

Plant-animal Interactions and Defaunation in Tropical Forests:  
How Animal Communities and Anthropogenic Disturbances Drive Patterns in Seed  
Predation, Seedling Damage, and the Regeneration of Tropical Forest Trees

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Dissertation submitted in partial fulfillment of  
the requirements for the degree of  
Doctor of Philosophy in Environment  
from the Graduate School of  
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ABSTRACT

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## **Abstract**

The biotic forces that shape plant communities across ontogenetic stages drive patterns in survival, vegetation structure, and species diversity. In tropical forests, many of these forces are facilitated by interactions with animals, which can either promote or inhibit plant reproduction. Disruptions to these interactions – such as defaunation resulting from hunting and logging – can generate broad changes in tree recruitment, forest structure, and carbon storage, with demographic filtering at the seed and seedling stages responsible for many of the effects. Research to date has largely focused on a subset of prominent interactions (especially seed dispersal), while concurrent disruptions to other less-studied ecological processes may drive changes of opposite directionality for individual species or entire communities. With a limited understanding of seed predation, seedling establishment, and seedling physical damage and survival – particularly in Central African forests – it remains difficult to predict the outcomes of defaunation for tropical forest plant communities. In this dissertation, I use a combination of literature reviews, field-based experimental methods (including telemetric seed tags, seed and seedling exclosures, and artificial seedlings) and statistical analyses to assess 1) the role of plant-animal interactions and the influence of hunting on the regeneration of timber trees across tropical forests; 2) patterns of secondary dispersal and seed fate for two tree species in northeastern Gabon; 3) the role of seed traits and

both seed density and distance from the parent tree in driving patterns of seed mortality and seedling establishment for ten tree species in northeastern Gabon; 4) the impacts of hunting on seed predation and seedling establishment for eight commercially important tree species across a defaunation gradient in northeastern Gabon; and 5) the role of physical damage by vertebrate trampling, rooting, and digging to artificial seedlings in intact and hunted and/or logged forests in Peru, Gabon, and Malaysian Borneo. I conclude that 1) hunting is likely to disrupt plant-animal interactions and tropical forest timber regeneration, but that these effects can be ameliorated given appropriate management; 2) seed fate is dependent on seed size and the identity of the seed predator, with evidence of scatterhoarding and secondary dispersal in northeastern Gabon; 3) seed traits, not density or distance from the parent tree, drive patterns in seed mortality and seedling establishment in northeastern Gabon, with vertebrate seed predation a stronger force than other mortality factors; 4) hunting-induced defaunation drives increased rodent seed predation and decreased seedling establishment of commercially-important tree species; and 5) vertebrate physical damage to seedlings is a consistent force in forests across the tropics, and hunting significantly reduces its strength. This dissertation highlights the important roles of wildlife in tropical forest ecological processes as well as the degree to which these interactions can be disrupted through hunting-induced defaunation, and emphasizes the value of appropriate management and continued comparative research across tropical forest regions.

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# **1. The Effects of Hunting on Tropical Forest Plant-Animal Interactions and Timber Tree Regeneration**

## ***1.1 Summary***

Avoiding the conversion of tropical production forests to non-forest land uses is a forestry and conservation priority, and is contingent on successful regeneration of commercially important species. The underlying ecological processes that facilitate regeneration, however, are poorly understood. Perhaps as a result, timber yields after regeneration can be lower than expected. Hunting is widespread in timber concessions, and may threaten regeneration by disrupting the various processes facilitated by wildlife. Vertebrate seed dispersers are often heavily hunted, resulting in reduced seed movement for many species and a shift in community composition to favor those plants dispersed by small animals and abiotic means. Timber species with large seeds and fleshy fruit are at particular risk for dispersal and recruitment failure. Hunting also alters granivore communities, resulting in increased predation on species favored by insects and small rodents, and changing the spatial template of seed predation, with detrimental effects on many timber species. Large vertebrate herbivores decline with hunting pressure, resulting in the potential release of insect herbivores and the modification of plant competitive interactions. This is disadvantageous to several traits that are common among timber trees, including relatively slow growth and high wood density. A lack of appreciation for – and management of – these interactions could threaten forest biodiversity, limit future timber production, and increase the likelihood

of forest conversion for other land uses. In this review, I highlight the plant-animal interactions that could influence timber regeneration in tropical forests, as well as how these processes might be expected to change under hunting pressure. The review concludes with recommendations for management and future research priorities.

## **1.2 Introduction**

Timber production represents a major land use for tropical forests worldwide, encompassing 403 million hectares (Blaser et al. 2011) – roughly half the area of the contiguous United States. Though logging can have various detrimental impacts on tropical forests (eg Johns 1988, Bawa and Seidler 1998, Fimbel et al. 2001), there is mounting evidence that timber concessions are not without environmental merit, potentially meeting both forestry and conservation goals (Johns 1985, Putz et al. 2000, Meijaard et al. 2005, Clark et al. 2009, Berry et al. 2010). Selectively logged forests under responsible management represent a valuable “middle way” between deforestation and absolute protection (Putz et al. 2012, but see also Rice et al. 1997). Avoiding the conversion of production forest to non-forest land uses is thus critical, and relies on continued regeneration of commercially important species.

Most selective timber systems with sustained yields (Putz et al. 2012) use one form or another of natural forest management (see reviews by Baur 1964, Buschbacher 1990, but see also Bawa and Seidler 1998). These management schemes rely to varying degrees on the natural regeneration of target timber species, often with simple

silvicultural treatments. Reproduction under close-to-natural forest conditions – for eventual harvest in future cutting cycles – is less labor intensive and expensive than other methods, and is thus a favored forestry scheme across much of the tropics (Weetman and Vyse 1990, Gómez-Pompa and Burley 1991).

Recent evidence shows that the post-harvest regeneration of timber species can be lower than expected (Fredericksen and Mostacedo 2000, Gourlet-Fleury et al. 2013), highlighting the need to understand the ecological requirements of these tree species and identify the causes of regeneration failure. Plant-animal interactions are increasingly recognized as critical to maintaining tropical forest integrity and composition, particularly the processes of seed dispersal (eg Terborgh et al. 2008), seed predation (eg Asquith et al. 1997), and herbivory (eg Clark et al. 2012). These processes may play a role in timber regeneration, given the extensive interactions between timber species and tropical forest wildlife (see Tables 1 and 2). Disruptions to plant-animal interactions can have consequences both for biodiversity and forest carbon production (Wright 2003, Brodie and Gibbs 2009, Jansen et al. 2010, Poulsen et al. 2013), though the specific effects on the regeneration of timber are largely unknown. As a result, logging companies generally lack any practical management of these processes, despite their apparent importance (Terborgh 1995, Hammond et al. 1996, Guariguata and Pinard 1998, Sheil and Heist 2000, Putz et al. 2012).

A major threat to the integrity of plant-animal interactions is the increasing impact of hunting for subsistence and the commercial wild meat trade (Redford 1992). Hunting is widespread in tropical forests (Robinson and Bennett 2000, Fa et al. 2002), and is further facilitated by logging through the creation of road networks and increased access to frontier forests (Wilkie et al. 2000). Hunting within concessions can be particularly intensive, as extractive industries promote immigration and timber companies rarely provide supplemental protein to their workers' diets (Robinson et al. 1999, Auzel and Wilkie 2000, Poulsen et al. 2009). Overall, hunting within concessions affects animal distributions more strongly than do the direct effects of logging (van Vliet and Nasi 2008, Poulsen et al. 2011).

Hunting alters ecological processes in many ways (see reviews by Wright 2003, Stoner et al. 2007, Abernethy et al. 2013, Kurten 2013). If these processes are important for the regeneration of timber, disruptions to them may threaten continued production and must be managed appropriately. In this review, I highlight the plant-animal interactions that could influence timber regeneration, as well as how these processes might be expected to change under hunting pressure, with a focus on seed dispersal, post-dispersal seed predation, and herbivory. I identify specific interactions between hunted wildlife and prominent timber tree species, with attention to the world's three main regions of tropical forest. The review concludes with recommendations for management and future research priorities.

### **1.3 Seed Dispersal**

Dispersal confers several potential reproductive advantages to the seed.

Dispersed seeds may benefit from colonizing novel and uncompetitive environments, landing in sites suitable for establishment, and escaping the vicinity of the parent (Howe and Smallwood 1982, Willson and Traveset 2000, Muller-Landau and Hardesty 2005). Escape through dispersal reduces the incidence of attack on seeds and seedlings by host-restricted natural enemies near the parent tree, as described by the Janzen-Connell model (Janzen 1970, Connell 1971). This model of distance- and density-responsive mortality mechanisms is well-supported scientifically (see reviews by Hammond and Brown 1998, Terborgh 2012), and dictates a major role of seed dispersal in regeneration success. Indeed, there is strong evidence that nearly all sapling recruits arise from seedlings of dispersed seeds (Howe and Miriti 2000, Terborgh and Nuñez-Iturri 2006, Terborgh 2013). Any disruption to the dispersal process may have impacts on individual trees, species, and communities. In particular, hunting threatens the integrity of animal-mediated dispersal, with potential consequences for timber regeneration in forests subject to such pressures.

The majority of tree species in humid tropical forests produce seeds with fleshy fruit or aril and are dispersed by animals (Howe and Smallwood 1982, Willson et al. 1989, Jansen and Zuidema 2001, Beaune et al. 2013). Many species producing a hard pericarp are also dispersed by vertebrates through caching and other pathways (Janzen

1971, Forget 1990, Jansen and Forget 2001, Hulme 2002, Beck 2005). Dispersal by animals is thus widespread, and is probably as common for potential timber species as for tropical forest tree species in general (Jansen and Zuidema 2001). Trees with vertebrate-dispersed seeds account for 72% of the 95 timber species in the Guianas (Hammond et al. 1996), and 74% of the 46 timber species in Bolivia (Jansen and Zuidema 2001). Although this over-represents animal dispersal among the few timber species most desired by current world markets (see Table 1), proportions of animal-dispersed timber trees are expected to increase with depletion of high-value, wind-dispersed timbers and growing demand for lesser-known species (Jansen and Zuidema 2001).

Dispersal by animals is clearly important for many timber species (see Tables 1 and 2), though few studies have determined its specific role in regeneration success. As noted above, dispersal which increases seed distance from the parent tree may be critical for timber regeneration. Pulp removal and gut passage may also improve survival and germination of animal-dispersed seeds (Traveset 1998, Traveset and Verdu 2002, Levi and Peres 2013). To assess the value of dispersal for the timber tree *Virola surinamensis* in Panama, Howe *et al.* (1985) monitored seeds and seedlings located near the parent, noting over 99% mortality by insects and mammals within 12 weeks; seeds dropped 45m from the fruiting tree were at an advantage of up to 44-fold compared to their undispersed counterparts. Similarly, undispersed seeds and seedlings of the timber species *Pycanthus angolensis* and *Canarium schweinfurthii* in Cameroon faced substantially

greater mortality by invertebrates and rodents than those that had been dispersed by primates (Mbelli 2002). Poor natural regeneration of the Guyanese timber tree *Hymenaea courbaril* beneath its own canopy supports the assertion that primate dispersal is critical for recruitment, with 98% of undispersed seeds suffering mortality due to bruchid beetle attack (Hammond et al. 1992). Hammond *et al.* (1999) found that while dispersal of the timber tree *Chlorocardium rodiei* did not completely preclude natural enemy attack, it did delay predation long enough to promote germination success with increasing distance from conspecific adults, thus dispersal benefitted trees through a combination of spatial and temporal factors.

Documented recruitment failure in the absence of dispersal is a concern for timber production, given that animal dispersers – and their services – are strongly impacted by hunting. Most highly desirable game animals of tropical forests are prominent seed dispersers, including large primates, duikers, deer, tapirs, and other ungulates (Redford and Robinson 1987, Feer 1995, Fa et al. 2005, Corlett 2007, Peres and Palacios 2007, Beaune et al. 2013). In general, frugivorous vertebrates suffer greater declines with hunting pressure than either granivorous or folivorous species, regardless of body size (Peres and Palacios 2007).

Animal dispersers can be partitioned into several non-overlapping “syndromes” based on morphological traits of the fruits they consume (Gautier-Hion et al. 1985). While there may be many potential dispersers for any one timber species (Howe and

Smallwood 1982), they can vary in their effectiveness (Schupp 1993), and actual redundancy may be lower than anticipated based on dietary overlap (Poulsen et al. 2002). Additionally, the removal of a given disperser may change regeneration patterns by altering the tree's seed shadow and susceptibility to predation (Janzen and Vázquez-Yanes 1991). Large-bodied vertebrates are capable of ingesting – and dispersing, via endozoochory – a greater quantity and size range of fruit than smaller animals (Corlett 1998, Peres and Van Roosmalen 2002, Knogge and Heymann 2003). Dispersal of timber trees reliant on large animals is thus unlikely to be compensated for by smaller non-game taxa, except perhaps in cases where a given species is additionally dispersed via synzoochory (as by bats). In the Guianas, for example, the seeds of most timber trees are animal-dispersed and larger than one gram – too large to be effectively dispersed by smaller animals (Hammond et al. 1996).

Some trees may have one or very few critical dispersers (Howe 1977, Hallwachs 1986, Tutin et al. 1991, Asquith et al. 1999), and face dispersal failure when these particular species are absent. In Uganda, chimpanzees are the primary – perhaps sole – dispersers of the timber tree *Cordia millenniumii* (Plumptre et al. 1994, Bakuneeta et al. 1995, Reynolds 2005), and in Gabon, the only known disperser for the timber tree *Cola lizae* is the lowland gorilla (Tutin et al. 1991). Even moderate hunting of important dispersers, as in “half-empty” forests (Redford and Feinsinger 2001), may be sufficient to alter timber regeneration patterns. McConkey and Drake (2006) found that hunted flying

foxes ceased to function as dispersers for three timber species (*Pouteria grayana*, *Syzygium clusiifolium*, and *S. dealatum*) long before they became rare.

Shifts in abundance of vertebrate dispersers may have variable effects on plants. While large-bodied dispersers are reduced or extirpated with hunting, densities of small-bodied fauna can increase through compensatory mechanisms (Peres and Dolman 2000, Rosin and Swamy 2013). As a result, hunting reduces dispersal of large-seeded trees, while those dispersed by small animals and wind tend to increase in abundance (Wright et al. 2007, Stoner et al. 2007, Nuñez-Iturri et al. 2008, Terborgh et al. 2008, Vanthomme et al. 2010, Effiom et al. 2013, Harrison et al. 2013, Kurten 2013). This shift in dispersal based on reproductive traits such as seed size has important consequences for timber trees specifically. When compared against the tree community as a whole, the seeds of fleshy-fruited timber species can be significantly larger than those of non-timber species (Hammond et al. 1996), and thus more negatively affected by changes to the disperser assemblage due to hunting.

For one particular guild of small-seeded plants, the wind-dispersed lianas, hunting can promote significantly increased abundance (Wright et al. 2007), though widespread evidence is limited. Lianas are detrimental to timber trees; they induce stem deformations and other mechanical damage, slow diametric growth, and increase the likelihood of the host tree falling (Putz 1982, 1991, Clark and Clark 1990). Infested trees may suffer reduced seed production (Stevens 1987, Nabe-Nielsen et al. 2009) and

possible recruitment failure in adjacent gaps, given that lianas can impede the successional process (Schnitzer et al. 2000). Combined, these factors lead to poor timber regeneration when lianas are abundant (Grauel and Putz 2004). Lianas also hinder timber harvest and complicate management, as liana-laden trees cause greater felling damage to the surrounding forest (Fox 1968, Appanah and Putz 1984, Johns et al. 1996) and raise costs associated with liana cutting and herbicide treatment (Putz 1991). By benefitting lianas, hunting may thus indirectly reduce timber production and profitability.

There is ample evidence both that animal-mediated dispersal is important for many timber species, and that hunting alters this process. Trees reliant on large vertebrates face dispersal failure, heightened natural enemy attack, and increased abundance of competitors such as lianas, all of which may hinder timber regeneration in forests subject to hunting pressure.

#### ***1.4 Seed Predation***

Seed predation is an important ecological interaction which can regulate plant population dynamics (Janzen 1971, Crawley 1992, Hulme 1998). As seed predators are abundant and diverse in tropical forests, and consume the seeds of many timber tree species (see Tables 1 and 2), it is reasonable to assume that they may impact regeneration processes, though direct evidence is limited. In particular, changes to

community composition of seed predators, as can occur under hunting, may alter seed predation regimes and differentially impact tree recruitment.

Large mammalian granivores such as pigs (Suidae) and peccaries (Tayassuidae) exert predation pressures that influence tree recruitment (Ghiglieri et al. 1982, Bodmer 1991, Curran and Webb 2000, Ickes et al. 2001, Silman et al. 2003, Beck 2005, Beaune et al. 2012). Small mammals, particularly rodents, can be voracious seed consumers as well (Fleming 1975, Smythe 1986, Hulme 1993, Blate et al. 1998), with potentially stronger seed predation pressures than larger mammals (Terborgh et al. 1993, DeMattia et al. 2004, Paine and Beck 2007). Rodents prey on seeds even when alternative resources such as pulpy fruits are available (Adler 1995), and can kill seedlings up to several weeks after germination, to exploit sprouts and seed reserves (DeSteven and Putz 1984, Forget 1997). Insects and other arthropods are also important seed predators of timber species (see below; Toy 1988, Hammond et al. 1992), and impact seeds differently than vertebrates (Janzen 1971, Terborgh et al. 1993, Notman and Villegas 2005).

Small rodents tend to favor seeds of small size (Blate et al. 1998, Vieira et al. 2003, Dirzo et al. 2007), exerting predation pressures unique from large mammals (DeMattia et al. 2004, Mendoza and Dirzo 2007, Hautier et al. 2010). Agoutis and peccaries also differ in their seed preferences based on the presence of chemical and/or physical defenses (Kuprewicz 2012), and specialized invertebrates such as bruchid beetles and other weevils can process seed compounds toxic to larger animals (Janzen 1971). Given that

different granivores have distinct seed preferences, changes that alter the relative abundance of these fauna may substantially alter seed predation pressures.

Hunting contributes to compositional change of seed predator communities, with potentially important consequences. Pigs and peccaries are frequently hunted, as are some large rodents like agoutis and porcupines, while smaller rodents such as squirrels, rats, and mice are much less favored (Redford and Robinson 1987, Clayton et al. 1997, Fa et al. 2005, Rao et al. 2005, Corlett 2007). This disparity of harvest rates can shift faunal community composition, while interspecific dynamics may further enhance these changes. As with primates (described above), compensatory responses can occur when two or more species share a common resource and are differently impacted by hunting, thus small rodents may increase in abundance with hunting pressure even while total animal biomass declines (Smythe 1987, Happold 1995, Phillips 1997, Wright 2003). Observational and experimental evidence support this, with greater abundance of small and medium-sized rodents documented in sites where their predators and/or competitors are absent (Glanz 1991, Adler and Levins 1994, Keesing 1998, Lambert et al. 2003, Laurance et al. 2006, Poulsen et al. 2011, Effiom et al. 2013).

Logging itself modifies forest habitat in ways that additionally benefit small mammalian seed predators, such as opening canopy gaps (Struhsaker 1997), and expanding road margins (Malcolm and Ray 2000), increasing the density of vegetation through post-harvest regeneration. Overall these factors lead to increased rodent

richness, diversity, and density in selectively logged forests (Isabirye-Basuta and Kasenene 1987), and potentially more so in those subject to hunting pressure.

Hunting may also indirectly benefit some invertebrate seed predators such as insects. Seeds that contain bruchid beetle larvae may be preferentially fed on by mammalian granivores (Silvius 2002, Gálvez and Jansen 2007). When hunting reduces populations of these mammals, larvae have a greater chance of surviving the seed stage to adulthood, increasing their abundance (Stoner et al. 2007). As a result, seed predation by insects dramatically increases with hunting pressure, at least on the several species of palm for which much data is available; two reviews have noted this increased predation, which ranges from 2- to 14-times higher (Kurten 2013) and from 4- to 70-times higher (Stoner et al. 2007) in hunted vs. nonhunted sites.

This change could have important consequences for timber trees, given the extent to which insects attack their seeds both pre- and post-dispersal, regardless of the dispersal mode. In Guyana, invertebrates heavily infest seed crops of the timber trees *Peltogyne* spp. and *Aspidosperma* spp. (ter Steege et al. 1996), and bruchid beetles destroyed nearly all undispersed *Hymenaea courbaril* seeds in one study (Hammond et al. 1992, see above). Weevils are a major predator of *Virola surinamensis* in Panama (Howe et al. 1985), and can kill up to 90% of the seed crop of dominant dipterocarps in Malaysia (Toy 1988).

Due to differential hunting intensity and potential compensatory responses, the functional make-up of the seed predator guild may be expected to change dramatically under hunting pressure. Such shifts in faunal composition and abundance directly affect species-specific and community-wide seed predation and recruitment (DeSteven and Putz 1984, Sork 1987, Asquith et al. 1997, DeMattia et al. 2004, Hautier et al. 2010). Asquith *et al.* (1997) documented increased seed and seedling predation in forests under extreme mammal defaunation – those in which only small rodents remained of the original terrestrial mammalian granivore/herbivore community – compared to forests with a more complete fauna. Rodent density was negatively correlated with the overall density of tree seedlings in a logged Ugandan forest (Kasenene 1980), and with the density of preferred small-seeded seedlings in a hunted Mexican forest (Dirzo et al. 2007).

Increased rodent abundance may play an important role in reducing the regeneration of many timber trees (Kasenene 1984, Struhsaker 1997). Rodents are significant seed predators of mahogany (*Aglaia sp.*) in Malaysia (Becker and Wong 1985), and true mahogany (*Swietenia macrophylla*) in Brazil (Grogan and Galvão 2006, Norghauer et al. 2006). In Guyana, rodents attacked 43% of monitored seeds of the timber tree *Chlorocardium rodiei*, as late as 566 days after implantation (Hammond et al. 1999). Abundant small rodents in hunted and logged Costa Rican forest sites removed significantly more seeds of three timber species (*Dipteryx panamensis*, *Minquartia*

*guianensis*, and *Virola koschnyi*) than in a comparable site protected from hunting (Guariguata et al. 2000, 2002). In experimental plantings of the timber species *Strombosia scheffleri* in Uganda, 74.8% (n=119) of seedlings died within 122 days, with 95.7% of mortality attributed to rodents (Lwanga 1994). Synnott (1975) documented comparably extensive rodent predation of the timber tree *Entandrophragma utile*, and Hall (2008) encountered predation pressure so intense that rodents dug under or squeezed through holes in wire mesh enclosure cages to consume 100% of experimentally scattered *Entandrophragma angolense* seeds. It is clear that rodent predation on seeds can be a significant filter on timber tree recruitment, particularly given their increased abundance in hunted forests.

The spatial aspects of seed deposition and granivore habitat preferences may also influence predation pressure on timber species. As small seed predators such as insects and rodents are generally more specialized and occupy smaller home ranges than large vertebrates, they may exert stronger Janzen-Connell type pressures (discussed above) on timber recruitment, increasing the value of seed dispersal away from parent trees. Rodents also favor the microhabitat conditions generated by young disturbed growth (Lambert and Adler 2000), thus their seed and seedling predation can be higher in gaps than under closed canopy (Schupp 1988, Schupp and Frost 1989, Hammond et al. 1992). Wind-dispersed seeds – a common trait among currently harvested timber species – arrive more frequently in gaps than in the understory (Augspurger and Franson 1988,

Loiselle et al. 1996), so predation on these tree species may be especially high with increasing rodent abundance. While wind-dispersal may continue to be effective even in forests where large animal dispersers are absent (see above), increased rodent predation in gaps may depress overall recruitment. Evidence of this is limited, and merits further attention (see Future Research Priorities, below).

Alteration of the granivore guild through hunting will variably release plant species from seed predation or impose greater mortality, depending on the seed species' attractiveness to the remaining small fauna. In sum, due to the changes in seed predation intensity and selectivity of an altered granivore community, hunting may have strong indirect impacts on tree recruitment and timber regeneration dynamics.

### **1.5 Herbivory**

While the term "herbivory" sometimes encompasses both frugivory and granivory (discussed above), this section will focus on the consumption of leaf tissue; here, the term is used synonymously with folivory. Herbivores reduce leaf tissue and photosynthetic capacity, killing seedlings and harming or potentially killing saplings by uprooting and breaking stems. Herbivory is increasingly being recognized as an interaction which shapes tropical forest tree communities (Dirzo and Miranda 1991, Marquis 2005, Terborgh et al. 2006, Clark et al. 2012), and disruptions to this process may alter plant competitive interactions and impact timber tree recruitment.

Tropical forest herbivores are abundant and highly diverse in character, from invertebrates to elephants. Given this diversity, the effects of hunting on the herbivore guild vary, mostly as a result of differences in body size and hunter preference. The extreme size classes of herbivores generally escape hunting pressure (illegal poaching for secondary animal products, as with elephants, is an exception, eg Maisels et al. 2013), while mid-sized herbivores are among the most heavily hunted vertebrates. Ungulate herbivores such as tapirs, deer, and bovids are highly desired game species (Redford and Robinson 1987, Fa et al. 2005, Poulsen et al. 2009), and their populations can be severely reduced in hunted sites (Redford 1992, Peres 2000, Laurance et al. 2006, Corlett 2007).

The removal of terrestrial herbivores by hunting may have both direct and indirect consequences for timber tree recruitment. In general, diminished herbivory results in increased survival and densities of seedlings and saplings, but reduced diversity (Dirzo and Miranda 1991, Terborgh and Wright 1994, Bulinski and McArthur 1999, Alves-Costa 2004, Dyer et al. 2010, Harrison et al. 2013). In their pioneering study of a defaunated Mexican forest, Dirzo and Miranda (1991) observed dense seedling carpets and a complete absence of vertebrate herbivore leaf damage; lacking herbivores, the understory became an impoverished mosaic of virtual monocultures, dramatically altered in structure. How well timber species might fare in such an altered system is mostly unknown.

In addition to consuming leaf tissues, terrestrial herbivores can physically damage plants through trampling, rooting, and digging. Seedling responses to this damage can differ among species (Clark and Clark 1989), which may result in disproportionately increased survival of more vulnerable species when large animals are no longer abundant (Roldán and Simonetti 2001). Both direct impacts of herbivores – consumption and physical damage – may thus differentially affect plant species, though again, their effects on timber tree performance are not well documented.

The hunting of vertebrate herbivores may indirectly affect timber trees both by increasing invertebrate herbivory and by altering plant competitive interactions. As with small mammals (discussed above), insect herbivores can compensate with increased abundance when large vertebrates are extirpated (Dirzo 2001). Insects exert strong and specialized herbivore pressures (Coley and Barone 1996, Massey et al. 2005) and are widely regarded as significant timber pests (Gray 1972, Nair 2007). Hunting may thus indirectly lead to added timber losses by prompting increased insect herbivory, though evidence is extremely limited.

Hunting may also indirectly modify plant competitive interactions. Herbivory is by definition a net loss for plants, regardless of the herbivore involved. However, these losses may be unevenly distributed across the plant community, particularly when hunting alters herbivore pressures. Plant species that are less often consumed by remaining herbivores as well as those that invest little in anti-herbivore defense may

realize a new competitive advantage within the plant community. Designating resources toward the production of plant defense compounds can promote increased seedling survival (Molofsky and Fisher 1993), but involves a trade-off with investment in growth (Coley et al. 1985). Fast growing, competitively dominant species thus typically suffer high rates of herbivory in intact forests because of the palatability of their tissues (Coley and Barone 1996), though this regulatory pressure is lost in the absence of herbivores. In an exclosure experiment by Kurten (2010), herbivore removal indeed favored less defended, higher leaf nutrient species. Seedlings which more quickly exhaust their reserves through fast growth also have less of a chance to be damaged by rodents (Forget 1997). In a community-level study, Poulsen *et al.* (2013) documented the proliferation of fast growing, low wood density species in forests subject to hunting pressure. By way of explaining this trend, the authors' *forest herbivore hypothesis* implicates the relaxation of browsing by hunted mammals as the key mechanism of change.

Overall, current evidence suggests that hunting will favor plant species with fast growth, disadvantaging well-defended, high wood density species at the community level. This poses a concern for the regeneration of many timber species in hunted forests. Through its direct and indirect impacts on herbivory, hunting may alter the "competitive balance" between plant species (Wright 2003), to the detriment of timber regeneration.

**Table 1: Ecological characteristics and plant-animal interactions of the 10 most commonly harvested timber tree species (based on volume exported in 2011 and 2012; ITTO 2012) from the world's three main regions of tropical forest. Note the disproportionate representation of wind dispersed species by current harvests; these species are often favored because of their long, straight boles.**

Scientific Name	Family	Disperser(s)	Seed Predator(s)	Herbivore(s)	Diaspore	Volume (1000m <sup>3</sup> )
<b>Neotropics</b>						
<i>Tabebuia</i> spp.	Bignoniaceae	wind	saki monkeys <sup>1</sup>	insects <sup>4</sup>	winged	142
<i>Peltogyne venosa</i>	Leguminosae	wind, monkeys	beetles, ants, saki monkeys ( <i>P. paniculata</i> ) <sup>15</sup>	insects	pod	79
<i>Swartzia</i> spp.	Fabaceae	bats, birds, rodents, monkeys	rodents, ants	insects, mammals	fleshy	68
<i>Dicorynia guianensis</i>	Leguminosae	wind, gravity	insects, rodents, brocket deer <sup>9</sup>	insects	pod	37
<i>Mora excelsa</i>	Leguminosae	water, fish, rodents (secondary)	rodents	insects	pod	35
<i>Chlorocardium rodiei</i>	Lauraceae	scatterhoarding rodents <sup>19</sup>	insects, rodents	insects	woody nut	32
<i>Goupia glabra</i>	Goupiaceae	birds	insects, rodents	insects	fleshy	11
<i>Eperua falcata</i>	Leguminosae	explosive dehiscence, scatterhoarding rodents (secondary) <sup>18</sup>	insects, rodents, peccaries <sup>18</sup> , saki monkeys <sup>1,15</sup>	insects, mammals <sup>19</sup>	pod	10
<i>Manilkara bidentata</i>	Sapotaceae	birds <sup>17</sup> , monkeys <sup>12</sup>	peccaries <sup>20</sup> , beetles	leaf miner insects	fleshy	10
<i>Catostemma commune</i>	Bombacaceae	monkeys, bats, other mammals	brocket deer ( <i>C. fragrans</i> ) <sup>9</sup>	<i>Atta</i> spp. ants	fleshy	9
<b>Afrotropics</b>						
<i>Aucoumea klaineana</i>	Burseraceae	wind		elephants; psyllids ( <i>Pseudophacopteron</i> spp.), caterpillars, chimpanzees (flowers)	winged	1063
<i>Entandrophragma cylindricum</i>	Meliaceae	wind	rodents ( <i>Entandrophragma</i> spp.) <sup>20</sup>		winged	509
<i>Triplochiton scleroxylon</i>	Sterculiaceae	wind	insects	psyllids, <i>Anaphe venata</i> silkworm, other insects	winged nut	364
<i>Chlorophora excelsa</i> / <i>Milicia excelsa</i>	Moraceae	birds, bats, and squirrels		iroko gall fly, gorillas	fleshy	306
<i>Ceiba pentandra</i>	Malvaceae	wind	<i>Dysdercus</i> cotton stainer, other	insects	cottony floss	202

				insects		
<i>Cylicodiscus gabonensis</i>	Leguminosae	wind	primates	insects	pod / winged	181
<i>Erythrophleum ivorense</i>	Leguminosae	gorillas <sup>29</sup> , other primates	colobus monkeys <sup>44</sup>	colobus monkeys <sup>44</sup> , insects	pod	143
<i>Pterocarpus soyauxii</i>	Fabaceae	wind, animals (secondary)		numerous animals	winged	75
<i>Tectona grandis</i>	Lamiaceae	wind	beetles	<i>Hyblaea</i> and <i>Eutectona</i> caterpillars, other arthropods	woody nut	71
<i>Entandrophragma utile</i>	Meliaceae	wind	rodents <sup>31,30</sup> antelopes, shoot borers, lepidopterous insects		winged	63
<b>Indo-Malayan Tropics</b>						
<i>Shorea spp.</i>	Dipterocarpaceae	wind, scatterhoarding	insects, rodents, primates, bearded pigs	insects <sup>42</sup> , rodents <sup>42</sup> , other mammals	winged nut	4041
<i>Dipterocarpus spp.</i>	Dipterocarpaceae	wind, scatterhoarding	insects, rodents, primates, bearded pigs	insects, mammals	winged nut	2700
<i>Tectona grandis</i>	Lamiaceae	wind	beetles	<i>Hyblaea</i> and <i>Eutectona</i> caterpillars, other arthropods	woody nut	965
<i>Dryobalanops spp.</i>	Dipterocarpaceae	wind, scatterhoarding	insects, rodents, primates, bearded pigs	insects, porcupines, other mammals	winged nut	810
<i>Xylocarpus xylocarpa</i>	Leguminosae	explosive dehiscence	insects	insects	woody pod	718
<i>Hevea brasiliensis</i>	Euphorbiaceae	explosive dehiscence			capsule	172
<i>Koompassia spp.</i>	Leguminosae	wind, orangutans <sup>32</sup>			winged	163
<i>Acacia mangium</i>	Fabaceae	birds, ants	beetles, ants	mammals, insects	coiled pod	152
<i>Parashorea spp.</i>	Dipterocarpaceae	wind, scatterhoarding	insects, rodents, primates, bearded pigs	beetles and other insects, snails, mammals	winged nut	85
<i>Anisoptera spp.</i>	Dipterocarpaceae	wind, scatterhoarding	insects, rodents, primates, bearded pigs	insects, mammals	winged nut	81

**General sources:** Pan-tropical: World Agroforestry Centre Database, PROTAbase, Jansen and Zuidema 2001; Neotropics: van Roosmalen 1985, Hammond *et al.* 1996; Afrotropics: Doucet 2003; Indo-Malayan tropics: Soerianegara and Lemmens 1993, Lemmens *et al.* 1995, Sosef *et al.* 1998.

**Specific sources (footnotes):** <sup>1</sup>Norconk and Veres 2011, <sup>2</sup>Lambert *et al.* 2005, <sup>3</sup>Terborgh *et al.* 1993, <sup>4</sup>Ribeiro *et al.* 1994, <sup>5</sup>Carvalho 1994, <sup>6</sup>Arnold and Fonseca 2011, <sup>7</sup>Embrapa Amazonia Oriental 2004, <sup>8</sup>Dick 2001, <sup>9</sup>Gayot *et al.* 2004, <sup>10</sup>Wenny 2000, <sup>11</sup>Howe *et al.* 1985, <sup>12</sup>Simmen and Sabatier 1996, <sup>13</sup>Henry *et al.* 2000, <sup>14</sup>Bodmer 1991, <sup>15</sup>van Roosmalen *et al.* 1988, <sup>16</sup>Altricher *et al.* 2001, <sup>17</sup>Snow 1981, <sup>18</sup>Forget 1989, <sup>19</sup>Hammond *et al.* 1999, <sup>20</sup>Beck 2005, <sup>21</sup>Sabater Pi 1979, <sup>22</sup>Williamson *et al.* 1990, <sup>23</sup>Tutin and Fernandez 1993, <sup>24</sup>Beaune *et al.* 2012, <sup>25</sup>Astaras and Waltert 2010, <sup>26</sup>Hawthorne 1995, <sup>27</sup>Lahm 1986, <sup>28</sup>Morgan and Sanz 2007, <sup>29</sup>Doran *et al.* 2002, <sup>30</sup>Hall 2008, <sup>31</sup>Synnott 1975, <sup>32</sup>Galdikas 1988, <sup>33</sup>Ungar 1995, <sup>34</sup>Blate *et al.* 1998, <sup>35</sup>Marshall *et al.* 2009, <sup>36</sup>McConkey and Galetti 1999, <sup>37</sup>Hamzah *et al.* 2010, <sup>38</sup>Davies 1991, <sup>39</sup>Mumford 2009, <sup>40</sup>Mudappa *et al.* 2010, <sup>41</sup>Fredriksson *et al.* 2006, <sup>42</sup>Turner 1990, <sup>43</sup>Kanwatanakid-Savini *et al.* 2009, <sup>44</sup>McKey *et al.* 1981

**Table 2: Ecological characteristics and plant-animal interactions of less commonly harvested timber tree species from the world's three main regions of tropical forest. Harvest rates are currently low but expected to increase as the market for lesser-known timber species increases (Jansen and Zuidema 2001). Species selected based on frequent mention in the literature and/or future market potential.**

Scientific Name	Family	Disperser(s)	Seed Predator(s)	Herbivore(s)	Diaspore
<b>Neotropics</b>					
<i>Amburana spp.</i>	Leguminosae	wind	insects	insects	winged
<i>Araucaria angustifolia</i>	Araucariaceae	birds, rodents, and other mammals <sup>5</sup>	peccaries, rodents	insects <sup>6</sup>	fleshy nut
<i>Brosimum utile</i>	Moraceae	monkeys <sup>3,12</sup> , tapirs ( <i>B. parinaroides</i> ) <sup>13</sup> , birds, peccaries <sup>14</sup>	brocket deer ( <i>Brosimum spp.</i> ) <sup>9</sup> , saki monkeys <sup>1,15</sup> , peccaries <sup>16</sup>		fleshy
<i>Carapa guianensis</i>	Meliaceae	scatterhoarding rodents	brocket deer <sup>9</sup> , saki monkeys <sup>16</sup> , rodents, peccaries	insects, deer	woody nut
<i>Cedrela spp.</i>	Meliaceae	wind	saki monkeys <sup>1</sup>	shootborer ( <i>Hypsiplya grandella</i> ), other arthropods	winged
<i>Cordia goeldiana</i>	Boraginaceae	birds, monkeys <sup>12</sup>	brocket deer <sup>9</sup>		fleshy
<i>Dinizia excelsa</i>	Leguminosae	wind/gravity, rodents and other mammals (secondary) <sup>7</sup>	parrots, macaws, beetles <sup>8</sup>		pod
<i>Hymenaea courbaril</i>	Leguminosae	monkeys, scatterhoarding rodents	saki monkeys <sup>1</sup> , peccaries, rodents, beetles <sup>3</sup>	<i>Atta spp.</i> ants	fleshy nut
<i>Ocotea spp.</i>	Lauraceae	numerous birds and mammals	small rodents <sup>10</sup> , insects, brocket deer <sup>9</sup> , peccaries	insects, mammals	fleshy
<i>Pradosia ptychandra</i>	Sapotaceae	monkeys <sup>12</sup>	saki monkeys <sup>1</sup> , peccaries ( <i>P. surinamensis</i> ) <sup>45</sup> , beetles	insects, mammals	fleshy
<i>Swietenia spp.</i>	Meliaceae	wind, rodents (secondary)	beetles, rodents <sup>2</sup>	shootborer ( <i>Hypsiplya grandella</i> )	winged
<i>Trattinickia spp.</i>	Burseraceae	birds <sup>17</sup> , monkeys <sup>12</sup>			fleshy
<i>Virola spp.</i>	Myristicaceae	birds, monkeys <sup>11</sup>	beetles, rodents, peccaries, brocket deer <sup>9</sup> , saki monkeys <sup>3</sup>	insects, deer, tapirs	fleshy
<b>Afrotropics</b>					
<i>Austranella congolensis</i>	Sapotaceae	elephants, gorillas <sup>29</sup>	bush pigs, porcupines		fleshy
<i>Baillonella toxisperma</i>	Sapotaceae	elephants, giant pouched rats, monkeys	bush pigs, porcupines	bush pigs, antelopes, elephants	fleshy
<i>Copaifera mildbraedii</i>	Leguminosae	birds <sup>26</sup>			fleshy

<i>Dacryodes buettneri</i>	Burseraceae	numerous birds, squirrels, monkeys, apes <sup>21,22,23</sup>	red river hogs <sup>24</sup> , mandrills <sup>25</sup> , rodents	elephants	fleshy
<i>Diospyros crassiflora</i>	Ebenaceae	birds, gorillas <sup>29</sup> , mandrills <sup>27,25</sup> , other animals		jumping plant-lice	fleshy
<i>Gambeya africana</i>	Sapotaceae	gorillas <sup>29</sup> , chimpanzees, elephants, birds	red river hogs ( <i>G. lacourtiana</i> ) <sup>24</sup> , mandrills <sup>27</sup>		fleshy
<i>Gilbertiodendron dewevrei</i>	Leguminosae	explosive dehiscence, gorillas <sup>29</sup>	red river hogs <sup>24</sup> , antelopes, elephants, rodents, primates	forest buffaloes, bongos; elephants	pod
<i>Guarea cedrata</i>	Meliaceae	hornbills, monkeys, duikers, porcupines	<i>Menemachus</i> beetles		fleshy
<i>Khaya ivorensis</i>	Meliaceae	wind	beetles, rodents	psyllids, other insects	winged
<i>Lophira alata</i>	Ochnaceae	wind, mandrills <sup>27</sup>	rodents, mandrills <sup>27</sup> , colobus monkeys <sup>44</sup>	gall-forming insects, gorillas <sup>22</sup> , colobus monkeys <sup>44</sup>	winged
<i>Millettia laurentii</i>	Fabaceae	explosive dehiscence		caterpillars, apes <sup>23</sup> , colobus monkeys <sup>44</sup>	pod
<i>Nauclea diderrichii</i>	Rubiaceae	birds, elephants, duikers, monkeys, gorillas <sup>28</sup>		shoot-boring moth larvae	fleshy
<i>Staudtia spp.</i>	Myristicaceae	numerous animals	mandrills <sup>27</sup>		fleshy
<i>Testulea gabonensis</i>	Luxembourgiaceae	wind	grey parrots	gorillas <sup>22</sup>	winged
<b>Indo-Malayan Tropics</b>					
<i>Buchanania spp.</i>	Anacardiaceae	animals	rodents		fleshy
<i>Calophyllum spp.</i>	Guttiferae	birds <sup>17</sup> , orangutans <sup>32</sup> , gibbons <sup>33</sup> , bats, squirrels, monkeys	rodents <sup>34</sup>	insects	fleshy
<i>Canarium spp.</i>	Burseraceae	birds <sup>17</sup> , gibbons <sup>35</sup> , sun bears <sup>36</sup> , monkeys, bats	rodent <sup>34</sup>		fleshy
<i>Celtis spp.</i>	Ulmaceae	birds <sup>17</sup> , rodents			fleshy
<i>Dillenia spp.</i>	Dilleniaceae	orangutans <sup>33</sup> , monkeys, elephants, pigs, squirrels, birds			fleshy
<i>Gonystylus bancanus</i>	Thymelaeaceae	orangutans <sup>32</sup> , Malayan flying foxes <sup>37</sup> , fruit bats	squirrels, other rodents		woody capsule
<i>Heritiera simplicifolia</i>	Sterculiaceae	wind	beetles, moth larvae		winged
<i>Intsia spp.</i>	Leguminosae	birds <sup>17</sup>	red leaf monkeys <sup>38</sup> , rodents	deer, mouse deer, rats	pod
<i>Palaquium spp.</i>	Sapotaceae	birds, gibbons <sup>35,39</sup> , orangutans <sup>32</sup> , civets <sup>40</sup> , sun bears <sup>41</sup> , fruit bats	squirrels, other rodents <sup>34</sup> , birds	insects	fleshy
<i>Pometia pinnata</i>	Sapindaceae	bats, birds	<i>Conopomorpha</i> moths		fleshy
<i>Pouteria spp.</i>	Sapotaceae	monkeys, bats, birds, squirrels	squirrels, beetles		fleshy

<i>Syzygium spp.</i>	Myristicaceae	gibbons <sup>35,39</sup> , hornbills <sup>43</sup> and other birds, civets <sup>40</sup> , sun bears <sup>41</sup> , small fruit bats, squirrels	rodents <sup>34</sup>	insects	fleshy
<i>Terminalia spp.</i>	Combretaceae	birds <sup>17</sup> , monkeys <sup>34</sup>	rodents, insects	<i>Roesalia</i> moth caterpillars	fleshy

**General sources:** Pan-tropical: World Agroforestry Centre Database, PROTAbase, Jansen and Zuidema 2001; Neotropics: van Roosmalen 1985, Hammond *et al.* 1996; Afrotropics: Doucet 2003; Indo-Malayan tropics: Soerianegara and Lemmens 1993, Lemmens *et al.* 1995, Sosef *et al.* 1998.

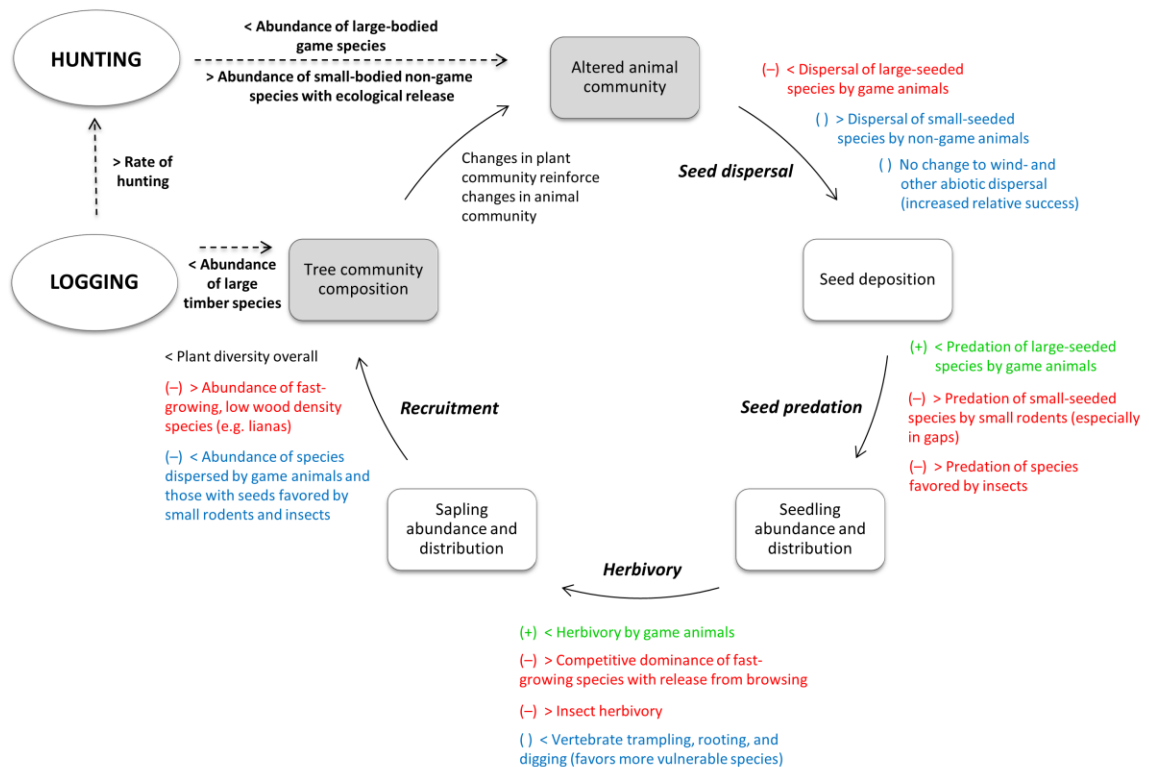
**Specific sources (footnotes):** <sup>1</sup>Norconk and Veres 2011, <sup>2</sup>Lambert *et al.* 2005, <sup>3</sup>Terborgh *et al.* 1993, <sup>4</sup>Ribeiro *et al.* 1994, <sup>5</sup>Carvalho 1994, <sup>6</sup>Arnold and Fonseca 2011, <sup>7</sup>Embrapa Amazonia Oriental 2004, <sup>8</sup>Dick 2001, <sup>9</sup>Gayot *et al.* 2004, <sup>10</sup>Wenny 2000, <sup>11</sup>Howe *et al.* 1985, <sup>12</sup>Simmen and Sabatier 1996, <sup>13</sup>Henry *et al.* 2000, <sup>14</sup>Bodmer 1991, <sup>15</sup>van Roosmalen *et al.* 1988, <sup>16</sup>Altricher *et al.* 2001, <sup>17</sup>Snow 1981, <sup>18</sup>Forget 1989, <sup>19</sup>Hammond *et al.* 1999, <sup>20</sup>Beck 2005, <sup>21</sup>Sabater Pi 1979, <sup>22</sup>Williamson *et al.* 1990, <sup>23</sup>Tutin and Fernandez 1993, <sup>24</sup>Beaune *et al.* 2012, <sup>25</sup>Astaras and Waltert 2010, <sup>26</sup>Hawthorne 1995, <sup>27</sup>Lahm 1986, <sup>28</sup>Morgan and Sanz 2007, <sup>29</sup>Doran *et al.* 2002, <sup>30</sup>Hall 2008, <sup>31</sup>Synnott 1975, <sup>32</sup>Galdikas 1988, <sup>33</sup>Ungar 1995, <sup>34</sup>Blate *et al.* 1998, <sup>35</sup>Marshall *et al.* 2009, <sup>36</sup>McConkey and Galetti 1999, <sup>37</sup>Hamzah *et al.* 2010, <sup>38</sup>Davies 1991, <sup>39</sup>Mumford 2009, <sup>40</sup>Mudappa *et al.* 2010, <sup>41</sup>Fredriksson *et al.* 2006, <sup>42</sup>Turner 1990, <sup>43</sup>Kanwatanakid-Savini *et al.* 2009, <sup>44</sup>McKey *et al.* 1981, <sup>45</sup>Fragoso 1999.

## 1.6 Conclusions

Hunting can affect regeneration through a variety of pathways (Figure 1).

Vertebrate seed dispersers are strongly impacted by hunting pressure, reducing seed movement for many species and shifting community composition to favor those plants dispersed by small animals and abiotic means. Timber species with large seeds and fleshy fruit are at particular risk for dispersal and recruitment failure. Hunting also alters granivore communities, resulting in increased predation on species favored by insects and small rodents, and changing the spatial template of seed predation. There is abundant evidence to suggest that many timber species will be detrimentally affected by such altered seed predation regimes. Large vertebrate herbivores decline with hunting pressure, resulting in the modification of plant competitive interactions. This process disadvantages several traits that are common among timber trees, including relatively slow growth and high wood density.

Timber species, like the broader tropical tree community, interact with wildlife through all stages of their life cycles. One cannot assume that regeneration will be successful in the face of hunting, when plant-animal interactions are so widely modified. A lack of appreciation for – and management of – these interactions could threaten forest biodiversity, limit future timber production, and increase the likelihood of forest conversion for other land uses.



**Figure 1: Conceptual model of pathways by which hunting may affect the regeneration of timber; adapted with permission from Poulsen *et al.* (2013). Hypothesized effects on timber regeneration are presented by subscripts: green (+) effects are beneficial, red (-) effects are detrimental, and blue ( ) effects are variable, depending on specific plant traits.**

### 1.6.1 Management Considerations

Hunting will no doubt continue to affect tropical forests worldwide, though there is great potential to curtail its effects in production forests, through improved management. Many natural management systems rely on unlogged concession lands both to preserve biodiversity and to promote recovery after harvesting from adjacent forest units. However, unlogged tracts may be too small to maintain viable animal populations and too isolated to allow re-colonization of logged areas (Pannell 1989).

Forest managers expecting sustained timber production must thus ensure that the processes that contribute to regeneration occur within logged areas themselves (Guariguata and Pinard 1998). This is only possible if wildlife populations are maintained and the impacts of hunting are reduced across concessions.

The most effective management modifications to reduce hunting in concessions are those which reduce market demand for wild meat and curb the transportation of hunters and their game (Auzel and Wilkie 2000, Clark et al. 2009). One way to curtail access would be to ban the transport of hunters and game meat on logging trucks, enforced with road blocks and spot checks, and to close or destroy unused bridges and roads post-logging (Auzel and Wilkie 2000). Removing the transportation infrastructure that hunters rely on can be a very successful intervention, as evidenced by the collapse of bushmeat markets and closure of local hunting camps that followed a brief halt in traffic of a large Congo concession (Pearce and Ammann 1995).

Demand for wild meat can only be reduced if alternatives are available at equal or lesser prices, perhaps subsidized by the logging companies themselves. This could be achieved by importing domestic animal meat, or by establishing livestock-raising programs within concessions (Auzel and Wilkie 2000). Poulsen *et al.* (2009) outline several additional recommendations to reduce hunting within concessions, including: concession support for wildlife law enforcement, ensuring that any workers who hunt

do so legally, formalizing resource management in land-use planning, especially for indigenous people, and avoiding urbanization in concessions.

Such management requirements may seem extensive, but are not beyond the capacity of most extractive enterprises. In the Congolaise Industrielle des Bois (CIB) concessions in the Republic of Congo, wildlife and biodiversity are specifically managed through a combination of land-use planning, hunting law enforcement, developing economic and protein alternatives to hunting and wild meat, and formalizing wildlife management (Poulsen and Clark 2010, Clark and Poulsen 2012). Gabon's Rabi concession, though focused on oil rather than timber, is another exemplary case. The concession prohibits nighttime driving, restricts access for non-employees, and forbids the possession of firearms, snares, and bushmeat (Laurance et al. 2006). Workers are well compensated financially and domestic animal meat is made available at competitive prices (Laurance et al. 2006). Similarly, logging companies in Sarawak are tasked with enforcing a wildlife trade ban in rural areas and providing meat for workers, and forestry laws in Bolivia mandate comparable practices (Robinson et al. 1999).

The options open to forest managers are typically influenced by short-term financial and political priorities, often resulting in the dismissal of plant-animal interactions and the long-term consequences of disruptions to them (Smith and Garnett 2004). However, these financial constraints are precisely why managers must strive to

make informed decisions that promote efficient and cost-effective practices (Green 2007). For example, protecting native seed dispersers can be much less expensive than artificially recreating lost dispersal services (Hougner et al. 2006).

Management schemes and certification bodies such as the Forest Stewardship Council (FSC) should strive to be as specific as possible regarding wildlife and ecological services; this process has benefitted in recent years from biologists becoming more involved in setting guidelines (Bennett 2001). Revised FSC principles and criteria now include mention of hunting and ecosystem function (FSC 2012), but the language remains non-specific and non-prescriptive. Additionally, there is currently little information on whether certification and improved practices actually reduce the pressures on wildlife associated with timber harvest (Kuijk et al. 2009), despite this being a stated goal of such management.

Ultimately, appropriate management decisions will come about only by recognizing the direct and indirect impacts the timber industry has on wildlife (Robinson et al. 1999, Poulsen et al. 2009). Few have acknowledged that wildlife management is a vital component of forest management (Smythe 1987, Pannell 1989, Terborgh 1995, Corlett 2011), though it is in many companies' best interests to do so, as such explicit consideration would benefit both biodiversity and timber regeneration.

## 1.6.2 Future Research Priorities

Knowledge of the ecological requirements and reproductive biology of most tropical timber species is sorely lacking (Bawa et al. 1990, Pinard et al. 1999). Though there is sufficient evidence to conclude that animals play many important roles (see Tables 1 and 2), few forestry studies directly address these relationships. The information presented here is far from exhaustive; these interactions are scattered few and far between in primary literature and natural history accounts, and very little is known on any generalizable scale. In particular, the impacts of potentially disruptive activities such as hunting must be documented and communicated well, so that governments, certifying bodies, and timber companies themselves can make informed management decisions.

One research priority is to obtain basic ecological data for timber trees and for hunted wildlife species, including their distribution, density, and rates of change under hunting (Milner-Gulland et al. 2003), particularly for animals that may play a role in timber regeneration. Such information is critically important for identifying important functional traits, as well as thresholds in plant-animal relationships beyond which wildlife are no longer ecologically effective in their roles (McConkey and Drake 2006), or compensatory increases become deleterious to regeneration processes (see above). Specific studies addressing the dispersal, predation, or overall recruitment of timber trees with relation to wildlife are needed. Responses to hunting among wildlife and

plant communities are not unidirectional; it is clear that disruptions to plant-animal interactions can vary in their downstream effects, promoting or inhibiting recruitment depending on several factors. Reconciling the sometimes contradictory outcomes of these processes will require manipulative field experiments.

Regardless of the focal theme, researchers must strive to promote access to ecological knowledge among the international forestry community, and to improve its translation into tangible management action (Sheil and Van Heist 2000). The most effective research to promote change and mitigate deleterious impacts on wildlife will be that which addresses silviculturally and financially viable alternatives to exploitative practices (Putz et al. 2001). Without such efforts, timber operations and the bodies that oversee them will be unable to make the important decisions that will define the future of tropical forestry.

Forest wildlife and the ecological processes that influence regeneration can be of great importance for many timber species, and the effects of impacts such as hunting must be well understood in order to maintain them. The sustainability of logging from both an ecological and economic perspective will rely on careful management with a strong scientific foundation.

## 2. Telemetric Tracking of Scatterhoarding and Seed Fate in a Central African Forest

### 2.1 Summary

In seed predation studies, removal of a seed is only the first step of a dynamic process that may result in dispersal rather than seed death. This process, termed seed fate, has received little attention in African forests, particularly in Central Africa. We experimentally assessed the initial steps of seed fate for two tree species – the large-seeded *Pentaclethra macrophylla* and the relatively small-seeded *Gambeya lacourtiana* – in northeastern Gabon. Specifically, we evaluated whether seed size and seed consumer identity are important determinants of seed fate. We established experimental stations under conspecific fruiting trees, each comprising three seeds fitted with telemetric thread tags to facilitate their recovery, and a motion-sensitive camera to identify visiting mammals. In total, animals removed 76 tagged seeds from experimental stations. Small Murid rats and mice primarily removed small *Gambeya* seeds, whereas large-bodied rodents and mandrills primarily removed large *Pentaclethra* seeds. *Gambeya* seeds were carried shorter distances than *Pentaclethra* seeds and were less likely to be cached. The two large-bodied rodents handled seeds differently: *Cricetomys emini* larderhoarded nearly all (n=15 of 16) encountered *Pentaclethra* seeds deep in burrows, while *Atherurus africanus* cached all (n=5 of 5) encountered *Pentaclethra* seeds singly under 1-3 cm of leaf litter and soil, at an average distance of 24.2 m and a maximum distance of 46.3 m from experimental stations. This study supports the hypothesis that seed fate varies based on

seed size and seed consumer identity, and represents the first telemetric experimental evidence of larderhoarding and scatterhoarding in the region.

## **2.2 Introduction**

Much seed predation research has equated the removal of a seed from an experimental plot with the seed's death. However, seed predators vary in their handling of seeds, with a diversity of consumption and hoarding behaviors (Janzen 1971, Vander Wall 1990, Hulme 1998, Forget *et al.* 2005, Vander Wall *et al.* 2005). Methodological advances in studying these processes – ranging from simple seed thread tags to radioisotopes to telemetric tracking (Forget and Wenny 2005) – have prompted the realization that seed predation is a dynamic process, comprising multiple steps, complex mechanisms, and varied outcomes (Vander Wall *et al.* 2005). The study of these pathways, collectively known as seed fate, follows seeds to either death or, in few cases, successful establishment as seedlings by way of various biotic and abiotic actors.

In tropical forests, seed fate has been examined most prominently in studies of acouchies, agoutis, and spiny rats: Neotropical seed-consuming rodents that can double as effective dispersers via the process of scatterhoarding (Morris 1962, Smythe 1978, Forget 1990, Adler & Kestell 1998, Brewer & Rejmánek 1999, Jansen *et al.* 2012). Though relatively well-studied in the Neotropics and in several temperate forests, scatterhoarding and seed fate have received very little attention in other tropical forest regions, particularly in Central Africa. For African forests as a whole, only a few studies

have examined seed fate and the role of rodents in seed dispersal (Doucet 2003, Nyiramana et al. 2011, Moupela et al. 2013, Aliyu et al. 2014, Dutton et al. 2014).

This research gap merits attention, as rodent seed predators are ubiquitous in tropical forests and can strongly influence plant population dynamics and patterns of tree recruitment (Janzen 1971, Fleming 1975, Asquith et al. 1997, Paine and Beck 2007). In Central African forests, large rodents – including Emin’s giant pouched rat (*Cricetomys emini*) and the African brush-tailed porcupine (*Atherurus africanus*) – are common seed consumers, though very little is known about the fate of seeds they handle. A single captive study (Ewer 1968) noted caching behavior in *A. africanus*, though this has never been explicitly assessed in the wild. As both species are heavily hunted for meat (Fa et al. 2005), developing an understanding of their ecological roles may also impact forest management decisions.

In this study we experimentally assess the initial steps of seed fate for two tree species, *Gambeya lacourtiana* and *Pentaclethra macrophylla*, in northeastern Gabon. Specifically, we evaluate whether seed size and the identity of the seed predator are important determinants of seed fate.

### **2.3 Methods**

We conducted this study in the forest surrounding the Ipassa Research Station, in the Ogooué-Ivindo region of northeastern Gabon. This region is dominated by lowland forest, and receives approximately 1700 mm of rain annually, with two rainy seasons

(September-December and March-June). Despite its protected status as part of Ivindo National Park, the Ipassa forest is occasionally hunted. A few species of game animals, including bay duikers (*Cephalophus dorsalis*) and red river hogs (*Potamochoerus porcus*), have been reduced in abundance as a result (Okouyi et al. 2001, van Vliet et al. 2007). Nonetheless, the forest boasts high mammal diversity (Okouyi *et al.* 2002, J. Poulsen, unpubl. data) and an apparently intact rodent community (Markham 2015).

We selected the seeds of two tree species, *Gambeya lacourtiana* (Sapotaceae; basionym: *Chrysophyllum lacourtianum* De Wild.) and *Pentaclethra macrophylla* (Fabaceae; Figure 2), because they were: a) locally abundant, b) divergent in size but both large enough for telemetric thread tagging, and c) known to be commonly preyed upon. *Gambeya lacourtiana* (hereafter *Gambeya*) is a large tree, reaching over 50 m tall, with large succulent globose fruits (mean mass= 320 g) that are widely consumed by small, medium, and large-bodied mammals. *Gambeya* seeds, of which there are 4-5 per fruit, are relatively small in size (mean mass=2.8 g) with a flattened ellipsoid shape (mean length=29 mm, mean width=14 mm). They have a prominent seed scar and a shiny brown seed coat that is hard but thin, and easily penetrated by mammalian seed predators. *Pentaclethra macrophylla* (hereafter *Pentaclethra*) is a medium to large tree, 20-30 m tall, with large woody seed pods (approximately 50 cm x 10 cm x 2 cm). Each pod contains 5-8 seeds, and dehisces explosively at maturity, scattering seeds up to 20 m from the tree (Archinewhu 1996). *Pentaclethra* seeds are very large (mean mass=29.4 g),

with a flat elliptical shape (mean length=64 mm, mean width=39 mm) and a shiny brown seed coat that is medium-hard, but is also easily penetrated by most seed predators.



**Figure 2: The seeds of two tree species, *Pentaclethra macrophylla* (on left) and *Gambeya lacourtiana* (on right), used in the study.**

We collected whole *Gambeya* fruits (July-August) and *Pentaclethra* seeds (September-October) from the ground beneath at least 5 fruiting individuals of each species, during their close but non-overlapping fruiting seasons. We extracted *Gambeya* seeds from their fruits, cleaned them of flesh, and dried them for 1-2 hours in the sun to prevent fungal growth. We assessed all seeds for damage, discarding seeds with fungus, arthropod exit holes, and any seeds that floated in water. We conducted the experiment for both species during the same period, from September 22, 2014 to November 2, 2014, which required us to store cleaned *Gambeya* seeds indoors under ambient air conditions for a period of approximately 45-60 days. Results from other

experiments using these seeds indicate that this brief storage period did not affect seed removal or germination rates.

Immediately prior to experimental placement, we fitted seeds with telemetric thread tags (Hirsch et al. 2012) by attaching a 7 mm screw eye and threading it with 30 cm of black nylon-coated stainless steel leader wire. We also tied on a small piece of pink flagging labeled with an identification code unique to its experimental placement. Each cylindrical radiotransmitter (Advanced Telemetry Systems, Isanti, MN) weighed 4.10 g, including a 20 cm long wire antenna, and featured a magnet-operated on-off switch (Hirsch et al. 2012). Prior experimental tests have shown that seeds with telemetric thread tags are removed at equal rates to untagged seeds (Hirsch et al. 2012). We tested this for our study by scattering three tagged and three untagged seeds in a clump (1 m<sup>2</sup> in area), and monitoring their fate for 14 days. We repeated the procedure four times in different locations for each species.

We intended to pair the telemetric thread tag method with more traditional thread tags (Forget 1990), using 60-cm lengths of brightly-colored line threaded to each seed, with a flagging tape label at the distal end. Initial use of these simple thread tags was unsuccessful, as the cotton thread frequently caught on understory vegetation and was difficult to re-locate visually. Nylon thread, fine metal wire, or plastic fishing line might have been suitable alternatives, but were unavailable for our study.

We established experimental seed stations under conspecific fruiting trees (5-10 m from the tree bole) for each species. Stations consisted of three telemetric thread tagged seeds, arranged 0.75 m apart in a triangle on soil cleared of leaf litter. We mounted a motion-sensitive trail camera (Bushnell Trophy Cam HD, set to 60-second video mode) on a nearby tree to identify visiting mammals and record their behavior (Figure 3). Each seed station was located at a different tree and spaced a minimum of 250 m from any other station. Due to the cost of telemetric thread tags, we were limited to running four seed station experiments at any one time.



**Figure 3: The major terrestrial mammalian seed predators of the Ipassa Reserve, “caught” removing seeds from experimental stations. Clockwise from top left: African brush-tailed porcupine (*A. africanus*), Emin’s giant pouched rat (*C. emini*), small Murid rodent (Family: Muridae; circled), and mandrill (*Mandrillus sphinx*). Still images were taken from motion-sensitive trail camera videos.**

We checked seed stations 3 days after seed placement and again 7 days after placement if seeds remained after the first check. To recover removed seeds, we first visually scanned the immediate area, and then used a handheld radio receiver with telemetry antenna, locating tagged seeds by their specific transmitter frequency. At each recovery location, we took the following data: movement distance (measured with a measuring tape), compass direction, and seed condition (intact, consumed, in burrow, or cached under soil or leaf litter).

If all seeds remained untouched after 7 days, we closed the station and established a new experimental site. If some or all seeds were removed, we recovered

the telemetric thread tags and attached them to new seeds, and we established a new station on the opposite side of the same tree (10-20 m away), or at an entirely new location if two experimental sites had already been used there. In one instance, we repositioned a trail camera to continue monitoring a tagged seed that had been removed and cached nearby. Equipment and field limitations prevented us from following seeds over time in all other cases; our data are limited to the first movement of seeds and their initial fate.

## **2.4 Results**

Tagged and untagged seeds were removed at equal rates in the pilot experiment, with no difference in time to removal or quantity removed; all seeds of both treatments were removed (n=42 seeds across four stations) except at one station, where none of the seeds of either treatment were removed (n=6 seeds). This supports previous experimental tests indicating that the telemetric thread tag does not affect seed removal (Hirsch *et al.* 2012). It is impossible to determine whether the telemetric thread tag affects eventual seed fate, as untagged seeds cannot be monitored.

In total, 76 telemetric thread tagged seeds were removed from experimental stations for the two species (*Gambeya*=36 seeds, *Pentaclethra*=40 seeds). Seeds for which the fate could not be determined (due to failure of the trail camera to capture the seed predator [n=6], the thread tag being tangled on vegetation [n=5], or transmitter failure [n=1]) were excluded from analysis, as were the data from the pilot study.

Small Murid rats and mice removed greater proportions of small *Gambeya* seeds, whereas large-bodied rodents and mandrills (*Mandrillus sphinx*) removed greater proportions of large *Pentaclethra* seeds (Table 3). For *Gambeya* seeds, the dominant seed predators were small-bodied Murid rats and mice, which removed 63% (n=20) of all seeds, followed by large-bodied rodents, *C. emini* (34%, n=11) and *A. africanus* (3%, n=1). For *Pentaclethra* seeds, the dominant seed predator was *C. emini*, which removed 56% (n=18) of all seeds, followed by *M. sphinx* (28%, n=9) and *A. africanus* (16%, n=5). No *Pentaclethra* seeds were removed by small-bodied Murid rodents.

**Table 3: Removal percentages (by seed consumer) and movement distances of telemetric thread tagged seeds.**

Species of Seed	Murid rodents	% removed by:			Movement Distance (m)	
		<i>C. emini</i>	<i>A. africanus</i>	<i>M. sphinx</i>	Mean	Max
<i>Gambeya</i> (n=36)	63	34	3	0	3.2	13.5
<i>Pentaclethra</i> (n=40)	0	56	16	28	15.9	46.3

Animals moved *Gambeya* seeds shorter distances (mean=3.2 m, max=13.5 m) than *Pentaclethra* seeds (mean=15.9 m, max=46.3 m), and consumed a higher proportion of *Gambeya* seeds on the spot, within 0.5 m of experimental placement (31% [n=11] for *Gambeya* vs. 18% [n=7] for *Pentaclethra*; Figure 4). A single *Gambeya* seed was cached (in a Murid rodent burrow), while 20 *Pentaclethra* seeds were cached (five seeds cached under 2-3 cm of soil and leaf litter by *A. africanus*, 15 seeds cached in burrows by *C. emini*). Of the five seeds cached by *A. africanus*, one was subsequently found and

removed by a *C. emini* individual, and the remaining four were still cached at the conclusion of the study, approximately two weeks after deposition. To assess the fate of seeds cached in *C. emini* burrows, we dug up one burrow, which had two entrances, a total length of 7.4 m, and a depth of 1.2 m at the center, where seeds were cached. A total of 104 seeds of four species (*Pentaclethra*, along with *Coula edulis*, *Pentaclethra eetveldeana*, and *Scorodophloeus zenkeri*) were recovered from this single burrow cache, of which 78 were *Pentaclethra*, with a total seed mass of 2.47 kg, approximately twice the average body mass of the rodent.

## **2.5 Discussion**

In this first telemetric examination of seed fate in Central Africa, we found that the fate of *Gambeya* and *Pentaclethra* seeds differed due to two related factors: the size of the seed and the identity of the seed predator. The 10-fold difference in seed size probably resulted in divergent rates of consumption by different animal species; small Murid rats and mice removed greater proportions of small *Gambeya* seeds, whereas large-bodied rodents and mandrills removed greater proportions of large *Pentaclethra* seeds. *Gambeya* seeds were also more likely to be eaten on the spot rather than carried away, particularly among larger-bodied rodents.

When removed, small *Gambeya* seeds were carried shorter distances than large *Pentaclethra* seeds, and were less likely to be cached. This result supports the conclusion of several studies that large seeds are more likely to be carried farther and to be cached

than small seeds (Hallwachs 1994, Forget et al. 1998, Jansen et al. 2004). Differential treatment of seeds along a seed size axis may allow seed-eating rodents to minimize exposure to predators, by consuming small seeds that are quick to process and carrying large seeds that are time-intensive to process to a safe space such as a burrow (Smith and Reichman 1984, Vander Wall 1990). Hoarding few large seeds is also energetically favorable and makes better use of limited caching sites than hoarding many small seeds (Stapanian and Smith 1978, Jansen et al. 2002). In our study, the weight of the transmitter and difficulty in dragging the tag may have inhibited small Murid rodents from caching *Gambeya* seeds, as the additional 4.1 g increased total seed mass by almost 250%. Thus, small rodents may cache small untagged seeds more often than observed. The transmitter-to-body mass ratio for the two large rodents was much lower (33.5 g [transmitter+*Pentaclethra* seed] vs. 1200 g [*C. emini* mass] or 2750 g [*A. africanus* mass]), so the added transmitter weight was unlikely to alter their removal or caching behavior.

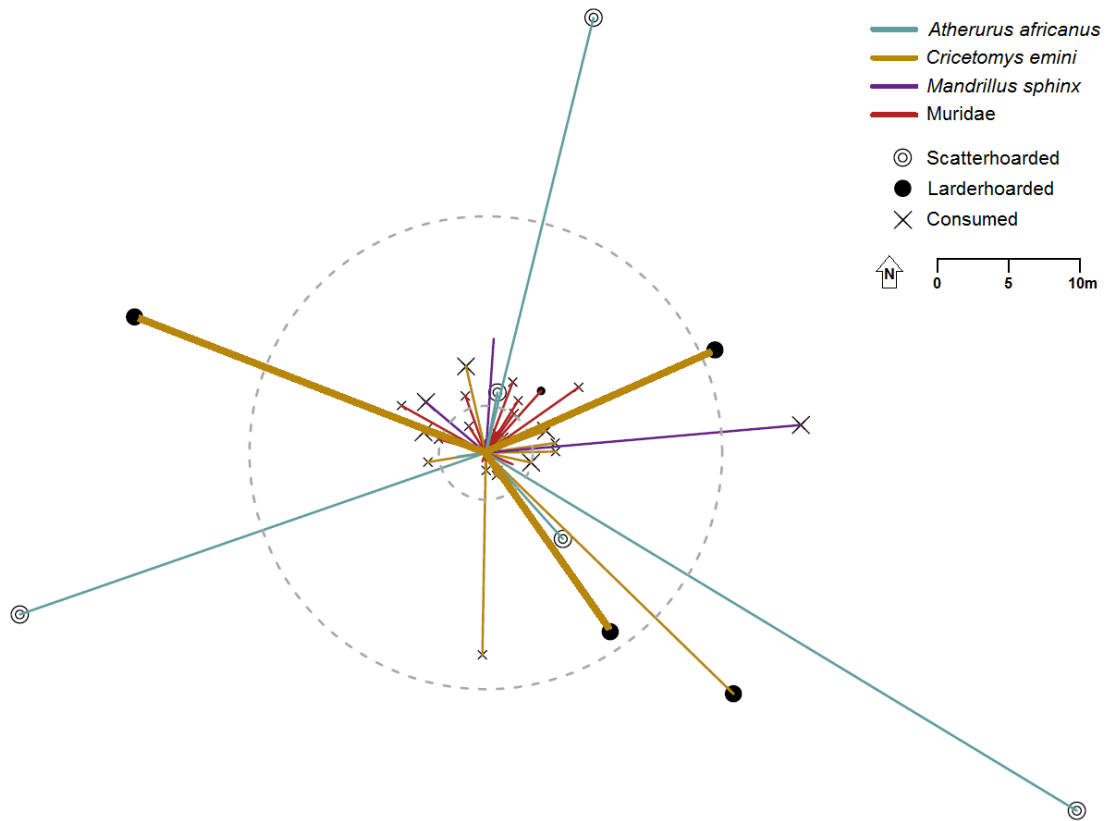
The two large-bodied rodents – *Cricetomys emini* and *Atherurus africanus* – consistently handled seeds differently from each other. *C. emini*, a large-bodied cheek-pouched burrowing rat, was responsible for the most seed removal (45% of 76 seeds overall), particularly for large seeds (56% of 36 seeds), and carried nearly all (n=15 of 16) encountered *Pentaclethra* seeds to their burrows to be larderhoarded (see Results for a description of one burrow and its recovered seeds). At a depth of 1 m underground, even seeds that germinate will be unable to establish as seedlings, thus the fate of seeds

removed by *C. emini* is death. This result supports the assertion that *Cricetomys spp.* rodents are primarily seed predators, not dispersers (Guedje et al. 2003, Kankam and Oduro 2009, Seufert et al. 2009). However, two recent studies have implicated *Cricetomys spp.* rodents as scatterhoarders of large seeds. Nyiramana *et al.* (2011) studied the fate of threaded *Carapa grandiflora* seeds in a montane forest in Rwanda, recovering several cached seeds and finding seedling cotyledon evidence that indicated scatterhoarding by seed-dispersing rodents. Aliyu *et al.* (2014) documented scatterhoarding of numerous threaded seeds in a fragmented montane forest in Nigeria, attributing this dispersal to *Cricetomys sp.* rodents, as they were the most commonly observed seed consuming animal visiting the seed plots. Though these studies have large seed sample sizes, neither study linked visual camera observations with specific seed movements, and neither used methods that allow for the recovery of seeds moved long distances or deposited deep in burrows. It is possible that the scatterhoarding observed in these studies has been incorrectly attributed to *Cricetomys spp.* rodents, as the anatomical and behavioral traits of this rodent taxon, along with the results presented here, suggest that it transports multiple seeds in its cheek pouches and hoards them in large burrow larders rather than small scattered caches. It is also possible, though perhaps less likely, that the differences among the several *Cricetomys* species and the habitats in which they live are sufficient to drive divergent seed handling behaviors. More research will be necessary to evaluate the degree to which these behaviors are

consistent across different forest types and with respect to variables such as rodent densities, fruiting phenology, and resource availability (P.-M. Forget, personal communication).

In contrast to *C. emini*, *A. africanus*, a rat-like porcupine that relies on natural-shelter burrows (Emmons 1983, Kingdon 2012), deposited all (n=5 of 5) encountered *Pentaclethra* seeds in shallow caches, at an average distance of 24.2 m and a maximum distance of 46.3 m from the experimental stations (Figure 4). In each case, seeds were cached singly under 1-3 cm of soil and leaf litter – an ideal microsite for germination and establishment. Due to equipment limitations, we were unable to continue monitoring seeds after their initial movement (e.g. Jansen *et al.* 2012), therefore it is impossible to quantify the proportion of scatterhoarded seeds that established as seedlings. Jansen *et al.* (2012) determined that most *Astrocaryum standleyanum* seeds hoarded by agoutis at one site in Panama were quickly recovered and eaten, but an estimated 14% of cached seeds survived to 1 year, with seeds being re-cached up to 35 times. Though the caching behavior of the two species is undoubtedly different, it is possible that a similar proportion of seeds scatterhoarded by *A. africanus* can survive to germinate and establish. However, *A. africanus* is frequently hunted (Fa et al. 2005) and occurs at lower densities than the other rodent species in our study (personal observation from trail camera footage), and it is likely that only a small minority of seeds removed by rodents in this region can survive to germination. Therefore, while scatterhoarding of seeds can

promote tree recruitment (Jansen and Forget 2001), this mechanism of dispersal may be of secondary importance to widespread endozoochory by abundant medium- and large-bodied mammals of African forests. The strongest benefit of scatterhoarding by rodents in the region may be to decrease clumping of previously dispersed seeds and to increase dispersal distances of seeds dispersed abiotically, both of which can reduce seed mortality due to distance- and density-responsive natural enemies (Janzen 1971, Hammond and Brown 1998, Terborgh 2012).



**Figure 4: Movement and fate of telemetric thread tagged seeds. Line color represents the identity of the seed predator, symbol type represents the fate of the seed, and symbol size represents seed size (small symbols for small-seeded *Gambeya*, large symbols for large-seeded *Pentaclethra*). The location of each point represents a given seed's movement direction and distance (in meters) from its experimental plot, with all plots combined into one figure. The gray dashed lines indicate mean dispersal distance for *Gambeya* (small circle, radius=3.2 m) and *Pentaclethra* (large circle, radius=15.9 m). Seeds for which movement distance was less than 0.5 m (n=17) were excluded from the figure, and seeds recovered intact on the leaf litter are represented by a line with no end symbol. In cases where multiple seeds were moved to the same location by the same seed predator (i.e. *C. emini* taking multiple tagged seeds from a single station back to its burrow), the data are represented by thicker lines.**

Our study supports the notion that telemetric thread tags can provide unique information on seed movement and fate beyond traditional tagging methods (Hirsch et al. 2012). Seeds removed and larderhoarded by *C. emini* would have been difficult or

impossible to recover using traditional thread tags, due to the length and depth of their burrows. In these cases, the entirety of a traditional thread tag (typically ~ 60 cm long) would be dragged underground. Additionally, the long distance movements of seeds scatterhoarded by *A. africanus* (three of which were moved  $\geq 30$  m from experimental stations) would have precluded the recovery of these seeds by a visual search alone. Though other methods of seed tracking can provide greater quantities of data with less expense in both research costs and time, many of the seed movements observed in our study might have been missed. Ideally, telemetric tagging could be paired with the use of traditional thread tags to maximize both the quality and quantity of observations.

This study represents the first use of telemetric thread tags to assess seed fate in Central Africa, an important step in determining potential seed fate pathways and the influence of factors such as seed size and seed predator identity. We also present the first telemetric experimental evidence of larderhoarding and scatterhoarding by large-bodied rodents of the region. However, this study was limited to observing only the first steps of the seed fate process and represents a relatively small sample for two tree species. Our results support the conclusion that seed removal is often just the beginning of a process with many possible outcomes (Hulme 1998, Forget *et al.* 2005, Vander Wall *et al.* 2005, Jansen *et al.* 2012). Future research in the region and elsewhere should focus on longer-term monitoring of removed seeds to examine the full seed-to-seedling transition and quantitatively evaluate the role of seed predators in both predation and

dispersal. Understanding the role these animals play in both intact and ecologically eroded (*sensu* Poulsen *et al.* 2013) tropical forests will be particularly important in establishing baselines for ecosystem function and integrity, and protecting critical ecological processes in forests under threat.

### **3. Seed Traits, Not Density or Distance From Parent, Determine Seed Predation and Seedling Establishment in an Afrotropical Forest**

#### **3.1 Summary**

Seed predators drive patterns in seed mortality and plant reproductive success, and are posited to contribute to the maintenance of plant species diversity through several mechanisms. Seed density and distance from the parent tree are likely major determinants of seed mortality and seedling establishment, with widespread evidence of negative density dependence and spatially-restricted patterns of recruitment in Neotropical forests. These processes are little studied in Afrotropical forests, however, where generalist vertebrates seem to contribute more to seed mortality than do host-restricted invertebrates and fungi. Generalist vertebrate seed predators may nonetheless contribute to the maintenance of tree species diversity if they disproportionately consume seeds near to the parent tree and/or at high density, or if they preferentially consume common species. We assessed these mutually-compatible hypotheses through a series of enclosure experiments for ten tree species in a forest in northeastern Gabon, isolating the effects of seed predator body size and examining the roles of seed density and distance from the parent tree. Overall, vertebrates caused the greatest seed mortality, driving the loss of more seeds than all other mortality agents combined. Seed density did not significantly affect seedling establishment. Unexpectedly, seeds under fruiting conspecific trees had significantly lower removal and higher seedling

establishment than those under heterospecific or non-fruiting canopies. Seed removal by vertebrates was positively correlated with seed mass (with marginal significance), but had no relationship with adult tree density (a measure of species commonness). The proportions of seeds removed and established as seedlings varied widely between species, with a clear influence of seed traits. Species with seeds undesirable to vertebrates – for which invertebrates and fungi cause proportionally greater seed losses – may be more likely to exhibit spatially-restricted recruitment. Our results highlight an apparent divergence in patterns of seed mortality and seedling establishment between the Neotropics and the Afrotropics, and emphasize the need for further comparative study.

### **3.2 Introduction**

Seed predation is a prominent ecological force determining patterns of seed mortality and plant reproductive success (Janzen 1971, Crawley 1992, Hulme 1998). In tropical forests, distance- and density-responsive seed consumers may also contribute to the maintenance of high plant species diversity (Janzen 1970, Connell 1971). Mechanisms of distance- and density-dependence are not limited to the seed-to-seedling transition, though demographic filtering is often greatest at these early life stages (Terborgh 2012). Thus, seed density and distance from parent are likely major determinants of mortality, and are posited to drive patterns of seed predation and seedling establishment (Howe and Smallwood 1982, Hammond and Brown 1998).

The process of seed predation is little studied in Afrotropical forests. Though the research is limited, strong evidence for host-specificity and Janzen-Connell patterns of seed mortality is so far lacking (Clark et al. 2012), though there is some evidence of these patterns in seedling herbivory (Matthesius et al. 2011). Compared to Neotropical forests that house diverse and abundant invertebrates and fungi – the actors principally responsible for driving patterns of spatially-restricted recruitment (Terborgh 2012, Bagchi et al. 2014, Fricke et al. 2014) – Afrotropical forests are drier and feature lower species diversity of plants and most other taxa (Corlett and Primack 2011), which may result in a lower frequency and intensity of host-restricted natural enemy attack. Indeed, in one Afrotropical forest, seed losses to generalist rodents were more than 5-fold higher than those to invertebrates and fungi combined (Rosin and Poulsen 2016). Despite little quantitative contribution to seed predation overall, specialized natural enemies may nonetheless generate distance and density effects for seedling establishment, but such patterns have not yet been documented in Afrotropical forests.

Even in the absence of strong effects by host-restricted natural enemies, seed predation may still contribute to the maintenance of tree diversity through the actions of generalist seed predators. In Peru, Paine and Beck (2007) found that rodents preferentially removed common and large-seeded species from experimental plots, and hypothesized that such selective seed consumption may generate a rare-species advantage. In Borneo, Hautier et al. (2010) documented that small mammals

significantly reduced the survival of seeds under conspecific – but not heterospecific – adult trees, as well as in high – but not low – densities, thereby generating the requisite Janzen-Connell distance and density effects typical of more specialized seed predators. They suggested that small mammals maintain small home ranges and preferentially select local (conspecific) seeds, thereby acting in a functionally host-restricted manner (Hautier et al. 2010). Whether either or both of these diversity-maintaining mechanisms are operating consistently – and in other tropical forest localities – remains to be seen.

We assessed three mutually-compatible hypotheses in a forest in northeastern Gabon: 1) rodents are the dominant seed predators and can significantly reduce seedling establishment, 2) seed mortality by rodents and/or other biotic agents is greater for seeds under conspecific adult trees, and for seeds in high densities, and 3) rodents preferentially remove seeds from common and large-seeded species. To isolate the effects of different size classes of seed consumers, we used exclosures allowing selective seed access to a) all vertebrates, b) small vertebrates  $\leq 4$  kg (rodents), and c) no vertebrates. We utilized the seeds of 10 tree species across four seed pairing experiments, with both high and low density seed treatments in locations under a) a conspecific fruiting tree, b) a heterospecific fruiting tree, and c) a neutral non-fruiting location, and followed all seeds for 60 days to determine patterns of seed mortality and seedling establishment.

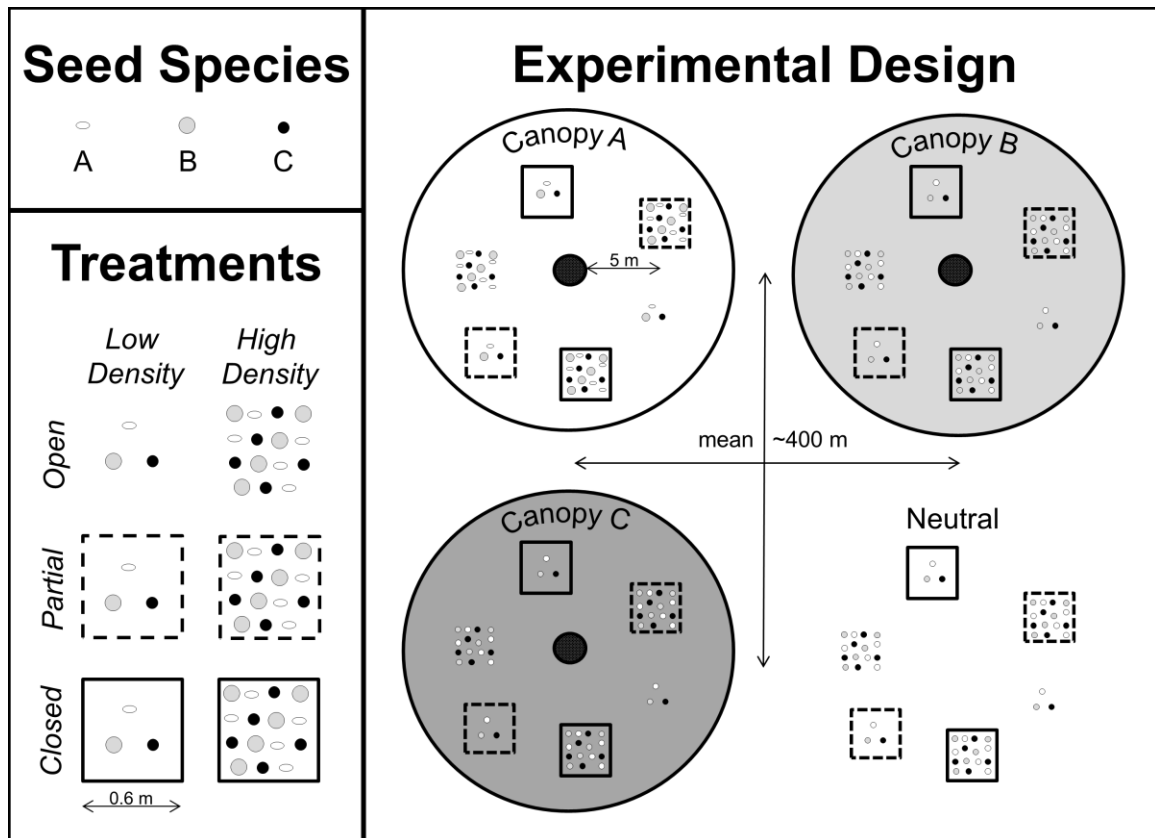
### **3.3 Methods**

#### **3.3.1 Study Site**

We conducted this study in the forest surrounding the Ipassa Research Station, in the Ogooué-Ivindo region of northeastern Gabon. The region is dominated by lowland forest, and receives approximately 1700 mm of rain annually, with two rainy seasons (September-December and March-June). Despite its protected status as part of Ivindo National Park, the Ipassa forest is occasionally hunted. A few species of game animals – including bay duikers (*Cephalophus dorsalis*) and red river hogs (*Potamochoerus porcus*) – have been reduced in abundance as a result (Okouyi et al. 2001, van Vliet et al. 2007). Nonetheless, the forest boasts high mammal diversity (Okouyi et al. 2002, Koerner et al. 2016) and an apparently intact small mammal community (Markham 2015).

#### **3.3.2 Experimental Design**

We established replicated seed exclosure experiments to assess the effects of a) seed consumer body size, b) seed density, and c) seed location on patterns of seed predation and seedling establishment for 10 tree species (Figure 5).



**Figure 5: Experimental design (based on Hautier et al. 2010).** Using two or three seed species (upper left panel), and six treatments with varying seed density (*Low* = 1 seed per species, *High* = 5 seeds per species) and vertebrate access (*Closed* = no access, *Partial* = rodent access, *Open* = all access; lower left panel), we established replicated experiments under one fruiting tree of each species, plus a random neutral non-fruiting location (with a mean distance of ~ 400 meters between nearest locations). We repeated this design for four consecutive experiments (establishing new locations for each experiment), using seeds from a total of 10 tree species.

To isolate the effects of seed consumer body size, we used three exclusion treatments: 1) *Open*, leaving seeds unprotected from predators, 2) *Partial*, excluding large but not small vertebrates from accessing seeds, and 3) *Closed*, excluding all vertebrates. For each treatment, we cleared approximately half the volume of leaf litter from a ground area of 0.6 m x 0.6 m to facilitate visual seed monitoring. To construct the

enclosures, we erected four 45 cm tall plastic-coated steel garden stakes to support galvanized 1.3 cm mesh hardware cloth walls and a roof, secured with zip ties. To exclude all vertebrates from the *Closed* enclosure, we folded the base of the hardware cloth flush with the soil and secured it with 15 cm lawn staples. To allow the terrestrial entry of small mammals in the *Partial* enclosure, we elevated the base of the hardware cloth 10 cm off the ground – this allowed for the entry of all rodents and other terrestrial mammals up to and including the African brush-tailed porcupine (*Atherurus africanus*; mass  $\leq 4$  kg), but excluded all larger mammals, including duikers (*Cephalophus spp.*), red river hogs (*Potamochoerus porcus*), and mandrills (*Mandrillus sphinx*). Terrestrial primates – mandrills, chimpanzees (*Pan troglodytes*), and gorillas (*Gorilla gorilla*) – could have reached under the elevated enclosures to access seeds, though we have no evidence that this occurred.

To assess the effects of seed density and location, we used a seed pairing approach modified from Hautier *et al.* (2010; Figure 5). We placed seeds of two or three tree species at both *Low* (1 seed per species) and *High* (5 seeds per species) density into each of the three enclosure types, creating six unique treatments of seed access and density. We established these treatments under one fruiting tree of each seed species and a random neutral non-fruiting location. We surveyed each location to ensure that no other fruiting trees were present within a ~30 m radius. The mean distance between nearest locations was ~ 400 m (range = 177 m to 794 m).

We repeated the experimental design for four consecutive experiments (establishing new locations for each experiment), using seeds from a total of 10 tree species (Table 1). We conducted each of these experiments during the active fruiting period of the species used, with experiments starting in September 2014 (Experimental Group 1; see Table 1), December 2014 (Experimental Group 2), February 2015 (Experimental Group 3), and March 2015 (Experimental Group 4). We selected species to encompass variation across several seed traits (size, diaspore type, and dispersal mode) as well as a range of adult tree abundance, from rare to common. Our focal species varied in seed mass 300-fold (from 0.1 g to ~30 g), spanned a range in seed coat hardness from very soft to hard, ranged in adult abundance 71-fold (from 0.3-29.4 stems/ha), and included four animal-dispersed, three wind-dispersed, and three gravity/ballistically-dispersed species.

**Table 4: Experimental groupings and characteristics of focal seeds. Seed hardness was determined manually according to the following categories: very soft (easily crushed with fingernail), soft (dented with fingernail), medium (dented by metal nail held by hand), hard (dented with metal nail and hammer), and very hard (difficult to dent with metal nail and hammer). Adult abundance was calculated as the number of stems  $\geq 10$  cm within 14 local 1-ha plots that included a total of 6140 stems (Poulsen, unpublished data).**

Exp. Group	Scientific Name	Family	Adult Abundance (stems/ha)	Seed Mass (g)	Seed Length (mm)	Seed Hardness	Diaspore Type	Dispersal Mode
1	<i>Pycnanthus angolensis</i>	Myristicaceae	0.6	1.4	18	medium	fleshy	animal
	<i>Pentaclethra macrophylla</i>	Fabaceae	1.8	29.4	64	hard	pod	ballistic/gravity
	<i>Pentaclethra eetveldeana</i>	Fabaceae	3.7	2.4	31	hard	pod	ballistic/gravity
2	<i>Cylicodiscus gabunensis</i>	Fabaceae	0.3	0.9	104	very soft	winged	wind
	<i>Pseudospondias microcarpa</i>	Anacardiaceae	0.9	0.9	19	hard	fleshy	animal
3	<i>Diospyros crassiflora</i>	Ebenaceae	6.1	18.1	47	medium	fleshy	animal
	<i>Scorodophloeus zenkeri</i>	Fabaceae	21.5	2.6	28	hard	pod	ballistic/gravity
	<i>Piptadeniastrum africanum</i>	Fabaceae	0.9	0.1	42	very soft	winged	wind
4	<i>Dacryodes buettneri</i>	Burseraceae	2.6	4.6	34	medium	fleshy	animal
	<i>Pterocarpus soyauxii</i>	Fabaceae	0.3	0.3	73	soft	winged	wind

We collected seeds from the ground beneath their parent canopies. Prior to seed sowing, we cleaned flesh off of fleshy-fruited seeds by hand or with a dull knife, and visually inspected all seeds, discarding seeds with any sign of fungal or arthropod damage. After placement, we assessed the condition of the seeds at days 15, 30, and 60, to allow sufficient time for the seeds to either establish as seedlings or die. We noted germination as the visible emergence of a shoot, and seed removal as the absence of the seed from the treatment area. We visually inspected all seeds that failed to germinate,

identifying the apparent agent of mortality when applicable: fungal spores indicated fungus, while larvae, bore holes, or hollowed seeds indicated invertebrates. We defined seedling establishment as the point at which the rooted living seedling had no seed endosperm remaining.

### **3.3.3 Statistical Analysis**

We used generalized linear models (GLMs) to model the relationships between the following variable pairs across all seed species: 1) the mean proportion of seeds removed and the mean proportion established as seedlings, 2) seed mass and the mean proportion of seeds removed, and 3) adult tree abundance and the mean proportion of seeds removed.

We used generalized linear mixed-effects models (GLMMs) with binomial error distributions to model seedling establishment (binary response: Established or Died) as a function of seed density (*Low* or *High*) and location (a proxy for dispersal, in which *Heterospecific* and *Neutral* treatments were lumped to represent dispersed seeds, while *Conspecific* treatments represented undispersed seeds), with seed species identity included as a random effect. Our first model included an interaction between seed density and location. Our second, simplified model included only fixed effects. Our third model assessed the three seed locations separately (*Conspecific* vs. *Heterospecific* vs. *Neutral*) to determine the significance of differences in establishment for each location separately, rather than lumping *Heterospecific* and *Neutral* locations together. We

followed the general recommendations for GLMMs outlined by Bolker et al. (2009), and performed all statistical analyses in R 3.2.3 (R Development Core Team 2015), using the lme4 package (Bates et al. 2015).

### **3.4 Results**

We assessed seed mortality and seedling establishment for a total of 648 seeds across 10 species, paired in four consecutive experiments (Table 4). Across all species in the *Open* treatments (n=216 seeds), 29% of seeds established as seedlings, 50% were removed by vertebrates, 10% killed by invertebrates, <1% killed by fungi, and 11% germinated but failed to establish for unknown reasons (Figure 6). In the *Partial* treatments (n=216 seeds), 29% of seeds established as seedlings, 46% were removed by vertebrates, 12% killed by invertebrates, 3% killed by fungi, and 10% germinated but failed to establish for unknown reasons. In the absence of vertebrates (*Closed* treatments, n=216 seeds), 64% of seeds established as seedlings, 19% were killed by invertebrates, 4% killed by fungi, and 13% germinated but failed to establish.

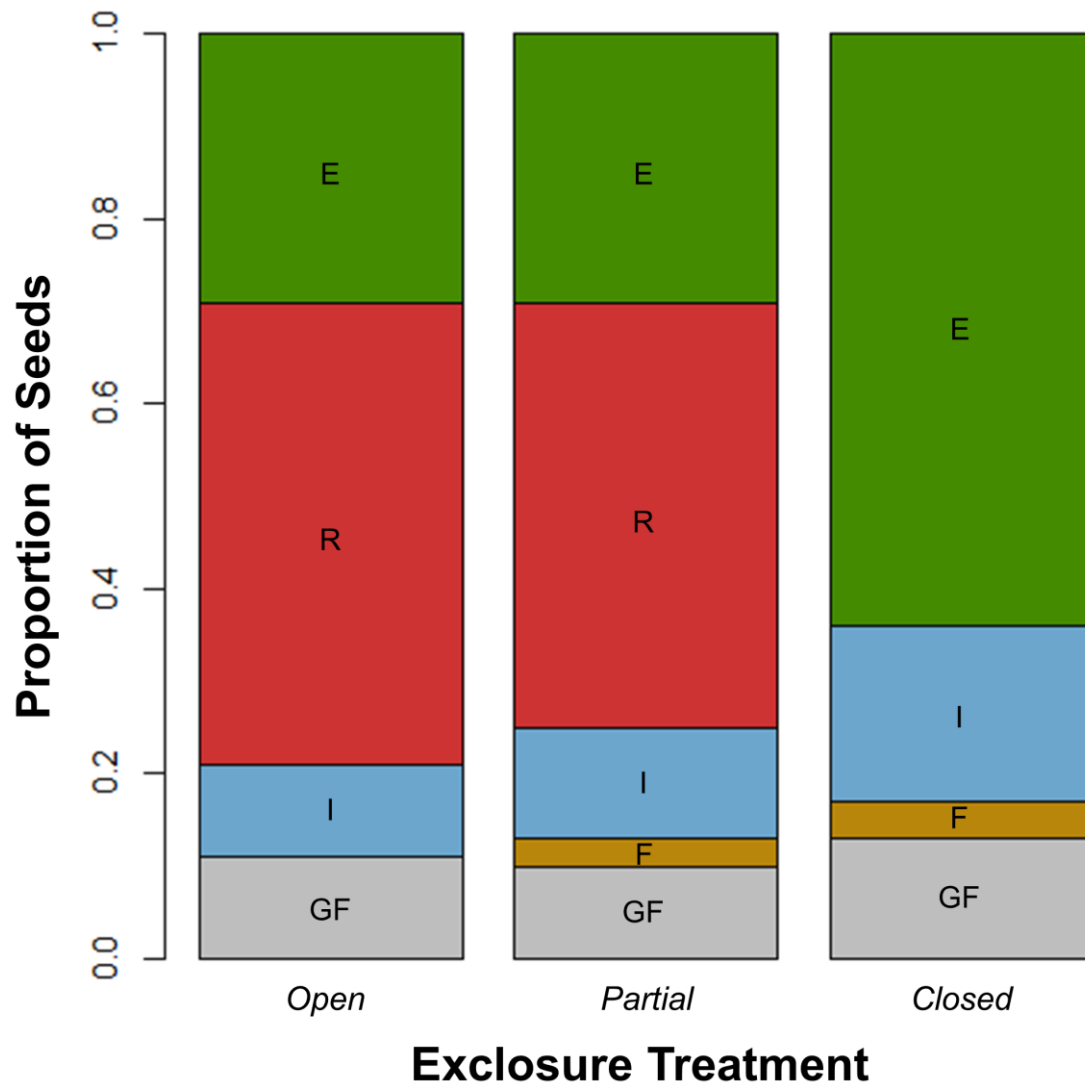


Figure 6: Fate of all seeds across three exclusion treatments: *Open* left seeds unprotected, *Partial* excluded large but not small vertebrates, and *Closed* excluded all vertebrates. Seed fate categories include: established (E), removed (R), invertebrate killed (I), fungus killed (F), and germinated but failed to establish for unknown reasons (GF).

Across all species and vertebrate access treatments, there was no significant difference in seedling establishment between seeds placed at *High* vs. *Low* densities

(GLMM:  $z=1.60$ ,  $df=647$ ,  $p=0.111$ ; Figure 7). Seed location significantly affected seedling establishment, with significantly lower seedling establishment among Heterospecific+Neutral (dispersed) seeds than among *Conspecific* (undispersed) seeds (GLMM:  $z=2.53$ ,  $df=647$ ,  $p=0.012$ ). Assessing the three seed locations separately, seedling establishment did not differ significantly between *Conspecific* and *Heterospecific* seeds (GLMM:  $z=-1.14$ ,  $df=647$ ,  $p=0.255$ ), but was significantly lower for *Neutral* seeds than *Conspecific* seeds (GLMM:  $z=-3.74$ ,  $df=647$ ,  $p<0.001$ ; Figure 7).

The proportions of seeds removed and established as seedlings varied widely among species (Figure 8). Overall, the proportion of seeds that established as seedlings in the *Open* and *Partial* treatments declined significantly with increasing seed removal (GLM:  $df=9$ ,  $p<0.001$ ). Seed removal ranged from 0% (*C. gabunensis*;  $n=36$  seeds) to 100% (*P. macrophylla*;  $n=48$  seeds), while seedling establishment ranged from 0% (*P. macrophylla*;  $n=48$  seeds) to 56% (*D. buettneri*;  $n=36$  seeds). In the absence of vertebrates (the *Closed* treatment), seedling establishment ranged from 33% (*S. zenkeri*;  $n=24$  seeds) to 96% (*P. macrophylla*;  $n=24$  seeds). The proportion of seeds removed (*Open* and *Partial* treatments) increased with increasing seed mass, though the relationship was only marginally significant (GLM:  $df=9$ ,  $p=0.081$ ). Seed removal had no relationship with adult tree abundance (GLM:  $df=9$ ,  $p=0.906$ ; Figure 8).

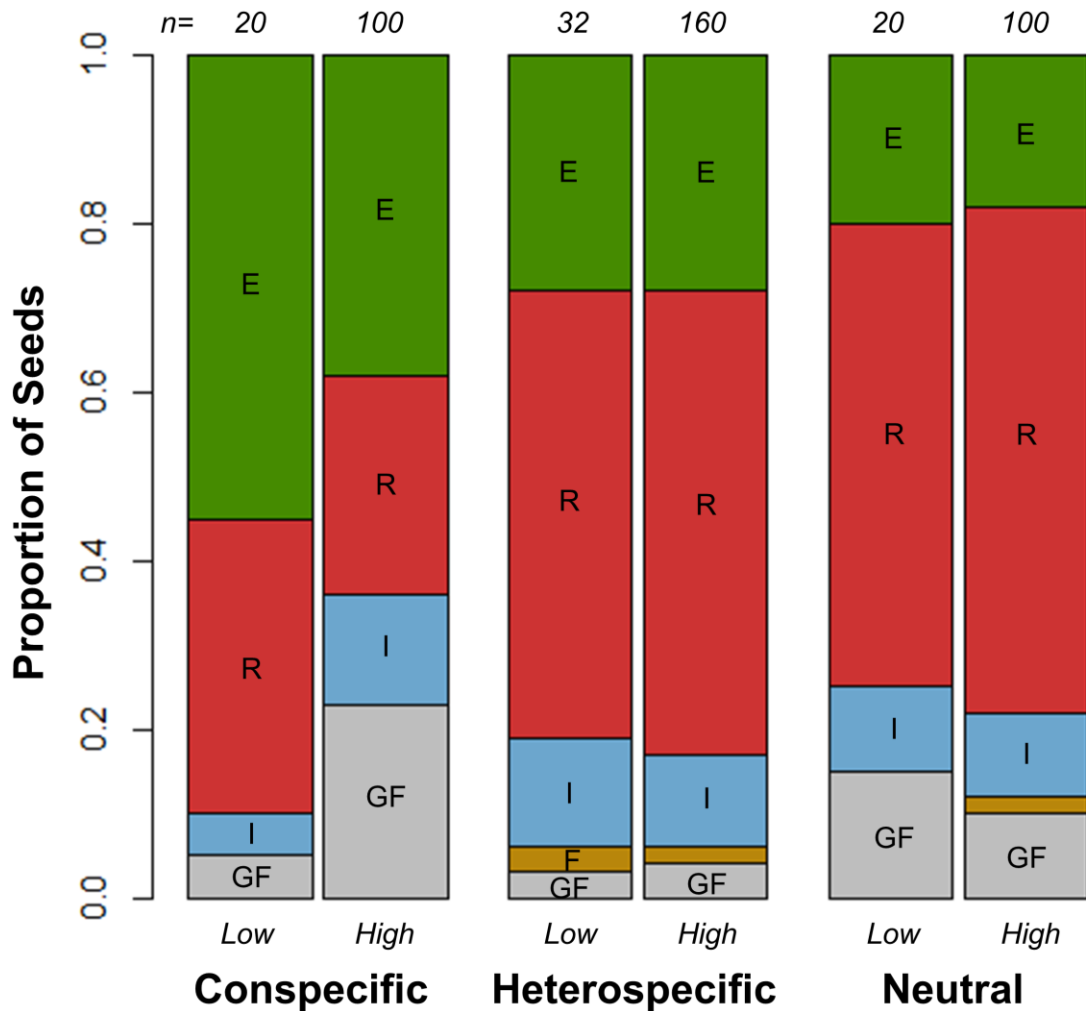


Figure 7: Fate of all seeds in the *Open* and *Partial* treatments (pooled together given the comparable fates of seeds in each; Figure 6) grouped by seed density (*Low*=1 seed, *High*=5 seeds) and location (beneath a *Conspecific* fruiting tree, beneath a *Heterospecific* fruiting tree, or in a random *Neutral* non-fruiting location). Fate categories include: E (established), R (removed), I (invertebrate killed), F (fungus killed) and GF (germinated but failed to establish for unknown reasons). Sample sizes are represented above each bar.

### 3.5 Discussion

Vertebrates caused the greatest overall seed mortality in our study, preying on more seeds than all other mortality agents combined (Figures 6, 7). Rates of seed removal were similar between the *Open* and *Partial* treatments (50% [n=216] and 46% [n=216], respectively), suggesting that rodents are the dominant seed predators in this system. Though our study directly measured seed removal, not seed predation, prior research indicates that the vast majority of seeds removed by vertebrates are killed (Rosin and Poulsen 2017). Rodent seed removal significantly reduced seedling establishment (Figure 6), resulting in 53% fewer established seedlings in their presence (30% of n=432 seeds, *Open* and *Partial* treatments) than in their absence (64% of n=216 seeds, *Closed* treatment). These results support our first hypothesis, and are consistent with studies that highlight the importance of vertebrate seed predators in Afrotropical forests (Clark et al. 2012, Rosin and Poulsen 2016).

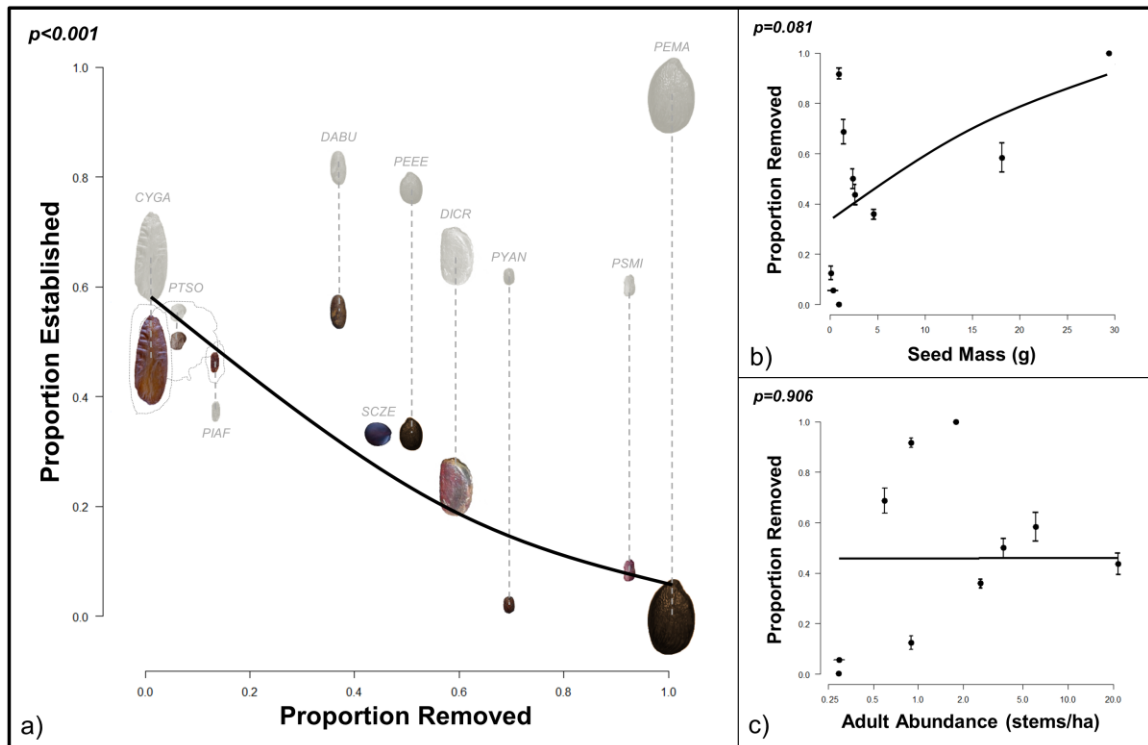
With no significant difference in seed removal or seedling establishment between seeds placed at *High* vs. *Low* densities (Figure 7), we found no support for seed density driving patterns of recruitment. However, we did not experiment with seeds at very high densities (eg Clark et al. 2013), and our two density treatments were located close to each other at all locations (Figure 5), so while seeds in the *Low* density treatments represented a lower nutritional reward and were likely less detectable than seeds in the *High* density treatment, they did not replicate long-distance dispersal in which a single

or few seeds are isolated from all others. How often such isolation of dispersed seeds actually occurs in nature is subject to debate, but most seeds are likely still subject to some aggregation via contagious dispersal (Howe 1989, Schupp et al. 2002, Clark et al. 2004). Additionally, the artificiality of the exclosures increases the conspicuousness of seeds within, even at very low densities.

Seed location (*Conspecific*, *Heterospecific*, or *Neutral*) did have a significant effect on seed removal and seedling establishment, but not as hypothesized. Using location as a proxy for dispersal and distance from the parent tree, dispersed seeds (those under *Heterospecific* and *Neutral* canopies) had significantly greater removal and lower establishment than undispersed seeds (those under *Conspecific* canopies; Figure 7). This trend was driven primarily by the significantly greater seed removal and lower seedling establishment of *Neutral* seeds than *Conspecific* seeds. Our results contrast with those of Hautier et al. (2010), in which rodents disproportionately reduced conspecific – but not heterospecific – seed mortality. Our results also fail to support the expectation of the Janzen-Connell hypothesis that seeds below the parent tree canopy face greater seed mortality and lower seedling establishment than those dispersed some distance away. High densities of seeds from natural seed rain may have partly satiated seed predators beneath fruiting trees, while seeds dispersed to neutral non-fruiting locations were more likely to be consumed given the potential local food scarcity; if an individual rodent's burrow and small home range does not include a fruiting tree at the time, any new seeds

that arrive are almost certain to be found and eaten, even those that are small and undesirable under more favorable conditions. Overall, these results do not support our hypothesis that seed mortality would be greater under conspecific trees. However, the full strength of Janzen-Connell conspecific mortality patterns extends well beyond the seed-to-seedling transition studied here (Swamy and Terborgh 2010, Terborgh 2012), and thus may not have been captured by our experimental design.

Seed removal was positively correlated with seed mass, but with only marginal significance (Figure 8). Large seeds provide a greater nutritional reward than small seeds, though within body size limits, smaller rodents generally consume smaller seeds, and larger rodents generally consume larger seeds (Rosin and Poulsen 2017). Seed removal did not vary strongly with adult tree abundance (Figure 8); though the mechanism of species maintenance by frequency-dependent seed selection is plausible (Paine and Beck 2007), we found no support for it in our study. Our results are limited to ten tree species, and therefore may not capture general trends. In a *post-hoc* analysis of a related seed predation dataset with larger sample sizes and a partly-overlapping but complementary suite of species (from Rosin and Poulsen 2016), we found no relationship between seed removal and adult tree abundance, mirroring the results of this study.



**Figure 8: The mean proportion of seeds that established vs. the mean proportion removed by vertebrates, both in the presence of vertebrates (*Partial* and *Open* treatments: colored seed images with GLM model curve) and in their absence (*Closed* treatment: gray seed images). The vertical dotted lines represent the degree to which vertebrate seed consumers reduced establishment for that species (note that establishment increased for PIAF and was equal for SCZE). Each seed species is identified by a four-letter code comprised of the first two letters of its genus and specific epithet. The wings of wind-dispersed seeds are outlined by gray dotted lines.**

**b) The mean proportion of seeds removed vs. seed mass (in grams). c) The mean proportion of seeds removed vs. adult tree abundance (stems  $\geq 10$  cm) / ha). All fitted curves represent GLM model results, with p-values displayed in the upper left corner of each pane.**

On an individual species basis, the proportions of seeds removed and established as seedlings varied widely (Figure 8). Vertebrates removed all *P. macrophylla* seeds – which are very large and dispersed ballistically – from *Partial* and *Open* treatments, resulting in zero seedling establishment, while 96% of seeds ( $n=24$ ) established as

seedlings when protected from vertebrates (*Closed* treatment; Figure 8). With such high seed losses to generalist vertebrates in all locations, strong patterns of spatially-restricted recruitment are unlikely. By contrast, all three wind-dispersed species (*C. gabunensis*, *P. africanum*, and *P. soyauxii*) had very low vertebrate removal in all locations, with greater proportional seed losses by invertebrates. The seeds of these species are small and papery, and are probably both inconspicuous and relatively undesirable to vertebrate seed consumers. The proportional seedling establishment of these species varied little with respect to vertebrate access (~50% in all treatments; Figure 8). It is possible that Janzen-Connell mortality patterns may occur for this subset of tree species with seeds that are undesirable to vertebrates – and thus face proportionally greater seed losses by more specialized natural enemies – though we have insufficient data to test that possibility explicitly.

Seed traits clearly affect patterns of seed removal and seedling establishment, and may determine recruitment differences among species, contributing more to the likelihood of success for an individual seed than do its density or distance from parent. Vertebrate seed predators – and their preferential selection of certain seed species over others – likely play a strong role in driving these patterns. It is difficult to establish an empirical basis for understanding seed preference among vertebrates, but it is likely a combination of the following factors: *seed size* (with larger seeds favored, within body size constraints; eg Mendoza and Dirzo 2007, Rosin and Poulsen 2017); *seed*

*conspicuousness* (related to size, but including characteristics of seed color, shape, and olfactory cues such as bits of fleshy fruit or seed deposition in dung; eg Janzen 1971, Hulme 1993); *physical defenses* (seed coat thickness and hardness, with thinner, softer seeds being more accessible to seed predators; eg Blate et al. 1998); *chemical defenses* (less defense means more palatable seeds, but this likely involves a trade-off with physical defenses; eg Janzen 1971); and *overall familiarity* (seed predators may develop a search image for common species, with adult abundance a good proxy for familiarity; eg Paine and Beck 2007). The divergence in seed traits between species likely reflects trade-offs in balancing traits that discourage seed predation with those that result in numerous and/or hardy seedlings.

Patterns of spatially-restricted recruitment documented in Neotropical forests have received little support in Afrotropical forests. This may be due to the relative dearth of ecological research, or it may be an indication that these patterns are actually less prominent. Given the many diverging biogeographical characteristics of forests across continents, there should be little expectation of absolute consistency among ecological processes that drive seed mortality and seedling establishment. Comparative studies are needed to address the many remaining questions of both ecological significance and conservation relevance.

## **4. Hunting-Induced Defaunation Drives Increased Seed Predation and Decreased Seedling Establishment of Commercially Important Tree Species in an Afrotropical Forest**

### **4.1 Summary**

Human hunting is widespread in tropical forests and can substantially alter the plant-animal interactions that drive tree recruitment. Seed predation is a strong determinant of plant reproductive success, but it remains unclear how defaunation modifies this process. We examined the effects of hunting-induced defaunation on seed predation and seedling establishment, using replicated exclosure treatments at six sites across a defaunation gradient in northeastern Gabon. We monitored 5580 seeds of eight commercially important tree species that varied in seed traits such as size and dispersal mode. Rodents caused the greatest seed mortality for all species, removing ~60% of accessible seeds. In comparison, invertebrates and fungi together caused just 6% of seed mortality. With protection from rodents, more than twice as many seeds established as seedlings, demonstrating that vertebrate seed predation was a strong filter on recruitment. With increasing defaunation, the proportion of seeds removed by rodents increased significantly, and seedling establishment decreased significantly for most species. In heavily defaunated sites, with the lowest abundances of large mammals, seed removal by rodents increased by 63% and seedling establishment decreased by 42% compared to sites with intact fauna. Diminished seedling establishment is likely to

reduce the regeneration of many tree species – including commercially important ones – in hunted forests, with detrimental economic consequences. In turn, declines in timber regeneration may increase the likelihood that selectively logged forests are converted to non-forest land uses with little conservation value. Appropriate management could preclude these outcomes, to the benefit of both wildlife and natural timber regeneration.

## **4.2 Introduction**

The ecological processes facilitated by wildlife are increasingly recognized as central to tropical forest tree recruitment. Human hunting disrupts these interactions when it causes defaunation of larger species, resulting in trophic cascades that can reduce plant diversity (Harrison et al. 2013, Camargo-Sanabria et al. 2014) and carbon storage (Poulsen et al. 2013, Kurten et al. 2015, Osuri et al. 2016), and may be detrimental to the regeneration of commercially important timber species (Rosin 2014). As hunting is widespread in timber concessions (Robinson et al. 1999, Auzel and Wilkie 2000, Fimbel et al. 2001) and can affect animal abundance more strongly than the direct effects of logging (van Vliet and Nasi 2008, Poulsen et al. 2011, Bello et al. 2015), understanding the consequences of defaunation is a priority for both forestry and conservation. Most studies of defaunation have focused on the reduction of large-bodied seed dispersers and the loss or modification of their services (eg Terborgh et al. 2008, Brodie et al. 2009, Beaune et al. 2013). Other plant-animal interactions have received substantially less

attention, and large gaps remain in our understanding of the consequences of defaunation for tree recruitment.

Seed predators play a crucial role in determining plant reproductive success and species coexistence, by shaping spatial and temporal patterns of seed mortality (Janzen 1971, Crawley 1992, Hulme 1998, Paine and Beck 2007). Mammalian seed predators, particularly rodents, are often implicated with causing the greatest seed mortality overall (Hulme 1998, DeMattia et al. 2004, Notman & Villegas 2005). Because changes in mammal composition and abundance can affect seed and seedling predation (DeSteven and Putz 1984, Sork 1987, Asquith et al. 1997), hunting may alter patterns of tree recruitment in defaunated forests, but the effects are not clear. Some studies posit that higher abundances of rodents in forests without large mammals increase levels of seed predation, but only for small-seeded trees, while large-seeded trees benefit from decreased seed predation by large-bodied vertebrates (Roldán and Simonetti 2001, Beckman and Muller-Landau 2007, Dirzo et al. 2007). In contrast, Asquith *et al.* (1997) and Galetti *et al.* (2015a) documented increased seed predation for medium and large-seeded tree species at sites where only rodents remained of the terrestrial mammalian herbivore/granivore community. With the studies to date limited to a few species and sites in the Neotropics, it is difficult to determine: a) whether these trends are generalizable, or represent site-specific or species-specific cases; b) whether these effects may be correlated with seed traits; and c) whether changes in the strength of seed

predation occur incrementally or only after some defaunation threshold has been reached.

Hunting may affect the strength of seed predation for many plant species, though our understanding of this process is limited, especially in Central Africa. There is some evidence that vertebrate seed and seedling predation are strong determinants of tree recruitment in the region (Clark et al. 2012). However, the importance of seed traits and the role of the different taxa of seed predators have yet to be determined, both for intact and anthropogenically disturbed forests. Such studies are rare, given the challenges of quantifying wildlife abundance and composition and establishing manipulative field experiments across a large geographic area. Ultimately, the effects of defaunation on seed predation may depend on the relative importance of the different taxa of seed predators, with little to no effect if invertebrates or fungi are greater seed mortality agents than rodents and other vertebrates.

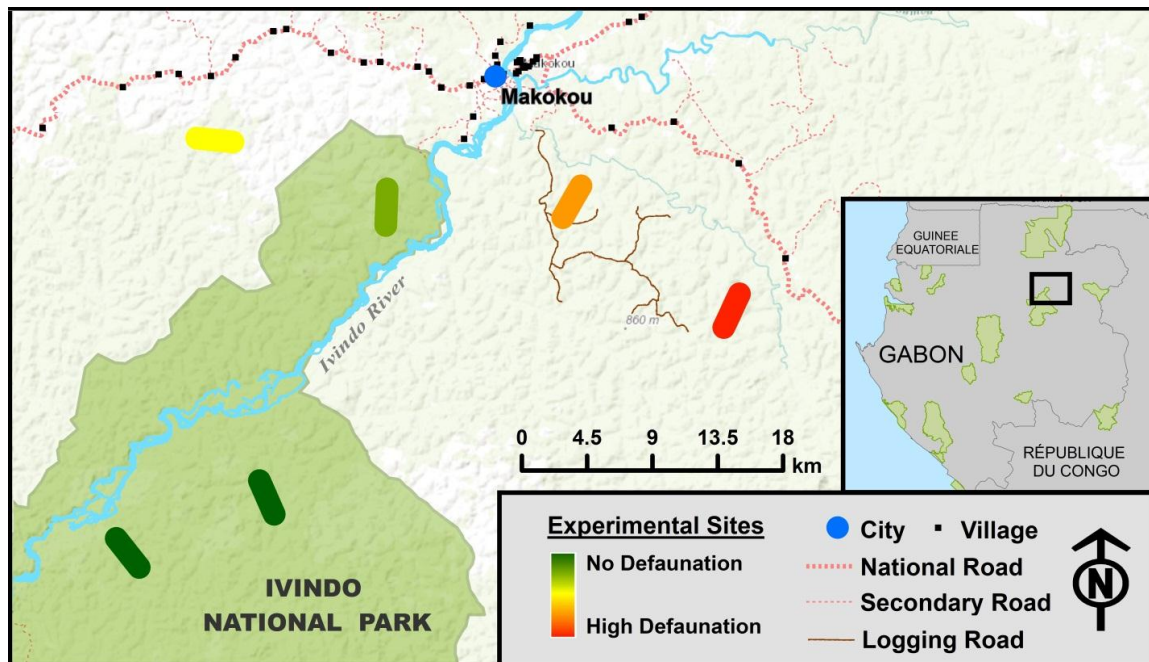
We took advantage of a known gradient in animal abundance and composition in northeastern Gabon to determine whether hunting-induced defaunation affects seed predation and seedling establishment of tropical forest trees. We selected eight common tree species that vary across seed traits such as size and dispersal mode, to determine the role of seed traits in removal and predation. We hypothesized that increasing defaunation would be positively correlated with seed removal by rodents, particularly for small and medium-sized seeds, resulting in decreased seedling establishment for all

but the largest seed species. We focused our study on tree species that are commercially important, to assess both the ecological and potential economic consequences of hunting-induced defaunation for seed predation and seedling recruitment.

## **4.3 Methods**

### **4.3.1 Study Area and Site Selection**

We conducted this study in the Ogooué-Ivindo province of northeastern Gabon. This region is dominated by lowland forest, and receives approximately 1700 mm of rain annually, with two rainy seasons (September-December and March-June). The study area includes the northern section of Ivindo National Park, the town of Makokou and surrounding villages, and two active logging concessions, which together form a roughly 2170 km<sup>2</sup> landscape with high heterogeneity in animal abundance and composition (Figure 1). Koerner *et al.* (2016) quantified wildlife community composition and abundance in the area using repeated surveys of 24 randomly-located 2-km transects over a period of 12 months. Their study demonstrated a 30-km gradient in defaunation, with declining diversity and relative abundance of large mammals near villages compared to the relatively intact forests of the Ivindo National Park, far from human settlements.



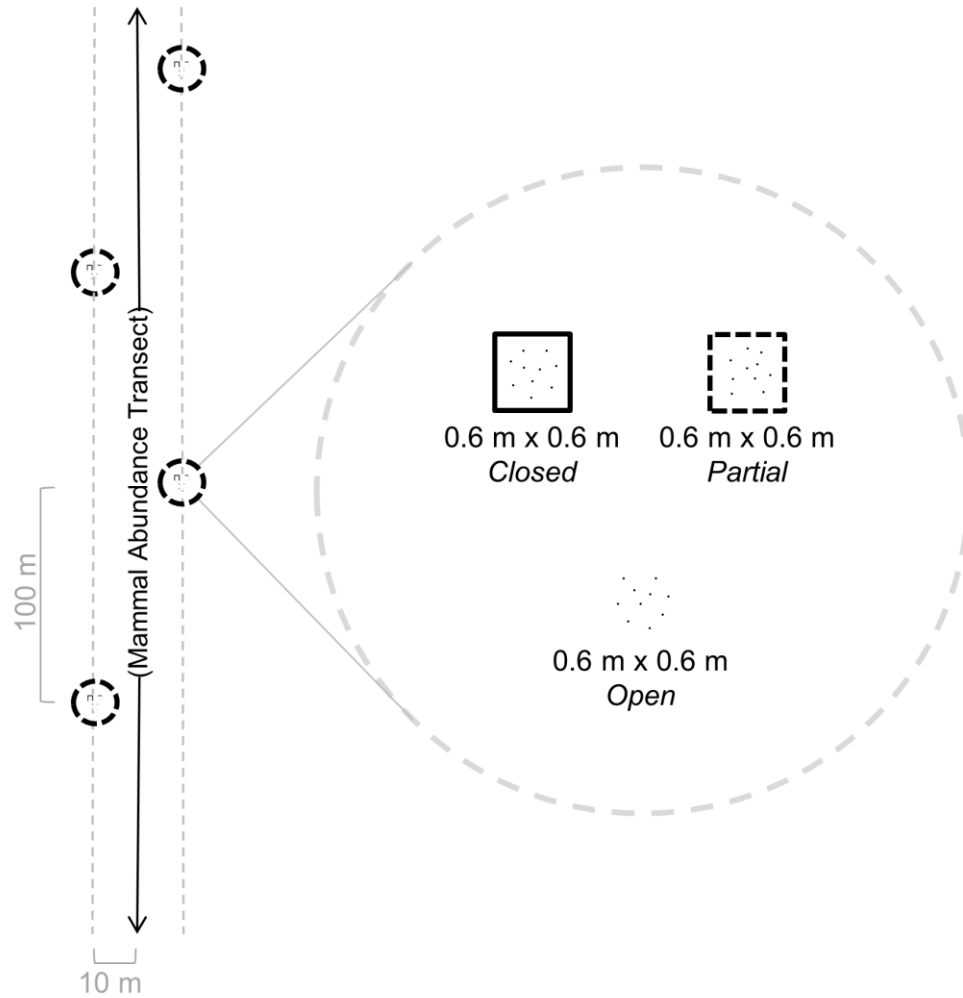
**Figure 9: Map of the study area (modified with permission from Koerner *et al.* 2016, with the six experimental sites depicted according to their defaunation score, ranging from 0 (no defaunation) to 1 (high defaunation). The inset map shows the location of the study area within Central Africa.**

Within this known defaunation gradient, we selected six of the 24 sites for our seed predation experiment. We selected sites to encompass the full gradient of mammal composition and abundance, including two protected nonhunted sites in the Park, a protected but occasionally hunted site in the buffer zone of the Park, an unprotected hunted site with minor selective timber extraction near a small village, and two hunted sites in an active selective logging concession (Figure 9). The distance between a site and its nearest neighbor ranged from 6.8 km to 13.5 km, with 49.5 km separating the two sites located farthest apart.

### 4.3.2 Seed Predation Treatments and Experimental Design

We quantified rates of seed predation using four enclosure replicates at each of our six sites along the defaunation gradient. A single replicate consisted of 10 scattered seeds of a single tree species in each of three treatments: 1) *Open*, leaving seeds unprotected from predators, 2) *Partial*, excluding large but not small vertebrates from accessing seeds, and 3) *Closed*, excluding all vertebrates (Figure 10). For each treatment, we cleared approximately half the volume of leaf litter from a ground area of 0.6 m x 0.6 m to facilitate visual seed monitoring. To construct the enclosures, we erected four 45 cm tall plastic-coated steel garden stakes to support galvanized 1.3 cm mesh hardware cloth walls and a roof, secured with zip ties. To exclude all vertebrates from the *Closed* enclosure, we folded the base of the hardware cloth flush with the soil and secured it with 15 cm lawn staples. To allow the terrestrial entry of small mammals in the *Partial* enclosure, we elevated the base of the hardware cloth 10 cm off the ground – this allowed for the entry of all rodents and other terrestrial mammals up to and including the African brush-tailed porcupine (*Atherurus africanus*; mass  $\leq$  4 kg), but excluded all larger mammals, including duikers (*Cephalophus spp.*), red river hogs (*Potamochoerus porcus*), and mandrills (*Mandrillus sphinx*). Terrestrial primates – mandrills, chimpanzees (*Pan troglodytes*), and gorillas (*Gorilla gorilla*) – were excluded from the *Partial* enclosures based on size but may have had the ability to reach under the elevated enclosures to access seeds if desired, though we have no evidence that this occurred. We established

all replicates 10 m to the right or left of the transect line and separated them by 100 m from each other.



**Figure 10: Seed predation experimental design, featuring four replicates (dashed circles) of three enclosure treatments, each with 10 scattered seeds of a single tree species. The *Open* treatment left seeds unprotected, the *Partial* treatment excluded large but not small vertebrates from accessing seeds, and the *Closed* treatment excluded all vertebrates. This design was repeated for eight seed species at each of six sites across a gradient of defaunation.**

We quantified seed predation for eight tree species: *Antrokyon klaineana*, *Aucoumea klaineana*, *Dacryodes buettneri*, *Gambeya lacourtiana*, *Lophira alata*, *Pentaclethra macrophylla*, *Piptadeniastrum africanum*, and *Pycnanthus angolensis* (Table 5). We selected these species based on the following criteria: a) they were available in sufficient quantities (with a minimum of three reproductive adult trees producing a collective minimum of 720 viable seeds); and b) they were commercially important, as known timber tree species (Mark et al. 2014). Among the tree species that met these two criteria, we chose species whose seeds varied across several plant functional traits, including seed size and hardness, diaspore type, and dispersal mode. Our focal species varied in seed mass 300-fold (from 0.1 g to 30 g), spanned a range in seed coat hardness from very soft to very hard, and included four animal-dispersed, three wind-dispersed, and one gravity/ballistically-dispersed species (Table 5). For each seed species, we collected and mixed seeds from a minimum of three trees. Prior to seed sowing, we cleaned any flesh off the seeds by hand or with a dull knife, and visually inspected each seed, discarding seeds with any sign of fungal or arthropod damage.

**Table 5: Focal tree species and their seed characteristics. Seed hardness was determined manually according to the following categories: very soft (easily crushed with fingernail), soft (can be dented with fingernail), medium (can be dented by metal nail held by hand), hard (can be dented with metal nail and hammer), and very hard (difficult to dent with metal nail and hammer). \* 1.7 g refers to mass of stone containing 4-5 seeds, <0.1 g refers to mass of each individual endosperm**

Scientific Name	Family	Seed Mass (g)	Seed Length (mm)	Seed Hardness	Diaspore Type	Dispersal Mode
<i>Antrokaryon klaineum</i>	Anacardiaceae	1.7/<0.1*	21	very hard	fleshy	animal
<i>Aucoumea klaineana</i>	Burseraceae	0.1	32	soft	winged	wind
<i>Dacryodes buettneri</i>	Burseraceae	4.6	34	medium	fleshy	animal
<i>Gambeya lacourtiana</i>	Sapotaceae	2.8	29	hard	fleshy	animal
<i>Lophira alata</i>	Ochnaceae	1.7	33	soft	winged	wind
<i>Pentaclethra macrophylla</i>	Fabaceae	29.4	64	hard	pod	ballistic/gravity
<i>Piptadeniastrum africanum</i>	Fabaceae	0.1	12	very soft	winged	wind
<i>Pycnanthus angolensis</i>	Myristicaceae	1.4	18	medium	fleshy	animal

After seed placement, we checked the experimental replicates monthly. We noted germination as the visible emergence of a shoot, and removal as the absence of the seed from the treatment area. For seeds that failed to germinate within one month of the first instance of germination in that replicate, we visually inspected seeds and identified the apparent agent of mortality when applicable: fungal spores indicated fungus, while larvae, bore holes, or hollowed seeds indicated invertebrates. We concluded each experiment after all seeds had established as seedlings (with no seed endosperm remaining), or had been removed or killed. As seed availability varied seasonally with fruiting phenology, we established new enclosure treatments for additional species over the course of a year.

### 4.3.3 Data Analysis

To evaluate the strength of seed predation in relation to the degree of defaunation, we developed an index of defaunation for our sites. From the wildlife data collected along transects, Koerner *et al.* (2016) calculated mammal species richness, evenness, and Shannon-Weiner diversity values for each transect, and used non-metric multidimensional scaling (NMDS) to represent transects in multidimensional space according to their similarity in these metrics. The NMDS axis scores correlated strongly with observed hunting signs along each transect. To create an index of mammalian defaunation, we re-scaled the calculated NMDS values to range from 0 (no defaunation) to 1 (high defaunation) across our sites, assigning a “defaunation score” for each site.

To assess the strength of seed predation across the defaunation gradient, we fitted generalized linear models (GLMs) to individually evaluate the number of seeds with a given fate (establishment, vertebrate removal, invertebrate mortality, and fungus mortality) as a function of the total number of seeds scattered. We included the enclosure treatment type and defaunation score (by site) as explanatory variables. We initially fit all models with a binomial error distribution, but re-fit all models with a quasibinomial error distribution to account for overdispersion. We used linear regression to graphically represent the relationship between defaunation and each seed fate category. We also used linear regression models to represent the effects of defaunation on seed removal for each species individually, but we replaced the linear

model with a polynomial one if the Akaike Information Criterion (AIC) value was  $\geq 3$  points lower. We performed all statistical analyses in R 3.2.3 (R Development Core Team 2015).

#### **4.4 Results**

We quantified seed predation on a total of 5580 seeds of eight species. Across all sites and species in the *Open* treatment (n=1860 seeds), 25% of seeds established as seedlings, 62% were removed by vertebrates, 5% killed by invertebrates, 1% killed by fungi, and 7% germinated but failed to establish for unknown reasons (Figure 11). In the *Partial* treatment (n=1860 seeds), 25% of seeds established as seedlings, 58% were removed by vertebrates, 8% killed by invertebrates, 1% killed by fungi, and 8% germinated but failed to establish for unknown reasons. In the absence of vertebrates (*Closed* treatment, n= 1860 seeds), 55% of seeds established as seedlings, 27% were killed by invertebrates, 5% killed by fungi, and 13% germinated but failed to establish.

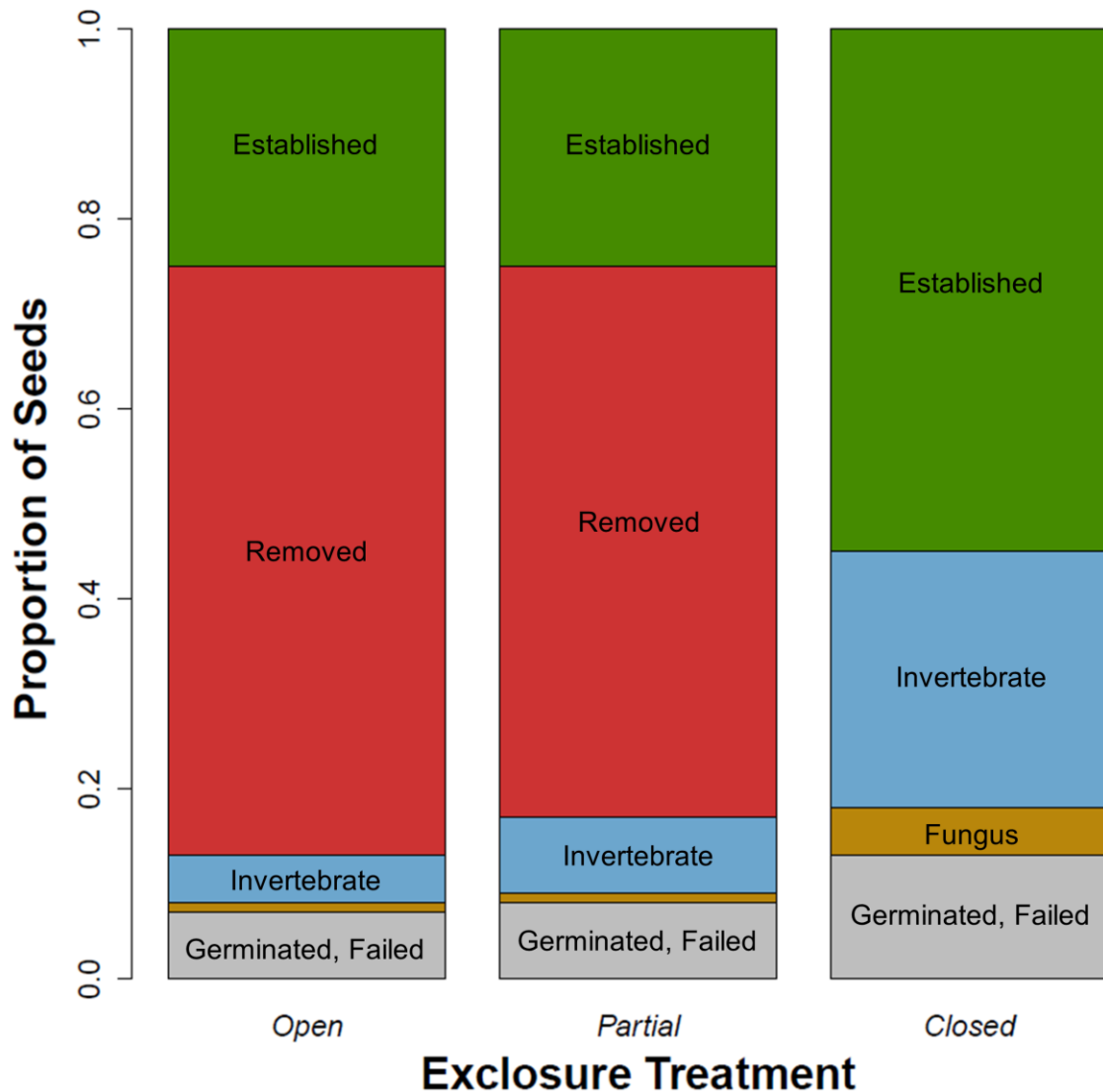
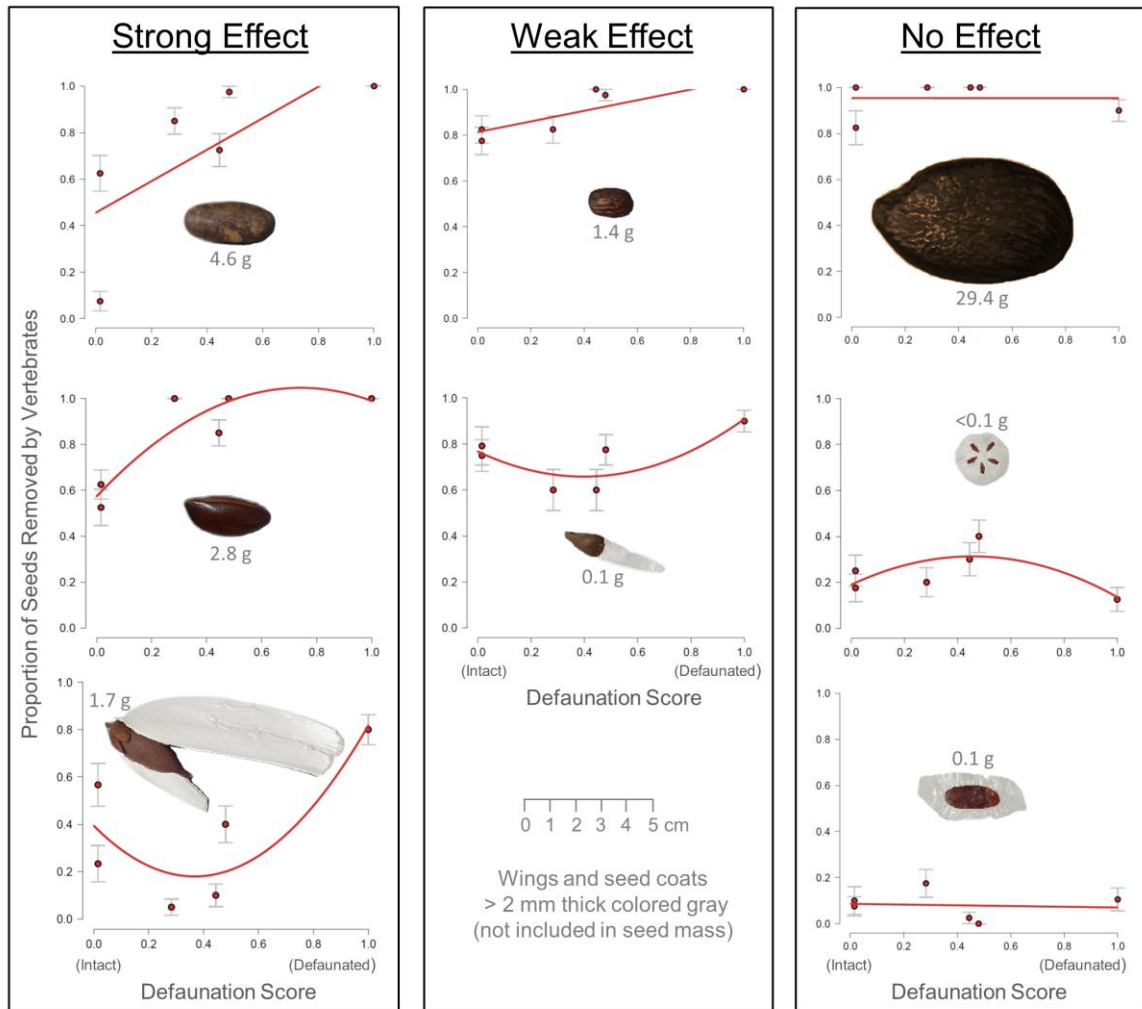


Figure 11: Fate of all seeds across three exclosure treatments: *Open* left seeds unprotected, *Partial* excluded large but not small vertebrates, and *Closed* excluded all vertebrates. Seed fate categories include: established (seedling with no seed endosperm remaining), removed, invertebrate killed, fungus killed, and germinated but failed to establish for unknown reasons. Removal from the *Open* and *Partial* treatments was approximately equal, attributable primarily to rodents, and seedling establishment was more than twice as high with their exclusion.

With increasing defaunation, the proportion of seeds removed by vertebrates increased significantly (Figure 13; seed removal GLM:  $df=560$ ,  $p<0.001$ ); this pattern can be attributed primarily to rodents, as the overall seed removal rates for the *Partial* (small mammals only) and *Open* (all mammals) treatments were nearly equal (58% and 62%, respectively; Figure 13). This trend held true for five of the eight species individually, while the three exceptions, *Pentaclethra macrophylla*, *Antrokyon klaineum*, and *Piptadeniastrum africanum*, showed no significant difference in removal across the defaunation gradient (Figure 12). *P. macrophylla* was removed at very high rates across all sites (90% of 440 seeds were removed from the *Partial* and *Open* treatments), while *A. klaineum* and *P. africanum* had low removal rates across all sites (29% and 13% of 480 seeds were removed, respectively).



**Figure 12: Strength of defaunation effect on vertebrate removal of the eight focal tree species individually, indicating the degree to which seed removal from the *Open* treatment increased (or was unchanged) with increasing defaunation. Species with a strong effect include (top to bottom): *Dacryodes buettneri*, *Gambeya lacourtiana*, and *Lophira alata*. Species with a weak effect include (top to bottom): *Pycnanthus angolensis* and *Aucoumea klaineana*. Species with no effect include (top to bottom): *Pentaclethra macrophylla*, *Antrokaryon klaineianum*, and *Piptadeniastrum africanum*. See Methods for a description of regression model selection.**

In contrast to the trend in vertebrate seed removal, the proportion of seeds killed by invertebrates and fungi did not change significantly across the defaunation gradient (invertebrate GLM:  $df=560$ ,  $p=0.315$ ; fungus GLM:  $df=560$ ,  $p=0.066$ ; Table 6).

**Table 6: Results from generalized linear models (GLMs) evaluating the number of seeds with a given fate (vertebrate removal, invertebrate mortality, fungus mortality, or establishment) as a function of the total number of seeds scattered. Coefficient outputs represent the comparison of the *Closed* enclosure treatment to the *Open* and *Partial* treatments, along with the influence of increasing defaunation.**

Vertebrate Removal				
	Estimate	SE	<i>t</i>	<i>p</i>
(Intercept)	-5.1464	0.6338	-8.12	3.01E-15
Open treatment	5.2465	0.6327	8.292	8.38E-16
Partial treatment	5.0946	0.6322	8.059	4.72E-15
Defaunation	1.0631	0.2652	4.009	6.93E-05

Invertebrate Seed Mortality				
	Estimate	SE	<i>t</i>	<i>p</i>
(Intercept)	-0.9498	0.1259	-7.545	1.85E-13
Open treatment	-1.7457	0.2016	-8.661	< 2e-16
Partial treatment	-1.423	0.1812	-7.852	2.11E-14
Defaunation	-0.2234	0.2224	-1.005	0.315

Fungal Seed Mortality				
	Estimate	SE	<i>t</i>	<i>p</i>
(Intercept)	-3.3582	0.2495	-13.459	< 2e-16
Open treatment	-1.6368	0.4046	-4.045	5.97E-05
Partial treatment	-1.6425	0.4046	-4.059	5.63E-05
Defaunation	0.7304	0.3965	1.842	0.066

Seedling Establishment				
	Estimate	SE	<i>t</i>	<i>p</i>
(Intercept)	-0.02073	0.12276	-0.169	0.865974
Open treatment	-1.39826	0.16287	-8.585	< 2e-16
Partial treatment	-1.34783	0.16083	-8.38	4.32E-16
Defaunation	-0.80102	0.20774	-3.856	0.000129

Corresponding to increased seed removal by rodents, the proportion of seeds that established as seedlings decreased significantly with increasing defaunation (Figure 13; seedling establishment GLM:  $df=560$ ,  $p<0.001$ ). This overall trend held true for five of the eight species individually. As with the proportions of seeds removed, the establishment of *Pentaclethra macrophylla*, *Antrokyon klaineum*, and *Piptadeniastrum africanum* did not change along the defaunation gradient: with no change in seed removal for these species, there was no change in seedling establishment.

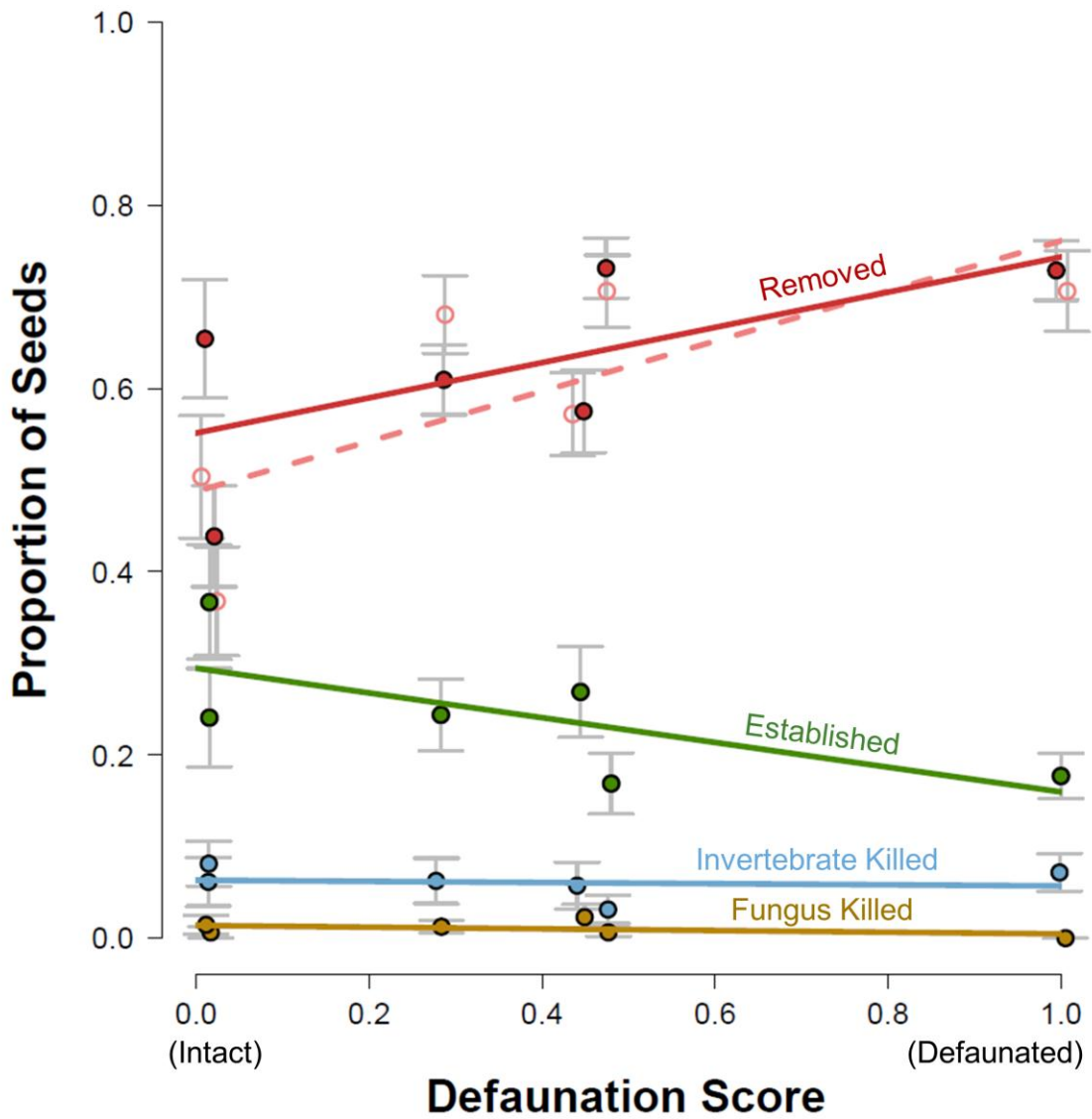


Figure 13: Fate of *Open* treatment seeds (all species) across the mammalian defaunation gradient, labeled and colored by fate category (see Figure 11); the dotted line represents seed removal from the *Partial* treatment, attributable to rodents. With increasing defaunation (values closer to 1), seed removal by rodents increased, seedling establishment decreased, and the proportion of seeds killed by invertebrates and fungi remained approximately the same.

## **4.5 Discussion**

### **4.5.1 Role of Vertebrates in Seed Predation and Seedling Establishment**

Vertebrates drove the loss of more seeds than all other mortality factors combined, for each tree species individually and for all eight species together. Rodents in particular removed approximately 60% of all accessible seeds, making them the most important actors in the seed predation process in this study. For seeds accessible to rodents, invertebrates and fungi were much less prominent mortality agents, killing just 6% of seeds combined. Though invertebrates and fungi can disproportionately generate distance- and density-responsive patterns of seed mortality (Hammond & Brown 1998, Terborgh 2012, Bagchi et al. 2014, Fricke et al. 2014; but see Hautier et al. 2010), our results support the assertion that mammalian seed predators, particularly rodents, cause the greatest seed mortality overall (Terborgh et al. 1993, DeMattia et al. 2004, Notman and Villegas 2005), at least for seeds not located under reproductive conspecific trees. Among the terrestrial rodent seed consumers in our study region (small Murid rats and mice [mass  $\leq 170$  g], Emin's giant pouched rat [*Cricetomys emini*; mass  $\approx 1200$  g]), and the African brush-tailed porcupine [*Atherurus africanus*; mass  $\approx 2750$  g], one species (*A. africanus*) is known to disperse intact scatterhoarded seeds, though the vast majority of seeds removed by the rodent community are larderhoarded or consumed on the spot (Rosin and Poulsen 2017). Based on this prior seed fate research, we suspect that *C. emini* is responsible for removing the majority of medium and large seeds in this study,

while smaller Murid rats and mice removed the smaller seeds, none of which were likely to have survived.

Given protection from rodents, more than twice as many seeds established as seedlings (55% vs. 25%; Figure 11), demonstrating that vertebrate seed predation was a strong filter on recruitment in our study. Rodents can clearly reduce the population of seeds that survive to germination and establishment, but whether seed predation affects plant demography at the community level has been subject to some debate. Seed predation may have little effect if establishment is limited by the availability of suitable microsites rather than the number of surviving seeds (Crawley 1992, Hulme 1998), though this appears to be uncommon in most plant communities (Hulme 2002). Indeed, in one study in the Congo Basin, seed limitation induced by vertebrate consumption was the strongest determinant of seedling recruitment (Clark et al. 2012). Rodents may be especially strong drivers of recruitment (Kasenene 1980, Asquith et al. 1997, Dirzo et al. 2007), reducing seedling density and potentially increasing seedling species richness by favoring common and large-seeded species, thus generating a rare-species advantage (Paine and Beck 2007). Though we did not assess the role of rodents or other vertebrates on long-term seedling survival or plant community composition, our results highlight the importance of rodent seed consumers in shaping the seed-to-seedling transition stage of a diverse group of tree species.

#### 4.5.2 Effects of Defaunation

Increasing defaunation drove increased seed removal and decreased seedling establishment in a consistent and unidirectional manner (Figure 13). Across the regional extremes of defaunation for our study – from the two sites in Ivindo National Park to the two hunted and logged concession sites – rodent seed removal increased by 63% and seedling establishment decreased by 42%. Our results indicate that hunting, logging, or a combination of the two can generate substantial changes in the rodent community and the ecological processes they facilitate.

The specific mechanism(s) by which defaunation alters tropical forest rodent communities is not well established. Hunters preferentially harvest large mammals rather than small ones (Fa et al. 2005, Poulsen et al. 2009), potentially releasing rodents from competition for resources with larger mammals and allowing them to expand their dietary breadth (Galetti et al. 2015c). The combination of uneven harvest rates of wildlife species and compensatory ecological responses may lead to increased rodent abundance with hunting, despite a decline in total animal biomass (Happold 1995, Phillips 1997, Wright 2003, Laurance et al. 2006, Poulsen et al. 2011, Effiom et al. 2013, Galetti et al. 2015c). For our region in Gabon, two recent studies have documented community-level increases in rodent biomass with hunting pressure (Markham 2015, Koerner et al. 2016). Logging itself may also benefit rodents, as the creation of new canopy gaps and expanded road margins increases vegetation density (Struhsaker 1997,

Malcolm and Ray 2000). As two of our most defaunated sites are within logging concessions, and a third has been subjected to some selective timber harvest by local villagers, it is possible that changes to the seed predation process presented here are a consequence of both pressures, rather than hunting alone. However, Koerner *et al.* (2016) examined the trends in mammal abundance and composition for these sites, and found that vegetation characteristics such as canopy cover and understory stem density were less important than hunting pressure in driving the abundance of all mammal taxa, with the exception of elephants. Hunting clearly exerts strong pressures on the animal community, and rodents can benefit as a result.

The effects of hunting-induced defaunation on rodent seed predation in our study were fairly consistent across a diverse group of tree species and seed traits, with increased seed removal and decreased seedling establishment for five of the eight focal timber tree species (Figure 12). The three tree species for which defaunation did not significantly affect seed predation and seedling establishment had traits that made them either very attractive or very unattractive to seed consumers across all sites (Table 5). The seeds of *P. macrophylla*, which had the highest rate of vertebrate removal among all species, are large and conspicuous (~30 g, and shiny brown), relatively unprotected physically (with a thin and easily penetrable seed coat), and are readily consumed by a variety of animals (Rosin, personal observation). Contrary to some results from the Neotropics (Roldán and Simonetti 2001, Beckman and Muller-Landau 2007, Dirzo et al.

2007), we found no upper-size-limit on rodent seed predation among our species, with high removal of even the largest seeds we studied. The seeds of *A. klaineana* and *P. africanum*, in contrast, were removed at very low proportions across all sites. *A. klaineana* seeds have very hard seed coats surrounding several tiny embryos, and *P. africanum* seeds have small and thin papery endosperms – both traits that apparently render these species’ seeds unattractive to rodent seed predators.

In defining plant community “winners” and “losers” in the defaunation process – those for which hunting appears to be beneficial or detrimental to their recruitment – it is clear that changes to the seed predation process produce disproportionately more losers, with declining seedling establishment for most species in our study and unchanged seedling establishment for the others. The few species that may benefit from defaunation are likely those possessing seed traits that deter rodent consumers, such as extremely small size or strong chemical and/or physical defenses, or perhaps those that are so rare as to escape the search image of foraging seed predators (Paine and Beck 2007, Galetti et al. 2015b). Although the scope of this study is limited to the seed-to-seedling transition, modifications to the seed predation process that affect the relative abundance of seedling species may persist through the sapling and adult tree stages, and could result in reduced stem density and altered plant community composition (Dirzo et al. 2007, Paine and Beck 2007).

### 4.5.3 Implications for Timber Regeneration and Management

The cascading effect of defaunation on seedling regeneration is likely to have economic consequences for timber harvest. Increased seed removal and decreased seedling establishment of many tree species – including but not limited to those harvested for timber – will result in fewer saplings, and eventually fewer harvestable trees in forests subjected to hunting. Many commercially important timber tree species could suffer reduced recruitment as a result (Rosin 2014). In Uganda, for example, increased rodent abundance drove reduced regeneration of several timber species (Kasenene 1980, 1984, Struhsaker 1997). Likewise, abundant small rodents in a defaunated Costa Rican forest removed significantly more seeds of three timber species (*Dipteryx panamensis*, *Minquartia guianensis*, and *Virola koschnyi*) than in a comparable nonhunted site (Guariguata et al. 2000, 2002). Forest managers expecting continued yields must weigh short-term financial and political priorities with the long-term benefits of maintaining intact animal communities (Smith and Garnett 2004). As it is essential that the processes that contribute to regeneration occur within logged areas themselves (Guariguata and Pinard 1998), managers must strive to maintain wildlife populations and reduce the impacts of hunting across entire concession areas.

Hunting is widespread in timber concessions, but could be reduced with appropriate management, to the benefit of both wildlife and the natural regeneration of timber species. Timber certification bodies such as the Forest Stewardship Council (FSC)

– which provide an external incentive for improved practices – should strive to promote the specific management of ecological processes facilitated by wildlife. As external incentives are not always effective, forest managers may be motivated by improved knowledge of an internal incentive: that hunting can be detrimental to timber regeneration, and may represent an overall economic loss for timber companies that allow hunting in their concessions. The best management strategies, regardless of the motivation, will be those that restrict forest access for hunters and their game, and reduce the demand for wild meat by providing or subsidizing other sources of protein (Auzel and Wilkie 2000, Poulsen et al. 2009, Clark et al. 2009, Rosin 2014).

To the extent that scientific evidence directs these management decisions, future research should focus on understanding how other ecological processes vary across a gradient of defaunation, as well as how these changes might translate to shifts in plant community composition and actual gains or losses in timber tree abundance. Selectively logged forests can represent a “middle way” between absolute protection and deforestation (Putz et al. 2012), but reduced regeneration as a result of hunting may increase the likelihood that these forests be converted to non-forest land uses, representing a great loss of conservation value. It is thus critical that researchers and managers alike strive to address specific conservation needs and identify viable alternatives to exploitative hunting practices.

## **5. A Pantropical Assessment of Physical Damage to Forest Seedlings and the Effects of Vertebrate Defaunation**

### **5.1 Summary**

Many of the forces that shape tropical forest plant communities are facilitated by interactions with animals, which can either promote or inhibit plant reproduction and survival across ontogenetic stages. Hunting-induced defaunation can disrupt these interactions, altering tree recruitment, forest structure, and carbon storage, with strong effects at the seed and seedling stages. Research to date has largely focused on how changes to prominent interactions (especially seed dispersal) affect plant species and communities, while concurrent disruptions to less-studied processes may have opposing effects. With a particularly limited understanding of non-trophic interactions – such as physical damage to seedlings by vertebrate trampling, rooting, and digging – it remains difficult to predict the outcomes of defaunation for tropical forest plant communities. We use 1800 artificial seedlings in 18 intact and disturbed sites across the three main tropical forest regions – the Neotropics (Peru), the Afrotropics (Gabon) and the Indo-Malayan tropics (Malaysian Borneo) – to isolate non-trophic vertebrate physical damage from other causes of seedling mortality (herbivory, pathogens, abiotic desiccation, etc.), and to understand its effects in intact and anthropogenically-disturbed forests. We demonstrate that vertebrate physical damage is a consistent force in forests across the tropics, and that hunting significantly alters its strength, with a ~70% decrease in

damage in hunted vs. intact sites that resulted in a ~350% increase in artificial seedling survival. Our results reveal an underappreciated mechanism that may contribute to changes in seedling survival, stem density, and plant community composition in tropical forests subjected to hunting.

## **5.2 Introduction**

Plant-animal interactions are prominent in tropical forests (Price et al. 1991), and can be beneficial (e.g. pollination, seed dispersal) or detrimental (e.g. herbivory, seed and seedling predation) to plant reproduction and survival. Disruptions to these interactions – such as defaunation resulting from hunting (Redford 1992) – can generate broad changes in tree recruitment (Terborgh et al. 2008), forest structure (Dirzo and Miranda 1990), and carbon storage (Osuri et al. 2016), with demographic filtering at the seed and seedling stages responsible for many of the effects (Kurten 2013). Research to date has largely focused on a subset of prominent bi-trophic interactions (especially seed dispersal), while concurrent disruptions to other less-studied ecological processes may drive changes of opposite directionality for individual species or entire communities (Wright 2003, Kurten 2013).

Largely ignored in recent research are non-trophic interactions (Ohgushi 2008), such as trampling, rooting, digging, and other incidental physical damage that occurs as animals use their habitat. The strongest of these ecological effects are obvious: elephants create vast networks of trails through repeated trampling (Blake and Inkamba-Nkulu

2004), and maintain forest clearings called *bais* (Klaus et al. 1998); foraging herds of peccaries root and dig, disturbing the soil and vegetation over large areas and acting as “ecosystem engineers” (Beck et al. 2010). While extensive localized damage is conspicuous, multitudinous small effects – such as the trampling of many individual seedlings across large spatial and temporal scales – could have equally consequential effects for plant communities. With very limited understanding of these interactions, it remains difficult to predict the outcomes of defaunation for tropical forests.

Little is known about the role of non-trophic vertebrate damage to seedlings in the tropical forest understory (Clark and Clark 1989), as well as how this force may be altered by defaunation. The assessment of physical damage can be difficult, given that vertebrate and invertebrate herbivory, pathogen attack, abiotic desiccation, and other factors can produce visually similar forms of seedling mortality. To isolate the effects of physical damage (by both vertebrates and falling plant debris) from other causes of mortality, we used a modified artificial seedling model designed to replicate natural seedlings in general shape, flexibility, and resilience to damage (Clark and Clark 1989; Figure 1). The model provides an index of damage that is ideal for comparison across sites (Clark and Clark 1989) and between forests with different human disturbances such as hunting (Roldán and Simonetti 2001).

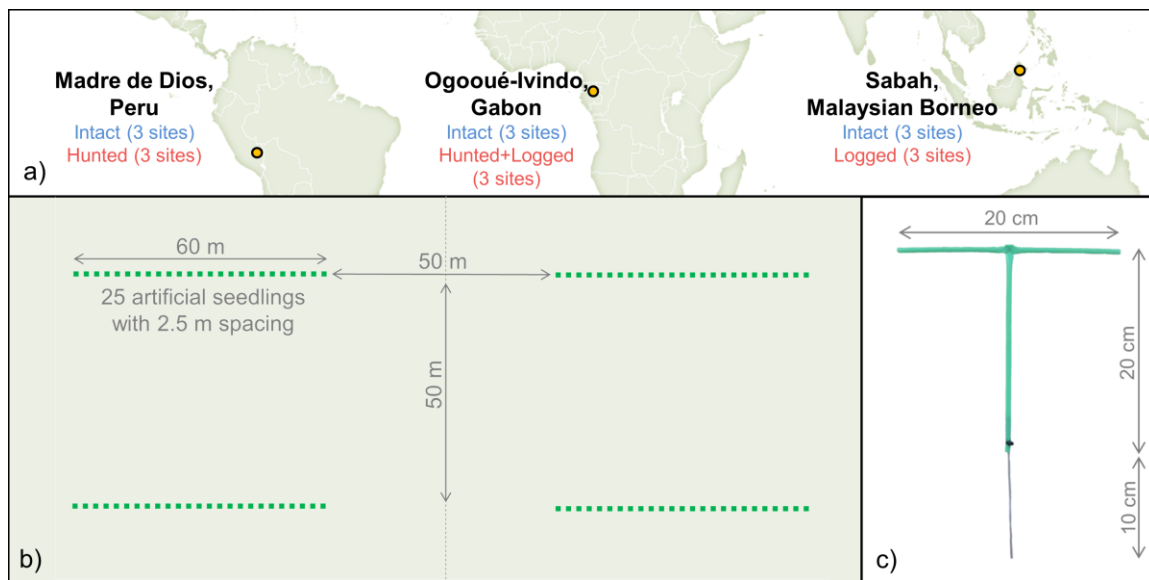
We sought to quantify non-trophic seedling physical damage in biogeographically distinct forests across the tropics, and to compare these effects

between intact forests (protected sites without any recent human disturbance) and those subjected to hunting and/or logging. We assessed damage to a total of 1800 artificial seedlings across 18 sites, with three sites in each of two forest conditions (intact vs. hunted and/or logged) in Peru, Gabon, and Malaysian Borneo. We expected that: 1) non-trophic vertebrate damage would cause more artificial seedling losses than would physical damage by plant debris, with certain terrestrial fauna (elephants [*Loxodonta cyclotis*, Gabon, Figure 15; and *Elephas maximus*, Malaysian Borneo], bearded pigs [*Sus barbatus*, Malaysian Borneo], and white-lipped peccaries [*Tayassu pecari*, Peru]) as strong actors in this process; 2) non-trophic vertebrate damage would be highest in Gabon and Malaysian Borneo, where megafauna remain abundant; and 3) the reduction in abundance of medium and large terrestrial mammals would significantly reduce non-trophic vertebrate damage in forests subjected to hunting-induced defaunation.

## **5.3 Methods**

### **5.3.1 Study Sites**

We conducted our study in both intact and disturbed forests of Peru, Gabon, and Malaysian Borneo (Figure 14). In total, we established 18 experimental sites, with three sites in each of two forest conditions (intact vs. hunted and/or logged) in each of the three regions. Sites within each forest condition were separated by at least 1 km (mean distance = 8 km; maximum distance = 34 km).



**Figure 14: a) Map of study areas, with three sites in each of two forest conditions (intact vs. hunted and/or logged) in each of the three main tropical forest continents; b) The experimental design for a single site, made of four parallel lines of 25 artificial seedlings (green dotted lines; grey arrows indicate spatial scale and distance between seedling lines; central grey dashed line represents the access route) – in total, we established 18 sites and 1800 artificial seedlings; c) The artificial seedling model, constructed of two green plastic drinking straws attached to a stiff wire “root”.**

In Peru, our experimental sites were located in the Madre de Dios region in the southeast, and included: 1) three intact sites near the Tambopata Research Center in the Tambopata National Reserve, and 2) three disturbed sites subjected to heavy hunting, located within Reserva Amazónica, a small privately-owned forest approximately 16 km from the regional population center of Puerto Maldonado. Transect surveys of the disturbed forest sites have documented the substantial reduction in abundance of medium- and large-bodied mammals, with a near absence of white-lipped peccaries (*Tayassu spp.*), tapir (*Tapirus terrestris*), and deer (*Mazama spp.*; Rosin, unpublished data),

and a highly impoverished primate community (Rosin and Swamy 2013). The nearest distance between the intact and disturbed condition sites was approximately 90 km.

In Gabon, our experimental sites were located within the Ogooué-Ivindo province in the northeast, and included: 1) three intact forest sites in northern Ivindo National Park, and 2) three disturbed sites near the town of Makokou, with one site near a village, and two sites within the Wang Chuan Timber Sarl concession, all of which were selectively logged and subjected to heavy hunting. Transect surveys of the disturbed forest sites have documented substantially reduced abundances of medium- and large-bodied mammals, including elephants (*Loxodonta cyclotis*), red river hogs (*Potamochoerus porcus*), duikers (*Cephalophus spp.*), mandrills (*Mandrillus sphinx*), and apes (Koerner et al. 2016). The nearest distance between the intact and disturbed condition sites was approximately 22.5 km.

In Malaysian Borneo, our experimental sites were located in eastern Sabah, and included: 1) three intact forest sites within the Danum Valley Conservation Area, and 2) three disturbed sites within the Sabah Biodiversity Experiment (SBE), which was selectively logged in the 1980s. This area has not been subjected to substantial hunting (Hector et al. 2011), in part due to security measures restricting forest access. In 2007, much of the surrounding forest was logged for a second time, though our specific study area was not (Hector et al. 2011). A comparative camera trap survey of the intact and disturbed sites indicated that despite differences in forest structure (Hector et al. 2011),

the two areas have comparable abundances of terrestrial mammals, including bearded pigs (*Sus barbatus*), sambar (*Rusa unicolor*), yellow muntjac (*Muntiacus atherodes*), and pig-tailed macaques (*Macaca nemestrina*; Granados et al. 2016). The nearest distance between the intact and disturbed condition sites was approximately 20 km.

### **5.3.2 Artificial Seedling Construction, “Planting,” and Monitoring**

We constructed 1800 artificial seedlings, following Clark and Clark (1989), with slight modification. Each artificial seedling was composed of two green plastic drinking straws (20 cm length x 0.5 cm diameter) stapled into a “T”, attached to a 13 cm “root” of 12-gauge wire with 3 cm of overlap, and secured with a plastic cable tie under a small duct tape lip (Figure 14). We numbered each artificial seedling using black permanent marker. The model mimicked natural seedlings in general size, flexibility, and resilience to damage, and required a strong upward force to uproot.

At each of our 18 sites, we established four parallel 60 m lines, separated by 50 m (Figure 14). For each line, we “planted” 25 artificial seedlings to a depth of 10 cm (so the cable tie attachment was flush with the soil), each separated by 2.5 m along the line. If a planting location was unavailable because of the presence of a tree bole, log, or stream, we avoided the obstacle and adjusted the rest of the line to maintain the separation among seedlings.

We censused all artificial seedlings monthly for a period of 12 months, during the following dates: December 2014 to December 2015 for Gabon; July 2015 to July 2016

for Malaysian Borneo, and November 2015 to November 2016 for Peru. Due to logistical limitations, we missed one census period in Peru and Gabon, and three census periods in Malaysian Borneo. In all cases, we continued with data collection at the following month's census period.

Following Clark and Clark (1989), we classified artificial seedlings as “damaged” when the model was bent such that either of the two arms of the “T” touched the ground, or when the whole model was flattened, uprooted, or bitten off. We defined three categories of damage: 1) Plant debris – artificial seedlings found directly under fallen branches, trunks, large fruits, or other heavy debris; 2) Vertebrates – artificial seedlings that had been trampled, knocked over, or buried, with evidence of vertebrate activity including animal trails, tracks, scrapings and diggings, and tooth marks; and 3) Unknown – damaged artificial seedlings that couldn't be assigned, with confidence, to either of the other categories. We categorized artificial seedlings as “Missing” for those that were uprooted and not found within a 10 m radius of their planting location. We categorized artificial seedlings as “Invertebrate damaged” for those with small cut marks and no evidence of vertebrate chewing. We removed all damaged artificial seedlings from their lines at the time of censusing.

### **5.3.3 Data Analysis**

To determine the significance of differences in non-trophic vertebrate damage and artificial seedling survival between intact vs. disturbed conditions for each of the three regions, we fitted generalized linear models (GLMs) with binomial error distributions to model artificial seedling fate (binary response: vertebrate damaged or survived) as a function of the total number of artificial seedlings established, with forest condition (intact vs. hunted and/or logged) as an explanatory variable. We performed all statistical analyses in R 3.2.3 (R Core Team 2015).

### **5.4 Results**

A total of 79% (of n=1800) of all artificial seedlings were damaged during the 12-month study period; 71% (n=600) were damaged in Peru, 65% (n=600) in Gabon, and 100% (n=600) in Malaysian Borneo (Figure 16). We excluded all “Missing” and “Invertebrate Damaged” artificial seedlings from further analysis, as they likely represented an unnatural novelty response to the model itself (see below). Excluding these data resulted in reduced sample sizes of n=540 artificial seedlings for Peru, n=592 for Gabon, and n=334 for Malaysian Borneo.

Across all sites, forest conditions, and regions, vertebrates predominantly drove artificial seedling losses (Table 7). Vertebrates damaged 49% (n=1466) of all artificial seedlings, compared to just 16% (n=1466) damaged by plant debris.

**Table 7: Damaged artificial seedlings, categorized by cause. The values represent average proportions across the three sites within each forest condition, with standard errors (averaged among all sites in the condition) in parentheses.**

<b>Vertebrates</b>	<b>Plant Debris</b>	<b>Unknown</b>	<b>Vertebrates</b>	<b>Plant Debris</b>	<b>Unknown</b>
<i>Peru Intact (n=278)</i>			<i>Peru Hunted (n=262)</i>		
0.770 (0.044)	0.144 (0.036)	0 (0)	0.099 (0.029)	0.290 (0.049)	0.046 (0.021)
<i>Gabon Intact (n=297)</i>			<i>Gabon Hunted+Logged (n=295)</i>		
0.593 (0.048)	0.047 (0.020)	0.152 (0.041)	0.322 (0.044)	0.061 (0.025)	0.115 (0.039)
<i>Malaysian Borneo Intact (n=143)</i>			<i>Malaysian Borneo Logged (n=191)</i>		
0.664 (0.069)	0.217 (0.061)	0.112 (0.030)	0.618 (0.060)	0.304 (0.057)	0.079 (0.031)

Hunting significantly reduced vertebrate damage to artificial seedlings, by 87% in hunted sites in Peru and 46% in hunted and logged sites in Gabon, compared to intact sites (Peru:  $z=-13.6$ ,  $df=539$ ,  $p<0.001$ ; Gabon :  $z=-6.52$ ,  $df=591$ ,  $p<0.001$ ). There was no significant difference in the level of damage by vertebrates in intact vs. logged sites in Malaysian Borneo ( $z=-0.88$ ,  $df=333$ ,  $p=0.382$ ).

Artificial seedling survival was significantly greater in the hunted sites of both Peru and Gabon than in intact sites (Peru:  $z=10.6$ ,  $df=539$ ,  $p<0.001$ ; Gabon:  $z=7.27$ ,  $df=591$ ,  $p<0.001$ ). In Peru, 9% ( $n=278$ ) of artificial seedlings survived the year in the intact sites, while 57% ( $n=262$ ) survived in the hunted sites. In Gabon, 21% ( $n=297$ ) survived in the intact sites, while 50% ( $n=295$ ) survived in the hunted and logged sites.

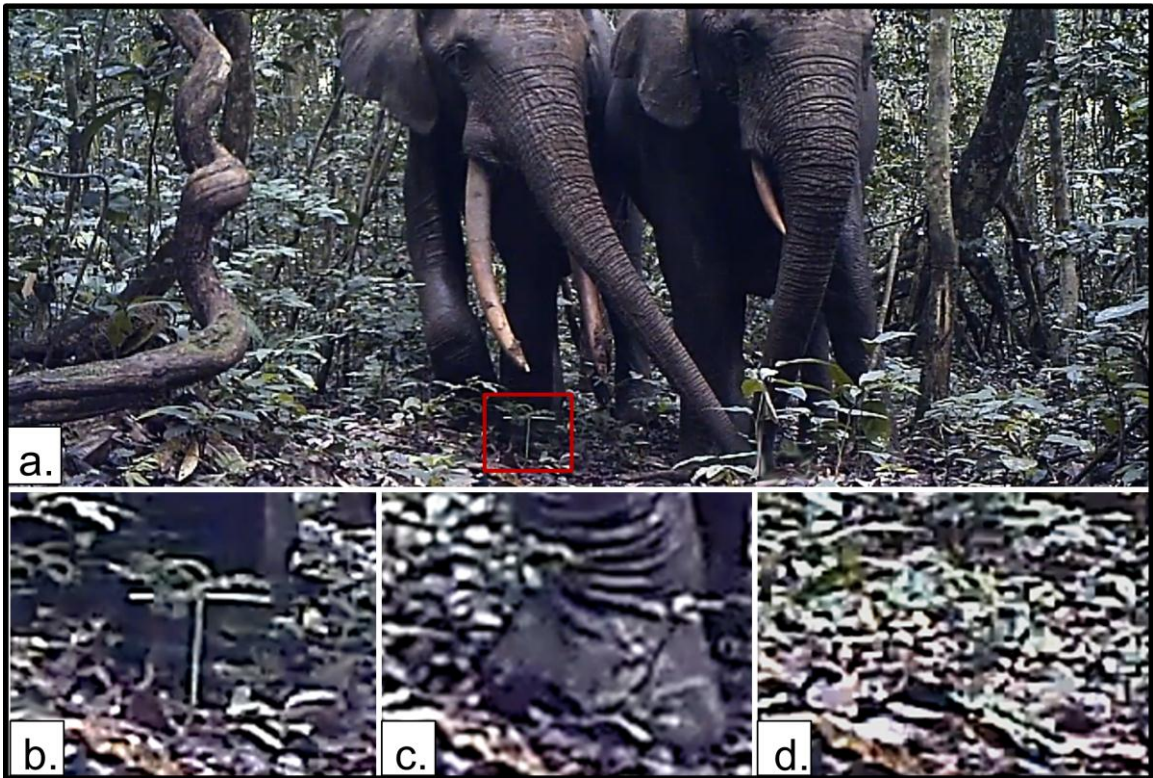


Figure 15: a) Foraging elephants in Gabon approach an artificial seedling (in red square), monitored by a motion-sensitive video camera; b) close up still photo of the artificial seedling, prior to trampling; c) the artificial seedling is crushed under the elephant's foot; and d) post-trampling, the artificial seedling and surrounding natural vegetation are flattened.

## 5.5 Discussion

### 5.5.1 Patterns of Damage

The magnitude of non-trophic vertebrate damage to the seedling layer was similar in intact sites across all three regions (Figure 16), despite the substantial natural differences in their animal communities. From observations of the damaged artificial seedlings and their surroundings, as well as knowledge of foraging ecology, white-lipped peccaries (Peru), elephants and red river hogs (*Potamochoerus porcus*, Gabon;

Figure 15), and bearded pigs (Malaysian Borneo) likely generated the strongest vertebrate effects.

The similarity in damage rates among continents contrasts with our expectation of greater damage in sites supporting abundant megafauna. There are several plausible explanations for this result. First, the artificial seedling model may not accurately capture differences in the quality of physical damage (for example, elephant trampling is a very different force than peccary rooting, though both damage artificial seedlings with quantitative equivalence). Second, trampling by megafauna not only damages vegetation but also compacts the soil, which may reduce the likelihood for seedling recolonization; thus, the effects of megafauna on stem density may extend beyond the direct damage investigated by our study. Third, the expected geographic divergence in damage could occur for plants of larger size classes – an effect not captured by using the small artificial seedling model. No Neotropical forest vertebrates, except humans, are capable of inducing the physical damage necessary to kill woody plants with diameters  $\geq 3\text{-}5$  cm, whereas elephants in the Afrotropics and Indo-Malayan tropics can and often do kill much larger trees (Mueller-Dombois 1972, Kortlandt 1984, Terborgh et al. 2016a). Plants in these forests thus experience vertebrate damage for a much longer period and across multiple growth stages, only escaping this window of mortality at a relatively large size. Non-trophic vertebrate damage may contribute to the observed biogeographic divergence in stem density and forest structure across the tropics (Corlett

and Primack 2011, Terborgh et al. 2016b), though assessing this would require further study through later life stages, when the filtering mechanism exerted only by megafauna takes effect.

As with very large animals, falling branches or trees (categorized as “plant debris”) can kill plants much larger than our artificial seedling model. While most plants are susceptible to vertebrate damage for a relatively short period of time, the risk of death by plant debris may span several decades or more of the life of a slow-growing understory plant. Thus, while plant debris accounted for only relatively minor losses of artificial seedlings, the true lifetime impact of this damage is underestimated by our 12-month experiment. For comparative purposes, however, the observed differences in plant debris damage between regions are likely to reflect actual differences in debris damage to natural seedlings (Gillman et al. 2002). Debris damage was consistently lower across sites in Gabon than in Peru and Malaysian Borneo (Figure 16). This may be a result of the lower overall tree density (Corlett and Primack 2011, Lewis et al. 2013) and/or lower turnover (Lewis et al. 2004) in Central African forests than elsewhere in the tropics; with fewer trees and lower turnover to generate debris, the likelihood of physical damage to the seedling layer is lower.

The unexpectedly high proportion of missing artificial seedlings at sites in Malaysian Borneo (32% of n=600) suggests that some of the observed vertebrate damage resulted from a novelty response of terrestrial mammals to the unnatural model.

Macaques (*Macaca fascicularis* and *M. nemestrina*) were the most likely culprits, uprooting artificial seedlings and carrying them elsewhere. These losses reduced the sample sizes for Malaysian Borneo considerably, and may have inflated the rates of damage observed beyond those to be expected for natural seedlings. Uprooting and missing seedlings occurred rarely in Peru and Gabon, with even distribution across sites, and we have no other evidence that the model was treated in a non-natural way.

After excluding missing artificial seedlings, we are confident that the remaining observations represent an accurate index of non-trophic vertebrate damage for comparative purposes. Studies using the same model have demonstrated similar rates of damage between natural and artificial seedlings in tropical forests (Clark and Clark 1989, Alvarez-Clare and Kitajima 2009). However, rates of damage to artificial seedlings likely overestimate rates of mortality of natural seedlings by an unknown factor (Gillman et al. 2002), given the potentially greater resilience of some natural seedlings to physical damage, particularly for those with large seeds and hypogeal germination (Harms and Dalling 1997), or for older seedlings with large, flexible stems. Indeed, tropical forest seedling mortality by all causes is often substantially lower than the rates of artificial seedling damage reported here (eg Metz et al., 2008). Therefore, artificial seedlings are most useful as an index for comparing physical damage potential across forest conditions and regions, rather than as an absolute estimation of damage or

mortality for natural seedlings in any particular locality (Clark and Clark 1989, Gillman et al. 2002).

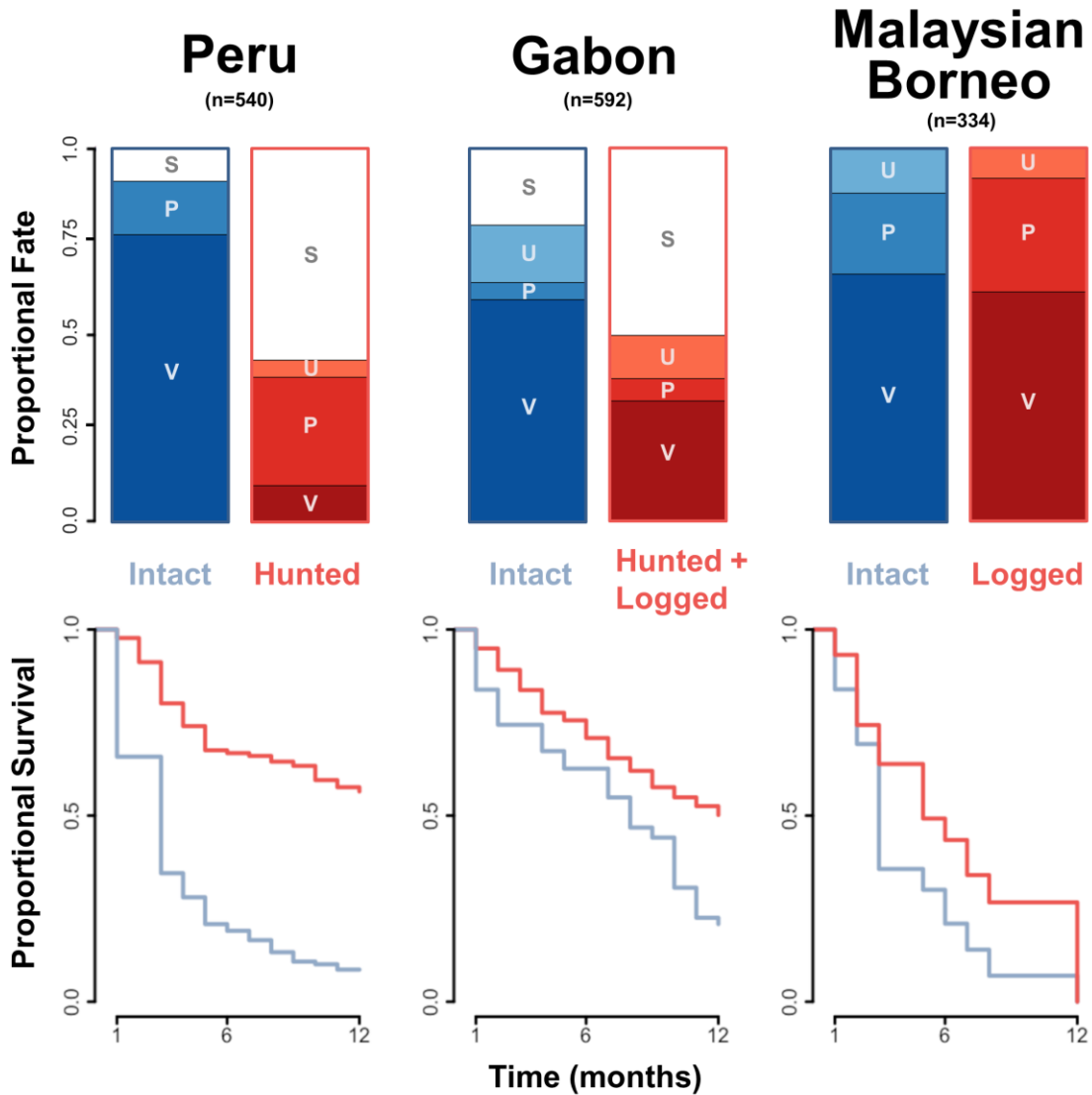


Figure 16: Top row: The final proportion of artificial seedlings in each forest condition, categorized by fate, including damaged by vertebrates (V), damaged by plant debris (P), damaged by unknown causes (U), and survived (S). Unexpectedly high rates of damage in Malaysian Borneo are at least partly a result of a novelty response of vertebrates to the unnatural model (see Discussion). Bottom row: Proportion of surviving artificial seedlings over time (blue line=Intact sites, red line=Disturbed sites).

### 5.5.2 The Effects of Hunting and Logging

Hunting strongly affected non-trophic vertebrate damage, reducing artificial seedling losses by 87% in hunted sites in Peru and 46% in hunted and logged sites in Gabon, compared to intact sites. In Malaysian Borneo, where the disturbed forest was selectively logged 30 years ago, but not hunted, there was no significant difference in the level of damage by vertebrates. Despite any logging-induced variation in forest structure and composition, the terrestrial mammal community in the disturbed sites was not significantly different from the intact sites (Granados et al. 2016), and vertebrate damage to artificial seedlings was nearly equal between the two forest conditions. Hunting generally affects animal abundance more strongly than do the direct effects of logging (Poulsen et al. 2011); in our study, hunting was also the key driver in modifying the rates of vertebrate damage to artificial seedlings.

As a consequence of reduced non-trophic vertebrate damage, artificial seedling survival was significantly greater in the hunted sites of both Peru and Gabon than in intact sites. In Peru, just 9% of artificial seedlings survived the year in the intact sites, while 57% survived in the hunted sites (an increase of 633%). In Gabon, 21% survived in the intact sites, while 50% survived in the hunted and logged sites (an increase of 238%). Several studies have demonstrated that hunting-induced defaunation can result in increased survival of natural seedlings (Dirzo and Miranda 1990, Roldán and Simonetti 2001, Poulsen et al. 2013), reflecting the trends presented here. While the absolute rates

of survival of natural seedlings may be greater than those of artificial seedlings (as noted above), the relative differences in artificial seedling survival between hunted and intact forests presented here likely represent the relative survival differences for natural seedlings as well.

In addition to altering seedling survival and stem density, hunting-induced modifications to the physical damage regime could potentially alter plant community composition. As seedling responses to physical damage can differ among species (Clark and Clark 1989), those most vulnerable to such damage could have disproportionately increased survival in hunted sites (Roldán and Simonetti 2001), with subsequent changes in seedling community composition. Specifically, this might favor fast-growing taxa that invest relatively few resources in strong and flexible stem structure and the capacity to resprout.

Several studies have demonstrated that hunting-induced defaunation can result in community-level shifts in seedling stem density and diversity (Dirzo and Miranda 1990, Wright 2003, Kurten 2013), though the mechanisms inducing change are not always well-established. Our study provides compelling evidence that the reduction of non-trophic vertebrate seedling damage is an under-appreciated mechanism that may contribute to changes in vegetation structure and composition in defaunated tropical forests. Determining the community-level importance of this ecological interaction – as well as its strength relative to others – will require its inclusion in future studies that

seek to understand the drivers of plant reproductive success in intact and anthropogenically-disturbed forests.

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## Biography

I was born on August 18<sup>th</sup>, 1984 in Madison, Wisconsin, USA, to Eberhard Rosin and Anne Ellen Rosin. I graduated from Macalester College in St. Paul, Minnesota in May, 2007, with a bachelor's degree in Biology and a strong interest in tropical ecology and conservation that largely resulted from my experiences on a semester-abroad program in Ecuador with the School for International Training.

After graduating college, I volunteered for 8 months with the WorldTeach program in Kwakwani, Guyana, teaching science and biology to middle and high school students. The experience solidified my interest in working abroad, and expanded on my experience living in and around tropical forests. Upon returning to the US, I gained more research experience with wildlife, ecology, and conservation biology working in both the UW-Madison Department of Forest and Wildlife Ecology and as a field technician for research in Belize studying jaguars, pumas, and other wild cats.

I entered the Master of Environmental Management (MEM) program at the Nicholas School of the Environment at Duke University in the fall of 2010, with a concentration in Ecosystem Science and Conservation. In May of 2011, I married Rachel Elizabeth Nordberg (now Rachel Nordberg Rosin) in Madison, Wisconsin. Very soon after, we traveled together to the Madre de Dios region of southeastern Peru to pursue my master's project research, which comprised transect surveys at three forest sites with differing levels of protection, to understand the impacts of hunting on primates,

medium and large terrestrial mammals, and large birds. I graduated from the MEM program in the spring of 2012, and entered the PhD program in Environment the subsequent fall.

After two years of doctoral study, my research again brought Rachel and me abroad; beginning in June 2014, we spent eleven months living at the Ipassa Research Station and conducting dissertation research in and around Ivindo National Park in northeastern Gabon. Very shortly after departing Gabon, I spent three weeks in the Danum Valley of Sabah, Malaysian Borneo, initiating an extension of one of my dissertation projects in collaboration with Alys Granados, and later with Varun Swamy. After returning to North Carolina, settling in, and reacquainting ourselves with the luxury of reliably-running water, Rachel and I welcomed our son Walter Eberhard Rosin in June of 2016. My doctoral work continued, despite the occasional loss of sleep.

My dissertation comprises five chapters, three of which have been published in peer-reviewed scientific journals: “Does hunting threaten timber regeneration in selectively logged tropical forests?” (in *Forest Ecology and Management*, 2014); “Telemetric tracking of scatterhoarding and seed fate in a Central African forest” (in *Biotropica*, 2017, with co-author John Poulsen); and “Hunting-induced defaunation drives increased seed predation and decreased seedling establishment of commercially important tree species in an Afrotropical forest” (in *Forest Ecology and Management*, 2016, with co-author John Poulsen). I also published one article resulting from my master’s project: “Variable

density responses of primate communities to hunting pressure in a western Amazonian river basin" (in *Neotropical Primates*, 2013, with co-author Varun Swamy). I expect to publish the remaining two dissertation chapters, with titles that reflect those presented in this document.

I have been privileged to receive several grants, fellowships, and academic honors during my graduate education. In 2011, I received the Nicholas School International Internship Award, the Lazar Foundation Award, and the Kuzmier-Nikitine-Lee Endowment Fund Award to support field research in Peru, and I was a Semi-Finalist for the Doris Duke Conservation Fellowship. In 2014, I received the Garden Club of America Award in Tropical Botany, the IDEA Wild Field Equipment Fund Award, and the James B. Duke International Research Travel Fellowship, to support field research in Gabon. In 2015, I received the Duke University International Research Travel Fellowship to support field research in Malaysian Borneo. From 2016-2017, I was a fellow of the Preparing Future Faculty (PFF) program.