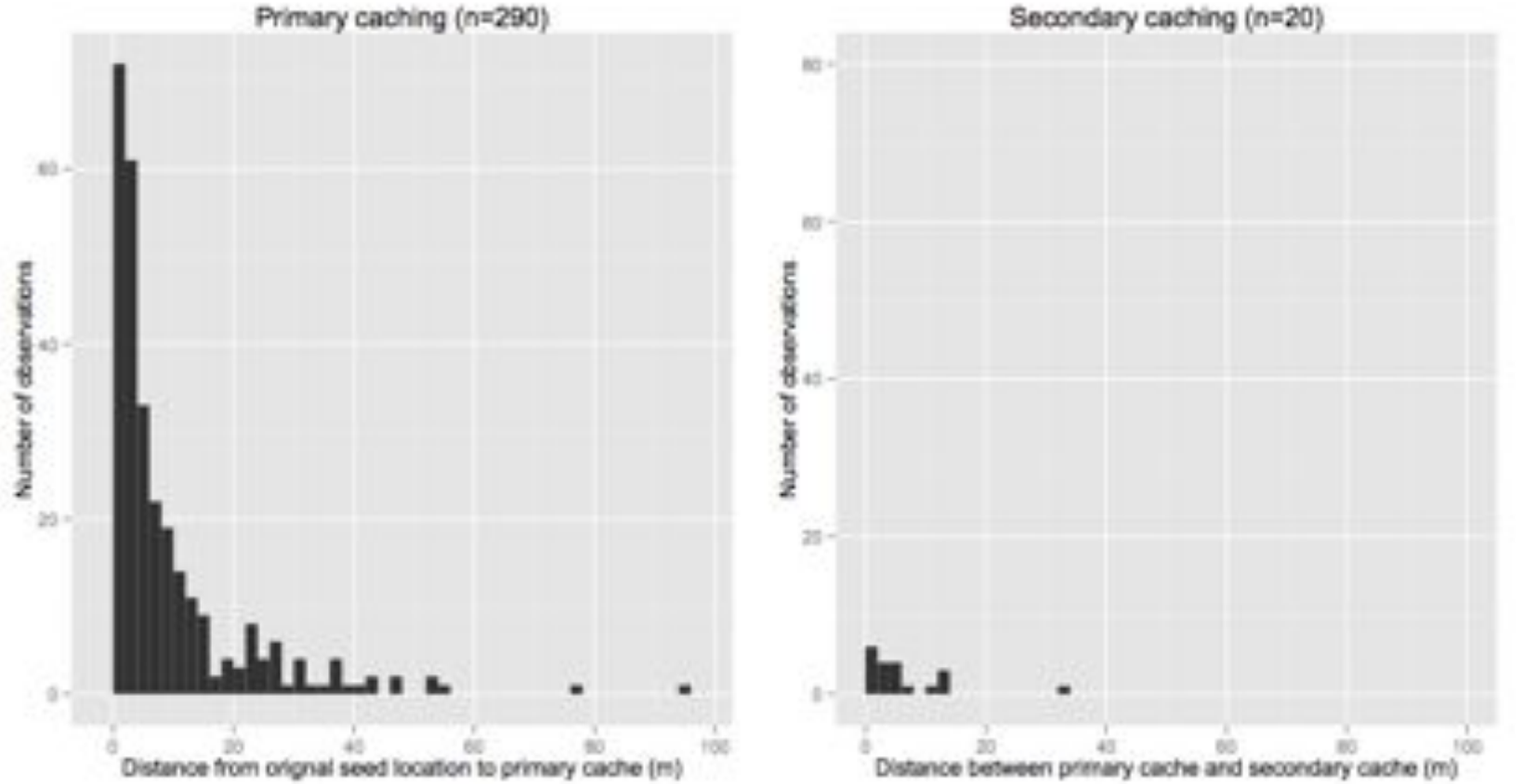

Table 3.1 Summary of the hypotheses and analyses

Summary of the important measured outcomes to be addressed, hypotheses of how the most important covariates will influence the outcomes, and the analyses used to explain the observed patterns.

Subproject	**Effect of increasing background fruit abundance**	**Effect of increasing seed mass**	**Analytical approach**
Effects of tags on seed removal	na	na	Mann Whitney U
Time until station discovery	More time	na	GLM (gamma family)
Time until seed removal	More time	Less time	Cox model
Seed fate after removal	More caching, less eating	More caching, less eating	Multinomial logistic regression
Cache distance	Shorter distance	Longer distance	Multiple linear regression
Time until removal from cache	More time	Less time	Cox model
Fate after cache removal	More caching, less eating	More caching, less eating	Multinomial logistic regression
Re-caching distance	Shorter distance	Longer distance	Multiple linear regression

Table 3.2 Hypotheses about the effects of rodent activity

Hypotheses about the effects of rodent activity on the same measures of interest as presented in Table 3.1.

Subproject	**Effect of increasing rodent activity**
Effects of tags on seed removal	na
Time until station discovery	Less time
Time until seed removal	Less time
Seed fate after removal	More caching?
Cache distance	Longer distance
Time until removal from cache	Less time
Fate after cache removal	More caching?
Re-caching distance	Longer distance

Table 3.3 Summary of the results as they relate to hypotheses

Summary of the findings as they relate to hypotheses presented in Table 3.1 and Table 3.2.

Subproject	Effect of increasing background fruit abundance	Effect of increasing seed mass	Effect of increasing rodent activity
Effects of tags on seed removal	-	-	-
Time until station discovery	NS	-	-
Time until seed removal	Initially decreases removal time, then increases	NS	Slight initial decrease in removal time
Seed fate after removal	NS	NS	NS
Cache distance	Slight	NS	NS
Time until removal from cache	NS	NS	NS
Fate after cache removal	NS	NS	NS
Re-caching distance	NS	NS	NS

Table 3.4 Linear model results of the distances seeds were dispersed to primary caches

Coefficient estimates and associated p-values of a linear model of the distances seeds were dispersed to primary caches. Distances were log transformed. Fruit abundance was the average number of fruits available in that plot in the observation interval before caching was recorded. Round refers to when the experiment started.

Coefficients	Estimate	Std. Error	t-value	P-value
(Intercept)	1.35	0.35	3.84	0.000
Fruit abundance	-0.58	0.23	-2.54	0.012
Seed mass	0.02	0.03	0.55	0.586
Round (1 or 2)	0.39	0.14	2.68	0.008
Fruit abundance:Seed mass	0.03	0.02	1.82	0.070

Table 3.5 Effects of background fruit abundance and rodent activity on time until seed removal from a seed station

Effects of background fruit abundance and rodent activity on time until seed removal from a seed station. The model includes where the seeds were originally collected (seed source) and round as stratifying factors. Number of removal events = 998.

Covariate	Coef	Exp(Coef)	SE(Coef)	z	p-value
Rodent activity	0.53	1.71	0.05	11.17	<0.001
Rodent activity:time	-0.03	0.97	0.01	-3.42	<0.001
Rodent activity:time^2	0.00	1.00	0.00	2.01	0.044
Fruit abundance	0.76	2.15	0.13	6.09	<0.001
Fruit abundance:time	-0.19	0.83	0.03	-7.08	<0.001
Fruit abundance:time^2	0.01	1.01	0.00	6.22	<0.001

4 SEED RAIN UNDER AND AWAY FROM BAT FEEDING ROOSTS

4.1 Abstract

Frugivorous bats throughout the tropics disperse seeds of many different plant species. In the paleotropics, the relative importance of bats compared to other vertebrate dispersers is still poorly known because many studies of seed rain have excluded bats. Furthermore, little is known about the role of paleotropical bats as seed dispersers in fragmented forest landscapes compared to intact forest habitat. I used 144 seed traps under and away from bat feeding roosts in continuous forest and forest fragments in submontane East African rainforest to capture approximately 20,253 intact seeds or fruits from 40 species and 66 morphospecies from bats and other dispersers over the course of about 4 months. Based on evidence of handling, fruit bats dispersed 24 species, with 13, 5, 5, and 4 species dispersed by birds, monkeys, unidentifiable mammals, and rodents, respectively. Seed traps below bat feeding roosts and in fragments captured more diaspores when considering all intact diaspores as well as only those from bats. Species richness was higher in traps below bat feeding roosts and in fragments, except when only considering diaspores from bats, when the continuous forest had higher richness. Rarefaction curves illustrate the noticeably lower species richness of seed rain in forest fragments. The differences in the quantity of seed rain in fragmented habitat may be driven by the presence of numerous seeds from small-seeded species ingested by bats, but other dispersers may be responsible for the greater species richness in fragments.

4.2 Introduction

Fruit bats are important seed dispersers in the tropics where frugivory evolved in two separate bat families: Phyllostomidae in the neotropics and Pteropodidae in the paleotropics. Pteropodid bats, all of which are frugivorous and/or nectarivorous, are much larger than their neotropical cousins. Along with the differences in body size come some differences in behavior. Phyllostomid fruit bats are recognized for their role in early succession in the neotropics and while pteropodids disperse economically valuable late successional species in the paleotropics (Fujita and Tuttle 1991, Muscarella and Fleming 2007). It is accepted that pteropodids frequently disperse large seeds, but was not widely recognized for phyllostomids before Melo et al. (2009) demonstrated the high abundance and richness of seeds that the small phyllostomids were dispersing even without ingestion. Similar studies for pteropodids are lacking. Several studies have quantified seed rain from neotropical bats using seed traps (Medellin and Gaona 1999, Martinez-Garza and Gonzalez-Montagut 2002, Arteaga et al. 2006, Henry and Jouard 2007), but only a handful have done the same for pteropodids (Duncan and Chapman 1999, Ingle 2003, Gonzales et al. 2009). Only one of those studies was in Africa (Duncan and Chapman 1999), where fruit bats have been less studied than many other types of dispersers (Chapter 1). Other seed trap studies in Africa have compared seed rain below and near isolated trees (Carrière et al. 2002) and beneath trees with different dispersal syndromes (Clark et al. 2001, Hardesty and Parker 2003). I am interested in how seed rain from African fruit bats compares to that from other animal dispersers.

The seed rain generated by bats compared to other animals is particularly important in the context of habitat loss and fragmentation. It is possible that bats can still be important seed

dispersers even in fragments, but studies explicitly testing pteropodid fruit bat response to fragmentation are lacking. African fruit bats often fly long distances to forage each night (Richter and Cumming 2008 recorded a 59-km one-way foraging trip for *Eidolon helvum*) and can carry large diaspores hundreds of meters, even in fragmented landscapes (Duncan and Chapman 1999). However, fragmentation could alter the amount or richness of seed rain from bats (Melo et al. 2009). Following Melo et al. (2009), the objective of this study was to compare the amount and richness of seed rain below bat feeding roosts to control areas 5 m away in both forest fragments and continuous forest. I expected that the areas beneath bat feeding roosts would have significantly higher seed rain and species richness than areas away from bat feeding roosts. I also expected that the quantity and richness of seed rain would be similar in continuous forest and forest fragments.

4.3 Methods

4.3.1 Study site

Seed traps were placed in twelve different submontane forest sites in and around the Amani Nature Reserve (ANR), East Usambara Mountains, Tanzania (5° 06’ 00” S, 38° 38’ 00” E). The East Usambaras receive approximately 1900 mm/rain per year (Hamilton and Bensted-Smith 1989). All sites were 940 - 1140 m above sea level. Six sites were within ANR and two sites were in large forest fragments. These eight sites are collectively referred to as ‘continuous forest’ habitat here forward. Four sites were in small, more isolated forest fragments around ANR (‘forest fragment’ habitat). Non-forested land cover is dominated by tea plantations, small family farms, and non-native timber plantations. The forests include many plant species endemic to the

Eastern Arc Mountains as well as some endemic just to the East Usambaras (Lovett et al. 2006, Burgess et al. 2007).

4.3.2 Fruit bats and other arboreal seed dispersers

Seven species of bats have been recorded in the East Usambara Mountains that are primarily frugivorous, though may also take nectar (Nowak 1994) (see Chapter 1, methods). It was not possible to identify which species of the bat species is responsible for dispersal into the seed traps, but evidence of bat handling is easily distinguishable from other animals in the area. Other arboreal seed dispersers include two species of monkeys (*Colobus angolensis palliates* and *Cercopithecus mitis*), bush babies (*Otolemur garnettii*), two species of hornbills (*Bycanistes bucinator* and *B. brevis*), palm civet (*Nandinia binotata)*, turacos (*Tauraco fischeri*), squirrels (*Paraxerus lucifer*, *P. vexillarius*, and *Heliosciurus undulatus*), several smaller bird species (e.g. as noted in Cordeiro and Howe 2003, Cordeiro et al. 2004), and genets (Cordeiro and Seltzer 2012).

4.3.3 Seed trap construction

Seed traps were constructed out of dark green cotton/polyester blend cloth with a 20 x 20 cm square hole in the middle with two layers of dark blue mosquito netting sewn in. All four trap edges were folded over and sewn to create a tube to pass through rope for securing the trap in the field. Each trap was approximately 1 x 1 m.

4.3.4 Seed trap placement

In each of the twelve sites, I searched haphazardly for evidence of active bat feeding roosts by scanning the ground for bat-dispersed fruits, seeds, and ejecta within 100 m of the forest edge.

There had to be at least four diaspores with evidence of bat manipulation within a square meter to place a seed trap. Seed traps were erected using bamboo stakes or existing vegetation and sisal rope on all four sides approximately 0.3-1 m above the ground. A second trap ('non-bat trap') was placed in a random direction 5 m away (edge to edge) from the first trap. If there was evidence of bat dispersal in the location 5 m away, a different random direction was chosen instead. Each site had six bat seed traps ('bat traps') and six non-bat seed traps ('non-bat traps').

4.3.5 Checking traps

Traps were open day and night from late September to mid-November 2010 and again from mid-February to mid-April 2011. Traps were typically checked every 2-3 weeks (range 1 to 31 days). At each check, I measured the length and width of the open trap because there was some variation in trap sizes and the traps covered a smaller area when they sagged. These measurements were used to calculate the m^2*days that the trap was open since the previous visit. This measurement was used to account for variation among trap sizes and length of time traps were open.

I searched the contents of the trap for fruits and seeds in the field and recorded the type of item (e.g. fruit, seed, partial fruit or seed, capsule, bat ejecta), plant species, agent of dispersal, and quantity. Diaspores with unknown dispersal agents were noted. Unidentifiable plant material was saved and assigned a morphotype id. Bat handling was confirmed by characteristic teeth and claw marks or ejecta (as described in Chapter 1 and Chapter 1 appendix 1D). Bird dispersal was identifiable from bird feces, or characteristic seed coloration in the case of hornbills. Feces or characteristic tooth marks on fruit were used to identify monkeys as the dispersers. Rodents often broke open seeds or left distinctive tooth marks. In a few cases, the disperser was recorded as an

unidentifiable ‘mammal.’ If the disperser was completely unknown but an animal might have been involved, the disperser was recorded as ‘unknown’. Predated diaspores, fruit tissue without any seeds, and diaspores with no evidence of animal involvement in dispersal (such as wind dispersed seeds) were recorded but excluded from analyses unless otherwise noted.

Very small seeds (<2 mm long) were small enough to fall out through the mosquito netting in the middle of traps. Therefore, I estimated the numbers of small seeds. Nearly all very small seeds came from bats, mostly imbedded in ejecta with fruit pulp. Ejecta cannot always be distinguished as discrete units, so estimation of ejecta quantity was often necessary or a minimum number were counted and recorded (e.g. if there were at least 30 ejecta, I used 30 as the ejecta quantity). I counted *Anthocleista grandiflora* seeds in a subset of ejecta from a trap and used the mean to estimate seed count based on estimates of the number of ejecta. These methods provide conservative estimates of seed count.

4.3.6 Analyses

To account for the variation in area covered by open traps and the length of time that traps were open, I divided the number of diaspores recorded in each trap by the trap area (m^2) times the number of days the trap had been open for comparisons of diaspore quantity, except as noted below.

Because the species richness and diaspores/m^2*days data are not normally distributed, I used Generalized Linear Models (GLMs) to compare the effects of trap type (bat or non-bat) and habitat type (fragment or continuous forest) on species richness and diaspores per m^2*days. When only diaspores dispersed by bats were considered, I used the number of diaspores with a

Poisson distribution rather than diaspores/m^2*day since there were many traps with zero diaspores/m^2*days, and the Gamma distribution cannot include zero. The two measures were highly correlated for bat-dispersed diaspores (Pearson's product-moment correlation, t = 138.4168, df = 142, $p<0.001$).

Rarefaction curves were generated using 100 permutations of species accumulation with respect to number of diaspores in the package 'vegan' (Oksanen et al. 2013). All analyses were performed in R version 2.15.2 (R Core Team 2012).

4.4 Results

4.4.1 Plant species and their dispersers

Overall, approximately 20,253 intact seeds or fruits from 40 species and 66 morphospecies were recorded in the seed traps (hereafter, species and unidentified morphospecies will be referred to collectively as 'species'). Based on evidence of animal handling, fruit bats dispersed 24 species, birds 13 species, monkeys 5 species, rodents 4 species, and unidentifiable mammals 5 species (Table 4.1). For 96 species the dispersal agent was unknown on at least one occasion. With the exception of three unidentified morphotypes, all of the bat-dispersed species recorded here were also recorded in Chapter 1. Only one species, *Maesopsis eminii*, was recorded for all animal groups.

Small-seeded species (*Anthocleista grandiflora, Coccinia mildbraedii*, and all *Ficus* spp.) overwhelmingly contributed the greatest numbers of viable diaspores, nearly all of them dispersed by bats (Table 4.1). Most of the seeds were quantified from ejecta, but some also came

from bat feces. *A. grandiflora* and at least one *Ficus* spp. were found in traps at ten of the twelve sites, whereas *C. mildbraedii* was only observed in three sites (Table 4.2). The largest-seeded species were overwhelmingly dispersed by bats with some unknown dispersers (*Cephalosphaera usambarensis*, *Maranthes goetzeniana*, and *Parinari excelsa*) were found in six, seven, and all twelve sites, respectively (Table 4.2).

Macaranga capensis had the highest quantity of seeds dispersed by birds. Many *Bridelia micrantha* seeds were probably also dispersed by birds, but nearly all its diaspores were assigned to an unknown disperser. Other commonly recorded species attributed to unknown dispersers include *Shirakiopsis elliptica* and *Syzygium guineense* which were also dispersed by birds and bats, respectively (Table 4.1). Since there were few feces in the traps, most of the dispersal attributed to monkey or unknown mammals based on tooth marks. These seeds and fruits were probably dropped while feeding. In the case of rodents, the observed diaspores were usually mostly intact fruits with tooth marks, since predated seeds were excluded.

Sites varied considerably in the number of traps with bat activity, total number of intact diaspores, and species richness (Table 4.3). Out of 144 seed traps, 71% captured at least one seed, fruit, or ejecta from fruit bats. There were seven traps placed below bat feeding roosts and 35 non-bat traps that never captured dispersal from bats. Species richness in individual traps ranged from 1 to 17 (mean = 4.3, median= 4). Site species richness ranged from 15 to 37 species. The highest richness was recorded in a forest fragment that had a high number of unidentified morphotypes.

4.4.2 Diaspore quantity and species richness for all dispersers

When diaspores from all dispersers were considered together, both factors of interest (trap type and habitat type) had a significant effect on the number of diaspores and number of species in an individual trap.

4.4.3 Trap type

Bat traps captured more diaspores (mean= 3.1 vs. 0.49 diaspores/ m^2*days, GLM with Gamma distribution (log link), t=-4.102, $p<0.001$) and had higher species richness (mean= 5.1 vs. 3.4 species, GLM with Poisson distribution (log link), z= -4.696, $p<0.001$) than non-bat traps (Table 4.3, Figure 4.1 a, b). Since both the number of diaspores and richness were higher in bat traps and fragments, it is important to consider the species accumulation curves for both trap type and habitat type. Rarefaction curves reveal that bat traps attained higher observed species richness, but the non-bat traps are actually on a trajectory for higher species richness (Figure 4.2 a).

4.4.4 Site type

Seed traps in forest fragments captured greater numbers of diaspores (mean= 3.4 vs. 1.0 diaspores/m^2*days, GLM with Gamma distribution (log link), t= 2.696, p=0.008) and had higher species richness compared to continuous forest (mean= 5.1 vs. 3.8 species, GLM with Poisson distribution (log link), z= 3.557, $p<0.001$) at the level of individual traps (Figure 4.1 c, d). Although species richness in fragments is higher on a per-trap basis, species richness across all traps accumulates much faster and reaches a higher level in continuous forest for each individual diaspore added (Figure 4.2 b).

4.4.5 Rarefaction on dispersers

By far, bats were observed to disperse the greatest number of diaspores, followed by diaspores from unknown dispersers (Figure 4.3). The diaspore species richness of unknown dispersers was higher, primarily due to a high number of unidentified morphospecies. The number of very small seeds dispersed by bats (and almost nothing else) heavily influences the rarefaction curve for bats. Comparing species accumulation on a per-diaspore basis, birds would be expected to disperse a greater number of species than bats. The leveling off of the bat curve also suggests that I captured nearly all of the bat-dispersed species that were fruiting in the vicinity of the seed traps during that time. Since a large amount of species richness is attributed to unknown dispersers, I separately analyzed just the observations attributed to bats.

4.4.6 Diaspore quantity and species richness for bats only

When only diaspores dispersed by bats were considered, both trap type and habitat type still had significant effects on the number of diaspores and species richness recorded in a trap, but the direction of effect reversed for continuous forest and fragments from the results for all dispersers.

4.4.7 Trap type

Unsurprisingly, bat traps had more bat-dispersed diaspores than non-bat traps (mean= 204.4 vs. 17.7 diaspores, Figure 4.4 a, GLM with Poisson distribution (log link), $z= -47.03$, $p<0.001$), as well as higher species richness of bat dispersed diaspores (mean= 2.3 vs. 0.7 species, Figure 4.4 c, GLM with Poisson distribution (log link), $z= -7.439$, $p<0.001$). Richness of bat dispersed species per trap ranged from 0 to 8 (mean= 1.5, median= 1). Comparison of rarefaction curves for bat and non-bat traps show the lines are nearly on top of each other, which suggests that bat-

dispersed species accumulation is following a similar trajectory in non-bat traps as observed in bat traps (Figure 4.5 b).

4.4.8 Site type

Traps in forest fragments had greater numbers of bat-dispersed diaspores than continuous forest sites (mean= 219.6 vs. 56.7 diaspores, Figure 4.4 b, GLM with Poisson distribution (log link), $z= 81.64$, $p<0.001$). However, in contrast to the higher species richness observed in fragments for all dispersers, fragments had lower species richness of bat-dispersed diaspores than continuous forest sites (mean= 1.2 vs. 1.6 species, Figure 4.4 d, GLM with Poisson distribution (log link), $t= -2.013$, $p=0.044$). The lower species richness of bat-dispersed diaspores in fragments compared to continuous forest is apparent in rarefaction curves comparing species accumulation in the two types of sites (Figure 4.5 b).

4.5 Discussion

This study quantified bat-dispersed diaspores, which has rarely been done in Africa, and confirms in a quantifiable way many of the observations of bat dispersal in Chapter 1. Although none of the bat-dispersed species are identifiably new, these observations offer insight into the quantity and variety of diaspores in bat diets in a diverse Afrotropical forest.

4.5.1 Diaspores from all sources together

I expected that seed rain and richness would be higher below bat feeding roosts and similar in fragments and continuous forest. As predicted, traps placed below bat feeding roosts had both higher numbers of diaspores and higher richness compared to traps away from feeding roosts

(Figure 4.1 a, c). The same pattern was true for fragments compared to continuous forest at the level of individual traps (Figure 4.1 b, d). The rarefaction curves for species richness in the two habitat types, however, tell a different story. When compared across all traps in all sites, the species richness is higher for continuous forest sites than forest fragments (Figure 4.2 b). This suggests that species composition may be more similar among fragments than among continuous forest sites.

4.5.2 Diaspores only from bats

Similar trends as observed with the diaspores from all dispersers were observed for diaspores from bats alone for the trap type and for diaspore quantity in fragments. The traps below feeding roosts had higher abundance and richness at the level of individual traps (Figure 4.4 a, c). However, the results were different for species richness. Instead of higher richness in fragments, traps had higher richness in the continuous forest (Figure 4.4 d), and the difference is even more pronounced when using rarefaction curves to compare species accumulation among habitat types. When traps are pooled together, continuous forest had much higher species richness of bat-dispersed diaspores than forest fragments which leveled off at a much lower species richness.

At first, the result that bats dispersed more seeds in fragments appears to contradict what was found by Melo et al. (2009) where they had fewer seeds in small reserves compared to large ones. However, they were only counting seeds >8 mm long. The observed trends with bats may be strongly driven by the overwhelming numbers of small diaspores (94% of bat-dispersed diaspores). It is clear that fruit bats disperse large numbers of seeds from small-seeded species, which is difficult to observe without seed traps (or trapping bats themselves) since the small seeds are easily lost in the leaf litter, especially when defecated. The small seeded species

dispersed by bats in this study are all species commonly found in gaps or edges, and can grow in degraded areas. *A. grandiflora* is a common and distinctive tree reaching about 30 m in height that was found in traps at ten of the 12 different sites (Table 4.2). Fruit bats are also likely pollinators for this species (Sewall et al. 2003). *C. mildbraedii* is a non-woody cucurbitaceous vine which was notably found in only two sites, both small fragments, but its numerous seeds and popularity at those sites launched it to the top of the diaspore list. The two *Ficus* species, *F. mucuso* and *F. sur*, are both fast-growing gap-dependent species that can become large trees (Lovett et al. 2006). Only one other bat-dispersed species has seeds small enough to be swallowed- *Adenia lobata*. Although the greatest numbers of diaspores were from ingestible small-seeded species, the greatest species richness was among species with larger seeds. This observation is consistent with the conclusion of Muscarella and Fleming (2007) that Pteropodid fruit bats disperse some early-successional species (especially *Ficus* spp.), but most of the species are larger-seeded, later successional species.

Although the focus of the study was dispersal by bats, some dispersal by other species was also captured. Previous research in African forests has demonstrated that hornbills (e.g. Whitney et al. 1998, Cordeiro et al. 2004), other birds (e.g. Farwig et al. 2006, Flörchinger et al. 2010), monkeys (e.g. Clark et al. 2001, Koné et al. 2008, Gross-Camp et al. 2009), civets, and genets (Engel 2000) disperse numerous plant species. This study identifies a gap in the richness from seed traps in forest fragments compared to continuous forest that is not attributable to bats (compare Figures 4.2 b and 4.5b). Most of the increase in species richness in bat traps in fragments compared to continuous forest appears to be due to dispersal of species by unknown dispersal agents, since bat-dispersed species alone have *lower* richness in fragments. Which

animals are dispersing the greatest number of species in fragments? Most likely, much of the dispersal is from birds. Rain, long intervals between checks, and a lack of noticeable uric acid in the feces of some frugivorous birds (Duncan and Chapman 1999) probably contributed to the low numbers of diaspores attributed to birds.

The one plant species that was dispersed by all animal groups (along with many unknown dispersers) was *Maesopsis eminii*, an invasive species introduced from central and western Africa. Its popularity with hornbills (*Ceratogymna brevis*), turacos (*Tauraco fischeri*), and monkeys (*Cercopithecus mitis*) was documented by Cordeiro et al. (2004) but not its popularity with fruit bats. Many *M. eminii* seeds were also found predated by both large and small rodents (based on the size of tooth marks). Whether or not the seeds are scatterhoarded by rodents is unknown, but I suspect it is highly likely. Unlike hornbills, fruit bats cannot ingest *M. eminii* seeds, so they are not responsible for seed dispersal on the order of kilometers, but bats may be important mid-range dispersers. Understanding the role of fruit bats in seed dispersal has relevance to management of bat-dispersed invasive species like *M. eminii* and other invasives in Africa such as the neem tree (Ayensu 1974).

Overall, this research demonstrates that Pteropodid fruit bats can disperse enormous quantities of small seeds in both forest fragments and continuous forest, but other animals such as birds may be responsible for a greater richness of seeds in fragments.

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4.7 Figures and Tables

Figure 4.1 Box plots of intact diaspores from all dispersers

Box plots displaying cumulative values for individual seed traps of intact diaspores from all dispersers. a) Diaspores/m^2*days dispersed into bat traps (B) and non-bat traps (NB) ($p<0.001$), b) diaspores/m^2*days dispersed into traps in continuous forest (C) and fragments (F) ($p=0.008$), c) species richness of diaspores dispersed into bat traps (B) and non-bat traps (NB) ($p<0.001$), d) species richness of diaspores dispersed into traps in continuous forest (C) and fragments (F) ($p<0.001$). All differences are statistically significant (see section 4.4.2). Boxes show the second quartile, median, and third quartile. Whiskers indicate highest and lowest values within 1.5 times the interquartile range and dots indicate values outside that range. Asterisks indicate the means.

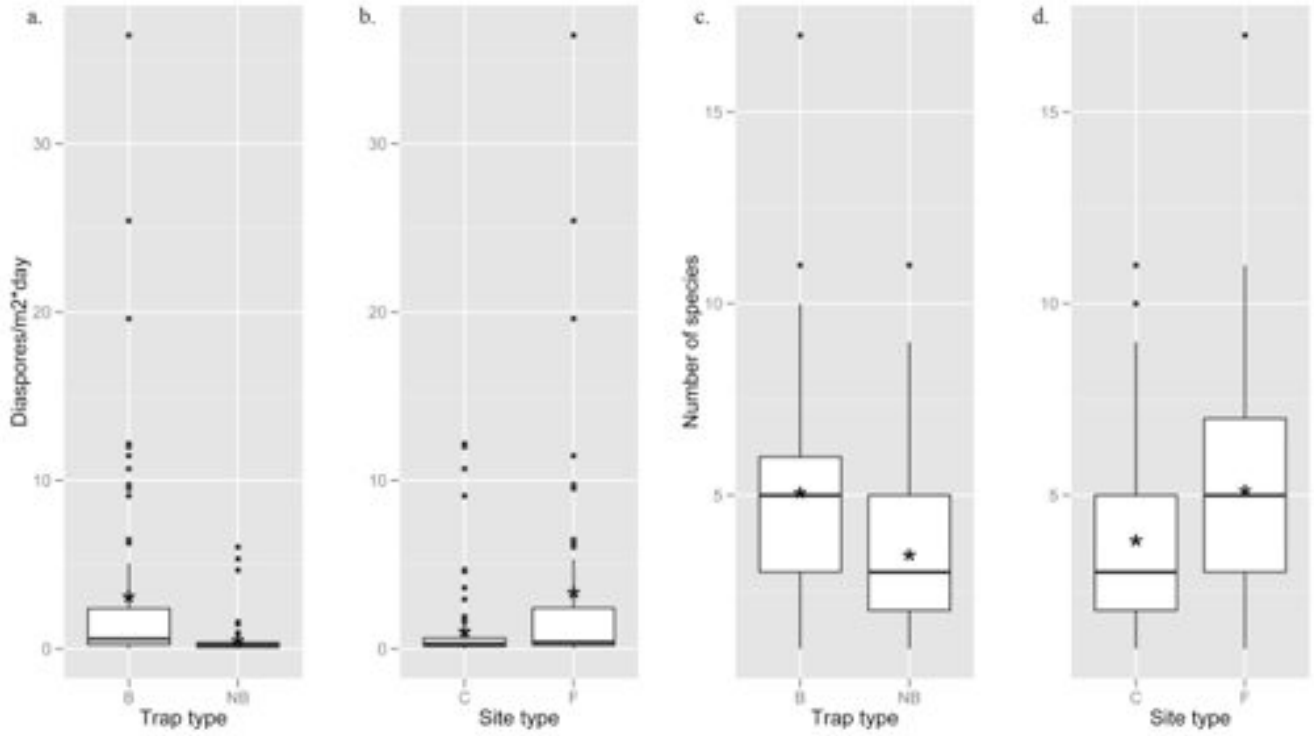

Figure 4.2 Rarefaction curves based of number of diaspores and species richness

Rarefaction curves based on 100 permutations of number of diaspores and species richness for a) bat traps (solid) and non-bat traps (dashed), b) continuous forest (solid) and forest fragments (dashed).

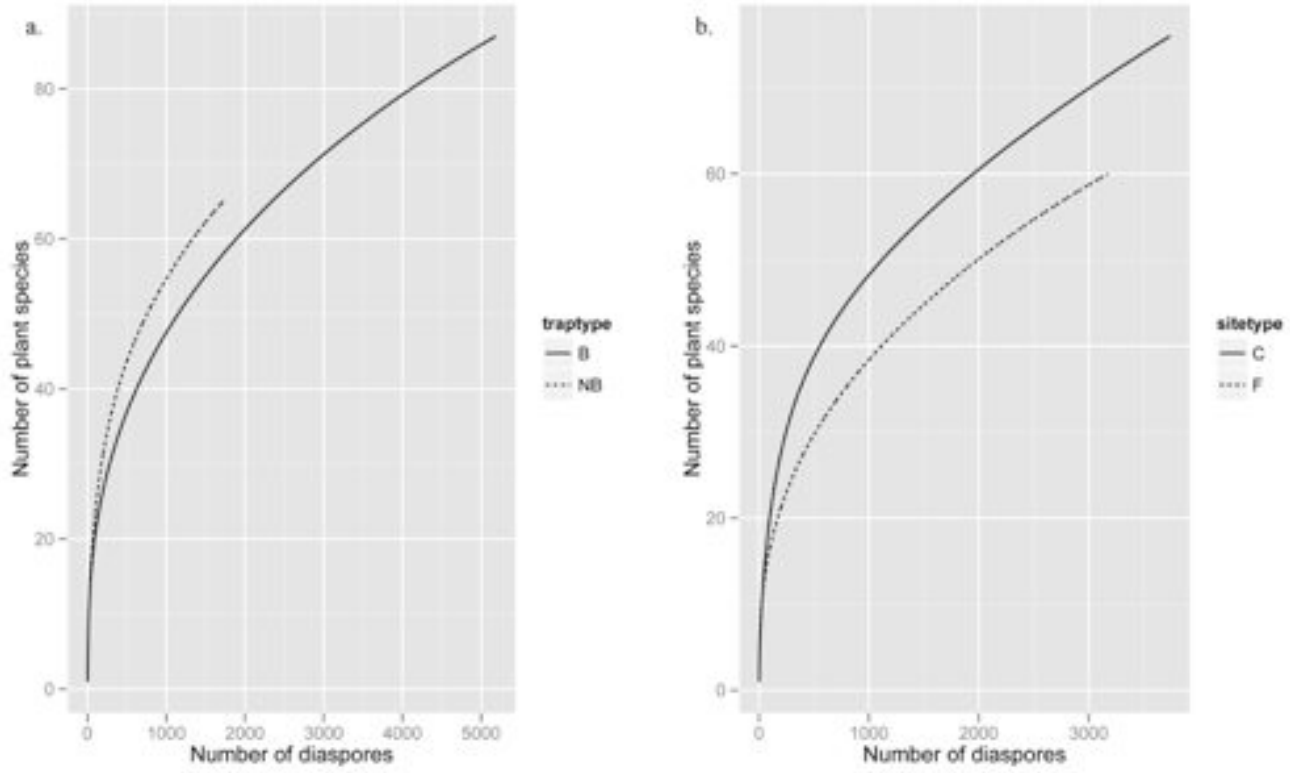

Figure 4.3 Rarefaction curves for different types of dispersers

Rarefaction curves based on 100 permutations of number of diaspores and species richness for different types of dispersers. The inset zooms in on the disperser types that did not have many diaspores attributed to them.

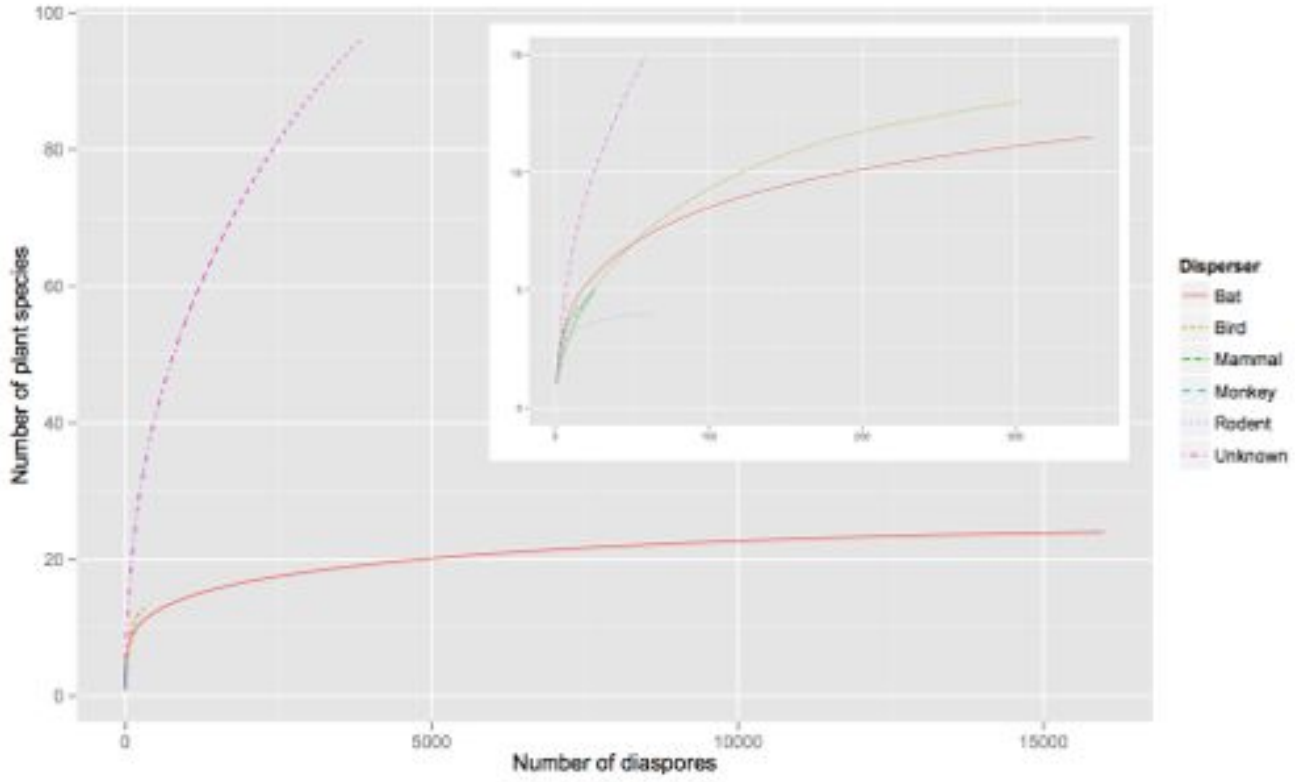

Figure 4.4 Box plots of intact diaspores dispersed by bats

Box plots displaying cumulative values for individual seed traps of intact diaspores dispersed by bats. a) Diaspores/m^2*days dispersed into bat traps (B) and non-bat traps (NB) ($p<0.001$), b) diaspores/m^2*days dispersed into traps in continuous forest (C) and fragments (F) ($p<0.001$), c) species richness of diaspores dispersed into bat traps (B) and non-bat traps (NB) ($p<0.001$), d) species richness of diaspores dispersed into traps in continuous forest (C) and fragments (F) ($p=0.044$). All differences are statistically significant (see section 4.4.4). Boxes show the second quartile, median, and third quartile. Whiskers indicate highest and lowest values within 1.5 times the interquartile range and dots indicate values outside that range. Asterisks indicate the means.

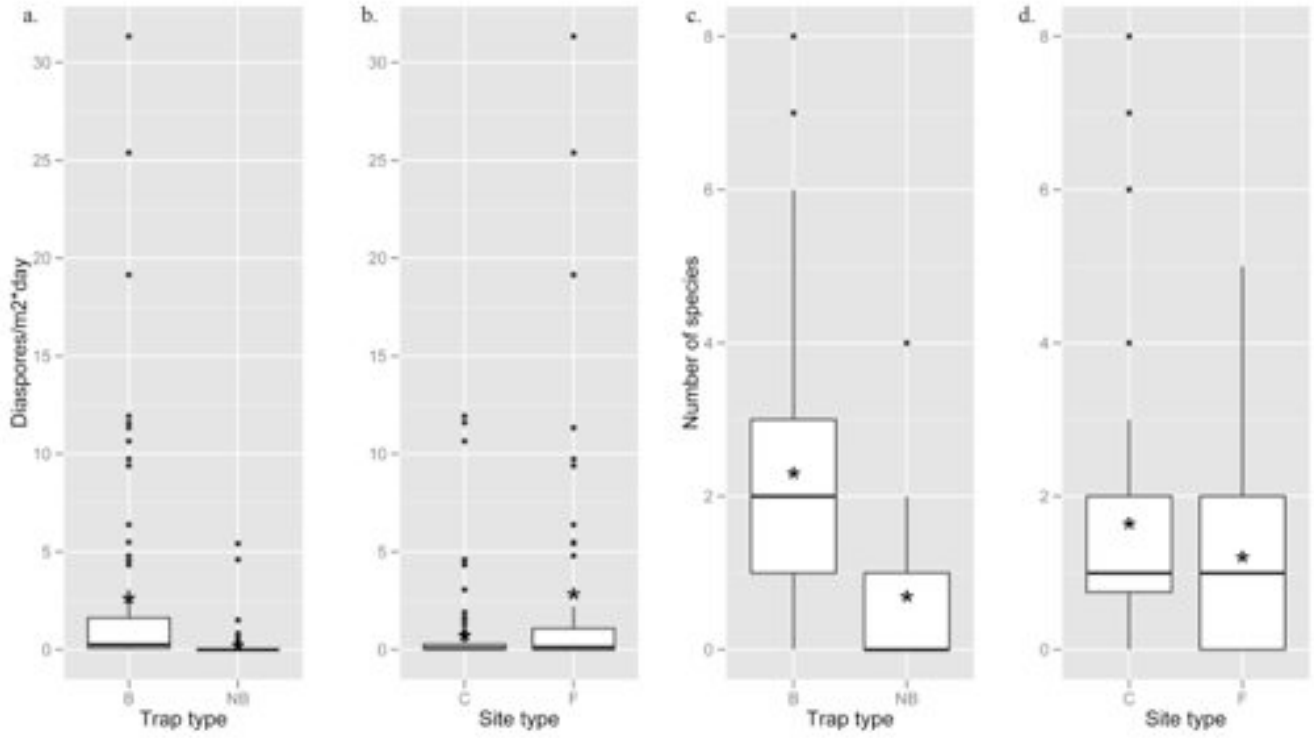

Figure 4.5 Rarefaction curves of bat-dispersed diaspores and species richness

Rarefaction curves based on 100 permutations of number of bat-dispersed diaspores and species richness for a) bat traps (solid) and non-bat traps (dashed), b) continuous forest (solid) and forest fragments (dashed).

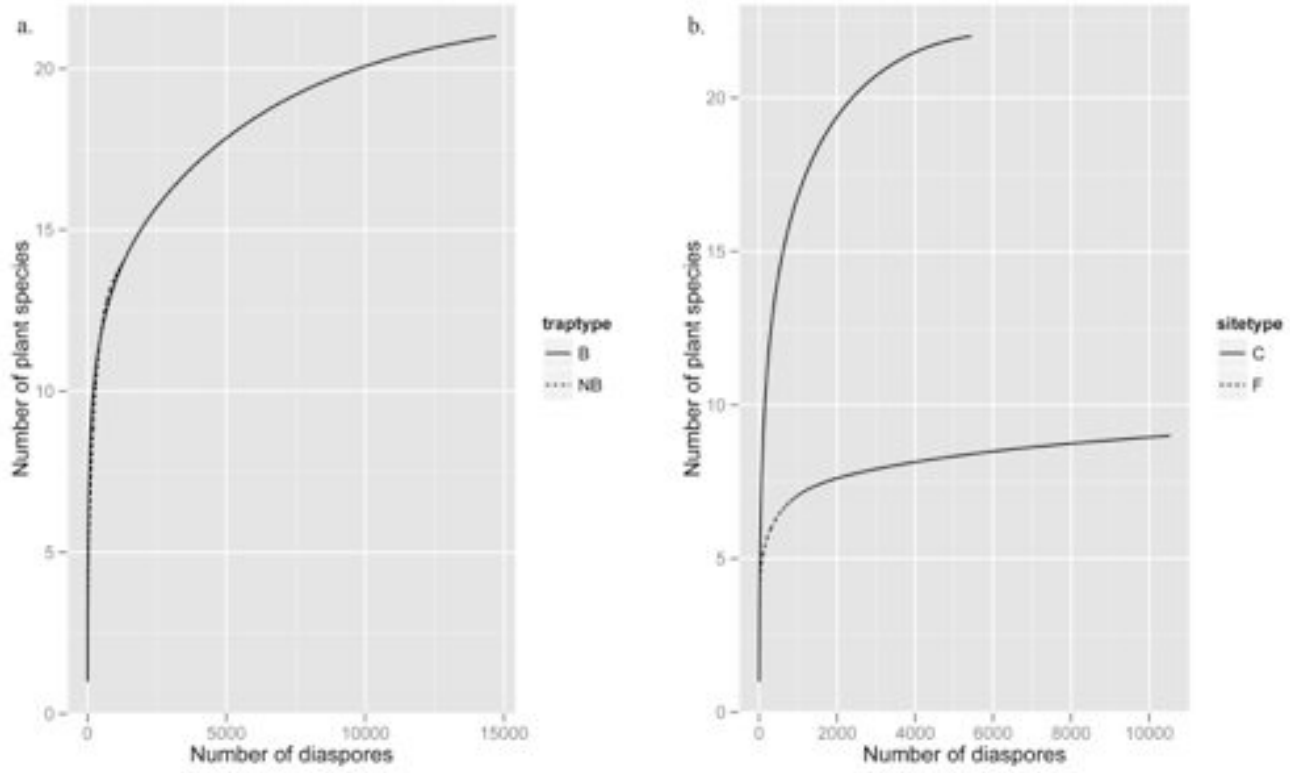

Table 4.1 Summary of intact diaspores recorded for each plant species and animal type

Total number of intact diaspores recorded for each plant species and animal type.

Plant species	Bat	Bird	Mammal	Monkey	Rodent	Unknown	Total
Adenia lobata	1	0	0	0	0	0	1
Alangium chinense	0	0	0	0	0	44	44
Albizia gummiferae	0	0	0	0	0	11	11
Allophylus sp.	0	3	0	0	0	0	3
Anisophyllea obtusifolia	2	0	0	0	0	5	7
Annickia kummeriae	0	0	0	0	0	45	45
Anthocleista grandiflora	6594	0	0	0	0	16	6610
Blighia unijugata	0	0	0	0	0	2	2
Bridelia micrantha	0	1	0	0	0	271	272
Camellia sinensis	0	0	0	0	0	1	1
Cephalosphaera usambarensis	148	0	0	0	0	2	150
Coccinia mildbraedii	1049	0	0	0	0	3	1052
Dracaena afromontana	0	1	0	0	0	3	4
Drypetes gerrardii	29	0	0	0	0	3	32
Eucalyptus sp.	0	0	0	0	0	4	4
Ficus mucuso	408	0	0	0	0	0	408
Ficus natalensis	7	0	0	0	0	0	7
Ficus spp.	3928	0	10	0	0	59	3997
Ficus sur	3029	40	0	0	0	2	3071
Greenwayodendron suaveolens	8	0	0	0	0	4	12
Harungana madagascariensis	0	0	0	0	0	10	10
Landolphia sp.	22	0	0	3	0	2	27
Lantana camara	0	0	0	0	0	1	1
Macaranga capensis	0	217	0	0	0	561	778
Maesopsis eminii	388	4	8	20	33	569	1022
Maranthes goetzeniana	187	0	0	0	12	23	222
Morpho 8	2	0	0	0	0	0	2
Morpho 9	0	10	0	0	0	0	10
Morpho B	0	3	0	0	0	1	4
Morpho BG	0	15	0	0	0	0	15
Morpho BT	0	2	0	0	0	2	4
Morpho D	0	0	5	1	0	1	7
Morpho EA	3	0	0	0	0	4	7
Morpho EX	1	0	0	0	0	0	1
Morpho FB	0	1	0	0	0	0	1

Myrianthus holstii	0	0	0	0	20	8	28
Parinari excelsa	109	0	0	2	2	2	115
Paullinia sp.	0	0	0	0	0	2	2
Pouteria adolfi-friedericii	21	0	0	0	0	0	21
Rauvolfia caffra	0	4	1	0	0	27	32
Rinorea sp.	0	0	0	0	0	2	2
Rourea minor	37	0	0	0	0	81	118
Shirakiopsis elliptica	0	4	1	0	0	323	328
Strombosia scheffleri	3	0	0	0	0	2	5
Strychnos sp.	2	0	0	1	0	3	6
Synsepalum cerasiferum	4	0	0	0	0	27	31
Syzygium guineense	7	0	0	0	0	560	567
Viscum sp.	0	0	0	0	0	2	2
Xylopia aethiopica	0	0	0	0	0	17	17
58 additional morphotypes	0	0	0	0	0	1135	1135

Table 4.2 Plant species with >100 intact diaspores dispersed by bats

The number of seed traps per site (max= 12) with diaspores of each plant species with more than 100 diaspores dispersed by bats. All observed *Ficus* spp. have been lumped together in this table.

Seed size	Most abundant bat-dispersed plant species	Continuous forest habitat								Fragmented forest			
		C1	F17	F18	K1	K2	N2	P1	S1	F13	F22	F4	F9
Small	*Anthocleista grandiflora*	1	6	6	6	2	0	0	2	1	6	4	1
	Coccinia mildbraedii	0	0	0	0	0	0	0	0	3	1	0	0
	Ficus spp.	4	1	1	2	1	0	0	0	1	8	5	5
Large	*Cephalosphaera usambarensis*	5	5	3	7	5	0	0	0	0	0	2	0
	Maesopsis eminii	11	6	4	3	8	7	3	8	2	0	1	0
	Maranthes goetzeniana	3	2	6	0	3	1	0	0	1	0	6	0
	Parinari excelsa	4	2	0	0	1	7	2	4	3	2	2	2

Table 4.3 Site summaries of seed traps

Site summaries of traps with bat dispersal, total diaspores dispersed per m^2*days, and species richness.

Habitat Type	Site	Traps with evidence of bat dispersal (max=6)		Total diaspores/m^2*days		Species richness		Species richness
		Bat traps	Non-bat traps	Bat traps	Non-bat traps	Bat traps	Non-bat traps	
Continuous forest	C1	6	6	14.2	1.4	18	13	24
	F17	6	5	15.3	2.2	16	11	19
	F18	5	3	6.6	1.3	17	11	21
	K1	6	4	18.6	6.8	14	6	16
	K2	6	2	8	1.7	16	9	18
	N2	5	4	10.1	1.4	14	10	17
	P1	5	1	2.4	0.8	13	10	15
	S1	6	5	6.3	1.5	16	10	19
Forest fragments	F13	5	0	19.6	1.3	13	9	15
	F22	6	4	72.2	8	16	15	20
	F4	6	1	19.5	0.8	9	12	16
	F9	3	2	31.4	8.1	32	20	37

5 ANALYSIS OF A CONTINENT-WIDE SEED DISPERSAL NETWORK AT THE FAMILY LEVEL

5.1 Abstract

Plant-animal interactions can be characterized using network analysis. What is known about seed dispersal networks to date comes from many small-scale studies on subsets of seed disperser communities. Studies have shown that these networks tend to be nested and modular. It is unknown whether similar patterns also exist at broader geographic scales and lower taxonomic resolution. This study aggregates records of vertebrate seed dispersal across Africa and examines the network properties of these interactions at the level of animal and plant families, rather than species. The Africa Tree Database was created to enter frugivory and seed dispersal interactions in Africa from published literature. I created an unweighted (binary) interaction matrix of African plant and animal families based on the records entered in the database, then applied common network analysis methods such as nestedness and modularity to analyze the interactions. Results from the observed family-level network were compared to 1000 randomizations Patefield's null model that maintained marginal matrix sums from a weighted matrix. I found that the observed network was less nested and more modular than the null models. Seven modules were identified based on the density of interactions recorded among different families. The plant families Moraceae (e.g. figs) and Leguminosae (e.g. Acacia), and animal families Hominidae (e.g. apes), Cercopithecidae (e.g. monkeys), and Elephantidae (elephants) were particularly well-connected within and between their modules. Although these results are preliminary due to the incompleteness of interactions in the database, this approach

has great potential to reveal broad-scale patterns in plant-animal coevolution and could be applied to other geographic areas.

5.2 Introduction

Plant-animal interactions have long been of interest to ecologists, but it is only in the past decade that network analysis methods have been rigorously applied to pollination, seed dispersal, and frugivory networks (Bascompte et al. 2003, Bascompte and Jordano 2007, Olesen et al. 2007, Schleuning et al. 2011). Research on seed dispersal networks has previously focused on sampling small geographic areas (though often analyzing several networks from different areas, e.g. Fortuna et al. (2010)) and almost always just a subset of vertebrate seed dispersers such as birds (Burns 2012, Plein et al. 2013), bats (Mello et al. 2011), or primates (Tutin et al. 1997). Bird dispersal networks have overwhelmingly received the most attention (Mello et al. 2011). One notable exception for the breadth of sampling in terms of animal groups is Donatti et al. (2011) who observed seed dispersal by 46 different animal species including mammals, birds, fish, and tortoises in the Brazilian Pantanal. These studies have informed what we know about the nature of seed dispersal networks.

Seed dispersal and pollination networks, unlike most social networks, are bipartite (or two-mode) because there are two distinct types of players: plants and animals. There are several different metrics used to characterize plant-animal interaction networks (Dormann et al. 2009). Connectance, species degree, nestedness, and modularity are some of the most commonly applied metrics (Blüthgen et al. 2008). Connectance is simply the proportion of possible

interactions within a network that are actually observed (range 0-1). Species degree is the number of other species each species interacts with. Nestedness was originally observed in species presence at different sampling sites, where sites with fewer species contained species that were subsets of more diverse fauna at other sites (Patterson and Atmar 1986, Atmar and Patterson 1993). The concept of nestedness was first applied to plant-animal interactions by Bascompte et al. (2003). In this context, a highly nested network is one in which specialist species interact with generalist species, rather than specialists interacting with each other. Most plant-animal interaction networks exhibit a high level of nestedness (Joppa and Pimm 2010). Modularity is a metric quantifying to what extent the network has distinct subgroups. Each plant and animal species is assigned to a module, which involves identifying the subgroups (usually by the density of interactions among species) and then compares the density of interactions within modules to the density of links outside of modules (Labatut and Balasque 2012). A network with modules that have as many links to other modules as within modules would have low modularity, regardless of how many modules were identified. Larger networks (more plant and animal species) tend to be more modular and have more modules (Olesen et al. 2007). Such compartmentalization of networks is thought to increase network stability (Krause et al. 2003, Teng and McCann 2004). These various metrics are used to characterize the interactions of plants and animals.

To date, seed dispersal network analyses have focused on the species level within small geographic areas to attempt high sampling completeness. It is important to restrict the sampling area enough to meet the assumption that all plant species can theoretically interact with all animal species. At broader geographic scales, this is clearly impossible. However, higher-order

taxonomic groups exhibit wider distributions than individual species (except in the case of monotypic groups). Therefore, it is possible to examine networks at a coarser taxonomic and geographic scale by looking at records of interaction between genera, families, or orders. It is presently untested whether network patterns observed at the local, species level also exist at the continental, family level. My goal is to decipher the structure of frugivory and seed dispersal at a continental, family level by aggregating observations from all groups of vertebrate seed dispersers across Africa, and compare the network properties of these plant-animal interactions to other network studies that have been done at the local, species level.

One advantage of this approach is that it allows for the inclusion of many disparate observations. The most comprehensive seed dispersal studies in Africa to date have missing animal taxa, even at the local level. In particular, Gautier-Hion et al. (1985)'s landmark study of dispersal syndromes in Gabon did not include fruit bats or most birds. But there are thousands of observations published in different journals, including detailed descriptions in hard-to-access natural history journals. In aggregate, these observations can reveal patterns that may be undetected at smaller scales. For example, is there evidence for disperser-plant coevolution at the family level? Species-level network approaches that take plant taxonomy into account, such as the approach used by Donatti et al. (2011) suggest that there is considerable diversity within plant families in terms of dominant seed dispersers. Indeed, this is obviously true even at the species level for many 'charismatic' fruits that attract a variety of frugivores. However, local studies are limited by the plant diversity within sites. At the continental level, some plant families may show specialization on particular animal groups, which would be difficult to discern by looking only at local networks.

Here I present the first attempt of continent-wide, family-level interactions of seed dispersal and frugivory using data compiled to date from Africa in the Africa Tree Database (www.africatreedatabase.com).

5.3 Methods

5.3.1 Data compilation

Several journals that were known or suspected to include published reports of seed dispersal and frugivory in Africa were systematically searched by reading through the journals' tables of contents (Table 5.1). The research team only read articles suspected to contain relevant information, and parsed information relevant to the reported interactions. Interactions were entered into the Africa Tree Database (ATD) (www.africatreedatabase.com) which was created specifically for this purpose.

Plant nomenclature was verified with the Plant List (http://www.theplantlist.org/) using the R package 'Taxonstand' (Cayuela 2012, Cayuela et al. 2012). If an entry failed to match using Taxonstand (which is true for anything with a misspelled genus), it was run through the Taxonomic Name Resolution Service (TNRS) (Boyle et al. 2013) using a script adapted from TNRS (iPlant Collaborative 2013). iPlant and TNRS both identify synonyms and offer the currently accepted family, genus, and species. A small number of entries required manual correction of the spelling or family name. Analyzing data at the family level allows for the inclusion of observations that cannot be assigned to a particular genus or species, but can be assigned to family. This is common in the tropics where flora may be incompletely described, or expert identification is not available.

Some non-target interaction types were entered in the database because they were in papers that contained target interactions (Table 5.2). For example, reports of wind dispersal were entered, but excluded from analyses. Other types of excluded interactions are listed in Table 5.2. After removing problematic or non-target data, there were 4381 interactions with 3273 unique plant-animal species combinations. The animal family and plant family was extracted from each individual interaction (mostly at the level of animal species – plant species) which resulted in 639 unique plant-animal family combinations.

5.3.2 Analyses

Plant-animal interactions are commonly represented in matrices where rows correspond to plants and columns correspond to animals. Usually these refer to individual species, but in this case each row (column) is a plant (animal) family. Interaction matrices can either be qualitative (binary) or quantitative (weighted). Binary matrices have 1s where an interaction between the plant and animal was observed, and 0s where no interactions were observed. Weighted matrices have some magnitude of observation, such as the number of individual visits of an animal to a tree (Schleuning et al. 2011). Since the database aggregates observations from numerous studies with a variety of methods and observation efforts, I use a binary interaction matrix for analyzing the data.

All analyses were run in R version 2.15.2 (R Core Team 2012) with additional packages as mentioned below.

5.3.3 Nestedness

Numerous methods of quantifying nestedness and numerous different null models have been proposed against which to compare levels of nestedness in observed networks (Ulrich et al. 2009, Mello et al. 2011). For plant-animal interaction networks, the current consensus is that the preferred metric is 'NODF' (Almeida-Neto et al. 2008) which is an acronym for nestedness metric based on overlap and decreasing fill. Another popular metric for nestedness is temperature *T*, which uses the relative distances of observations that fall outside the line of perfected nestedness in a matrix to quantify the deviation of an observed matrix from a perfectly nested matrix (Atmar and Patterson 1993). NODF is recommended rather than *T* because it is size invariant which allows inter-network comparisons of nestedness (Almeida-Neto et al. 2008). NODF also separately calculates nestedness of rows and columns to distinguish if they exhibit different levels of nestedness. Calculations of NODF were made in the R package 'vegan' (Oksanen et al. 2013).

The appropriate selection of a null model against which to compare the observed data is extremely important, and varies according to the question at hand (Ulrich et al. 2009). I used a null model (Patefield's algorithm (Patefield 1981)) that incorporated the number of "observations" for each individual plant family- animal family observation in a weighted interaction matrix. Each unique entry in the ATD constituted an observation of a particular plant and animal species from a specific journal article. This means that better-studied taxa have more observations in the database because there are more journal articles that have studied them. In order to compare the level of nestedness observed in the data to what would be expected taking into account the number of times each taxon was recorded in the database, I used a weighted

matrix to generate null models, then converted them back to binary matrices. The elements of the weighted matrix contained the number of records in the database where frugivory or seed dispersal was reported for a particular plant family and animal family. Since the records in the database are at the highest taxonomic resolution reported by the original authors, a single study of closely related taxa may produce many observations in the database that are all included in the same element of the matrix. For example, Tutin and Fernandez (1985) observed gorillas eating *Dictyophleba stipulosa* (Apocynaceae) fruits and chimpanzees eating *Landolphia* sp. (Apocynaceae) fruits. Each of these observations is a separate entry in ATD and results in two weights in the weighted family-level for the interaction between the animal family Hominidae (apes) and plant family Apocynaceae. This means that the weighted matrix is weighted not only by research effort but also by taxonomic diversity within the families, since a study of elephants can report observations from at most two animal species (*Loxodonta africana* and *L. cyclotis*), both in the same family. In contrast, a study of birds could report observations from several species in one or more families simply because there is greater bird diversity. In the binary interaction matrix, additional interactions between two previously recorded families does not add any weight.

The weighted matrix contained 4,381 observations among 124 plant families and 44 animal families. I used Patefield's null model (Patefield 1981), which keeps marginal (row and column) totals fixed and randomizes the interactions within that constraint. The null models were generated using the R package 'bipartite' (Dormann et al. 2008, 2009). Before calculating nestedness (NODF) of the null models, they were converted back to binary matrices. One

thousand randomizations were run to calculate the probability of the observed nestedness compared to random models based on the observation bias in the dataset.

5.3.4 Modularity

Network modularity was calculated using a multi-level modularity optimization algorithm (Blondel et al. 2008) implemented in the R package 'igraph' (Csardi and Nepusz 2006). The algorithm identifies highly connected groups of plants and animals and calculates a value between -0.5 and 1, where positive values have more connections within modules than expected from random interaction assignment among plants and animals. Modularity was calculated using the same algorithm for each of the 1000 matrices generated using Patefield's null model for the analysis of nestedness (above see 5.3.2.1). Testing for both nestedness and modularity on null models in R allowed me to run the tests on the exact same null models, rather than using different software to separately calculate nestedness and modularity. Network module visualization was done using the R packages 'igraph' and 'RColorBrewer' (Neuwirth 2011).

5.4 Results

5.4.1 Nestedness

The family-level, continent-wide network of seed dispersal interactions has a level of nestedness that is much *lower* than what would be expected when the observation bias of different taxonomic groups is taken into account using Patefield's null model (NODF= 52.44, $p<0.001$). For comparison, NODF for matrices generated under the null model was 66.36 $\pm$ 1.71 (mean $\pm$ sd). Patefield's null model kept the marginal totals constant (i.e. total number of observations for each plant and animal family), but does not keep connectance constant. As a result, all of the null

models have higher connectance (proportion of possible interactions observed) than the observed network (observed= 0.117, null models mean 0.165 $\pm$ 0.002). This means that for most plant and animal families, the null model predicts a *greater* number of interactions than have been observed. The higher fill (and higher nestedness) is noticeable when comparing a depiction of a random matrix (Figure 5.1) to the observed matrix (Figure 5.2).

Rows (plants) had higher nestedness than columns (animals) (53.56 and 43.44, respectively) in the observed matrix. This means that plant families exhibit a more continual decrease in the number of interactions across animal families, whereas the animal families show a less continual decrease down through plant families. This is visually evident in a depiction of the observed matrix with columns and rows arranged in order of decreasing fill (Figure 5.2).

5.4.2 Modularity

Seven different modules containing plant and animal families were identified by the algorithm, and the overall level of modularity is 0.285. For comparison, the null models had a mean modularity of 0.163 (range= 0.147 - 0.191) and had from 5-10 separate modules. This suggests that the observed family-level network is *more* modular than would be predicted when taking into account taxonomic observation bias in null models ($p<0.001$).

5.4.3 Module assignment

The families in each of seven different modules are detailed in Table 5.3 and pictured in Figure 5.3 and Figure 5.4. Module 1 has browsing and grazing ungulates (zebras, antelopes, & duikers) along with gulls, and many of the plant families contain mostly herbaceous species (e.g. Amaranthaceae, Asteraceae, Brassicaceae, and Oxalidaceae). Monkeys and baboons are the sole

animal family in module 2 (Cercopithecidae), along with a handful of plant families that are unconnected or poorly connected to other animal families (Figure 5.4). The high number of connections between Cercopithecidae and plant families outside its own module is evident in Figure 5.4. Elephants are responsible for most of the connections in module 3. Other animal families in module 3 include mongooses, fruit bats, parrots, and warblers. A handful of plant families are only connected to elephants. Nearly all of the bird families are in module 4, where there are several highly connected plant families (e.g. Moraceae, Burseraceae, Cannabaceae). Contrary to most other modules, the peripheral families in this module are mostly animal families rather than plant families.

Module 5 contains plant and animal families that are more prevalent in African savanna-giraffes, rhinos, ostriches, jackals, grasses (Poaceae), and acacias (Leguminosae). Similar to module 4, there are more peripheral animal families than plant families. The vast majority of connections to other modules are via the plant family Leguminosae. In contrast, module 6 is a highly connected module with all of the rodent families as well as chevrotains (mouse-deer) and hornbills. Only one plant family in module 6 is peripheral, and most of the plant families in this module are highly connected within and between modules. Module 7 is dominated by the apes (Hominidae) and turacos (Musophagidae), which are both well-connected to plant families in many other modules. There are several peripheral plant families that are only connected to the apes as well as a few plant families in module 7 (Euphorbiaceae, Malvaceae, Phyllanthaceae) with several connections to animal families in other modules.

5.5 Discussion

Comparing the observed family-level network to random matrices generated from fixed marginal sums illustrates three important results about the observed network: 1) it has fewer interactions, 2) lower nestedness, and 3) higher modularity than predicted. This begs the question, why?

Bluthgen et al. (2008) emphasize that it is important to consider the reasons for the absence of interactions in a matrix where the null model would predict them. It could be a result of incomplete sampling, or it could be indicative of a lack of plant-animal incompatibility. For the relatively well-studied groups, such as primates, the observed absences may truly be absences due to geographic or morphological incompatibility. The species diversity and geographic distribution within plant and animal families certainly also plays a role that was not addressed in this study. A small family with few species and restricted distribution (such as Tragulidae or Penaeaceae) is intrinsically more limited than monkeys and baboons (Cercopithecidae) or figs (Moraceae) which have representatives all over sub-Saharan Africa. Other types of incompatibility in plant-animal networks, such as temporal mismatches between plants and pollinators (Olesen et al. 2008) or seed dispersers (González-Castro et al. 2012), are less likely to be pervasive at the family level.

Most other studies of plant-animal networks have shown higher nestedness than predicted from null models (reviewed by Joppa and Pimm 2010), but the variety of null models used by different studies makes it difficult to compare. Still, Joppa et al. (2010) concluded that "Unusually non-nested networks are generally rare." Although I found lower nestedness, incorporation of additional literature could fill in the gaps suggested by the null model.

The lower-than-predicted nestedness combined with higher-than-predicted level of modularity in the observed network is in contrast to trends in other seed dispersal networks. Fortuna et al. (2010) found high correlation between nestedness and modularity at low levels of connectivity (comparable to that observed in this study). However, they note that the trend reverses in networks with high connectivity, so the pattern is sensitive to the proportion of realized interactions. By looking at Figure 5.4, it is easy to imagine how the distinctions between modules fall apart as more and more interactions are added to a network. Based on the work of Fortuna et al. (2010), I expect the observed network to become less modular as the sampling increases.

A drawback of aggregating numerous studies is the highly heterogeneous nature of sampling and data quality. We did not control for sampling methods, which differ among studies, and may be different among animal groups (e.g. dung surveys of elephants versus focal tree watches of birds). In our review of the literature, studies tend to have one of two general approaches: plant-focused studies, which include records of many different animal species visiting one or a few species of plants, or animal-focused studies, which closely follow the diet (e.g. through dung or observations) of one or a few animal species, resulting in records with many different plant species. There is considerable overlap in the plant families dispersed by different animal groups, meaning that the assemblages are taxonomically similar. Also, the locations of interaction records are not random. Each study focuses on a smaller geographic area (usually a protected area) and the distribution of studies to date is neither random nor complete (many African countries lack observations entirely).

Furthermore, some animal groups lack sufficient sampling. The peripheral placement of some animal families (especially module 5, Figure 5.4) illustrate that there is a wide range of sampling effort for different taxa. Primates in Africa have received considerable, devoted research attention that has involved meticulous recording of diets for decades (Wrangham 1977), although any records in books are not currently in the database. Elephant dung is fairly easy to study, but the number of individual studies contributing elephant observations to our database is surprisingly few (22 articles). It is currently impossible to determine the relative importance of under-represented animal groups such as bats, carnivores, and odd-toed ungulates as seed dispersers. Fruit bats have been relatively neglected by other broad surveys of frugivory in Africa (Gautier-Hion et al. 1985), although they are predicted to be important seed dispersers throughout African forests for a wide range of species (Chapter 1).

Birds are also notably under-represented in the database at present. No family of frugivorous birds is suspected to rely on a single plant family, yet that is what the data suggest in module 4 (Figure 5.4). This is likely because the appropriate journals have not yet been included rather than a lack of research emphasis. Web of Science searches on seed dispersal and frugivory in Africa found a greater number of searches for birds than for elephants or primates (Chapter 1, Figure 1.3B), both of which are well-represented in the database so far. One way to address some of the taxonomic gaps going forward is to do directed keyword searches to identify relevant literature such as theses and books that might be missed in the journal scanning approach.

This broad-scale approach may reveal nuances in the selective pressure within plant families to appeal to vastly different dispersers. Two places where this approach may be particularly suitable

are Madagascar and Australia, due to their unique fauna and distinct biogeographical boundaries. Although some interactions from Madagascar have been included in the database, they were excluded from this analysis due to the fact that several families of frugivores (all in the superfamily Lemuroidea) are endemic to Madagascar and not found on mainland Africa.

There are other ways in which a similar approach could be used on existing datasets. For example, the Database of Neotropical Bat/Plant Interactions (Geiselman et al. 2002) has taken an approach to compiling published data that is somewhat similar to ours. Since all neotropical fruit bats belong to the same family (Phyllostomidae), an analysis could be done at the level of plant and animal genera. This approach to the data could more clearly reveal dietary trends among neotropical fruit bats, definitively confirming some relationships that have been hypothesized (such as bat genera specializing on different types of fruit (Fleming 1986)) and perhaps uncovering new patterns.

Finally, if this same approach is taken with other continents, then intercontinental comparisons become possible. The dominant animal dispersers at the plant family level on different continents can help inform studies examining the evolutionary history of frugivory, such as Fleming and Kress (2011). There is no doubt that it is important to continue pursuits of detailed, thorough, local-scale studies of frugivore and seed disperser communities, but I also encourage the aggregation of numerous incomplete studies as these may reveal a landscape that can only be seen by stepping back.

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5.7 Figures and Tables

Figure 5.1 Illustration of a random plant-animal matrix generated using Patefield's algorithm

Illustration of a random plant-animal matrix generated using Patefield's algorithm (Patefield 1981). Each row corresponds to a plant family and each column to an animal family. Tan and red elements of the matrix represent present and absent observations, respectively.

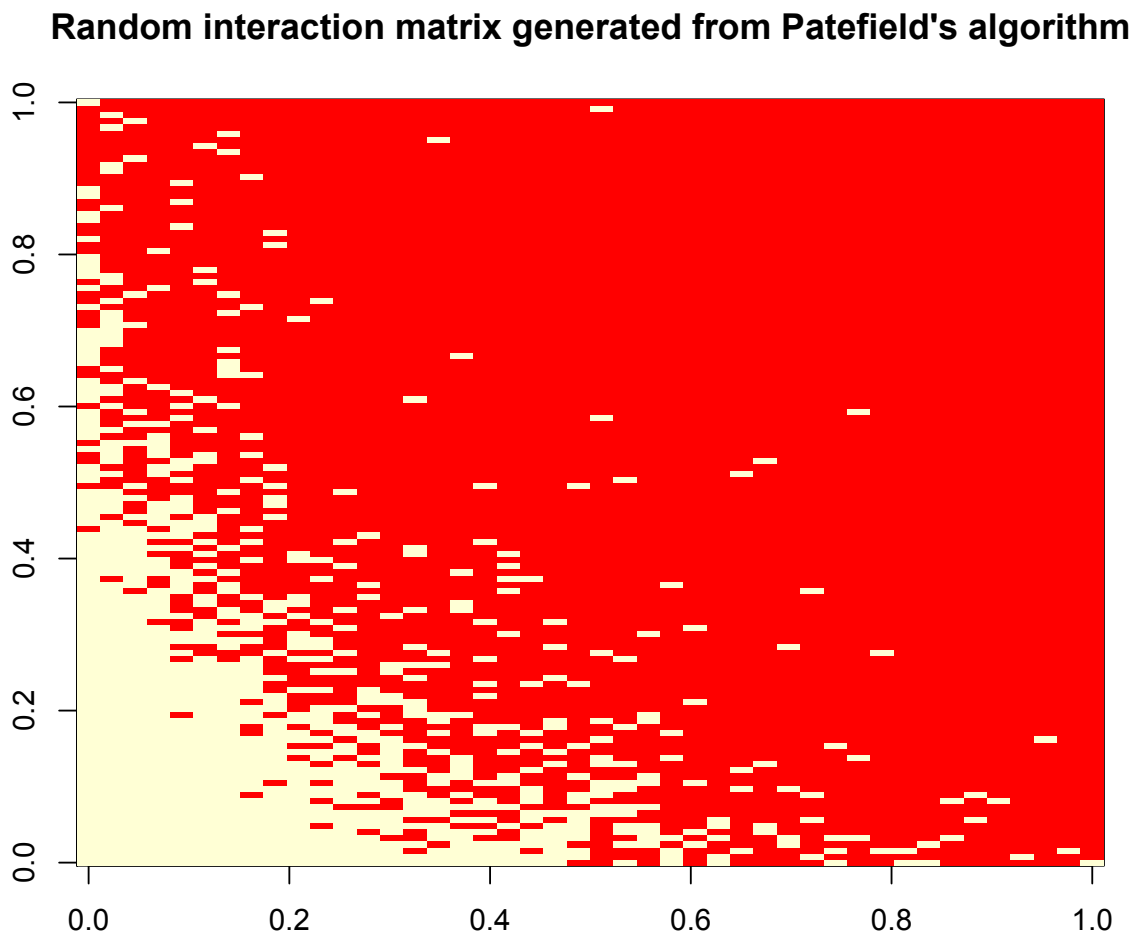


Figure 5.2 Illustration of the observed plant-animal interactions at the family level

Illustration of the observed plant-animal interactions at the family level. Each row corresponds to a plant family and each column to an animal family. Tan and red elements of the matrix represent present and absent observations, respectively.

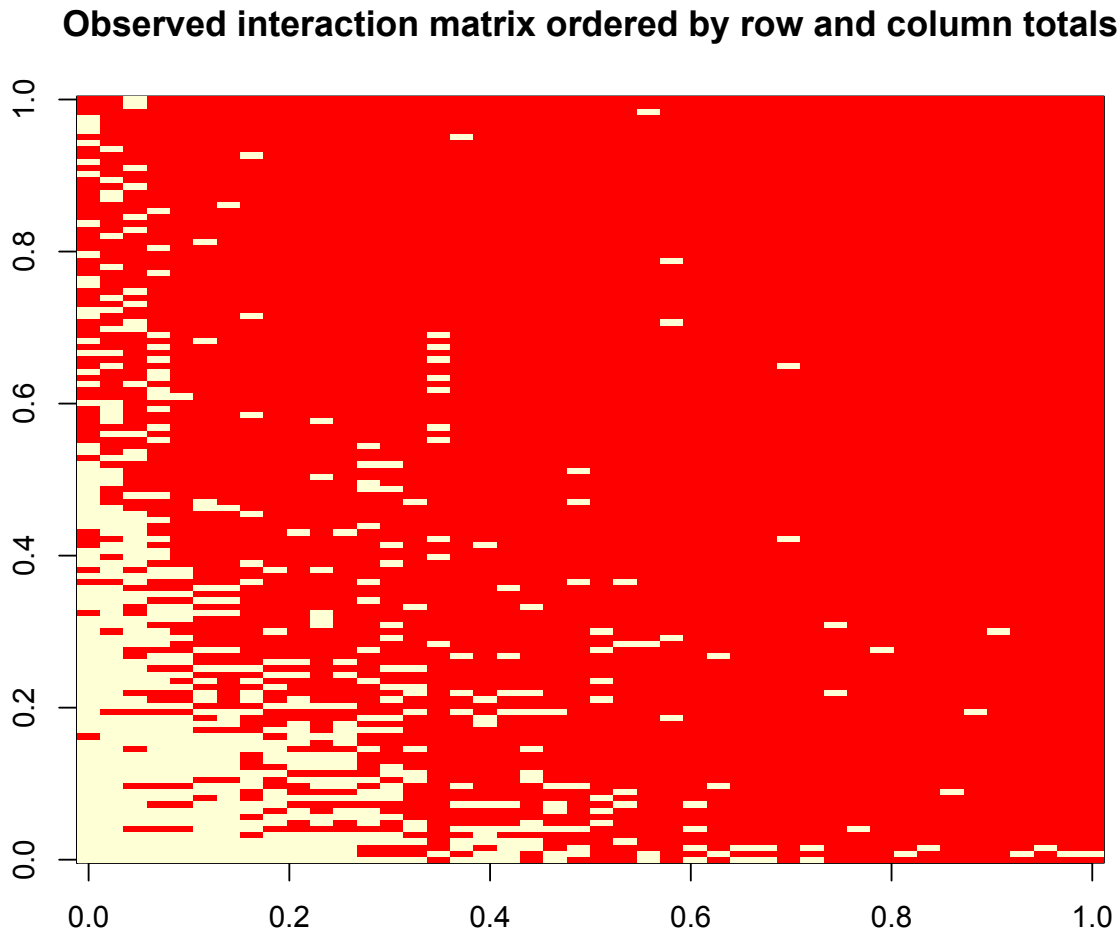


Figure 5.3. Bipartite network diagram

Bipartite network diagram of animal families (top) and plant families (bottom). The thickness of individual families represents how many different families it interacts with, not a quantification of interaction strength (i.e. each gray line is of equal thickness). Families are colored by module assignment. See also Figure 5.4 and Table 5.3.

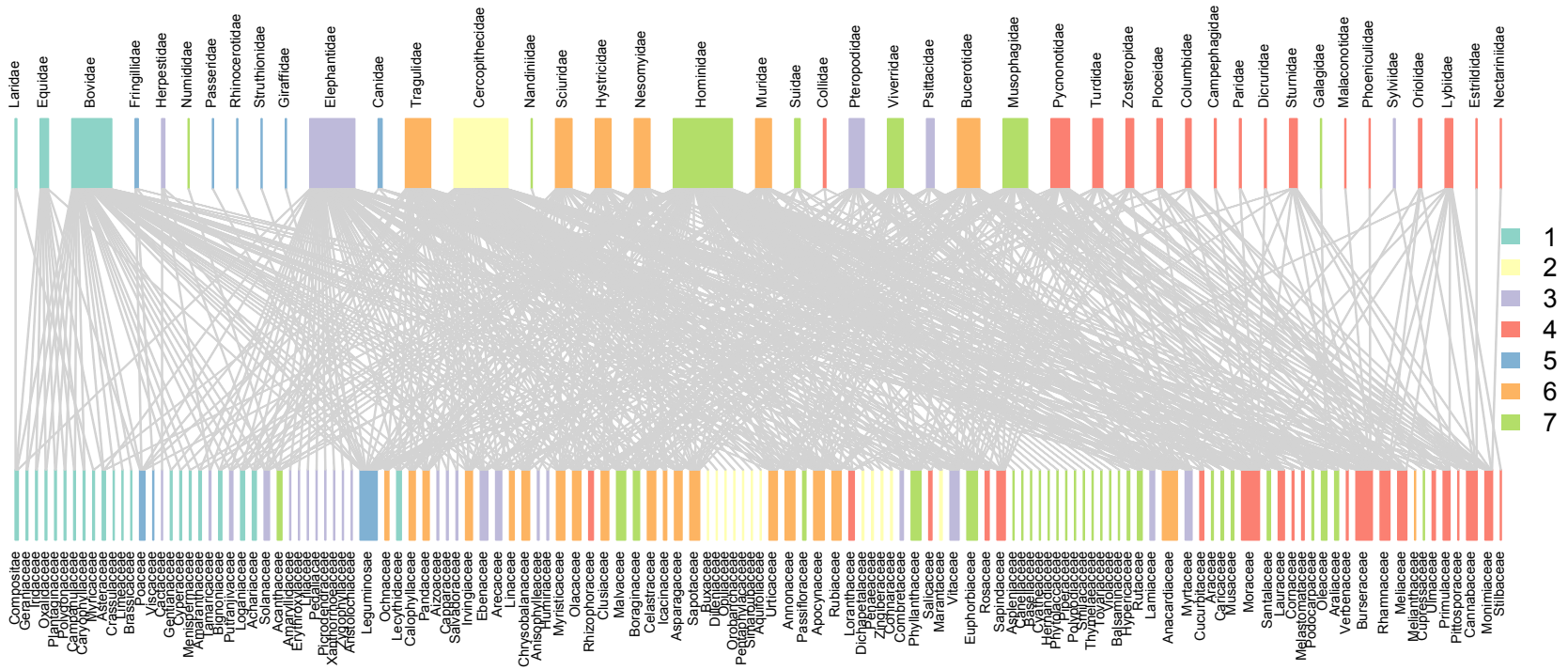
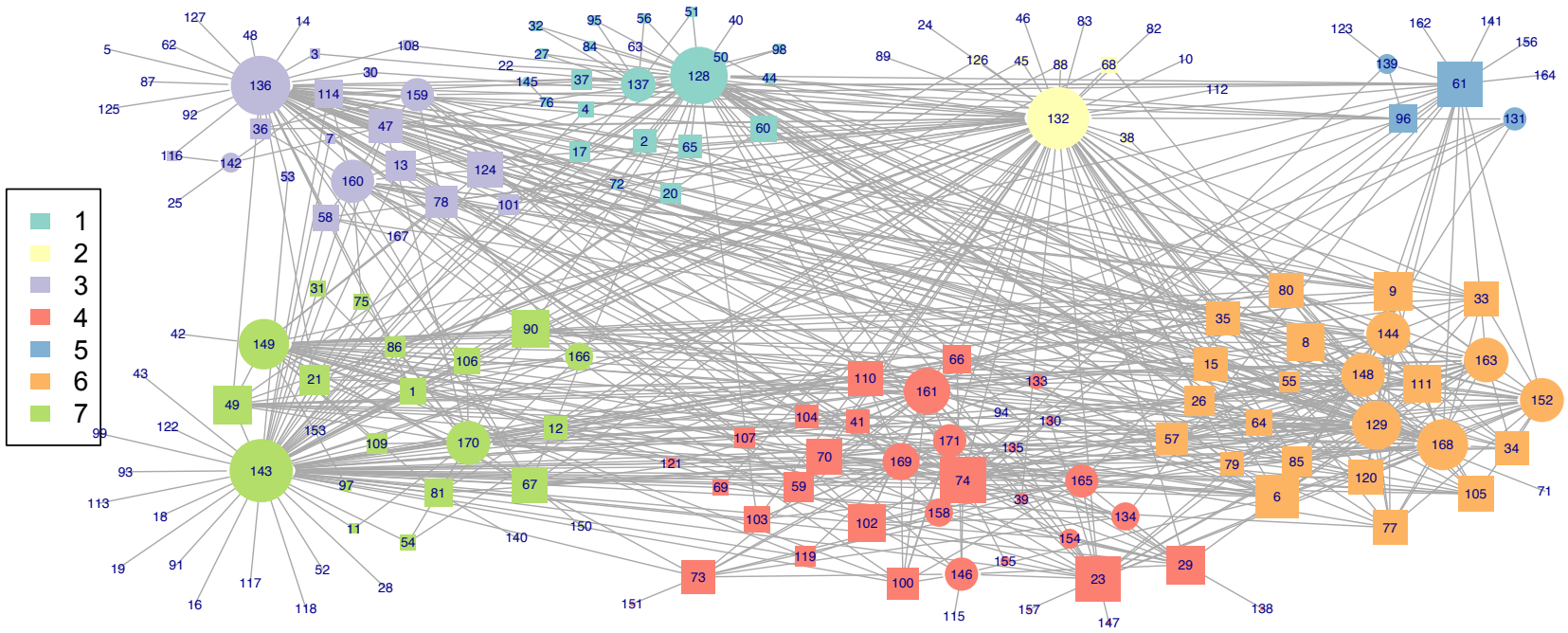


Figure 5.4 Modules within the network of African plant-animal family interactions

Modules within the network of African plant-animal family interactions. Colors indicate separate modules determined using multi-level modularity optimization algorithm (Blondel et al. 2008). Plant families are squares, animal families are circles. The number in each vertex identifies a unique family in Table 5.3. Each line connecting two vertices indicates an interaction between two families. Animal families only connect directly to plant families and vice versa (i.e. there are no plant-plant or animal-animal interactions). Vertex symbols are scaled according to the number of interactions.


1
2
3
4
5
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7

Table 5.1 Journals reviewed to date for potential plant-animal interactions in Africa.

Journal name	Series	Years reviewed	Number of interactions in database
Acta Oecologica	1997-present	2008-2013	0
African Journal of Ecology	1963-present	1963-2011	833
American Journal of Physical Anthropology	1918-present	1918-1978	0
Biodiversity and Conservation	1992-present	1992-2012	456
Biotropica	1969-present	1969-2012	868
Bulletin of the British Ornithologists' Club	1993-present	1993-2012	0
Conservation Biology	1987-present	1987-2012	78
Ecology Letters	1998-present	1998-2012	0
Ecotropica	1995-present	1995-2012	43
Gorilla Journal	1994-present	1994- 2011	0
Honeyguide	1962-2004	1969-1997	42
International Journal of Primatology	1980-present	1980-2012	628
Journal of Ecology	1913-present	1998-2012	296
Journal of Mammalogy	1919-present	1919-2012	2
Journal of Tropical Ecology	1985-present	1985-2011	954
Mammalia	1936-present	1936-2011	0
Oecologia	1968-present	1968-2012	2850
Oikos	1949-present	1990-2012	23
Ostrich	1930-present	1930-1947	1
Plant Ecology	1948-present	1948-2012	387
Scopus	1977-present	1979-1998	23
Small Carnivore Conservation	1989-present	1989-2006	47

Table 5.2 Criteria for exclusion

Interactions from the Africa Tree Database with the following criteria were excluded from analysis.

-From Madagascar or Mayotte

-Wind, water, or ballistic dispersal.

-Seed predation, herbivory, pollination, or flower predation.

-Insects (such as dung beetles).

-Plant species that could not be matched to a species, genus, or family in iPlant or TNRS.

-“Animal” or “vertebrate” dispersal (without a more specific animal identification).

-The following families were excluded due to errant observations: Macroscelididae, Crodidura, Hyraciodea, Anomaluridae, Felidae, Muscicapidae, and Trogonidae.

Table 5.3 Plant and animal family module assignments

Plant and animal family names, module assignments, vertex numbers (for reference in Figure 5.4), Order, Class, and example taxa from each family. Families are sorted by module number and then by vertex number. Animal families and associated data are highlighted in **bold** font.

Family	ertex umber	Order	Class	Commonly known examples
Module 1				
Achariaceae	2	Malpighiales	Rosids	None
Amaranthaceae	4	Caryophyllales	Core eudicots	Amaranth
Asteraceae	17	Asterales	Asterids	Aster, Daisy, Sunflower
Bignoniaceae	20	Lamiales	Asterids	Nandi flame tree
Brassicaceae	22	Brassicales	Rosids	Crucifers
Campanulaceae	27	Asterales	Asterids	Bellflower
Caryophyllaceae	32	Caryophyllales	Core eudicots	Carnations
Compositae	37	Asterales	Asterids	Marigold
Crassulaceae	40	Saxifragales	Core eudicots	Jade plant
Cyperaceae	44	Poales	Commelinids	Sedges
Gentianaceae	50	Gentianales	Asterids	Gentians
Geraniaceae	51	Geraniales	Rosids	Geraniums
Iridaceae	56	Asparagales	Monocots	Iris
Lecythidaceae	60	Ericales	Asterids	Brazil nut
Limeaceae	63	Caryophyllales	Core eudicots	None
Loganiaceae	65	Gentianales	Asterids	Strychnine tree
Menispermaceae	72	Ranunculales	Magnoliopsida	None
Myricaceae	76	Fagales	Rosids	Bayberry
Oxalidaceae	84	Oxalidales	Rosids	Starfruit
Plantaginaceae	95	Lamiales	Asterids	Herbaceous plantains
Polygonaceae	98	Caryophyllales	Core eudicots	Buckwheat, rhubarb
Bovidae	**128**	**Artiodactyla**	**Mammalia**	**Antelopes & duikers**
Equidae	**137**	**Perissodactyla**	**Mammalia**	**Zebras**
Laridae	**145**	**Charadriiformes**	**Aves**	**Gulls**
Module 2				
Aquifoliaceae	10	Aquifoliales	Eudicots	Holly
Buxaceae	24	Buxales	Magnoliopsida	Pachysandra
Connaraceae	38	Oxalidales	Rosids	None

Dichapetalaceae	45	Malpighiales	Rosids	Poison leaf
Dilleniaceae	46	(unplaced)	Core eudicots	Guinea flower
Marantaceae	68	Zingiberales	Commelinids	Arrowroot
Opiliaceae	82	Santalales	Core eudicots	None
Orobanchaceae	83	Lamiales	Asterids	Broomrape
Penaeaceae	88	Myrtales	Magnoliopsida	None
Pentaphylacaceae	89	Ericales	Asterids	None
Simaroubaceae	112	Sapindales	Rosids	Tree of Heaven
Zingiberaceae	126	Zingiberales	Commelinids	Ginger
Cercopithecidae	**132**	**Primates**	**Mammalia**	**Monkeys & baboons**
Module 3				
Aizoaceae	3	Caryophyllales	Eudicots	Carpet Weeds
Amaryllidaceae	5	Asparagales	Monocots	Amaryllis
Anisophylleaceae	7	Cucurbitales	Rosids	None
Arecaceae	13	Arecales	Commelinids	Palms
Aristolochiaceae	14	Piperales	Magnoliids	Pipevine
Cactaceae	25	Caryophyllales	Eudicots	Cactus
Capparaceae	30	Brassicales	Rosids	Caper
Combretaceae	36	Myrtales	Magnoliopsida	White mangrove
Ebenaceae	47	Ericales	Asterids	Ebony, Persimmon
Erythroxylaceae	48	Malpighiales	Rosids	Coca
Humiriaceae	53	Malpighiales	Rosids	None
Lamiaceae	58	Lamiales	Asterids	Herbs
Liliaceae	62	Liliales	Monocots	Lillies
Myrtaceae	78	Myrtales	Magnoliopsida	Myrtle, Guava, Eucalyptus
Pedaliacae	87	Lamiales	Asterids	Sesame
Picrodendraceae	92	Malpighiales	Rosids	None
Putranjivaceae	101	Malpighiales	Rosids	None
Salvadoraceae	108	Brassicales	Rosids	None
Solanaceae	114	Solanales	Asterids	Tomatoes, Peppers, Nightshade, Tobacco, Petunia, Nightshade
Tamaricaceae	116	Caryophyllales	Core eudicots	Tamarisk
Vitaceae	124	Vitales	Magnoliopsida	Grapes
Xanthorrhoeaceae	125	Asparagales	Monocots	Aloe
Zygophyllaceae	127	Zygophyllales	Rosids	Creosote
Elephantidae	**136**	**Proboscidea**	**Mammalia**	**Elephants**
Herpestidae	**142**	**Carnivora**	**Mammalia**	**Mongoose**
Psittacidae	**159**	**Psittaciformes**	**Aves**	**Parrots**
Pteropodidae	**160**	**Chiroptera**	**Mammalia**	**Fruit bats**
Sylviidae	**167**	**Passeriformes**	**Aves**	**Warblers**

Module 4				
Burseraceae	23	Sapindales	Rosids	Myrrh
Cannabaceae	29	Rosales	Rosids	Hemp, Hops
Cornaceae	39	Cornales	Asterids	Dogwood
Cucurbitaceae	41	Cucurbitales	Rosids	Squashes, Melons, Gourds
Lauraceae	59	Laurales	Magnoliids	Sassafras
Loranthaceae	66	Santalales	Core eudicots	Mistletoe
Melastomataceae	69	Myrtales	Rosids	Soapbush
Meliaceae	70	Sapindales	Rosids	Mahogany
Monimiaceae	73	Laurales	Magnoliids	None
Moraceae	74	Rosales	Rosids	Figs
Pittosporaceae	94	Apiales	Asterids	None
Primulaceae	100	Ericales	Asterids	Primrose
Rhamnaceae	102	Rosales	Magnoliopsida	Buckthorn
Rhizophoraceae	103	Malpighiales	Rosids	Red mangrove
Rosaceae	104	Rosales	Rosids	Plums, Cherries, Peaches, Apricots, Almonds
Salicaceae	107	Malpighiales	Rosids	Willow
Sapindaceae	110	Sapindales	Rosids	Maple
Stilbaceae	115	Lamiales	Asterids	None
Ulmaceae	119	Rosales	Magnoliopsida	Elm
Verbenaceae	121	Lamiales	Asterids	Verbena
Campephagidae	**130**	**Passeriformes**	**Aves**	**Cuckooshrikes**
Coliidae	**133**	**Colliformes**	**Aves**	**Mousebirds**
Columbidae	**134**	**Columbiformes**	**Aves**	**Pigeons & doves**
Dicruridae	**135**	**Passeriformes**	**Aves**	**Drongos**
Estrildidae	**138**	**Passeriformes**	**Aves**	**Estrilid finches**
Lybiidae	**146**	**Piciformes**	**Aves**	**Barbets**
Malaconotidae	**147**	**Passeriformes**	**Aves**	**Bushshrikes**
Nectariniidae	**151**	**Passeriformes**	**Aves**	**Sunbirds**
Oriolidae	**154**	**Passeriformes**	**Aves**	**Orioles**
Paridae	**155**	**Passeriformes**	**Aves**	**Tits**
Phoeniculidae	**157**	**Coraciiformes**	**Aves**	**Wood hoopoes**
Ploceidae	**158**	**Passeriformes**	**Aves**	**Weavers**
Pycnonotidae	**161**	**Passeriformes**	**Aves**	**Bulbuls**
Sturnidae	**165**	**Passeriformes**	**Aves**	**Starlings**
Turdidae	**169**	**Passeriformes**	**Aves**	**Thrushes**
Zosteropidae	**171**	**Passeriformes**	**Aves**	**White-eyes**
Module 5				

Leguminosae	61	Fabales	Rosids	Acacia, Legumes
Poaceae	96	Poales	Commelinids	Grasses
Viscaceae	123	Santalales	Core eudicots	Mistletoe
Canidae	**131**	**Carnivora**	**Mammalia**	**Jackals**
Fringillidae	**139**	**Passeriformes**	**Aves**	**True finches**
Giraffidae	**141**	**Artiodactyla**	**Mammalia**	**Giraffes**
Passeridae	**156**	**Passeriformes**	**Aves**	**Sparrows**
Rhinocerotidae	**162**	**Perissodactyla**	**Mammalia**	**Rhinos**
Struthionidae	**164**	**Struthioniformes**	**Aves**	**Ostriches**
Module 6				
Anacardiaceae	6	Sapindales	Rosids	Mangos, Poison Ivy
Annonaceae	8	Magnoliales	Magnoliids	Custard apple
Apocynaceae	9	Gentianales	Asterids	Frangipani, Plumeria
Asparagaceae	15	Asparagales	Monocots	Asparagus
Calophyllaceae	26	Malpighiales	Rosids	None
Celastraceae	33	Celastrales	Rosids	Bittersweet
Chrysobalanaceae	34	Malpighiales	Rosids	Coco plum
Clusiaceae	35	Malpighiales	Rosids	Mangosteen
Icacinaceae	55	(unplaced)	Asterids	None
Irvingiaceae	57	Malpighiales	Rosids	None
Linaceae	64	Malpighiales	Rosids	Flax
Melianthaceae	71	Geraniales	Magnoliopsida	None
Myristicaceae	77	Magnoliales	Magnoliids	Nutmeg
Ochnaceae	79	Malpighiales	Rosids	None
Olacaceae	80	Santalales	Core eudicots	None
Pandaceae	85	Malpighiales	Rosids	Bamboo
Rubiaceae	105	Gentianales	Asterids	Coffee
Sapotaceae	111	Ericales	Asterids	Shea
Urticaceae	120	Rosales	Magnoliopsida	Nettles
Bucerotidae	**129**	**Coraciiformes**	**Aves**	**Hornbills**
Hystricidae	**144**	**Rodentia**	**Mammalia**	**Porcupines**
Muridae	**148**	**Rodentia**	**Mammalia**	**Rats & mice**
Nesomyidae	**152**	**Rodentia**	**Mammalia**	**Pouched rats**
Sciuridae	**163**	**Rodentia**	**Mammalia**	**Squirrels**
Tragulidae	**168**	**Artiodactyla**	**Mammalia**	**Chevrotains (mouse-deer)**
Module 7				
Acanthaceae	1	Lamiales	Asterids	Mangrove
Araceae	11	Alismatales	Monocots	Aroid
Araliaceae	12	Apiales	Asterids	Ginseng
Balsaminaceae	18	Ericales	Asterids	Impatiens

Basellaceae	19	Caryophyllales	Core eudicots	None
Boraginaceae	21	Incertae sedis	Asterids	Forget-Me-Not
Canellaceae	28	Canellales	Magnoliids	None
Caricaceae	31	Brassicales	Rosids	Papaya
Cupressaceae	42	Pinales	Pinopsida	Juniper, Redwood
Euphorbiaceae	49	Malpighiales	Rosids	Cassava, rubber tree
Hernandiaceae	52	Laurales	Magnoliids	None
Hypericaceae	54	Malpighiales	Rosids	None
Malvaceae	67	Malvales	Rosids	Hibiscus
Musaceae	75	Zingiberales	Commelinids	Bananas
Oleaceae	81	Lamiales	Asterids	Olive
Passifloraceae	86	Malpighiales	Rosids	Passionfruit
Phyllanthaceae	90	Malpighiales	Rosids	None
Phytolaccaceae	91	Caryophyllales	Core eudicots	Pokeweed
Piperaceae	93	Piperales	Magnoliids	Black Pepper
Podocarpaceae	97	Pinales	Pinopsida	Podocarps
Rutaceae	106	Sapindales	Rosids	Citrus fruits
Santalaceae	109	Santalales	Core eudicots	Sandalwood
Smilacaceae	113	Liliales	Monocots	Greenbier
Thymelaeaceae	117	Malvales	Rosids	Ramin
Tovariaceae	118	Brassicales	Rosids	None
Violaceae	122	Malpighiales	Rosids	Violets, Pansies
Galagidae	**140**	**Primates**	**Mammalia**	**Galagos (bush babies)**
Hominidae	**143**	**Primates**	**Mammalia**	**Apes**
Musophagidae	**149**	**Cuculiformes**	**Aves**	**Turacos**
Nandiniidae	**150**	**Carnivora**	**Mammalia**	**Palm civets**
Numididae	**153**	**Galliformes**	**Aves**	**Guineafowl**
Suidae	**166**	**Artiodactyla**	**Mammalia**	**Bush pigs & warthogs**
Viverridae	**170**	**Carnivora**	**Mammalia**	**Genets and civets**

APPENDIX A

UIC UNIVERSITY OF ILLINOIS AT CHICAGO

Office of Animal Care and
Institutional Biosafety Committees (MC 672)
Office of the Vice Chancellor for Research
206 Administrative Office Building
1737 West Polk Street
Chicago, Illinois 60612-7227

August 29, 2013

To: University of Illinois Graduate College

From: Dr. Mary Bowman, Director, Office of Animal Care and Institutional Biosafety

Re: Thesis dissertation work involving the use of vertebrate animals conducted by Carrie Seltzer

This letter is to inform you that the animal work conducted by Carrie Seltzer for her dissertation was conducted under the University of Illinois at Chicago ACC protocols listed below:

ACC Number: 07-274
Title of Application: Effects of Fragmentation on Seed Dispersal by Bats
Approval Period: 1/24/2008-1/15/2011

ACC Number: 10-205
Title of Application: The Role of Rodents and Fruit Bats in Forest Regeneration
Approval Period: 1/4/2011-12/21/2011

Should you have any questions regarding this matter, please contact the Office of Animal Care and Institutional Biosafety at the number listed below.

APPENDIX B

May 9, 2013

Dear Carrie Seltzer,

Thank you for your request.

Permission is granted for you to use the material requested for your thesis/dissertation subject to the usual acknowledgements and on the understanding that you will reapply for permission if you wish to distribute or publish your thesis/dissertation commercially.

Permission is granted solely for use in conjunction with the thesis, and the material may not be posted online separately.

Any third party material is expressly excluded from this permission. If any material appears within the article with credit to another source, authorisation from that source must be obtained.

Kind Regards

Emma Willcox
Permissions Assistant

WILEY

VITA

Carrie E. Seltzer

Education

Ph.D.	Biological Sciences	University of Illinois at Chicago	2013 (expected)
B.A.	Biology	Earlham College, Richmond, IN	2004

Publications

Seltzer, C.E., H.J. Ndangalasi, and N.J. Cordeiro. 2013. Seed dispersal in the dark: shedding light on the role of fruit bats in Africa. Biotropica 45(4):450-456.

Druschke, C.D., and C.E. Seltzer. 2012. Failures of Engagement: Lessons Learned from a Citizen Science Pilot Study. Applied Environmental Education and Communication 11(3-4):178-188.

Cordeiro, N.J. and C.E. Seltzer. 2012. First record of the Servaline genet (*Genetta servalina*) new for the East Usambara Mountains, Tanzania. Journal of East African Natural History 101(1):17-27.

Mitchell, J.C., and C. Seltzer. 2007. Field notes: *Thamnophis sirtalis*. Catesbeiana 27(1):44-45.

Mitchell, J.C., and C. Seltzer. 2006. Early emergence and unusual coloration in eastern milk snakes (*Lampropeltis triangulum triangulum*) in the northern Blue Ridge Mountains of Virginia. Banisteria 28:56-59.

Grants, Fellowships, and Travel awards

£5996	Rufford Small Grants Foundation, 2011.
$2075	UIC Presenter's Awards, total 2011-12.
$90,000	NSF Graduate Research Fellowship, 2010-13.
$3500	The Field Museum's Council on Africa, 2009.
$2225	UIC Deiss Award for Graduate Research, 2009.
$60,000	NSF IGERT in Landscape, Ecological, and Anthropogenic Processes, 2008-10.
$1500	UIC Bodmer Travel Award, 2008.
$2500	Bat Conservation International Student Research Scholarship, 2008.
$3000	The Field Museum's Council on Africa, 2008.
$1500	American Society of Mammalogists Grant-in-Aid of Research, 2008.

Honors and Awards

2012 Finalist, Dance Your PhD 2012 (sponsored by AAAS)
2012 Finalist, UIC Graduate College Image of Research competition
2009 Teaching Assistant Award in Biological Sciences

2008 NSF Graduate Research Fellowship Honorable Mention

Conference Presentations

Seltzer, C.E., C.T. Kremer, H.J. Ndangalasi, and N.J. Cordeiro. In search of sustainable seed harvest: Seed removal and establishment of an endemic African rainforest tree. *Ecological Society of America 97th Annual Meeting*, 2012 August 5-10. Portland, Oregon. (oral)

Seltzer, C.E. and C.G. Druschke. Lessons learned from evaluating a citizen science pilot study. *Public Participation in Scientific Research Conference 2012*. August 3-4. Portland, Oregon. (poster)

Seltzer, C.E., C.T. Kremer, H.J. Ndangalasi, and N.J. Cordeiro. Seedling establishment from experimentally planted seeds of an economically important African tree. *Mid-Atlantic Ecological Society of America Chapter Meeting*, April 14, 2012. Blacksburg, Virginia. (oral)

Seltzer, C.E., C.T. Kremer, H.J. Ndangalasi, and N.J. Cordeiro. Plants, rats, and people: Seed dispersal of an economically important rainforest tree in Tanzania. *Ecological Society of America 96th Annual Meeting*, 2011, August 7-12. Austin, Texas. (poster)

Seltzer, C.E., C. Gottschalk-Druschke, E. Kuroiwa, C. Shierk, and J. Howell-Stephens. Citizen scientists: Self-reported attitudes, behaviors, and knowledge before and after participation. *Ecological Society of America 96th Annual Meeting*, 2011, August 7-12. Austin, Texas. (poster)

Shierk, C.L., C. Gottschalk-Druschke, J. Howell-Stephens, E. Kuroiwa, and C. Seltzer. Bee species richness and abundance in an urban landscape: Chicago Area Pollinator Study as a citizen science project. *NSF Conference for Sustainability IGERTs 2*. Arizona State University, October 2009. (poster)

Seltzer, C.E. and C. Currie. Symbiotic associations between antibiotic producing bacteria and ants, termites, bees, and mushrooms. *Butler Undergraduate Research Symposium*, Butler University, Indianapolis, IN, April 2004. (poster)

Seltzer, C.E. and C. Currie. Symbiotic associations between antibiotic producing bacteria and ants, termites, bees, and mushrooms. *Earlham Undergraduate Research Conference* sponsored by MERC/AAAS Undergraduate Science Research Program, Earlham College, Richmond, IN, November 2003. (poster)

Invited Seminars

Plants, rats, and fruit bats: Seed dispersal and regeneration in a Tanzanian rainforest. Invited seminar Earlham College, Richmond, IN. March 1, 2012.

Bee Monitoring: The Chicago Area Pollinator Study. C. Seltzer and C. Shierk. Garfield Park Conservatory 2nd Annual Bee Forum. November 2009.

Mentoring & Leadership

Advised undergraduates on post-college career options in biology during an alumni-student networking event at Earlham College. October 2012.
Advised eight undergraduate and two MSc students from Roosevelt University on projects related to plant-animal interactions in Africa. 2009-2012.
Coordinated volunteer opportunities in forest restoration around the Amani Nature Reserve for an Earlham College student. November 13-21, 2011.
Supported field work for female MSc in Biodiversity Conservation at the University of Dar es Salaam with funds from Rufford Small Grant for Conservation to work on a project related to *Allanblackia stuhlmannii* regeneration. 2011-2012.
Hosted six undergraduates from Earlham College in Tanzania to provide an introduction to research in the Amani Nature Reserve. November 9-14, 2010 and October 14-17, 2011.
Hosted eight undergraduates from Earlham College in Chicago to learn about research at The Field Museum. March 2009.

Non-specialist Publications

Seedling Guide to Trees, Shrubs, and Liana of the Eastern Arc Mountains. Ndangalasi, H.J., N.J. Cordeiro, L.E. Mshana, C.E. Seltzer, H.E. Pilla, and C. Challange. 2012. Available from The Field Museum Rapid Color Guides online in 2013.
Giant pouched rats (*Cricetomys* spp.) as Extreme Mammals. 2012. For *In The Field*, The Field Museum's member magazine.
Synthesis of findings in the survey of participants in the Chicago Area Pollinator Study (CAPS). A report for the Lincoln Park Zoo.

Outreach & Public Presentations

Choreographed and filmed a dance depicting the relationship between giant pouched rats and Allanblackia seeds for the Dance Your PhD 2012 contest (selected as a finalist). All other dancers were undergraduates at Earlham College.
Presented museum specimens of several species of "Extreme Bats" to guests at a fundraising event for The Field Museum. June 2, 2012.
Featured in a fundraising letter for UIC's College of Liberal Arts and Sciences. Spring 2012.
On-site presentation about seed dispersal research in Amani Nature Reserve to 40+ 8th grade students from the International School of Tanganyika. February 8, 2011.
Internet scientist expert for reading/science integration in 6th grade Chicago charter school classroom. February-March 2011.
Radio interview on TerraInforma, a Canadian podcast syndicated on several Canadian radio stations about biodiversity. Available on my website. First aired on October 23, 2010.
Seed dispersal by fruit bats in a Tanzanian rainforest. Presentation to The Field Museum's Council on Africa (2010) and The Field Museum Member's Night (2009).

Teaching Experience

Plant-Animal Interaction seminar leader

Roosevelt University
May-August 2012
Led literature-based weekly seminar for seven Africa Tree Database interns.
Coordinated lessons on common edible fruits and their origins, cultivation, and morphology.
Advised students (six undergraduate and one MSc) on projects related to plant-animal interactions in Africa.

Curriculum Consultant
The Field Museum
June-August 2010
Provided advice on the content and teacher training for a partnership with Chicago Public Schools and the Field Museum's education department to strengthen elementary science education.

Teaching Assistant, Intro to Cells & Organisms/Intro to Populations & Communities
University of Illinois at Chicago
August 2007- August 2008
Led laboratory exercises for two sections of ~30 students each per term.
Graded lab reports and exams.

Growing Native Curriculum Committee Member
Potomac Conservancy, Silver Spring, MD
2005-2006
Designed a lesson about the natural and political boundaries of the Potomac River watershed for teachers of grades 4-6 to be part of the Growing Native Curriculum Guide.
Reviewed lesson plans written by other members of the Curriculum Committee.

School Program Presenter
University of Virginia's Blandy Experimental Farm
October 2004- July 2006
Presented science and environmental themed presentations for 10,000+ K-12th graders.
Managed Microsoft Access database for program scheduling.
Designed a self-guided nature activity book for families visiting the Arboretum.
Planned and presented themed weekend and summer programs for children.
Created and revised pre and post-program curricula for teachers and parents.

Teaching Assistant
Ecological Biology, Earlham College
August- December 2003
Assisted with weekly laboratory activities and field trips.
Led study sessions and graded exams.

Pre-Graduate Experience
Enhancing Linkages between Mathematics and Ecology
Michigan State University's Kellogg Biological Station

June-July 2007
Used Maximum Likelihood Analysis to compare theoretical models to empirical data.
Modeled systems in field ecology and evolution using Mathematica and R.

Field Research Assistant
University of Auckland, New Zealand
October- December 2006
Radio tracked bats during foraging and to day roosts using radio telemetry.
Monitored bat activity using echolocation detectors, mist nets, and harp traps.
Measured, weighed, sexed, aged and banded *Chalinolobus tuberculatus* specimens.

Summer Environmental Exchange Participant
Tahoe Baikal Institute
June- August 2004
Studied watershed management issues in Lake Tahoe (California and Nevada) and Lake Baikal (Russia) with a group of U.S., Russian, Mongolian, and Ukrainian participants.
Collaborated with Russian scientists to conduct a survey of littoral zone gammarids (Amphipoda) in Lake Baikal to assess impact of near-shore human settlement.

Research Experiences for Undergraduates Intern
Ecology & Evolutionary Biology, University of Kansas
May-August 2003
Designed and carried out a research project under the direction of Dr. Cameron Currie.
Collected ants and bees using sterile techniques from four different field sites and cultured bacteria from specimens.
Presented results at an REU seminar.

Invertebrate Collection Intern
Field Museum of Natural History, Chicago, IL
May-August 2002
Sorted mollusks in microscopic ocean-bottom sediment samples from the Florida Keys as part of research by Rüdiger Bieler and Paula Mikkelsen.
Added new specimen information to collection database.

Tour Leader & Collections Curator
Joseph Moore Museum of Natural History at Earlham College
September 2000- May 2004
Interpreted the natural history of Indiana to school children (preschool- 10th grade).
Curated the invertebrate collection and live animal exhibits.

International Experience

Tanzania	Ph.D. research in the East Usambara Mountains, 2008-2011
New Zealand	Field research assistant for bat research, 2006
Russia	Summer Environmental Exchange, Tahoe Baikal Institute, 2004
Kenya	Earlham College Foreign Study Program, Fall 2002

Galapagos Is. Earlham College Foreign Study Program, May 2001

Professional Organizations
Ecological Society of America
Association of Tropical Biology and Conservation
Society for Conservation Biology
Association for Environmental Studies & Sciences
Union of Concerned Scientists
American Society of Mammalogists
Bat Conservation International

Additional Training
Improv for Scientists, University of Illinois at Chicago, 2012
How to Manage Ecological Data for Effective Use and Re-Use, Austin, TX, 2011
Communicating Science Workshop by NSF, Chicago, IL, 2008
Bat Conservation & Management Workshop, Portal, AZ, June 2007
Project Underground & Project Learning Tree Facilitator Training, Clifton Forge, VA, 2006
Virginia Master Gardener Training, White Post, VA, 2005
Certified Interpretive Guide Training from the National Association for Interpretation, Boyce, VA, 2005
Wilderness First Responder Course, SOLO, NH, 2003, Recertification 2006 and 2010.