



Seed Banks in Savanna, Forest Fragments, and Continuous Forest Edges Differ in a Tropical Dry Forest in Madagascar

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ABSTRACT

Rapid deforestation has fragmented habitat across the landscape of Madagascar. To determine the effect of fragmentation on seed banks and the potential for forest regeneration, we sampled seed viability, density and diversity in 40 plots of 1 m² in three habitat types: forest fragments, the near edge of continuous forest, and deforested savanna in a highly fragmented dry deciduous forest landscape in north-western Madagascar. While seed species diversity was not different between forest fragments and continuous forest edge, the number of animal-dispersed seeds was significantly higher in forest fragments than in continuous forest edge, and this pattern was driven by a single, small-seeded species. In the savanna, seeds were absent from all but three of the 40 plots, indicating that regeneration potential is low in these areas. Several pre- and post-dispersal biotic and abiotic factors, including variation in the seed predator communities and edge effects could explain these findings. Understanding the extent to which seed dispersal and seed banks influence the regeneration potential of fragmented landscapes is critical as these fragments are the potential sources of forest expansion and re-connectivity.

Abstract in French is available with online material.

Key words: anemochory; forest fragmentation; Madagascar; restoration; seed dispersal; zoochory.

GLOBALLY, IT IS ESTIMATED THAT 2.3 MILLION KM² OF FOREST WAS LOST BETWEEN 2000 AND 2012, and forest loss in the tropics increased by 2101 km² per year during this time (Hansen *et al.* 2013). These forests are typically not destroyed entirely, but are broken into fragments of varying sizes. Forest fragments can support animal species with important ecological roles, but critical mutualisms between animals and plants, such as seed dispersal and predation are altered by fragmentation (Chapman 1995, Estrada & Coates-Estrada 1996, Estrada *et al.* 1999, Wright & Duber 2001, Chapman *et al.* 2003, Wright *et al.* 2007a, Markl *et al.* 2012). Such mutualisms strongly influence the future composition of fragments (Santo-Silva *et al.* 2013). The need to understand seed banks and the mutualisms that maintain them is illustrated by the extent of regenerating forest. Wright and Muller-Landau (2006) estimated that secondary forests have replaced at least one of each 6 ha of primary forest deforested in the 1990s and Emrich *et al.* (2000) estimated that secondary forests represent 35 percent of all existing tropical forests. With increasing trends for urbanization and land abandonment in some tropical countries (Wright & Muller-Landau 2006, Jacob *et al.* 2008, Rudel 2013) forest restoration will be a vital component of future conservation strategies (Omeja *et al.* 2012).

To be able to use restoration of fragmented landscapes as an effective conservation tool the response of the plant community must be predictable. Some generalizations have been made, but more research is needed to verify these generalizations for particular regions. For example, one of the most commonly suggested generalizations is that large-seeded trees are dependent on the mutualistic relationship with large frugivores for fruit removal and that these animals are likely unable to persist in fragmented landscapes, particularly if hunting and fragmentation co-occur. Thus, researchers suggest that these tree populations are particularly vulnerable to collapse due to reduced seedling recruitment (Chapman & Onderdonk 1998, Rolan & Simonetti 2001, Cordeiro & Howe 2003, Beckman & Muller-Landau 2007, Terborgh *et al.* 2008). But even here results are equivocal, as evidence on the association between seed size and recruitment probabilities are still controversial (Wright *et al.* 2000, 2007b, Beckman & Muller-Landau 2007, Nunez-Iturri & Howe 2007, Brodie *et al.* 2009, Chaves *et al.* 2011). For example, in Uganda (Chapman & Onderdonk 1998, Chapman *et al.* 1999), Bolivia (Pacheco & Simonetti 2000), Mexico (Melo *et al.* 2010), and the Central African Republic (Vanthomme *et al.* 2010), reduced numbers of large-bodied frugivores were associated with reduced seedling densities and/or diversity of large-seeded trees species and greater aggregation of seedlings under parent trees (Chapman & Onderdonk 1998,

Received 28 July 2014; revision accepted 23 February 2015.

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Pacheco & Simonetti 2000). In contrast, in other parts of Mexico and in Panama, seedling densities were higher in areas with depleted mammalian communities (Wright *et al.* 2000, Dirzo & Mendoza 2007, for a meta-analysis of this phenomenon see Kurten 2013). The situation is complex as mammals, insects, and fungal pathogens play varying roles influencing the association between seed size and recruitment probabilities dependent on their presence and density.

The vast majority of studies of the effects of fragmentation on seed banks or seedling recruitment have been done in South and Central America, with few studies conducted in Africa and Asia. For restoration from fragments to be a viable conservation option globally, knowledge of how fragmentation influences the future potential of forest regeneration is needed for all tropical areas. Such information is critically needed in Madagascar. Although there is no consensus on the amount of anthropogenic deforestation that has occurred since humans arrived on the island (McConnell & Kull 2014), landscape analyses by remote imaging indicate that since the 1950s approximately half of the forest cover has been converted to agricultural fields or deforested grasslands (Green & Sussman 1990, Harper *et al.* 2007, Allnutt *et al.* 2008). The net deforestation rate in Madagascar is nine times higher than that in the Congo Basin (Mayaux *et al.* 2013). Research on the effect of removing primate seed dispersers may be particularly critical in managing the forests of Madagascar because the Malagasy fauna lacks many of the mammalian (*e.g.*, ungulate, large rodent) and avian (*e.g.*, hornbills, guans) frugivores that play important roles elsewhere (Dew & Wright 1998, Overdorff & Strait 1998).

Quantifying the fate of seeds is often evaluated by following individual seeds over time (Wenny 2000, Balcomb & Chapman 2003, Chaves *et al.* 2011), but this is difficult and results in a small sample of the total seed production of a tree or a tree species being evaluated. A more common method used to evaluate the effect of fragmentation on forest dynamics is through monitoring the seed bank (Nunez-Iturri & Howe 2007, Wright *et al.* 2007a). Here, we measure the effect of forest fragmentation and loss on dispersed seeds in a highly fragmented dry deciduous forest in northwestern Madagascar by determining: (1) if viable seeds are present in the soils of deforested areas, forest fragments, and the edges of continuous forest; and (2) whether there is variation in the density, richness, and dispersal mechanism of seeds in deforested areas, forest fragments, and continuous forest edges.

METHODS

STUDY SITE.—We carried out sampling between March and May, 2012 (end of the wet season) in a heavily fragmented landscape approximately 12 km west of the Ampijoroa Forestry Station in Ankarafantsika National Park (ANP-15° 59' -16°22S, 47°56' -47° 12E), northwestern Madagascar. The landscape lies approximately 300 m asl and comprises several fragments surrounded by a matrix of anthropogenic savanna dominated by invasive grasses, such as *Aristida barbicollis*, *Hyparrhenia rufa*, and *Heteropogon contortus* (Bloesch 1999). There are no remaining trees in the matrix.

Typically members of the local community burn these grasslands at the end of the dry season each year to improve the quality of the grazing lands. The vegetation of fragments and continuous forest is similar and characterized as semi-deciduous dry forest (Lourenco & Goodman 2006). The climate is highly seasonal, with rainfall ranging from 1100 to 1600 mm per year, most falling in January and February, and a mean annual temperature of 27°C, an average maximum temperature of 37°C in the rainy season and average minimum temperature of 16°C during the dry season (Rendigs *et al.* 2003).

We sampled seeds in 40 plots in the savanna, the continuous forest (7048 ha), and in four fragments (10 plots in each forest fragment) for a total of 120 plots (Fig. S1). The fragments we sampled, fragments 3, 4, 6, and 9 were 12, 15, 20, and 118 ha, respectively. Maps derived from aerial photos show that the fragments existed as early as 1975 (FTM, 1996). We chose seed plot locations with a stratified random sampling technique using ArcGIS (ESRI, version 10.1). We selected plot locations randomly, except in the case of continuous forest, where we placed plots within 318 m of the forest edge – hereafter called continuous forest. This distance corresponds to the greatest depth of the largest sampled fragment to control for potential edge effects (Lehman *et al.* 2006a).

Each seed plot was 1 m², and we excavated soil to a depth of 30 cm. All soil and plant parts within each plot were collected and returned to the lab for sorting and identification. The contents were passed through a 1-mm² mesh sieve and all plant parts were collected. Where possible, we identified plant parts to genus or species level, and in all cases, we classified seeds as either wind- or animal-dispersed, based either on knowledge of the species or morphology (Table S1). Voucher specimens of seeds were not collected; however, a photographic data base of seeds is available (10.6084/m9.figshare.1327747). We counted the number of seeds in each plot and calculated seed species richness. To assess seed viability, we recorded any signs of seed damage and death, and planted all seeds in marked containers, watered them, and monitored them for germination. To determine if there were differences in seed bank traits between habitats we compared the number of seed species, number of seeds, proportion of broken seeds, and the number of seeds by dispersal method (animal-dispersed, wind-dispersed, and unknown dispersal) between continuous forest and forest fragments. We did not do this for the savanna plots because the number of seeds found in these plots was extremely low ($N = 6$). Thus, we restricted our analyses to seeds found within continuous forest plots ($N = 201$) and forest fragments ($N = 305$), using generalized linear models (GLM) and compared seed composition in forest fragments ($N = 40$) versus continuous forest ($N = 40$). Prior to this analysis we used a Kruskal–Wallis rank sum test to determine if there was a difference in seed composition among fragments for each dependent variable (the number of seed species, number of seeds, proportion of broken seeds, and the number of seeds by dispersal method). We found no significant difference in seed composition among fragments for any of the variables except proportion of broken seeds. Therefore, we dropped this variable from our analysis. We then

continued using pooled fragment plots ($N = 40$). Because seed plot variables comprise count data and are not normally distributed, we used a GLM with each of the five seed bank characteristics as the dependent variables and habitat type (continuous or fragmented forest) as the factor with a Poisson log link function and Pearson's scaling parameter. Diagnostic tests revealed there were varying proportions of zero values within each of the five dependent seed variables: species richness (12.5% or 10 of 80), total number (15% or 12 of 80 are zero), animal dispersed (17.5% or 14 of 80), wind dispersed (81% or 65 of 80), and unknown (96% or 77 of 80). To confirm that low count numbers did not influence statistical results (*i.e.*, zero-inflation), we remodeled the dependent variables for the two habitat types using a Zero-Inflated Poisson Regression (ZIPR). This model determines whether or not excess zeros are generated by a separate process from the count values. ZIPR models include excess zeros in each seed variable independently from the data containing observed seeds. Values are expressed as the mean \pm 1 SD. All analyses were conducted using SPSS (V20, IBM, Chicago Illinois, U.S.A.) and alpha was set to 0.05.

RESULTS

Of all of the seeds planted, we found that no damaged seeds germinated, while 90 percent of undamaged seeds germinated within 8 mo of planting. There were no differences in seed bank characteristics among the four forest fragments (Kruskal–Wallis ($df = 3$); species richness $KW = 3.68$, $P = 0.30$; total seed number $KW = 4.73$, $P = 0.19$; number of animal-dispersed seeds $KW = 4.78$, $P = 0.19$; number of wind-dispersed seeds 6.76 , $P = 0.08$; number of unknown dispersed seeds $KW = 3.00$, $P = 0.39$), with the exception of the number of broken seeds ($KW = 8.99$, $P = 0.03$). However, the number of broken seeds was very low, and we therefore dropped this variable from subsequent analyses.

With the exception of the number of animal-dispersed seeds, none of the dependent variables was significantly predicted by forest fragmentation (Table S2). The number of animal-dispersed seeds was higher in forest fragments (7.08 ± 8.66) than in continuous forest (4.13 ± 4.34 , $P = 0.04$; Table S2). This pattern was driven by the high frequency of one species, *Securinega seyrigii* (species uncertain due to the lack of availability of plant parts other than fruits during sampling), in forest fragments (3.6 ± 6.49) versus continuous forest (1.75 ± 4.09). Conversely, the number of wind-dispersed seeds and the number of seeds of unknown dispersal mechanism appeared higher in continuous forest, but the difference was not significant (Table S2).

We only found six seeds in the deforested savanna areas and seeds were absent from all but three of the 40 sampled plots.

DISCUSSION

Our finding that forest fragments in this area of Madagascar have a significantly higher number of viable animal-dispersed seeds relative to continuous forest could have resulted from several fac-

tors and has important implications for forest restoration. First, the increase in animal-dispersed species in forest fragments was driven primarily by the increased density of a single, small-seeded tree species, *Securinega seyrigii*. Seeds of this species average 4 mm in each dimension (Table S1), and are thus small enough to be dispersed by birds and all lemurs in this area of Madagascar. In Ankarafantsika National Park, only five primate species are known seed dispersers (Mittermeier *et al.* 2010)—*Microcebus murinus*, *M. ravelobensis*, *Cheirogaleus medius*, *Eulemur fulvus*, and *E. mongoz*—and only three species of birds are known frugivores and putative dispersers—*Treron australis*, *Alectonenas madagascariensis*, and *Upupa epops* (Langrand 1990, Razafindratsima 2014). Seed size likely plays an important role in which species arrive and survive in forest fragments, and fragments may become progressively dominated by tree species with small seeds. Previous studies have shown that a greater proportion of the seedlings in forest fragments are from small-seeded species that might not require large mammals, like primates, or large birds for their dispersal (Chapman & Onderdonk 1998, Vidal *et al.* 2013, Albert *et al.* 2014). While more needs to be known about the habitat requirements for regeneration of *Securinega seyrigii* (*e.g.*, whether it favors edges or gaps), its presence suggests animals are depositing seeds in forest fragments.

Second, fragmentation causes habitat area to shrink; thus, primate density increases because of crowding (Silver *et al.* 1998, Ostro *et al.* 1999, Chapman *et al.* 2006, Irwin 2008) at least initially (Twinomugisha & Chapman 2007), and this can influence seed dispersal. This pattern may be especially applicable in Madagascar, where previous studies have shown that *Microcebus* species, an important seed disperser in an otherwise relatively depauperate frugivore community, not only tolerate disturbed forests, but show a strong positive edge response (Lehman *et al.* 2006a,b). Out of the five potential seed-dispersing mammalian species within the national park, four were observed within the fragments (T. S. Steffens, pers. comm.). An earlier study at this site indicated that species richness of seed-dispersing lemurs is positively related to fragment size (Steffens & Lehman 2013). *Microcebus murinus* and *Microcebus ravelobensis* are found in all four fragments we studied, *Cheirogaleus medius* is found in all but fragment 4, and *Eulemur fulvus* exists in fragments 3 and 4 (Steffens & Lehman 2013). In the fragments we studied, *Microcebus murinus* occurs at higher densities in the smaller than the larger fragments, while *Microcebus ravelobensis* occurs at similar densities in the larger and smaller fragments (Steffens & Lehman In press). Thus, while habitat loss results in an overall decrease in vertebrate abundance, it may result in increased local vertebrate density, with implications for seed dispersal and forest regeneration in disturbed habitats.

Third, the increase in animal-dispersed seeds in forest fragments relative to continuous forest may also result from variation in the secondary seed disperser and predator communities in Malagasy forest fragments and their selection of seed type. Dausmann *et al.* (2008) found an increased rate of successful seed dispersal in a Malagasy dry forest fragments relative to continuous forest because of an absence of rodent seed predators in fragments and increased secondary dispersal of small seeds by ants.

Similarly, in Brazil Andreazzi *et al.* (2012) found that low predation of palm fruits (*Attalea humilis*) by rodents and bruchid beetles produced a greater abundance of palms in small fragments despite the scarcity of the main dispersers of the fruit. This suggests that, even where primary disperser communities are disrupted or absent, post-dispersal effects driven by habitat change can critically alter seed communities and subsequent forest regeneration.

Fourth, the complex interplay of seed dispersal and post-dispersal variables is complicated where habitat is disturbed. Habitat disturbance affects abiotic factors controlling seedling survival in forest edges; different resources are available for the first stages of germination and growth and are thus differentially influenced by edge effects on different time scales (Zanne *et al.* 2005). In tropical dry forests, primary succession in disturbed areas is expected to comprise primarily wind-dispersed species, since wind-dispersed species generally demonstrate increased edge tolerance (Vieira & Scariot 2006). However, the extra resources often available in animal-dispersed seeds may give this type of seed an advantage under some conditions (Zanne & Chapman 2001, 2005).

Our finding that savanna areas in this region of Madagascar have very few seeds suggests that regeneration potential is low and that savannas will regenerate only from the expansion of forest fragments or continuous forest. Thus, understanding the forest community on the edges of fragments and continuous forest is particularly important. The low number of seeds likely results because few seeds arrive in these areas via animals and because those seeds that do arrive, *e.g.*, wind-dispersed seeds or those brought by animals such as birds that move among fragments (Duncan & Chapman 1999), are destroyed by the annual fires (Uhl & Kauffman 1990, Bloesch 1999).

Our sampling design placed plots in the continuous forest near the edge so that they were similarly affected by edge effects as the fragmented forest at least with respect to the biotic and abiotic factors that came from the edge side of the plot. In the future, it would be interesting to examine plots in a larger continuous forest in the deep interior of the park, to examine if there are similar trends when edge effects are removed. This can be done only once edge effect processes are more fully understood. For example, it is difficult to know how far edge effects that might influence the seed bank will extend into the forest interior (*i.e.*, how far the large lemurs travel from the edge into the interior carrying edge-species seeds).

Understanding the effect of habitat loss and disturbance on seed and seedling communities is critical, especially in Madagascar with a unique, relatively small animal disperser guild (Ganzhorn *et al.* 1999, Bollen *et al.* 2004), high rates of plant and animal endemism (Goodman & Benstead 2005), and rapid habitat loss (Mayaux *et al.* 2013, Schwitzer *et al.* 2014). Both anthropogenic disturbance and climatic change are projected to continue in Madagascar (Myers *et al.* 2000) and understanding the capacity for ecosystem resiliency and recovery in the face of this disturbance is essential.

Evaluation of the seed bank in continuous and forest fragments provides reason to be optimistic for conservation. We

found that the number of animal-dispersed seeds was significantly higher in forest fragments than in continuous forest, although this result was related to the high frequency of a single, small-seeded species, *Securinega seyrigii*. However, the similar species richness between fragments and continuous forest edges emphasizes the high conservation value of forest remnants and edges in fragmented landscapes, which are so common in Madagascar today. These fragments are more or less interspersed in the landscape matrix, providing valuable stepping stones allowing some animals to move among habitat patches that may in the long run maintain the functional connectivity of the landscape (Arroyo-Rodriguez *et al.* 2013). The fragments also represent the sources for forest expansion and re-connectivity should the political and economic situation change and population demands on the lands decline; as has occurred in North America and Europe (Lawler *et al.* 2014).

ACKNOWLEDGMENTS

We thank MICET and Madagascar National Parks for permission to conduct this research. We are grateful to Mr. Paul Tsiveraza, Tosy, Alfa, Jean-Paul, Velonkasi, Modeste and the villages of Mavatanbary and Andranahobaka for their support and for contributions in the field. This study complies with all national and regional laws dealing with ethics and animal welfare in both Madagascar and Canada. We are grateful for the comments and suggestions of two anonymous reviewers and the editors of *Biotropica*, and to C.W. Mcdougall and Dr. V.A.M. Schoof for valuable commentary on the manuscript. For funding we thank Sigma Xi, GM Women in Science (KV), the University of Toronto, and Natural Sciences and Engineering Research Council of Canada (NSERC) (KV, SML). NSERC and CRC grants (CC) helped fund the writing stage.

SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

TABLE S1. *Species and local names of the 15 most commonly found seeds in fragments and continuous forest edge, dispersal mechanism, and seed size in three dimensions.*

TABLE S2. *Seed bank characteristics of seeds sampled in continuous forest and forest fragments, with results of GLM with a normal identity link function and standard deviation, and a zero-inflated Poisson regression.*

FIGURE S1. Map of study site showing location of fragments and sample plots.

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