

IMPLICATIONS OF MAMMALIAN DEFAUNATION FOR WOODY-PLANT REGENERATION
DYNAMICS AND COMMUNITY COMPOSITION IN TROPICAL PREMONTANE FORESTS

by

Christopher J. Graham

(Under the Direction of Chris J. Peterson)

ABSTRACT

My research investigated potential implications of mammalian defaunation for tropical woody plant communities. I couched my studies in terms of two filters that large mammals apply to woody plant regeneration: seed predation and seedling/sapling herbivory. I found that small—medium-seed predation, rather than large-seed predation, differentiated mortality in isolated seed groups between sites. Herbivory on juvenile plants was equivalent between sites, evincing a lack of large-herbivore effect. Finally, tree species compositions differed between sites, but no evidence was found for juvenile tree community shifts due to diminished large-seed predation at the defaunated site. Although mine is a case study of premontane forests, I believe it to be an important addition to a compendium of defaunation papers dominated by lowland rainforest studies. My sites were buffered against differential effects of large herbivore activity by idiosyncrasies of small rodent populations, scale-dependent ungulate behavior, and, perhaps, the novel climate of the study systems.

INDEX WORDS: defaunation, fragmentation, seed predation, herbivory, tree communities, tropical premontane wet forest

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DEDICATION

For Mom and Dad, the most loving, encouraging, and understanding parents one could hope to have; and for lovely Laura, who kept me well-fed during the final months of this process, and who made the fourth year worth it.

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CHAPTER 1

INTRODUCTION AND LITERATURE REVIEW

Defaunation, the loss of part or all of the fauna within an ecosystem, threatens not only forest animals but also forest vegetation itself. This anthropogenic phenomenon occurs throughout the tropics (Wright 2003) and, at the global scale, contributes to rapidly diminishing animal biodiversity (Dirzo and Raven 2003, Ceballos *et al.* 2005). At smaller scales, recent research reveals a picture in which myriad mammal species have undergone drastic range contractions, going locally extinct over large parts of their original ranges. For example, Ceballos & Ehrlich (2002) found that 173 mammal species had disappeared from greater than 50% of their historic ranges. Study after study has exposed forest sites in which defaunation threatens local fauna and, in turn, entire forest communities (e.g. Peres 2000, Peres 2001, Dirzo *et al.* 2007, Bodmer 1995).

Defaunation has numerous causes, from wholesale destruction of a forest for timber extraction to the competitive effect of human extraction of forest fruits on resident frugivores (Redford 1992). Perhaps the two commonest drivers are hunting and forest fragmentation (Peres 2001, Dirzo 2001). Already, most neotropical landscapes outside of the Amazon Basin are highly fragmented (FAO 2006), and most of the world's tropical forests are expected to exist in the near future as small to moderate sized fragments, as tropical nations plan development of their remaining large forest blocks (Laurance *et al.* 2001). I focus on fragmentation induced

defaunation in my study, though the consequences, both direct and indirect, of the two defaunation mechanisms are often virtually the same.

Large mammals are the most vulnerable to human impacts (Cardillo *et al.* 2005), because they are favored by hunters (Redford 1992, Bodmer *et al.* 1997, Peres 2000), and because of their greater territorial requirements, which makes them are more sensitive to fragmentation (Dirzo 2001, Wright 2003). Differential defaunation, in fact, often proceeds along what Dirzo *et al.* (2007) call a defaunation gradient, in which the size of affected mammals decreases with increasing human pressure. That is, the largest members of respective guilds, such as jaguars (carnivores) and tapirs (herbivores), may disappear with only moderate fragmentation or hunting pressure, while the smallest mammals (e.g. mice, rats) persist even under severe human impact. Accordingly, Peres (2000) found in a study of Amazonian mammal communities that animal density and mean body size were positively correlated with hunting intensity for small species (≤ 1 kg), and negatively correlated with hunting intensity for large animals (> 5 kg).

Mammals interact with forest plants in myriad ways, and therefore shifts in mammal community structure may frequently produce substantial changes in vegetation dynamics and composition (Emmons 1989, Terborgh 1992, Wright 2003). My study is concerned with possible plant community consequences of fragmentation-induced changes in mammal populations. Specifically, I investigate early stages of forest regeneration, which set the template for future forest composition, structure, and spatial patterns.

Mortality rates due to post-dispersal seed predation are among the highest of any stage of forest regeneration (Muller-Landau *et al.* 2004, Hubbell *et al.* 1999), and seed predation by

neotropical mammals often plays a major part in limiting woody seedling recruitment (Janzen 1971, Sork 1987, Forget 1993, Asquith *et al.* 1997, Wright *et al.* 2000). Large ungulate frugivores, in particular, consume great quantities of fruit (Bodmer 1991). Bodmer (1991) found that fruit makes up 59% and 66% of the diets of collared (*Tayassu tajacu*) and white-lipped peccary (*T. pecari*), respectively. *T. pecari* alone can account for 50% of all terrestrial mammalian granivore biomass; indeed, during a natural local extinction of *T. pecari* at Cocha Cashu Reserve, seed survival close to mother trees in two palm species increased between 5000 and 6000% (Wyatt and Silman 2004). Further, peccaries and deer (Cervidae) destroy most of the seeds that they consume (Bodmer 1991).

Depredation of young plants, particularly foliar herbivory, can also be an important bottleneck in the recruitment to later life stages (Coley and Barone 1996). While any size class of terrestrial mammals can exert substantial foliar herbivory pressure (Paine and Beck 2007, DeMattia *et al.* 2006), most research has focused on larger mammals, especially ungulates. Deer and tapir, especially, rely heavily on vegetative browsing to meet dietary needs. Large ungulate “removal”, via extirpation or experimental exclusion, has led to increased relative growth rates (Osunkoya *et al.* 1993, Wahungu *et al.* 2002) and recruitment and survival (Terborgh and Wright 1994, Ostfeld *et al.* 1997, Connell *et al.* 2005, Wright 2003) of woody seedlings and saplings.

Predatory seed mortality also tends to be size- and frequency-dependent, and thus helps to control (and balance) community composition of understory plants. Density- (frequency-) dependent seed predation by mammals prevents dominance of any particular species near its mother trees, freeing up space for recruitment of other, potentially

competitively inferior, species (Armstrong 1989). It thus promotes species coexistence and increases understory plant diversity (Janzen 1970, Connell 1971, Harms *et al.* 2000). Size-dependent seed predation is also suspected to offset the competitive advantage that large-seeded seedlings naturally enjoy over small-seeded species, due to the positive correlation between seed size and seedling performance (Foster 1986, Dalling *et al.* 1997). That is, large mammal seed predators may prefer large seeds (Dirzo *et al.* 2007) and thus should prevent competitive dominance by large-seeded seedlings (Grubb 1998, Mendoza 2005). Removal of large seed predators can translate to dominance by large-seeded species and reduced diversity in the seedling layer (Dirzo and Miranda 1991, Wright *et al.* 2007) and even in the adult tree community (Putz *et al.* 1990).

Research in the Los Tuxtlas rainforest of Veracruz, Mexico (Dirzo *et al.* 2007, Dirzo and Miranda 1991), has evinced a striking pattern of defaunation-induced effects on vegetation, encompassing all three facets that I sought to investigate. The Los Tuxtlas rainforest is highly defaunated: it contains no large terrestrial mammals and low densities of medium mammals (i.e. caviomorph rodents), but does harbor abundant small rodents, perhaps due to release from predation. First, Dirzo and Miranda (1991) observed no foliar herbivory damage at Los Tuxtlas and a 29% damage rate at a faunally intact comparison site. Seedling and sapling densities were also 2.3 times higher at Los Tuxtlas. Further, complete mammal-exclusion at the defaunated site increased seed survival significantly. However, the magnitude of the effect depended strongly on seed size: small-seed survival rate was 30 times greater in cages than in open controls, while large seed were only 2.3 times more likely to survive in exclosures than in the open, and were much more likely to survive than small-seeds, overall. The researchers

conclude that such differential seed predation, by a much-diminished suite of terrestrial mammal species, has led to dominance in the understory by several large-seeded species and to a diversity that is one third that found in understory plants of the intact comparison site.

My research aimed to detect potential consequences of mammalian defaunation for regeneration of forest woody plants. I was most interested in the direct effects of large-herbivore loss on seed and juvenile plant survival and plant community composition. However, I also looked for evidence of a trophic cascade, in which woody plant dynamics and composition could be altered by greater abundances of small rodents, which may have been released from competition and predation by extirpation of larger herbivores and top carnivores, respectively. I focused on woody, non-climbing plants throughout my investigation.

I conducted my research at two primary, premontane, wet forests in southern Costa Rica (Holdridge *et al.* 1971, Kohlmann *et al.* 2010). One forest is a medium-sized fragment in a matrix of active and abandoned pasture and much smaller remnant forest patches; it contains no large terrestrial herbivores or top carnivores. The other site, part of a block of contiguous forest exceeding 500,000 ha, harbors a virtually complete mammal fauna. I monitored seed predation and sampled juvenile and adult woody plants at the two sites between spring 2009 and fall 2010.

In Chapter 2, I present results from a two-season seed predation study that utilized partial exclosures to differentiate among size classes of mammalian seed predators. I created survival models of seed predation to detect differences between sites, fenced exclosure treatments, seed sizes, and years. I interpret results of these analyses, and, specifically, highlight evidence for structuring of seed survival patterns by granivore fauna composition.

Chapter 3 discusses a 16-month juvenile-plant foliar herbivory experiment comparing browsing effects at the two sites. I quantified herbivory and key demographic metrics pertaining to large seedlings and small saplings under exposure to different mammal size classes. I also present a baseline description of juvenile plant communities at my two sites.

Building on the work presented in chapter 3, chapter 4 presents a community analysis based on augmented juvenile plant sampling and adult tree sampling. I performed multivariate analyses of composition and diversity of adult and juvenile woody plant communities, looking specifically for divergence in the juvenile plant communities of the two sites due potentially to disparate mammal community compositions.

My research fits into a burgeoning literature of investigations into defaunation-induced changes in tropical forest vegetation (see Redford 1992, Terborgh 1992, Wright 2003 for reviews). To my knowledge, mine is one of the first studies to apply multiple levels of partial mammal exclusion to an assessment of vertebrate seed predation and juvenile plant herbivory (see Paine and Beck 2007). It may be the first to do so in both a continuous forest and a defaunated fragment. I also performed this work in mid-elevation, premontane wet forest, an uncommon ecosystem in studies of defaunation. Perhaps this divergence may help to explain several of my results that go against the grain of typical patterns elicited by defaunation research in lowland rainforest ecosystems.

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CHAPTER 2

SMALL- AND MEDIUM-SIZED MAMMALS DRIVE DIFFERENCES IN SEED PREDATION BETWEEN A DEFAUNATED AND A FAUNALLY INTACT SITE IN TROPICAL PREMONTANE WET FOREST¹

¹ Graham, C. J. and C. J. Peterson. To be submitted to *Biotropica*.

Abstract

Defaunation of fragmented tropical forests is a worldwide trend, and the potential effects on seed predation, among many plant-animal interactions, may in turn threaten the integrity of plant communities. The local reduction or loss of mammals, in particular, typically proceeds along a size gradient, in which larger mammals succumb earlier to anthropogenic forces. This size-dependent defaunation is likely to differentially alter seed predation levels, in turn differentially favoring or hindering regeneration of across tree taxa, based on associated seed characteristics. I studied the impact of defaunation on seed predation patterns in a defaunated forest fragment and in a continuous forest having a nearly complete fauna, both in mid-elevation wet forest of southwestern Costa Rica. I conducted seed predation trials during summers of 2009 and 2010 on 14 tree species, ranging in seed mass over two orders of magnitude, placed into two mammal exclusion treatment levels: open (access to ALL mammals) and SMALL (access only to small rodents). I found, most importantly, that (1) medium-sized mammals and ground birds are the predominant predators of isolated groups of large seeds at both my sites, and (2) predation of small and medium seeds is the dominant factor driving greater overall predation rates at LA than at LCBS

Introduction

Defaunation, the loss of part or all of the fauna within an ecosystem, occurs throughout the tropics (Wright 2003). At the global scale, mammalian biodiversity is rapidly diminishing due to anthropogenic defaunation (Dirzo and Raven 2003, Ceballos *et al.* 2005). At smaller scales, recent research reveals a picture in which myriad mammal species have undergone

drastic range contractions, going locally extinct over large parts of their original ranges. For example, Ceballos & Ehrlich (2002) found that 173 mammal species had disappeared from greater than 50% of their historic ranges. Numerous other studies have exposed forest sites in which defaunation threatens local fauna and, in turn, entire forest communities (e.g. Peres 2000, Peres 2001, Dirzo *et al.* 2007, Bodmer 1995).

Defaunation has numerous causes, from wholesale destruction of a forest for timber extraction to the competitive effect of human extraction of forest fruits on resident frugivores (Redford 1992). Perhaps the two commonest drivers are hunting and forest fragmentation (Peres 2001, Dirzo 2001). Already, most neotropical landscapes outside of the Amazon Basin are highly fragmented (FAO 2006), and most of the world's tropical forests are expected to reach a state of small to moderate sized fragments as tropical nations plan development of their remaining large forest blocks (Laurance *et al.* 2001). I focus on fragmentation induced defaunation in my study, though the consequences, both direct and indirect, of the two defaunation mechanisms are often virtually the same.

Defaunation does not affect all mammal species equally, and large mammals are the most vulnerable to human impacts (Cardillo *et al.* 2005). Hunters generally favor large-bodied mammals (Redford 1992, Bodmer *et al.* 1997, Peres 2000), and large mammals are more sensitive to fragmentation because of their greater territory requirements (Dirzo 2001, Wright 2003). Differential defaunation, in fact, often proceeds along what Dirzo *et al.* (2007) call a defaunation gradient, in which the size of affected mammals decreases with increasing human pressure. That is, the largest members of respective guilds, such as jaguars (carnivores) and tapirs (herbivores), may disappear with only moderate fragmentation or hunting pressure,

while the smallest mammals (e.g. mice, rats) persist even under severe human impact.

Accordingly, Peres (2000) found in a study of Amazonian mammal communities that animal density and mean body size were positively correlated with hunting intensity for small species (≤ 1 kg), and negatively correlated with hunting intensity for large animals (> 5 kg).

Because mammals and plants in tropical forests interact in numerous important ways, any significant alteration of a forest's mammalian fauna may affect plant populations and communities (Emmons 1989, Terborgh 1992, Wright 2003). My study is concerned with possible plant community consequences of fragmentation-induced changes in mammal populations. Specifically, I focus on mammalian seed predation, which is a crucial filter in the transition from dispersed seed to established seedling (Harms *et al.* 2000) and helps set the template for future forest composition, structure, and spatial patterns. Indeed, seed predation produces higher mortality rates than at any other stage of forest regeneration (Muller-Landau *et al.* 2004).

Large ungulate seed predators, in particular, have the potential to consume and destroy enormous quantities of seeds (Bodmer 1991). Bodmer (1991) found that fruit makes up 59% and 66% of the diets of collared (*Tayassu tajacu*) and white-lipped peccary (*T. pecari*), respectively, and 81% of red brocket deer's (*Mazama americana*) diet. *T. pecari* alone can account for 50% of all terrestrial mammalian granivore biomass; indeed, during a natural local extinction of *T. pecari* at Cocha Cashu Reserve, seed survival close to mother trees in two palm species increased between 5000 and 6000% (Wyatt and Silman 2004). Further, peccaries and deer (Cervidae) destroy most of the seeds that they consume (Bodmer 1991).

The consequences of extirpation of such large frugivores can be extreme. Research in the highly defaunated Los Tuxtlas rainforest of Veracruz, Mexico (Dirzo *et al.* 2007, Dirzo and Miranda 1991), has evinced a striking pattern of differential effects on vegetation. In mammal exclusion experiments, complete-exclusion cages produced a small-seed survival rate 30-fold greater than that of seeds left in the open; survival proportion of large seeds, in contrast, was only 2.3 times higher under protection from predators, and on average was much higher than that of small-seeds. Dirzo *et al.* (2007) conclude that the absence of large seed predators has greatly improved survival of large seeds (their preferred prey), while an abundance of small rodent granivores (Sanchez-Cordero 1993, Mendoza 2005), possibly due to the extermination of top carnivores, has led to extreme predation on small-seeded species (their preferred prey). Such a bias can translate to dominance by large-seeded species and reduced diversity in the seedling layer (Dirzo and Miranda 1991, Wright *et al.* 2007) and even in the adult tree community (Putz *et al.* 1990).

I assessed mammalian seed predation at both a faunally intact, premontane wet forest and a similar forest depauperate of large mammals. At my defaunated study site, all five species of large terrestrial herbivores once common in the region are currently rare or extinct (Pacheco *et al.* 2006) (table 2.1). I was most interested in the direct effects on seed predation of the loss of these mammals, which comprise ungulates in the families Tayassuidae, Cervidae, and Tapiridae. I was also interested in the potential indirect effects of mammal extinction on seed predation, via what Wright (2003) terms compensatory mechanisms, which often result when release from predators and/or competitors frees remaining small mammals to reach great abundances. At the defaunated site, the absence of top carnivores in the Felidae and of

competing seed predators may have spurred population growth, and seed predation pressure, of small rodents (Muridae, Echimydae, Sciuridae) and even medium-sized caviomorphs (Central American agouti, *Dasyprocta punctate*; lowland paca, *Agouti paca*).

I conducted seed predation trials on a variety of plant species and in three levels of mammal exclusion: one open treatment and two selective-exclusion treatments. I predicted that (1) large-seeded species would experience lower predation rates at the defaunated site than at the faunally intact site; (2) small-seeded species would experience higher predation rates at the defaunated site; (3) seed predation rates would differ more between open and partial-exclusion treatments at the intact site than at the defaunated site; and (4) seed predation would focus on small-seeded species in exclosures passable to only small mammals, and on medium and large seeds in open plots and exclosures permitting small and medium mammals.

Several factors set my seed predation study apart from the majority of previous such investigations. To my knowledge, my study is the first to apply mammal exclusion treatments to seed predation studies at both a continuous forest and a defaunated fragment. I also repeated my study during the same season (July-September) in two consecutive years, whereas many studies have relied on only a single season's data (Holl and Lulow 1997, Osunkoya 1994, Myster and Pickett 1993). Rather than use a typically small number of plant species (≤ 3 ; Asquith *et al.* 1997, Beck and Terborgh 2002, Terborgh and Wright 1994), I utilized 14 species, across two orders of magnitude in seed mass, in my trials. And, finally, I performed this work in mid-elevation, premontane wet forest, which stands apart from a literature of seed predation studies severely biased toward lowland rainforest ecosystems.

Methods

Sites

I evaluated seed predation in two tropical premontane wet forests of southern Costa Rica (Coto Brus County) (figure 2.1). One of my sites, the forest of the Las Cruces Biological Station (LCBS), comprises some 250 ha of forest, about 200 ha of which are primary (figure 2.2). The surrounding landscape is a matrix of pasture containing myriad small forest fragments. LCBS has grown increasingly isolated as a large forest fragment since the 1950's, when non-native human settlement spurred accelerating forest destruction, until today, when forest covers only 27% of the landscape within 15 km of the Reserve (Daily *et al.* 2003) (figure 2.3). LCBS contains premontane wet forest (Holdridge *et al.* 1971, Kohlmann *et al.* 2010), with elevations between 1000 m and 1450 m above sea level (ASL). LCBS has a mean annual temperature of 22° C and annual precipitation of about 3500 mm, most of which occurs from May through November, with a pronounced dry season from January through March (Daily *et al.* 2003).

My other site is about 20 km north of LCBS and occurs within the 10,000 ha of Las Alturas (LA), a privately owned reserve that retains most of its cover, the majority of which is primary forest (figure 2.4). LA, in turn, is contiguous with nearly 600,000 ha of mostly unbroken forest contained in La Amistad Biosphere Reserve (Costa Rica and Panama). My study area occupies the lower slopes of the reserve, also premontane wet forest (Holdridge *et al.* 1971, Kohlmann *et al.* 2010). While climatological data have not been taken at the LA site, models predict a mean annual temperature of about 20°C and annual precipitation between 3000 and 4000 mm (Barrantes *et al.* 1985)

My experiments required two sites that share in common as many major environmental and ecosystem attributes as possible, but with a pivotal difference: one should be defaunated, and the other, “control” site, should retain its native fauna. There is no accessible, extensive, faunally intact forest in the immediate vicinity of LCBS. However, LA and LCBS share similar climate, elevation, topography, and inceptisol soil substrates; have similar forest structure; and harbor many of the same woody species (see Chapter 4 of this thesis for a more detailed community comparison).

Mammals in the study areas

The mammal faunas of the two sites are starkly different. LA is contiguous with an extensive intact forest ecosystem and therefore possesses a virtually complete fauna. Among large herbivores, I know that collared peccaries (frequent observation) and deer (*Odocoileus virginianus* and/or *Mazama Americana*) (scat) are present in my study area within LA. Tapirs (*Tapirus bairdii*) are known to occur elsewhere within LA and may or may not visit my study area. LCBS, on the other hand, stands apart as a medium-sized fragment in a landscape of cattle pasture and mostly small (<25 ha) forest fragments. Due to its size and a legacy of hunting by locals, LCBS lacks terrestrial herbivorous mammals larger than the paca, as well as all large carnivores and most large arboreal mammals (Pacheco *et al.* 2006; LCBS station director R.A. Zahawi, personal communication; see table 2.1).

Mammal exclosures

I sought to test how mammals of differing sizes affect seed survival, and therefore divided the terrestrial mammalian fauna into three size categories. Small mammals mostly comprise small rodents such as mice and rats (Muridae, Echimydae). Medium mammals include mammals larger than rats, up to the size of the larger caviomorph rodents (agoutis, pacas) and coatimundis (*Nasua narica*). Any mammal larger than these qualifies as large.

I used exclosures to exclude different size categories of mammals : one that allowed entry only to small terrestrial mammals (hereafter, the SMALL treatment); one that allowed entry by small- and medium-sized mammals (SMALL+MEDIUM); and a control treatment, which allowed entry by all mammal size classes (ALL). All exclosure treatments were applied to 1 m x 2 m plots. SMALL exclosures consisted of 1 cm-aperture mesh fence, between 0.5 (LCBS) and 1 m (LA) in height, wrapped around bamboo poles placed at the plot corners. I cut multiple 7 cm x 7 cm openings into the bottom of the fencing (two each on short sides, three each on long sides) to allow access to small mammals. I constructed SMALL + MEDIUM exclosures by placing several wraps of barbed wire around corner bamboo poles, leaving ~25 cm of space below the bottom wrap,. All bamboo poles were buried deep enough to prevent upheaval by local mammals (up to 0.7 m deep). All structures also had open tops, allowing equal access at both sites to flying and climbing mammals and birds. Finally, ALL plots had no structure, but were marked with 4 small plastic or metal stakes at the corners.

I had expected SMALL+MEDIUM and ALL treatments to produce similar survival curves at LCBS, where there are no large mammals to differentiate the two treatments. To the contrary, survival curves showed noticeably higher seed predation under the ALL treatment.

Pearson's chi-square tests at approximately three weeks ($X^2 = 12.317$, $p < 0.001$) and five weeks ($X^2 = 18.034$, $p < 0.001$) after seed placement confirmed that SMALL+MEDIUM plots experienced less predation than ALL plots. I suspect that the SMALL+MEDIUM structure itself had a deterrent effect on potential medium-sized seed predators, and I therefore excluded the treatment level from further analyses.

Study design

Seed predation exclosures were arrayed over approximately 100 ha areas of forest at each site, within elevation bands encompassing 1150 m to 1300 m ASL. I employed a block design within each site. Blocks were chosen such that the distribution of elevations, slopes, and distance to forest edge was similar between sites. Eight blocks per site each contained one randomly located array of three plots (one plot for each exclusion treatment). All arrays were placed under closed-canopy primary forest and at least 50 m from the nearest forest edge. Each plot array was at least 200 m away from all other arrays, in order to minimize non-independence due to the same seed predators' visiting multiple plots over the course of the experiment.

I used a split-plot design within sites to organize two treatment factors: size class of seed predators (exclosure treatments) and seed species. Thus, I assigned one exclosure treatment to each of three 1 m x 2 m plots in an array, constituting the "among" factor. Each plot contained four to six species of seeds at any one time ("within" factor). The three plots of an array were arranged in an L-shaped configuration with approximately 20-m sides (Figure 2.5).

To augment the number of species and seeds that could be studied, I later established a second set of 8 blocks at each site, independent of the first set. Plot arrays in this second set adhered to the same internal spacing rule (>200 m apart), but were placed a minimum of 50 m from the arrays of the first set. This was acceptable because no species was ever placed in both sets of plots at the same time, thus maintaining the 200 m spacing at the species level. Most importantly, the second set of blocks differed in that each “array” consisted only of a control (ALL) plot; hence the ALL treatment has much higher replication than other exclusion treatments in my analyses.

Seed collection and processing

I collected seeds from several regional sites during the summers of 2009 and 2010, as they became available. Species were chosen based on several criteria. I only used seeds from woody, non-epiphytic species. Seeds also had to be abundant and accessible enough for us to collect the necessary quantity for a given species (200-600). When possible, seeds of a given species were collected from at least 2-3 source trees. Finally, target species also had to be native to the forests at my sites, even if not collected from those sites (table 2.2).

Seeds were collected either in intact fruits or as bare seeds, having already been cleaned by primary dispersal agents. Both fruits and seeds were kept slightly moist at room temperature until final cleaning and placement. One to two days before placement, I cleaned all seeds in a cold water bath using rubber gloves, removing all remaining exocarps as well as human oils and scents (figure 2.6). Endocarps, when present, were generally left on the seeds, although the bony endocarps of *Calatola costaricensis* were removed in order to encourage

mammalian predation. I only used those seeds with no visible signs of insect attack or decay, and discarded those that floated in the water bath due to possible infestation.

Seed monitoring

I tracked seed fates for four to twelve weeks during the summers of 2009 and 2010. Plots contained four to six seed species, arranged in monospecific clusters spaced evenly around the perimeter of the plot. The number of seeds per cluster varied by species, increasing with decreasing mean seed mass (table 2.2). To facilitate tracking of seeds and prevent seeds' rolling down the often steep slopes in my study areas, I placed each group of seeds into a small mesh basket, or depot. Depots were constructed either solely of fine mosquito-screen mesh folded into a shallow square basket (1 cm-tall sides); or from 10 cm-wide, 1 cm-tall plastic rings with mesh glued to them as a floor. All depots were placed at least 30 cm from the plot perimeter, to preclude animals' "reaching" in to take seeds from outside the plot, and seed groups were arranged haphazardly within a plot with respect to seed species.

Seed tracking durations depended on feasibility and on the availability of new seed crops. I was able to track one set of four species for almost 12 weeks in summer 2009. I tracked most species for at least five to six weeks, and checked seeds every four to seven days. I considered a seed as predated if it had clearly been attacked or consumed (by mammals) at deeper than a surficial level, so as to kill the embryo (figure 2.7); or if it could not be found after a brief search. In searching, I removed (and replaced) leaf litter within about 15 cm of depots and farther out in down-slope directions, as well as scanned the litter surface of the entire

1 m x 2 m plot. I ignored insect predation, which was minimal. All intact seeds remaining at the end of the monitoring periods were censored in my survival analyses.

Camera traps

To identify the seed predators visiting my plots, I employed “heat-in-motion”-detecting digital cameras (model Cuddeback® Capture IR™). I placed cameras near four randomly chosen plots, two ALL and two SMALL+MEDIUM, at each site, positioned for optimal photography of visitors to seed depots within respective plots. The cameras were set to a minimum between-photographs time lapse of 30 seconds and captured color or black-and-white images, depending on light conditions. I monitored seed predators throughout the duration of my 2010 experiments.

Statistics

I performed marginal Cox proportional hazards (MCPH) survival analysis, using the covs(aggregate) option within the PHREG procedure, in SAS® 9.2. MCPH analysis corrects for non-independence of failure times (i.e. predation times) among clustered study individuals (Paul Allison, personal communication), which traditional survival analyses eschew, by assigning a unique identifier (ID) number to each group of individuals and then treating ID as a covariate in the Cox survival analysis (Lee *et al.* 1992). In my experiments, I presumed that predation risks of seeds within the same depot were not independent. However, whereas similarly designed seed predation studies have previously resorted to less powerful analysis techniques, or have simply run survival analyses with an unstated and unproven assumption that seeds

within a cluster are independent, the MCPH method allowed us to accurately analyze the survival of individual, though non-independent, seeds. Mine is the first study of which I am aware to apply this powerful method to seed survival data.

Year, site, seed size, and exclusion treatment served as explanatory variables in the marginal Cox regressions, i.e. survival analyses. Seed size in tropical forests can span five to six orders of magnitude (Coomes and Grubb 2003). Based on fresh masses, seed size at my sites broke down naturally into three categories (small, medium, large) spanning two orders of magnitude (figure 2.8).

I ran Cox regressions in conjunction with a stepwise model selection algorithm to create a global model of the entire data set. I further explored significant interactions by applying the same procedure to each level of the interacting terms. I focus on p-values and hazard ratios (HR) of model variables in my outputs, where a hazard is the per-capita risk of failure (predation) over a specified time under a certain treatment. In my analyses, hazard ratios represent the *mean* ratio of hazards for two treatment levels over the duration of the experiment (Allison 1995), and are reported if significant according to 95% Wald robust confidence intervals.

I also performed Pearson's chi-square and Fisher's exact tests on count data from camera trap imagery, in order to assess the distribution of visitation among sites, exclusion treatments, and animal classes.

Results

I monitored 3167 seeds distributed among 516 depots, representing 14 species, between 2009 (1104 seeds) and 2010 (2063). In total, 51.3% of seeds (1624 seeds) experienced mammalian predation during my trials, the remainder being censored at the ends of respective trials. The percentage of seeds predated was remarkably similar between years, at 51.5% (569 seeds) in 2009 and 51.1% (1055) in 2010.

Marginal Cox regression models

I created a global marginal Cox regression model (Wald chi-square=103.265, $p < 0.0001$) and, based on one significant interaction of explanatory variables, subsequently built five additional subset models (M1 through M5). Stepwise selection on the global data set excluded seed size and year as main effects but found site ($p < 0.0001$) and exclusion treatment ($p = 0.0050$) to have significant main effects. The effect of seed size, while not significant overall, varied significantly with site ($p = 0.015$), leading us to create the subset models for respective levels of site and seed size (models were created across both dimensions in order to calculate all relevant hazard ratios) (table 2.3).

Site

LA experienced greater seed predation rates than LCBS in the overall model ($p < 0.0001$, LA/LCBS HR=1.969). 60.7% of 1610 seeds were predated at LA, while only 41.6% of 1557 seeds were predated at LCBS. Site effect also varied across seed sizes (site*size, $p = 0.015$), with significant HR's of 2.600 (medium) and 2.010 (small) and no significant effect on large-seed

predation in the global model (site HR's always given as [LA hazard]/[LCBS hazard]). Site effects in M4-M6 corroborate these results for large (HR=1.246, not significant), medium (2.543), and small (1.969) seeds (table 2.3).

Exclusion treatment

A substantially greater fraction of seeds was predated in ALL exclusion treatment (60.5% of 2057 seeds) than in SMALL treatment (34.1% of 1110 seeds). Predation risk was greater in ALL than in SMALL treatment in the global model (M1, $p=0.0050$, ALL/SMALL HR=2.691; table 2.3)

Seed size

The fraction of seeds predated decreased marginally with decreasing seed size as 56.2% of 633 large seeds, 52.6% of 876 medium seeds, and 48.7% of 1658 small seeds. Seed size had no main effect in the global model (1) but interacted with site ($p=0.0153$). From subset models M2 and M3, predation rates did not vary among seed sizes at LA, but did vary at LCBS, where large seeds had greater predation risk than small (large/small HR=1.602) or medium (large/medium HR=1.624) seeds, the latter two experiencing the same predation risk (medium/small HR=0.987) (table 2.3)

Year

Study year did not occur as a significant factor in the global model, so effects of other treatment factors are statistically consistent across years.

Camera traps

I recorded 136 distinct animal visits across eight plots, where two visits of the same species were considered distinct when they occurred more than 15 minutes apart (sample photographs: see figure 2.9). As expected from seed survival data, far more seed predator observations occurred in ALL plots (115) than in SMALL+MEDIUM plots (21). I recorded no large mammal, including collared peccary, visitation at LA. I also photographed far more animal visitors at LCBS than at LA ($X^2=8.767$, $df=1$, $p = 0.003$) (figure 2.10), although one camera at LA (SMALL+MEDIUM plot) stopped capturing images three weeks early due to malfunction.

Caviomorphs (agoutis+pacas) and ground-dwelling birds (e.g. tinamous, ground-doves) were the most important visitors both in the medium animal class and overall (figure 2.10), and were equally important to each other at both sites (Fisher exact test: $p = 0.424$). Further, site had no effect on the proportion of visitations, among medium animals, accounted for by either caviomorphs (Fisher exact: $p = 1.000$) or ground birds (Fisher exact: $p = 0.147$).

Two caveats are in order here. First, due to the low replication of photographed plots at both sites, all results should be viewed with caution. Second, small rodents at both sites may be underrepresented relative to other animal classes, because my cameras are triggered by “heat in motion”. Small rodents emit less heat (infrared radiation) than larger animals, and therefore probably have lower distance and higher speed-of-motion thresholds for triggering the camera sensors.

Discussion

I expected LA to experience greater seed predation rates than LCBS due to the presence of a large herbivore class at LA. Peccaries (*Tayassuidae*) prefer seeds/fruits to other dietary components (Bodmer 1991) and may constitute at least 50% of granivore biomass in tropical forest ecosystems (Wyatt and Silman 2004). While evidence exists for compensatory effects after removal of large mammals (Wyatt and Silman 2004, Fonseca and Robinson 1990), at least one study has found that removal of large game species can increase seed survival on the forest floor by an order of magnitude (Wright *et al.* 2000; Wright & Duber 2001). I did not expect small- and medium-sized granivores at LCBS to fully compensate for the loss of the enormous seed consumption capabilities of collared peccaries and other large seed predators. Indeed, seeds at LA had approximately twice the risk of predation as seeds at LCBS over the course of my study.

However, I also expected that the greatest site difference would occur for large seeds, because large-bodied seed predators often prefer larger-seeded species (Bodmer 1991, Wyatt and Silman 2004, Dirzo *et al.* 2007). An analysis of site effect within each seed size, however, offers contrary, and potentially key, insights. First, site has no effect on predation of large seeds, despite the commonness at least of collared peccary (among large seed predators) at LA. On the other hand, small and medium seeds experienced significantly greater predation risk at LA than at LCBS. The fact that small- and medium-seed predation patterns match the site effect found in the global model indicates that patterns of predation on these smaller seeds drives elevated overall predation at LA.

Surprisingly, site effect did not vary between exclusion treatments. I had expected that site effect would be reversed between the two exclusion treatments; specifically, that greater large herbivore abundance at LA would lead to higher seed predation rates in ALL treatments than at LCBS, and that elevated abundances of small rodents at LCBS would result in greater predation risk at that site in SMALL treatments. However, predation risk in the global model was significantly greater at LA than LCBS regardless of exclusion treatments (HR=1.969), indicating that seed predation by even small rodents was greater at LA.

Why should small mammals be less important seed predators at the defaunated site? In response to this puzzle, I can only suggest that idiosyncratic and/or historical site differences are at work. LCBS seems to harbor rather low abundances of granivorous mice and rats (Bob Timm, personal communication; Graham, unpublished trapping data), and no such mammals were caught in camera traps at LCBS, compared to five occurrences at LA. It is unclear why small rodent populations have not responded to the suspected paucity of large carnivores. Regardless, this finding emphasizes the fact that results of defaunation studies are highly dependent on the particulars of the study system, especially the composition of the residual fauna and the operation of compensatory behaviors (Asquith *et al.* 1997, Adler 1995).

Overall, exclusion treatment affected risk of seed predation ($p=0.0050$). ALL experienced 2.691 times more predation than SMALL treatment; that is, medium and large mammals were responsible for 1.691 times more predation risk than were small mammals, or about 63% of mortality risk. This is not at all surprising, considering that ALL treatment allows predation by two *additional*, larger animal size classes than SMALL. That said, small mammals accounted for a surprisingly large fraction of seed predation, given that large terrestrial

mammal biomass typically exceeds biomass of medium or small mammals in neotropical forests by large margins (400, 57, and 14 kg/km², respectively, in faunally intact forest; Janson and Emmons 1990).

I previously noted that large-seed predation risk is similar between sites, despite the lack of large herbivores at LCBS. Coupled with evidence that seed predation (including that of large seeds) is driven by medium to large mammals, and the notion that larger mammals prefer larger seeds (Bodmer 1991), this suggests that the combined, medium- to large-sized mammal group exerts similar predation pressures between sites.

I can think of two conceivable, non-mutually exclusive explanations for this surprising relationship. First, other animals may be compensating for the lack of large seed predators at LCBS. Given evidence from the camera traps, the animals most likely to be compensating are large caviomorph rodents and ground-dwelling birds. Rodent seed predation pressure was amplified in response to large-frugivore absence from Amazonian disturbed sites (Wyatt and Silman 2004)

Second, collared peccaries, while present, may simply not have visited my seed predation plots at LA. Two lines of reasoning support this second hypothesis. As Paine and Beck (2007) point out, small mammals, which are generally ubiquitous (Beck *et al.* 2004), may effectively “sample” the forest understory better than do large herd mammals, which have enormous ranges and may visit any particular area infrequently (Beck 2006). Indeed, Beck and Terborgh (2002) uncovered a “hit-or-miss” effect of peccary predation on large seed arrays, supporting the idea that large herd animals sample potential fruit resources unevenly over space and time.

The Janzen—Connell (JC) model, which predicts that density-dependent seed predation will lead to greater seedling recruitment farther from con-specific adults, may also be an important factor (Janzen 1970; Connell 1971). While reviews by Hammond and Brown (1996) and Wright (2002) conclude that only invertebrate seed predation follows the JC model, two studies of peccary-palm interactions strongly indicate density-dependence in such systems. Wyatt and Silman (2004) found negative distance-dependence, with respect to mother trees, of seed predation by white-lipped peccaries on two palm species; moreover, the median distance (from mother trees) of surviving seeds was 8.5 to 9.3x higher at a disturbed site lacking the peccaries. Perhaps most relevant is Beck and Terborgh's (2002) research showing that predation rates by white-lipped peccaries on *Astrocaryum murumuru* seeds were greater in groves of the palm than around solitary palms, as well as greater in large seed arrays (21-40 seeds) than in small arrays (≤ 20 seeds). They attribute this pattern to the metabolic inefficiency of foraging over small resource patches.

Summary and conclusions

From my results of site and site*seed size analyses, I am left with the surprising interpretation that predation upon small and medium seeds is the dominant factor driving greater overall predation rates at LA than at LCBS. One explanation might be the state of small mammal faunas of the two sites. Dirzo *et al.* (2007) argue that small-mammal preference increases with decreasing seed size. I found that small mammals alone exert a substantial portion (37%) of seed predation pressure across seed sizes. Therefore, the small mammal size class may help largely drive the fates of small seeds. Moreover, recall that LCBS is strangely

depauperate of granivorous mice and rat, so these mammals may destroy many more seeds at LA than at LCBS. Again, this underscores the fact that results of defaunation studies are highly dependent on the particulars of the study system, especially the composition of the residual fauna and the operation of compensatory behaviors (Asquith *et al.* 1997, Adler 1995).

My work also suggests that medium-sized mammals and ground birds may be the predominant predators of *isolated* groups of large seeds at both my sites. My seeds were placed in small clusters with the idea of mimicking the piles that seeds often fall into after being dispersed by frugivorous birds and bats. Such primary dispersal, when it occurs away from the mother tree, plays a crucial role in many tropical forests in the escape of seeds from predation by invertebrates and vertebrates alike. Among vertebrates, this may be especially true for the largest of frugivores. As Paine and Beck (2007) point out, small and medium sized rodents are ubiquitous in tropical forests and forage over relatively small areas, so they are more likely to find small seed groupings than are widely ranging large frugivores. My finding fits well with such size-dependent spatiotemporal patterns of seed predation.

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Table 2.1: Selected species from the historical fauna of the LCBS region, and current statuses.

Species	Common name	Status	Primary guild(s)
<i>Mustela frenata</i>	Long-tailed weasel	common	carnivore
<i>Urocyon cinereoargenteus</i>	Gray fox	common	carnivore
<i>Canis latrans</i>	Coyote	rare	carnivore
<i>Leopardus pardalis</i>	Ocelot	rare	carnivore
<i>Puma concolor</i>	Puma	rare	carnivore
<i>Panthera onca</i>	Jaguar	extinct	carnivore
<i>Didelphis marsupialis</i>	Common opossum	abundant	omnivore
<i>Nasua narica</i>	White-nosed coati	common	omnivore
<i>Procyon lotor</i>	Raccoon	common	omnivore
<i>Myrmecophaga tridactyla</i>	Giant anteater	extinct	insectivore
<i>Tamandua mexicana</i>	Northern tamandua	rare	insectivore
<i>Mazama americana</i>	Red brocket deer	rare	folivore/frugivore
<i>Odocoileus virginianus</i>	White-tailed deer	rare	folivore/frugivore
<i>Tapirus bairdii</i>	Baird's tapir	extinct	folivore/frugivore
<i>Tayassu pecari</i>	White-lipped peccary	extinct	seed predator/ frugivore
<i>Tayassu tajacu</i>	Collared peccary	rare	seed predator/ frugivore
<i>Sciurus granatensis</i>	Red-tailed squirrel	abundant	seed predator/ disperser
5 spp. (Muridae)	mice/rats	abund/common	seed predator/ disperser
7 spp. (Muridae, Heteromyidae)	mice/rats	rare/unknown	seed predator/ disperser
<i>Cuniculus paca</i>	Lowland paca	common	seed predator/ disperser
<i>Dasyprocta punctata</i>	Central Am. Agouti	common	seed predator/ disperser
2 spp. (Echimyidae)	caviomorph rats	unknown	seed predator/ disperser

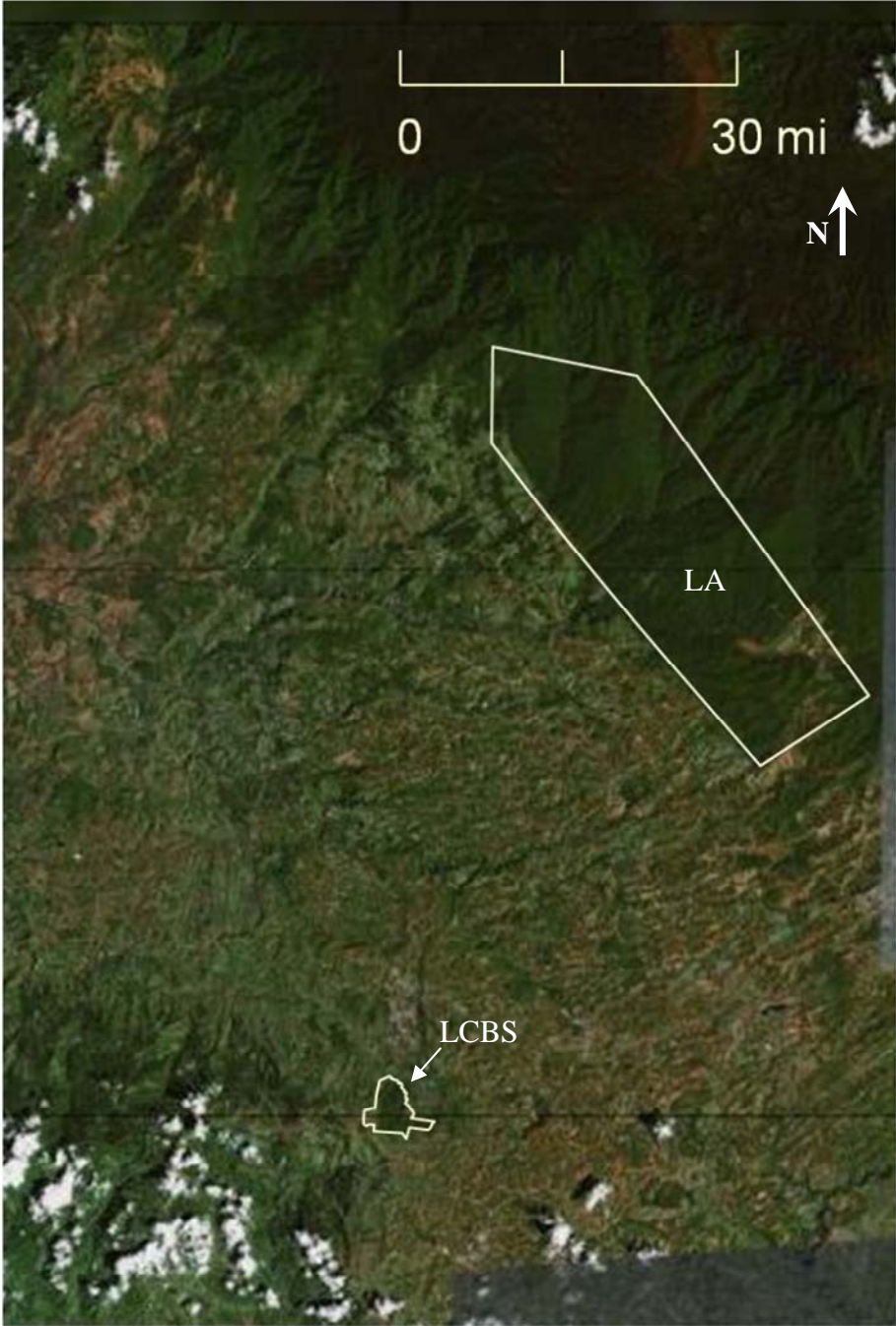


Figure 2.1: Landscape situation and relative sizes of the two study sites

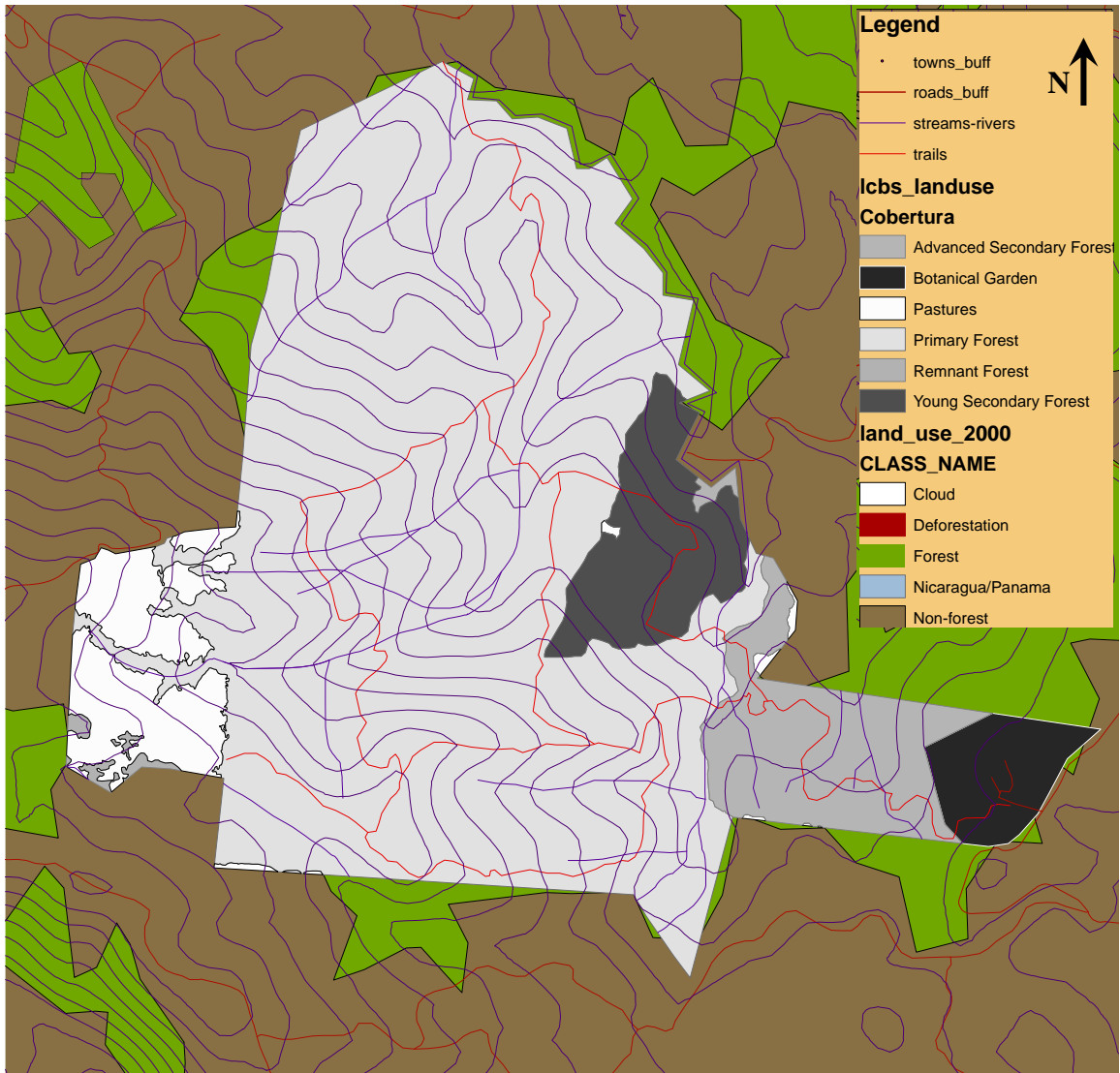


Figure 2.2: Topographic map of LCBS showing trails and cover types.

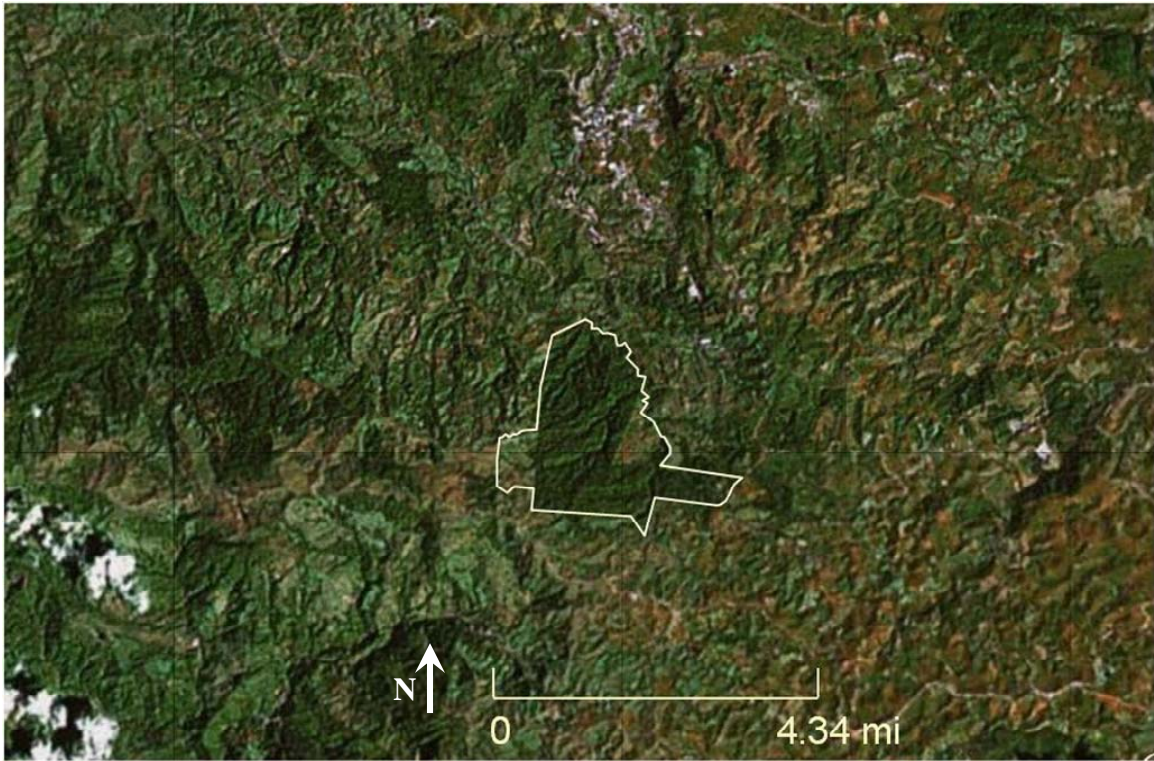


Figure 2.3: Satellite imagery of LCBS. Note deforestation, especially east of Station.

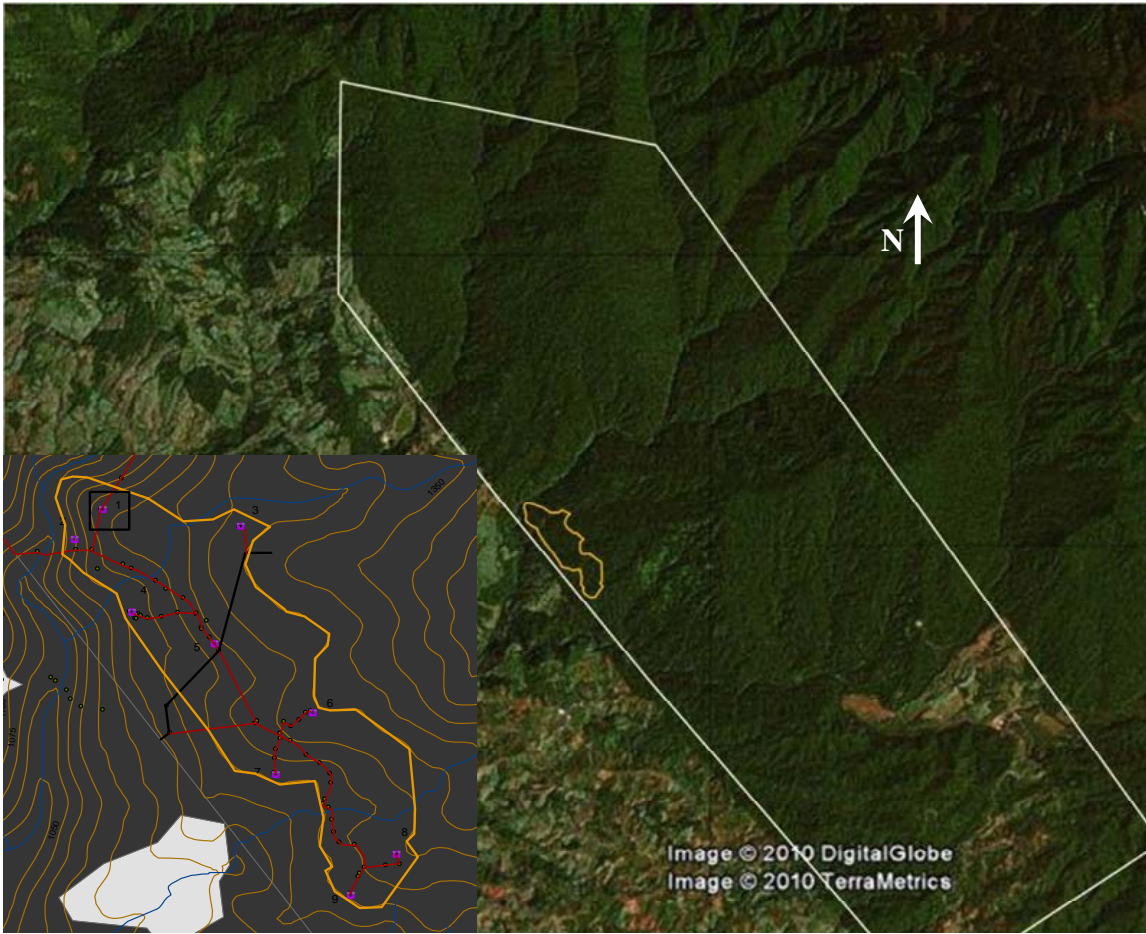


Figure 2.4: Satellite imagery of LA (inset: topographic map of study area). Thick orange line delineates study area; thin orange lines are contours; trails are drawn in red, streams in blue.

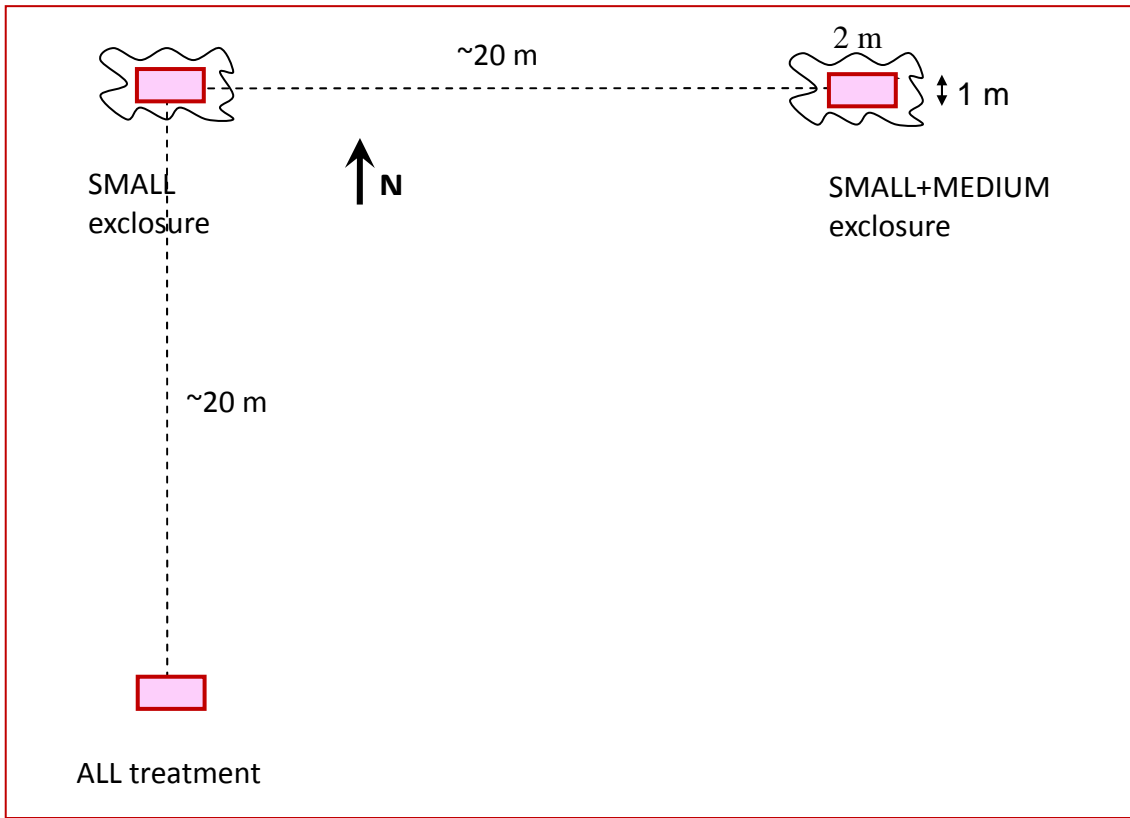


Figure 2.5: Experimental plot layout within a block.

Table 2.2: Summary of woody plant species used in seed predation experiments.

Species	Family	Year	Seed mass (g)	Seeds/depot
			[mean ± st.error]	
<i>Meliosma idiopoda</i>	Sabiaceae	2010	0.19 ± 0.01	10
<i>Trophis mexicana</i>	Moraceae	2009	0.2 ± 0.01	10
<i>Chrysoclamys glauca</i>	Clusiaceae	2010	0.21 ± 0.01	10
<i>Chamydorea crucensis</i>	Arecaceae	2009/10	0.28 ± 0.01	10
<i>Erythrina costaricensis</i>	Fabaceae	2010	0.35 ± 0.01	12
<i>Ocotea sp.</i>	Lauraceae	2010	1.23 ± 0.06	6
<i>Persea albida</i>	Lauraceae	2009	1.23 ± 0.06	6
<i>Tapirira guianensis</i>	Anacardiaceae	2009	1.54 ± 0.07	4
<i>Persea albida</i>	Lauraceae	2010	1.67 ± 0.06	6
<i>Symphonia globulifera</i>	Clusiaceae	2010	1.8 ± 0.04	7
<i>Meliosma glabrata</i>	Sabiaceae	2010	1.99 ± 0.1	4
<i>Tapirira guianensis</i>	Anacardiaceae	2010	2.38 ± 0.05	4
<i>Otoba novagranatensis</i>	Myristicaceae	2010	4.32 ± 0.07	5
<i>Ocotea endresiana</i>	Lauraceae	2009	4.56 ± 0.08	4
<i>Pseudolmedia mollis (a)</i>	Moraceae	2009	6.7 ± 0.3	4
<i>Pseudolmedia mollis (b)</i>	Moraceae	2009	8.49 ± 0.3	4
<i>Calatola costaricensis</i>	Icacinaceae	2010	15.17 ± 0.37	3



Figure 2.6: Seeds of several woody plant species used for seed predation experiments. Top panel (L to R): *Senna papillosa* (data not analyzed), *Chrysoclamys glauca*, *Erythrina costaricensis*, *Symphonia globulifera*, *Otoba novagranatensis*, *Calatola costaricensis*. Bottom panel (L to R): *Persea albida*, *Ocotea endresiana*, *Pseudolmedia mollis*.



Figure 2.7: Rodent damage to a *Calatola costaricensis* seed (without endocarp).

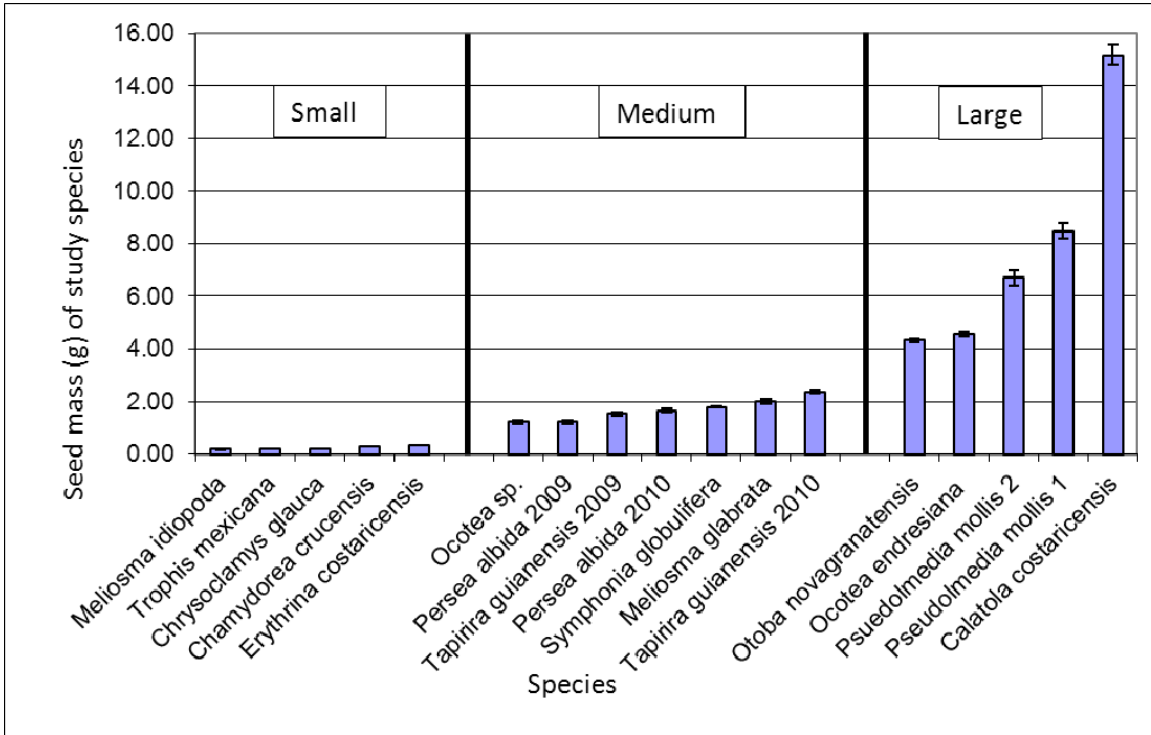


Figure 2.8: Seed mass categories used in predation data analysis. Error bars represent standard errors.

Table 2.3: MCPH models created using stepwise selection procedure. All included terms significantly improved the global model fit during stepwise selection ($\alpha=0.05$); only asterisked terms are individually significant in the presence of other model terms ($\alpha=0.05$). Treat stands for exclusion treatment; size indicates seed size. Chi-squares are sandwich-based Wald values.

Name	Conditions	Model terms	χ^2	P
M1	Global data-set	site*, size, treat*, site-size*, size·treat	103.265	<0.0001
M2	LA only	size	2.538	0.281
M3	LCBS only	size*	7.954	0.019
M4	Large seeds only	site	1.456	0.228
M5	Medium seeds only	site*	26.221	<0.0001
M6	Small seeds only	site*	15.062	0.0001

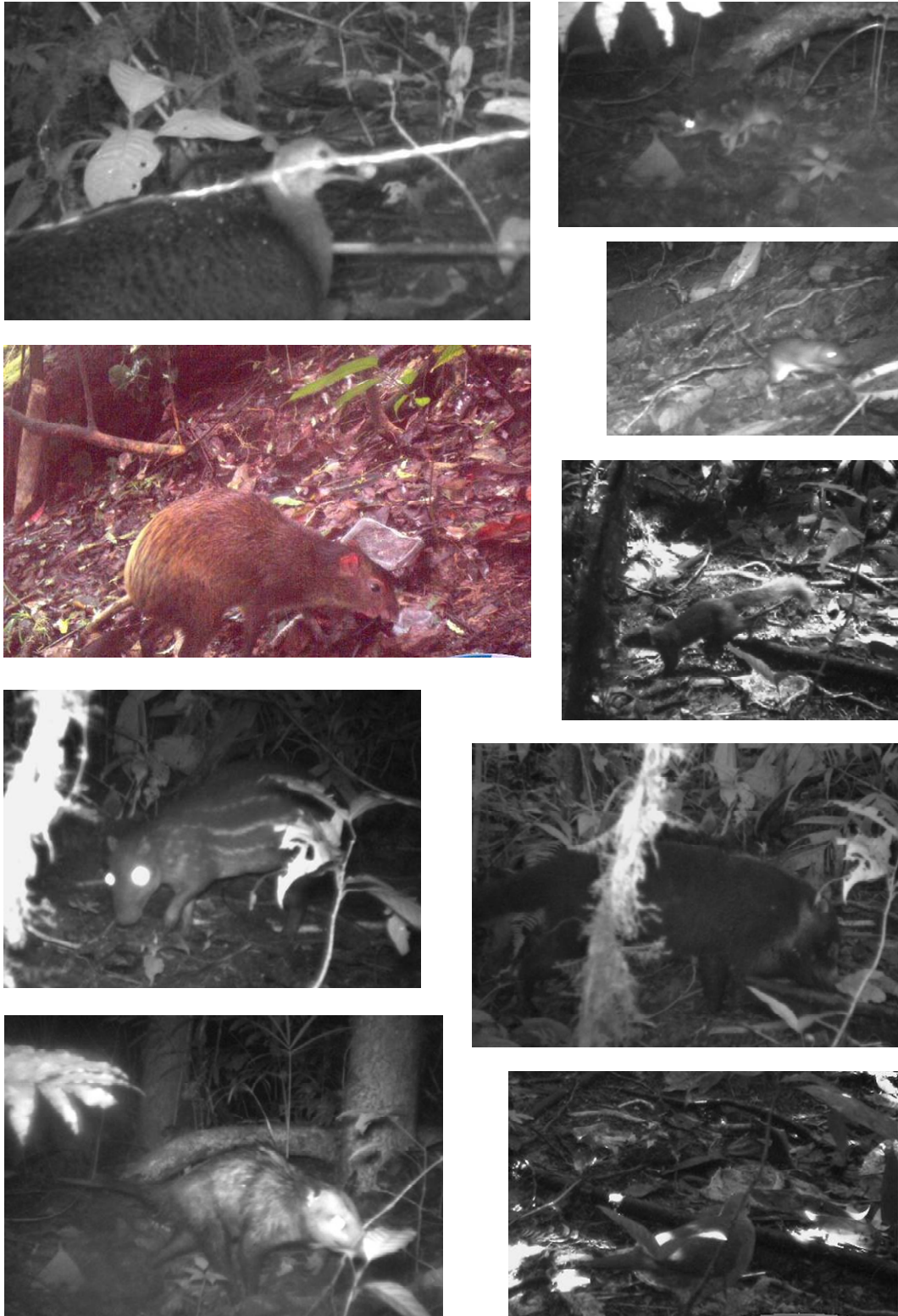


Figure 2.9: Animal visitors to seed predation plots: (CW from top-left) great tinamou, gray four-eyed opossum, rat, red-tailed squirrel, coatimundi, ground dove, common opossum, lowland paca, Central American agouti.

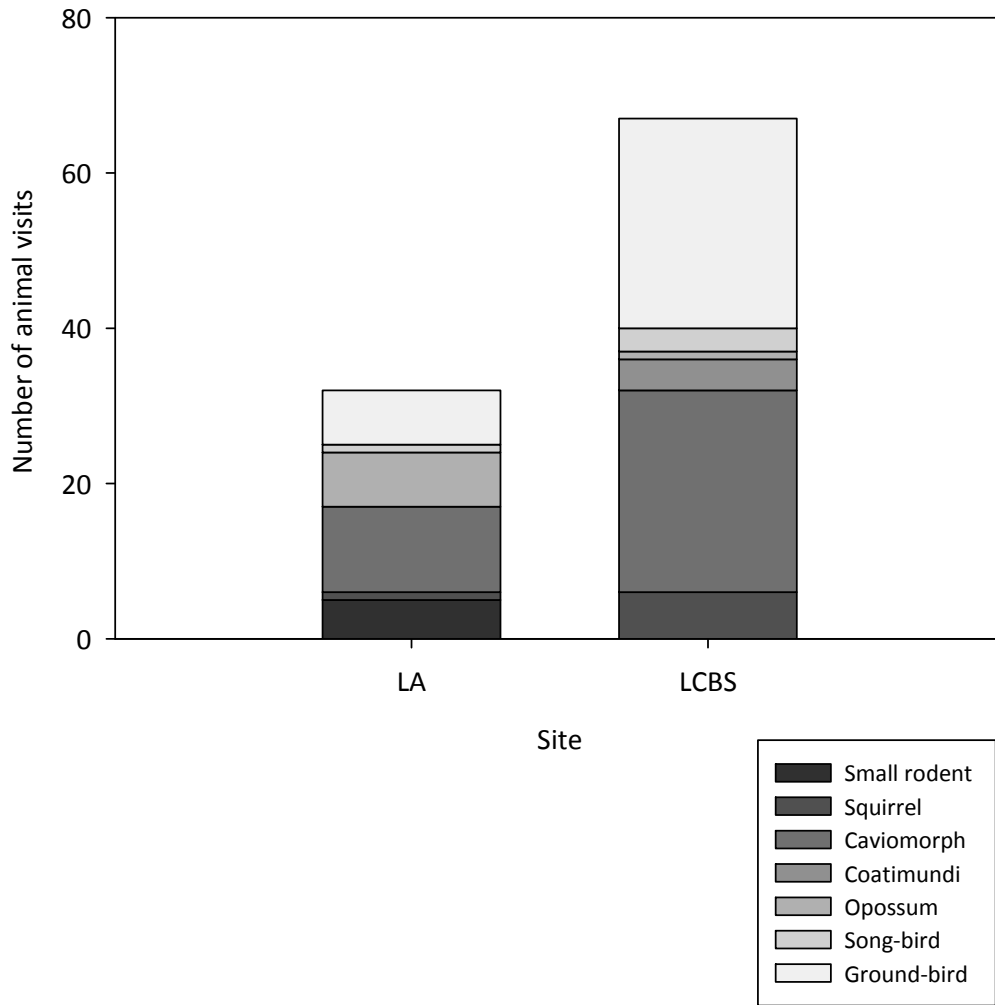


Figure 2.10: Distribution of visitors to plots among major animal categories.

CHAPTER 3

DEFAUNATED AND FAUNALLY INTACT PRIMARY, TROPICAL, PREMONTANE WET FORESTS

DEMONSTRATE ABSENCE OF LARGE-MAMMAL BROWSING EFFECTS²

² Graham, C. J. and C. J. Peterson. To be submitted to *Journal of Tropical Ecology*.

Abstract

Mammalian defaunation can have cascading effects through a forest ecosystem, including those mediated by the absence of extirpated herbivores. Herbivory by large mammals, in particular, is a major force in limiting seedling and sapling recruitment and structuring community composition. Mammalian herbivores in tropical forests are often polyphagous, thus killing or limiting growth of individual plant species in a non-density-dependent fashion. Therefore, removal of such herbivores, especially large-bodied ones, should markedly improve survival and recruitment into later stages of forest regeneration. I tested this hypothesis by establishing mammal exclusion treatments in a defaunated forest fragment and a faunally intact continuous forest. At both sites, I found no effect of either enclosure treatment on herbivory rates, plant growth, or seedling recruitment and mortality. Despite my somewhat limited sampling, this suggests that large herbivores, particularly collared peccaries and deer, exert little herbivory pressure at my premontane sites, a pattern that runs counter to accepted knowledge about neotropical lowland rainforests.

Introduction

Mammalian biodiversity is rapidly diminishing due to anthropogenic defaunation (Dirzo and Raven 2003, Ceballos *et al.* 2005). Defaunation, the loss of components of the fauna within an ecosystem, occurs throughout the tropics (Wright 2003). At smaller scales, recent research reveals a picture in which myriad mammal species have undergone drastic range contractions, going locally extinct over large parts of their original ranges (Ceballos & Ehrlich 2002).

Two major drivers of defaunation are hunting and forest fragmentation (Redford 1992, Peres 2001, Dirzo 2001). Large mammals are the most vulnerable to both human impacts (Cardillo *et al.* 2005), because hunters generally favor large-bodied mammals (Redford 1992, Bodmer *et al.* 1997, Peres 2000), and because their greater habitat requirements make them more sensitive to fragmentation (Dirzo 2001, Wright 2003). Consequently, differential defaunation usually proceeds along a size gradient (Dirzo *et al.* 2007), in which the suite of reduced or extirpated creatures grows to encompass smaller mammals as human impact increases (e.g. Peres 2000). Although I focus on fragmentation-induced defaunation, the consequences of the two mechanisms are often virtually the same.

Changes to the mammalian fauna of a forest may alter the plant community via numerous modes of plant-mammal interaction, not least of which is foliar herbivory (Emmons 1989, Terborgh 1992, Wright 2003). Foliar herbivory by mammals, i.e. consumption of vegetative plant parts (hereafter, used interchangeably with *herbivory*), is important in intact tropical forests, occurring in up to 29% of seedlings (Dirzo and Miranda 1991) and easily killing the often small, delicate plants (Wright 2003). Not surprisingly, then, herbivory decreases plant survival during early life-stages and helps determine future plant distribution and community composition (Coley and Barone 1996, Wright 2002, Krueger and Peterson 2006).

Almost universally, seedling survival (Coley and Barone 1996) and densities (Terborgh and Wright 1994) increase when freed from large-mammal herbivory. Experimental mammal-exclusion in previous investigations has produced increased seedling recruitment and survival (Ostfeld *et al.* 1997, Connell *et al.* 2005, Paine and Beck 2007, Wright 2003) as well as greater height-relative growth rates (Osunkoya *et al.* 1993, Wahungu *et al.* 2002). Natural “exclusion”,

via defaunation, has also produced dramatic shifts in understory vegetation. In a lowland rainforest in central Mexico, from which large-mammal browsers have been eliminated and medium browsers severely reduced, Dirzo and Miranda (1991) have observed dense seedling carpets and 0% herbivory of woody seedlings. Conversely, a faunally intact rainforest in southern Mexico evinced much higher rates of herbivore damage (29% of woody seedlings) and seedlings densities 2.3 times less than those found at the disturbed site (Dirzo and Miranda 1991).

I assessed mammalian herbivory in both a faunally intact premontane wet forest and a similar but fragmented forest depauperate of large mammals, posing the broad question, *how does the removal of large mammalian herbivores from a forest influence juvenile woody plant success?* At my defaunated study site, all five species of large terrestrial herbivores once common in the region are currently rare or extinct (Pacheco *et al.* 2006) (table 2.1). Further, foliage is a major dietary component of two of these (white-tailed deer, *Odocoileus virginianus*; Baird's tapir, *Tapirus bairdii*) (Bodmer 1990, Foerster 1998, Tobler 2002), while peccaries (collared, *Tayassu tajacu*; and white-lipped, *T. pecari*) can significantly elevate seedling mortality rates via trampling (Asquith *et al.* 1997; Dirzo and Miranda 1990; Wright and Duber 2001). There is potential for compensatory mechanisms (see Wright 2003) at my defaunated site, in that populations of small- and medium-sized rodents may undergo partial release from competition (with absent large herbivores) and/or predation (by absent top carnivores). Several studies have found that small and/or medium mammals can be more important than large mammals as seedling herbivores (Demattia *et al.* 2004, Asquith and Mejia-Chang 2005, Paine and Beck 2007). However, because of their extreme biomass advantage (Janson and

Emmons 1990), I hypothesized that the absence of large herbivores at the defaunated site should result in widely reduced foliar herbivory levels and improved juvenile (i.e. large seedlings and small saplings) woody plant performance.

Over a 14- to 16-month period during 2009 and 2010, I monitored naturally recruited juvenile, non-climbing, woody plants in partial mammal exclusions and in open controls. I endeavored to compare herbivory levels and plant performance among plants exposed to varying combinations of mammalian herbivore size classes. Given the status of large herbivores at the two sites, I predicted that mammal exclusion would have no effect at the defaunated site, but that, at the intact site, plants protected from mammals would see lower herbivory levels, higher growth rates, and increased recruitment than unprotected plants. Several factors set my herbivory study apart from the majority of previous such investigations. To my knowledge, my study is the first to apply mammal exclusion treatments to herbivory studies at both a continuous forest and a defaunated fragment. It also appears to be the first to apply multiple partial-mammal exclusion treatments to naturally-recruited woody plants. Finally, I performed this work in mid-elevation, premontane wet forest, which stands apart from a literature of tropical herbivory studies severely biased toward lowland rainforest ecosystems.

Methods

Sites

I evaluated demography of naturally occurring, juvenile, woody plants (large seedlings and small saplings) in two tropical premontane wet forests of southern Costa Rica (Coto Brus County) (figure 2.1). The regional landscape is dominated by cleared (mostly pastoral) land and

dotted with myriad small (<25 ha), remnant forest fragments, the legacy of 60 years of land-clearing by non-indigenous settlers (Daily *et al.* 2003).

One of my sites, the forest of the Las Cruces Biological Station (LCBS), comprises some 250 ha of forest, including 200 ha of primary forest (figure 2.2). Only 27% of original forest cover remains within a 15 km radius of LCBS, leaving the reserve as an isolated, mid-sized fragment (Daily *et al.* 2003) (figure 2.3). My other site, about 20 km to the north, occupies the lower slopes of a 10,000 ha tract called Las Alturas (LA), a privately owned reserve that retains most of its forest cover, the majority primary forest (figure 2.4). Further, LA abuts the mostly unbroken, 568,000-ha forest of La Amistad Biosphere Reserve. Both sites are classified as premontane wet forest, with elevations between 1000 m and 1450 m above sea level (ASL) (Holdridge *et al.* 1971, Kohlmann *et al.* 2010). LCBS has a mean annual temperature (MAT) of 22°C and receives about 3500 mm of precipitation annually (Daily *et al.* 2003), while climate models at LA predict a MAT of about 20°C and 3000-4000 mm of precipitation per year (Barrantes *et al.* 1985). Both sites experience a pronounced dry season from January through March. In addition, the two sites offer similar elevation, topography, and soils (inceptisols). Forest structures seem comparable, and there is considerable overlap in woody plant species between sites (see Chapter 4 of this thesis).

Mammals in the study areas

The mammal faunas of the two sites are starkly different. Owing to its large size and low poaching activity (boundary areas of LA are consistently patrolled by armed forest guards), LA possesses a virtually complete fauna. Among large herbivores, I know that collared

peccaries (frequent observation) and deer (scat) are present in my study area within LA. On the other hand, due to its isolation, comparatively small size, and a legacy of hunting by locals, LCBS is highly defaunated. The reserve lacks terrestrial herbivorous mammals larger than the lowland paca (*Agouti paca*), as well as most large carnivores and large arboreal mammals (LCBS station director R.A. Zahawi, personal communication; table 2.1).

Mammal exclusion

I employed selective mammal exclusion treatments to test the effects of various mammal size classes on juvenile plant growth and survival. Small mammals mostly comprised small rodents such as mice and rats (Muridae, Echimydae). Medium mammals included mammals larger than rats, up to the size of the larger caviomorph rodents (agoutis, pacas) and coatimundis. Any mammal larger than these qualified as large.

Exclusion treatments were applied to 1 m x 2 m plots. One treatment (SMALL) was permeable only to small mammals, mostly small rodents (Muridae, Echimydae, Sciuridae). These exclusions consisted of 1 cm-aperture hardware-cloth fence, between 0.5 (LCBS) and 1 m (LA) in height, wrapped around bamboo poles placed at the plot corners. 7 cm x 7 cm openings along the bottom of the fencing (two each on short sides, three each on long sides) allowed access to small mammals. Another exclusion type (MEDIUM) excluded the small and large classes, permitting access to medium mammals such as the larger caviomorph rodents (agoutis, *Dasyprocta punctata*; pacas, *Agouti paca*) and coatimundis (*Nasua narica*). MEDIUM exclusions utilized 20-25 cm tall sheet metal flashing to ensure exclusion of small rodents, which could not climb up the metal. Several wraps of barbed wire, beginning 25 cm above the top of the

flashing, prevented access by large mammals. Lastly, a control treatment level (ALL) was open to all mammals, including the large size class (mammals larger than the caviomorphs or coati). All structures had open tops, allowing equal access at both sites to flying and climbing mammals and birds, and corners of ALL plots were marked with small metal or pvc stakes.

Approximately twelve months into the study, it was discovered that the hardware cloth on SMALL enclosures at LCBS had deteriorated sufficiently, sometime after month-six of the study, to no longer be an effective barrier to medium mammals. Thus SMALL-enclosure plot pairs at LCBS were not included in statistical analyses. The SMALL enclosures at LA did not experience the same problem.

Study design

Herbivore enclosures were arrayed over approximately 100 ha (1 km²) areas of forest at each site, within elevation bands encompassing 1150 m to 1300 m ASL. I employed a block design within each site. Blocks within a site were chosen to have similar elevations, slopes, and distance to forest edge between sites (see Results). Eight blocks per site each contained one randomly located array of four 1 m x 2 m plots. All arrays were placed under closed-canopy primary forest and at least 50 m from the nearest forest edge. I also set a minimum of three (naturally occurring) juvenile plants per plot, and any plot that did not meet this requirement initially was randomly relocated a short distance. All plot arrays were at least 200 m away from any other array, for maximum independence among mammalian visitors to respective arrays.

The four plots within an array were arranged into two pairs, in order to facilitate paired t-test analyses (figure 3.1). Each pair consisted of one enclosure plot and one open control (one

pair each for MEDIUM and SMALL exclosures). Plots within a pair were spaced one to three meters apart, to minimize non-treatment-related differences in seedling dynamics; and plot pairs were spaced approximately 20-m apart.

Woody plant monitoring

I followed recruitment, growth, and survival of juvenile woody plants, i.e. large seedlings and small saplings (≥ 25 cm height and < 2 cm dbh), for approximately 14 months beginning in spring 2009. I tagged, tallied, and measured heights of all such plants at the outset of the experiment. At the conclusion, I re-inventoried and identified plants, noting mortality and new recruitment into my size class range, and again measured heights of juvenile woody plants.

I also gauged mammal-inflicted herbivory in each plant inventory. I counted damage as mammal herbivory only if a living stem or branch had been severed; I did not count leaf damage, due to confusion with arthropod herbivory, or severed dead stems, as mammal herbivory.

Statistics

I compared various metrics of plant performance between exclosure treatments within a site, as well as between sites. I performed paired, two-sample t-tests on mean height-relative growth rate (hRGR) for each set of paired plots, separately for each site, using SAS 9.2. HRGR was calculated as the change in height of a plant during the measurement interval divided by its initial height; all hRGR were standardized to a per-year basis. I also compared rates of herbivory, and used paired t-tests to compare relative rates of mortality and recruitment

between neighbor-plots, separately for each site. I calculated relative mortality and recruitment rates as the number of plants that died and recruited, respectively, during the study divided by the number of plants present at the initial inventory. Analyses were performed in either SAS 9.2® or SigmaPlot 11.0®.

Results

In a total of 64 m² (32 -1 m x 2 m plots) at each site, I tallied and measured 264 juvenile, non-climbing, woody plants at LA and 220 such plants at LCBS. Due to logistical constraints, some plants experienced mortality before they could be identified even to family. Excluding such plants, I was able to identify, at LA, 21 of 247 plants only to family, 43 to genus, and 178 to species; and at LCBS, 17 of 201 plants to family, 44 to genus, and 122 to species (figure 3.2). Juvenile woody plants at LA comprised 26 families, with Rubiaceae (26% of tallied plants), Myrsinaceae (12%), and Lauraceae (9%) the most common. At LCBS, Melastomataceae (11%), Fabaceae (6%), and Meliaceae (6%) were the most common of 29 plant families registered (table 3.1). Summed across all plots, the distribution of juvenile plant heights at the outset of the study was remarkably similar between sites (figure 3.3).

I found no significant effect of mammal exclusion (either treatment) or site on mammalian herbivory rates or on several key demographic variables (relative growth rate, recruitment and mortality rates). I detected almost no mammalian herbivory. At LCBS, I recorded one herbivorized stem on only 1 of 181 plants at the outset of the study and on 1 of 195 plants near the end of the study. Similarly, at LA I found one mammal-damaged stem on 4

of 218 plants initially and on 2 of 240 plants at the study's termination. Because damage levels were so low, I did not perform statistical analyses on herbivory.

HRGR's did not vary between paired exclusion treatments at either site. At both LA and LCBS, juvenile plants grew at the same mean rate between SMALL plots and respective paired control plots, and between MEDIUM plots and respective paired control plots (all comparisons: $p \geq 0.202$).

Relative mortality and recruitment rates were also equivalent between paired plots at both sites. All comparisons were highly non-significant ($p \geq 0.195$), with one exception. At LA, juvenile plants saw marginally higher survival rates (i.e. lower mortality) in SMALL enclosures than in paired control plots ($t=2.30$, $df=6$, $p=0.061$).

Discussion

Contrary to my prediction, the presence of large mammalian herbivores at LA did not affect woody plant growth or survival. In fact, direct signs of mammalian foliar herbivory at both sites were almost totally absent. I may have overlooked mammalian herbivory occurring on leaves, given that I only searched for (more easily discernible) damage to stems and branches. HRGR's and relative recruitment rates also did not change with exclusion of the largest mammals at LA, and relative mortality rates were only marginally lower under exclusion of medium and large mammals than under exposure to all comers. While this latter, weak trend is in line with the expected effects of large-mammal exclusion, I do not place much weight on this single indicator, given the consistent absence of treatment effects in all other facets of the study.

At LCBS, on the other hand, my prediction was borne out. The woody plants in my study seemed to escape mammal herbivory altogether, regardless of mammal-exclusion status, and plants performed no better or worse when exposed to all mammals than when subjected to a reduced suite (although only one exclosure treatment, in which medium mammals were allowed, was successful).

My results indicate that large mammalian herbivores have no discernible effect on juvenile woody plant performance, a conclusion that would mesh well with a recent finding in the Peruvian Amazon that large mammals do not influence seedling recruitment (Paine and Beck 2007). I note that my replication was fairly low ($n=8$ at each site) and my plots small (1 m x 2 m), so my design may have limited my ability to discern spatially heterogeneous herbivory. Additionally, small plot sizes resulted in a very low number of woody plants in most replicates, which likely contributed to high among-plot variance in rate-quantities.

However, I believe the lack of mammal herbivore activity in my plots may reflect the true state of browser-plant interactions at LCBS and even LA. Paine and Beck have noted that because large mammals have large home ranges (Beck 2006), large-herbivore “sampling” of understory plants is likely to be highly irregular over space and time, and visitation to any particular spot infrequent. Such irregularity of visitation may be exacerbated at my intact site by my study design and by generally low population densities. Members of *Tapirus* have shown a strong preference for vegetation in secondary forest (Foerster and Vaughan 2002, Fragoso 1990), riparian forest (Willams 1984), and gap habitats (Salas and Fuller 1996) over closed canopy primary in several previous studies. I sampled none of these preferred habitat types, and thus may have missed the bulk of tapir browse effects. The scarcity of such habitat

(personal observations), in fact, may depress local tapir densities in the LA study area. Foerster and Vaughan (2002), for example, believe that lower availability of high-quality forage contributes to much greater home-range sizes, and lower population densities, at high-elevation sites than at their study site in Corcovado National Park, Costa Rica, a lowland rainforest.

Finally, despite the presence of tapirs in the LA Reserve at large, an edge effect may be at play at my study site. Tapirs are known to shy away from human activity (Flesher and Ley 1996, Tobler 2002), and my LA site is situated close to an active cattle pasture, a scenario not atypical of remaining large neotropical forest blocks. I believe that this combination of factors implicates a novel result in tropical defaunation studies. Among intact higher-elevation forests, especially those near sites of human activity, large-mammal herbivory pressure may be low enough that mammal defaunation has negligible consequences for browsing-based understory plant limitation.

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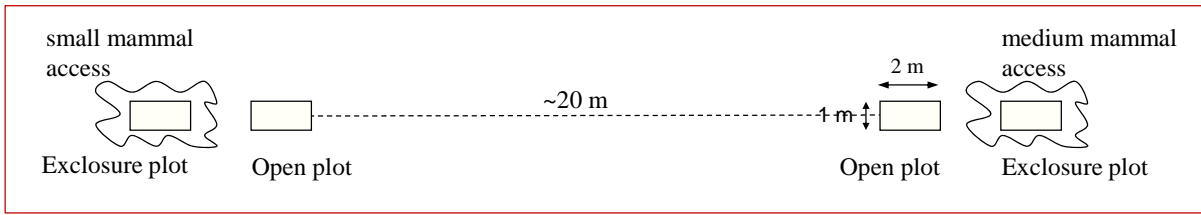


Figure 3.1: Layout of paired juvenile plant plots within a block.

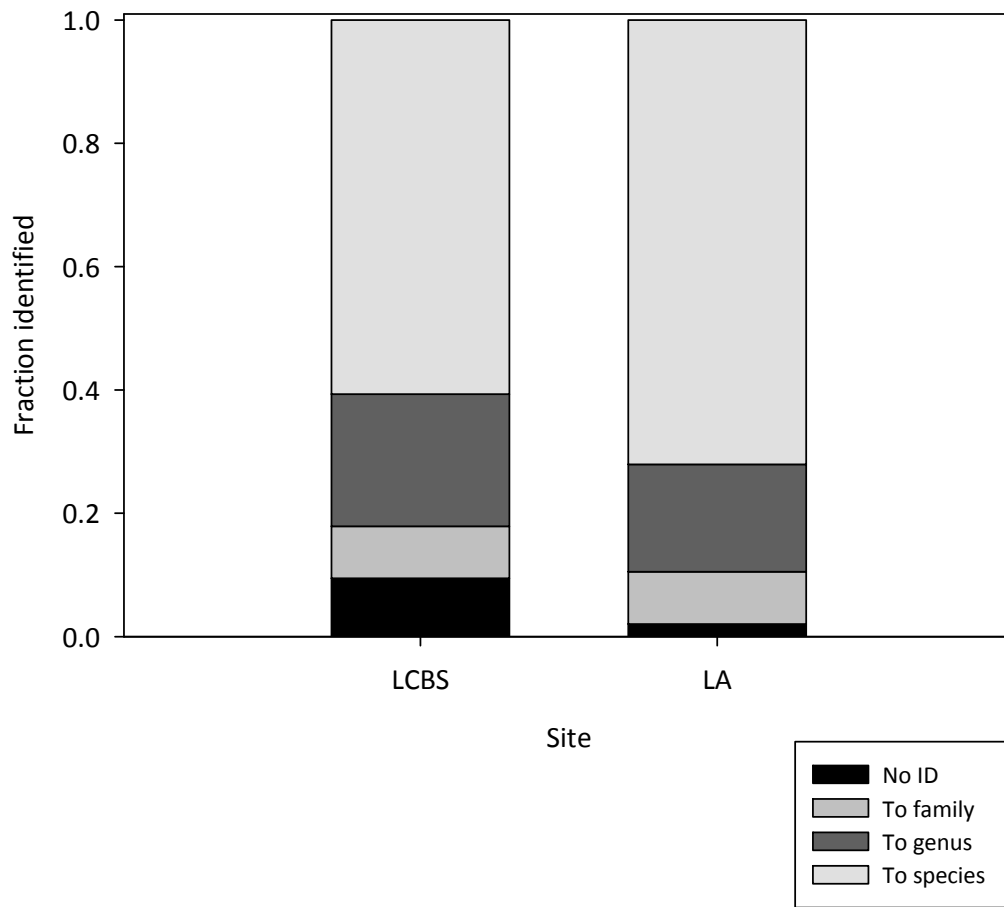


Figure 3.2: Identification precision of juvenile woody plants.

Table 3.1: Plant families of greatest abundance in juvenile plant plots at each site.

LCBS				LA			
Rank	Family	No. stems	% stems	Rank	Family	No. stems	% stems
1	Melastomataceae	23	11	1	Rubiaceae	65	26
2	Fabaceae	13	6	2	Myrsinaceae	30	12
3	Meliaceae	12	6	3	Lauraceae	22	9
4	Moraceae	12	6	4	Malvaceae	17	7
5	Myrsinaceae	12	6	5	Myristicaceae	16	6
6	Malvaceae	11	5	6	Myrtaceae	11	4
7	Rubiaceae	11	5	7	Annonaceae	9	4
8	Annonaceae	10	5	8	Clusiaceae	9	4
9	Lauraceae	10	5	9	Monimiaceae	8	3
10	Piperaceae	10	5	10	Moraceae	8	3

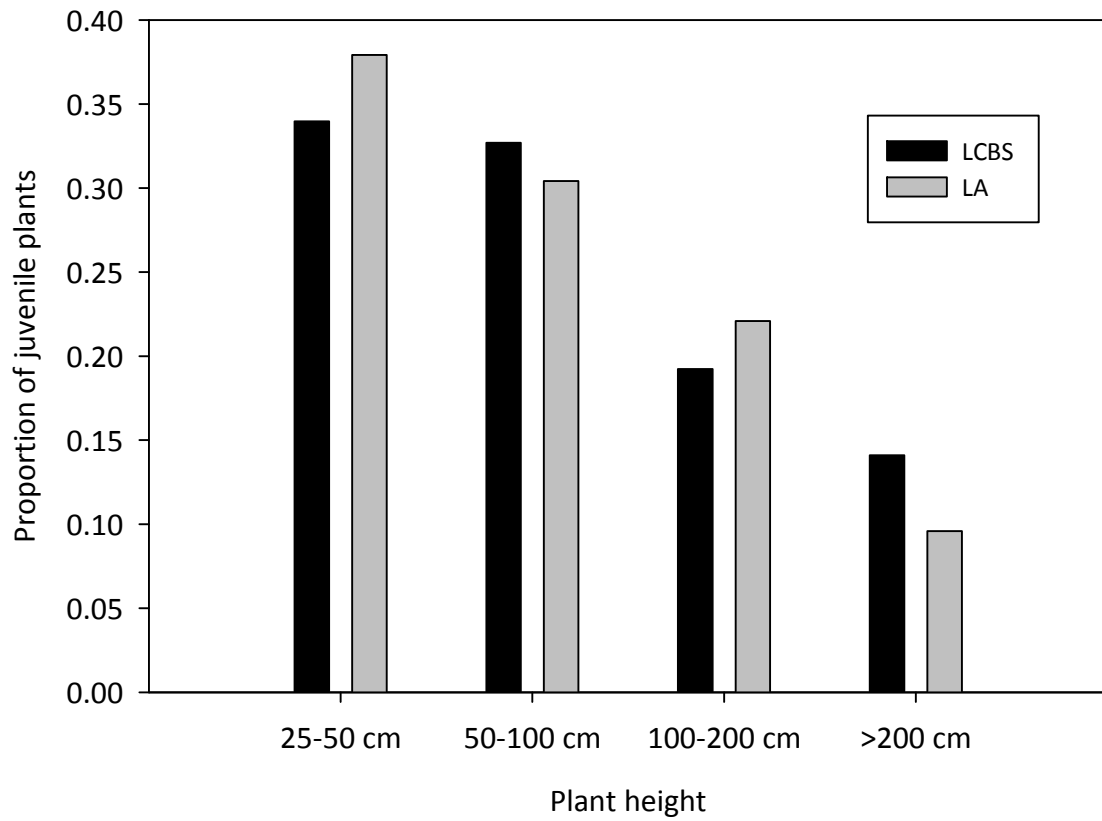


Figure 3.3: Height distributions for juvenile, non-climbing, woody plants at outset of study.

CHAPTER 4

TREE COMMUNITY COMPOSITION OF A DEFAUNATED AND A FAUNALLY INTACT PREMONTANE FOREST IN SOUTHERN COSTA RICA³

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Abstract

The anthropogenic purgation of native animals known as defaunation can have cascading effects through a forest ecosystem, threatening to alter not only the system's fauna, but the entire interconnected biota. One pathway to impacts on vegetation that has received much recent attention is the extirpation of terrestrial mammalian seed predators. Seed predation by large mammals is a major force in limiting seedling recruitment and mediating community composition and diversity. I hypothesized that large-granivore removal after forest fragmentation leads to competitive dominance by seedlings of large-seeded species, and I evaluated this hypothesis by describing and comparing tree compositions of two tropical, premontane wet forests, one defaunated and the other faunally intact. I found that the tree communities varied substantially, with only 31% similarity at the species level; and that the faunally intact site may have greater tree species richness than the defaunated site. However, using non-metric multidimensional scaling, I found no evidence for differential intergenerational (adult to juvenile) shifts in tree community composition between sites. A broader implication of this result is that extirpation of large seed predators may have limited influence on the competitive milieu of recently germinated seeds.

Introduction

Mammalian biodiversity is rapidly diminishing due to anthropogenic defaunation (Dirzo and Raven 2003, Ceballos *et al.* 2005). Defaunation, the loss of components of the fauna within an ecosystem, occurs throughout the tropics (Wright 2003). At smaller scales, recent research

reveals a picture in which myriad mammal species have undergone drastic range contractions, going locally extinct over large parts of their original ranges (Ceballos & Ehrlich 2002).

Two major drivers of defaunation are hunting and forest fragmentation (Redford 1992, Peres 2001, Dirzo 2001). Large mammals are the most vulnerable to both human impacts (Cardillo *et al.* 2005), because hunters generally favor large-bodied mammals (Redford 1992, Bodmer *et al.* 1997, Peres 2000), and because their greater habitat requirements make them more sensitive to fragmentation (Dirzo 2001, Wright 2003). Consequently, differential defaunation usually proceeds along a defaunation gradient (Dirzo *et al.* 2007), in which the suite of reduced or extirpated creatures grows to encompass smaller mammals as human impact increases (e.g. Peres 2000). Although I focus on fragmentation-induced defaunation, the consequences of the two mechanisms are often virtually the same.

Much recent work has focused on the top-down consequences of mammal defaunation for forest vegetation, as mediated by a multitude of interactions between trophic levels (see Redford 1992, Terbourgh 1992, Coley and Barone 1996, Wright 2003 for reviews). Seed predation is particularly important in tropical forest regeneration, as mortality rates due to post-dispersal seed predation are among the highest of any stage of forest regeneration (Muller-Landau *et al.* 2004, Hubbell *et al.* 1999). Seed predation by neotropical mammals, therefore, often plays a major part in limiting woody seedling recruitment (Janzen 1971, Sork 1987, Forget 1993, Asquith *et al.* 1997, Wright *et al.* 2000).

Predatory seed mortality also tends to be size- and frequency-dependent, and thus helps to control (and balance) community composition of understory plants. Density- (frequency-) dependent seed predation by mammals prevents dominance of any particular

species near its mother trees, freeing up space for recruitment of other, potentially competitively inferior, species (Armstrong 1989). It thus promotes species coexistence and increases understory plant diversity (Janzen 1970, Connell 1971, Harms *et al.* 2000). Size-dependent seed predation is also suspected to offset the competitive advantage that large-seeded seedlings naturally enjoy over small-seeded species, due to the positive correlation between seed size and seedling performance (Foster 1986, Dalling *et al.* 1997). That is, large mammal seed predators may prefer large seeds (Dirzo *et al.* 2007) and thus should prevent competitive dominance by large-seeded seedlings (Grubb 1998, Mendoza 2005).

Removal of large seed predators can translate to dominance by large-seeded species and reduced diversity in the seedling layer (Dirzo and Miranda 1991, Wright *et al.* 2007). Wright *et al.* (2007), for example, in a highly replicated study of hunted and protected sites in the Panama Canal Zone, found that woody seedling community composition of the hunted sites, relative to adult composition, had shifted toward greater dominance by large-seeded species than at the protected sites. They attributed the change to reduced abundances at the hunted sites of large mammals, who control recruitment of large-seeded species through depredation.

Such incipient compositional shifts in regenerating forest can have far-reaching ramifications. In a study of tiny islands in the Panama Canal, Putz *et al.* (1990) found almost complete dominance by large-seeded tree species. In contrast with the mainland and larger islands, the small islands were not large enough to support even small rodents, the smallest of mammalian granivores. Thus, in the 70 years since the formation of the tiny islands and the

local extinction of mammalian granivores, competitive imbalances in the seed stage had translated into canopy-level dominance of the un-predated species.

My objectives in this study were two-fold. First, I undertook a basic inventory and description of the woody vegetation in two primary forests, one of which has never been studied. Second, I sought to extend such questions of defaunation-induced plant community shifts, which have been largely focused on lowland rainforests, to the wet forests of a mountainous tropical landscape.

I assessed adult and juvenile tree communities at both a faunally intact, premontane wet forest and a similar forest that is depauperate of large mammals. At my defaunated study site, all five species of large terrestrial herbivores once common in the region are currently rare or extinct (Pacheco *et al.* 2006) (table 2.1). At least four of these consume fruits, especially large fruits, as major components of their diets (Bodmer 1991). Three (red brocket deer, *Mazama americana*; collared peccary, *Tayassu tajacu*; and white-lipped peccary, *Tayassu pecari*) were found to destroy most (94-95%) of the seeds they ingest, while a congener of the fourth (Baird's tapir, *Tapirus bairdii*) damaged roughly half of examined seeds (Bodmer 1991). While I could not directly test for seed-size based changes in juvenile plant community composition as did Wright *et al.* (2007), I looked for discrepancies between sites in the magnitude and direction of inter-generational changes in woody plant composition, which might be attributable to a paucity of large-seed predators at the defaunated site.

Methods

Sites

I investigated woody plant community composition in two tropical premontane wet forests of southern Costa Rica (Coto Brus County) (figure 2.1). The regional landscape is dominated by cleared (mostly pastoral) land and dotted with myriad small (<25 ha), remnant forest fragments, the legacy of 60 years of land-clearing by non-indigenous settlers (Daily *et al.* 2003).

One of my sites, the forest of the Las Cruces Biological Station (hereafter, LCBS), comprises some 250 ha of forest, including 200 ha of primary forest (figure 2.2). Only 27% of original forest cover remains within 15 km of LCBS, leaving the reserve as an isolated, mid-sized fragment (Daily *et al.* 2003) (figure 2.3). My other site, about 20 km to the north, occupies the lower slopes of a 10,000 ha tract called Las Alturas (LA), a privately owned reserve that retains most of its forest cover, the majority primary forest (figure 2.4). Further, LA abuts the mostly unbroken, 568,000-ha forest of the La Amistad Biosphere Reserve. Both sites are classified as premontane wet forest, with elevations between 1000 m and 1450 m above sea level (ASL) (Holdridge *et al.* 1971, Kohlmann *et al.* 2010). LCBS has a mean annual temperature (MAT) of 22°C and receives about 3500 mm of precipitation annually (Daily *et al.* 2003), while climate models at LA predict a MAT of about 20°C and yearly precipitation of 3000-4000 mm (Barrantes *et al.* 1985). Both sites experience a pronounced dry season from January through March. In addition, the two sites offer similar elevation, topography, and soils (inceptisols).

Mammals in the study areas

The mammal faunas of the two sites are starkly different. Owing to its large size and low poaching activity (boundary areas of LA are consistently patrolled by armed forest guards), LA possesses a virtually complete fauna. Among large herbivores, I know that collared peccaries (frequent observation) and deer (scat) are present in my study area within LA. On the other hand, due to its isolation, comparatively small size, and a legacy of hunting by locals, LCBS is highly defaunated. The reserve lacks terrestrial herbivorous mammals larger than the paca (*Agouti paca*), as well as most large carnivores and large arboreal mammals (LCBS station director R.A. Zahawi, personal communication; table 2.1).

Study design

Juvenile- and adult tree plots were arrayed over approximately 100 ha (1 km²) areas of forest at each site, within elevation bands encompassing 1150 m to 1300 m ASL. I employed a block design within each site, with four blocks at each site distributed to have similar elevations, slopes, and distance to forest edge between sites. Each block contained one randomly located adult-tree inventory plot (40 m x 40 m), from which I sub-sampled juvenile trees in a 24 m² area, as follows. First, each main plot contained an array of four 1 m x 2 m plots, established for complementary investigations. The four plots within an array were arranged into two pairs approximately 20 m distant (figure 1). Second, I randomly located one 4 m x 4 m plot within the central 25 m x 25 m area of the main plot. I considered the five sub-plots within each main plot as one aggregate juvenile tree plot in all analyses. All juvenile tree

plots were placed under closed-canopy primary forest and at least 50 m from the nearest forest edge, and all main plots were at least 200 m away from any other main plot.

Tree sampling

I sampled adult (≥ 10 cm dbh) and juvenile (large seedlings and small saplings; ≥ 25 cm height and < 2 cm dbh) trees in my study plots. I identified (when possible), mapped, and measured dbh of all adult trees in 40 m x 40 m (0.16 ha) main plots. Juvenile trees were tagged, tallied, and identified in all sub-plots (24 m² per main plot).

Data analysis

I performed community analyses and comparisons using PC-ord 5[®]. I summarized and compared stand structures of adult trees by distributing dbh-based size among seven classes. I calculated summary species and diversity information by site and tree size class and plotted stem-based species accumulation curves for each site. I also performed multi-response permutation procedure (MRPP) on rank-transformed Euclidean-distances to test for differences in community composition across sites and size classes, and quantified such differences with Sørensen indices. Finally, non-metric multi-dimensional scaling ordination (NMS) was used to graphically represent differences in species composition among plots, sites, and size classes (see McCune *et al.* 2002 for explanations of multivariate procedures).

Results

Far more adult than juvenile trees were captured in my inventories. I tallied 822 trees across the eight main plots, identifying 705 (85.8%) to species. Among juveniles, I only tallied those plants that could be identified as taxa exhibiting tree growth-habit, to facilitate comparisons with adult trees. A number of woody plants could not be identified precisely enough to make this determination, and I therefore excluded these plants from analysis (24 plants with no identification, 12 identified to family or genus). Subsequently, 264 juvenile plants remained for analysis, of which I identified 225 (85.2%) to species (figure 2)

It should also be noted that not all unidentified species and genera could be assigned to unique morphotypes. Where this is true, all occurrences of indistinguishable morphotypes were labeled as a single taxon (e.g., trees of the genus *Ocotea* that could not be identified to species and could not be distinguished as unique morpho-species were all called *Ocotea sp.*). Additionally, in relatively few cases, a unique morphotype at one site may not have been matched to the same morphotype at the other site, but rather given a different identifier. Thus my results may underestimate diversity at both sites and may underestimate community similarity between sites. To accommodate some of this taxonomic imprecision, I calculated community similarity indices at broader levels of organization (i.e. by genus and family).

Size structure of adult trees did not differ between sites when broken down into seven dbh classes (Chi-square= 8.276, df=6, p= 0.219). This was as expected based on my observations of the forests during field work. Figure 4.3 presents the distribution of adults at each site among the seven size classes.

Summary species data revealed considerable differences between sites and size classes. Consistent with total stem frequencies, adult tree plots included an average (across sites) of 103 stems, while juvenile plots only contained 33 stems on average. Likely because of this discrepancy, adult tree plots were both more species rich and diverse (Shannon's H) than juvenile plots, although juvenile plots exhibited greater species evenness (table 4.1).

Diversity metrics of adult tree communities differed between sites. First, LCBS plots contained more adult trees (111 per plot) than did adult plots at LA (95). LCBS also had greater adult tree absolute richness and diversity (Shannon's index (H)) than LA on a per-plot basis. LCBS harbored 46 species of adult trees per plot and a Shannon's H of 3.504, while LA's large tree plots contained only 40 species and had a diversity of 3.303; evenness was similar between sites. When adult tree plots were pooled within each site, species richness was similar between sites despite the greater number of sampled stems at LCBS. Plots of stem-based species accumulation curves standardize stem number between sites and indicate that LA may have a somewhat higher per-individual species richness than LCBS (figure 4.4). Species richness, evenness, and diversity were all similar between sites for juvenile plants, despite a higher stem density at LCBS (table 4.1).

I tested compositional differences between sites and size classes using MRPP. There was a significant difference in species compositions between adult and juvenile trees (pooled across sites) ($T=-4.935$, $p=0.0005$). Tree communities were also different between sites, both for adults only ($T=-4.131$, $p=0.006$) and for adults and juveniles combined ($T=-4.028$, $p=0.002$). Juvenile tree communities alone did not vary between sites ($T=-0.990$, $p=0.160$).

Community similarity indices and NMS plots corroborate these findings. I computed abundance-based Sørensen community similarity indices (SSI) at three taxonomic levels (species, genera, families) to compare adult community composition between sites. Adult tree communities were dissimilar between sites at the species (SSI=30.7%), genus (45.7%) and family (57.9%) levels, although they do share eight of the ten most abundant tree families at respective sites (table 4.2). In graphs of NMS plot ordinations (by species), juvenile plots are widely separated from adult plots (figure 4.5a), indicating compositional differences between size classes (within a site) at least as great as those between sites. Figure 4.5a also shows that juvenile tree plots from different sites mingle more closely together than do adult tree plots, which exhibit greater distances between site-specific plot clusters. Within-site pooling of plots illustrates this point more clearly, with much greater distances between sites in pooled adult plots than in pooled juvenile plots (figure 4.6). Note also that symbols representing adults and juveniles combined (labeled as “All”) are much closer to their respective adult plots than to respective juvenile plots, underscoring the larger sample sizes and dominance of adult plots in determining overall community compositions.

Discussion

Compositions varied between sites and size classes. Sørensen distances among juvenile plots within respective sites were large (figure 4.5a), leading to little between-site differentiation in juvenile plant composition (figure 4.6). On the other hand, there was considerable difference in adult community composition between sites, as evidenced by MRPP, Sørensen indices, and NMS plots (figures 4.5, 4.6). Furthermore, pooled juvenile plots and

pooled adult plots exhibited rather large compositional distances from each other, at respective sites. These observations are consistent with a conceptual “environmental filter”, in which environmental differences between sites cumulatively and differentially filter the composition of tree species reaching adulthood, producing increasing between-site differentiation in community compositions with increasing cohort age (Keddy 1992).

There may be scale dependence in patterns of adult tree species diversity. At the 40 m x 40 m plot level, LCBS had higher species richness, evenness, and diversity (Shannon’s H) than LA, though this may have arisen from the higher plot-level stem density at LCBS (111 vs. 95 stems per plot). At the site (i.e. pooled-plot) level, LA achieves greater species richness than LCBS, although, again, LCBS exceeds LA in species evenness. Based on my observations during field work, I am surprised by these results. LCBS had seemed to edge out LA in diversity, a discrepancy I thought might be attributable to differences in climatological variables (which have never been measure at the LA site) or to a “mass effect”, in which LA’s species composition is greatly influenced by contiguous higher elevation, and presumably lower-diversity, forest, while LCBS’ species composition may be more representative of its surrounding lower elevational forest. LCBS is also known to harbor tree species endemic only to its subsuming mountain range. However, the data did not bear out my anecdotal assessment.

To assess directional changes between adult and juvenile tree communities, I applied vectors to NMS plots of adult and juvenile plots (figure 4.5b). Because juvenile communities are of more recent origin than adult communities, representing more recent interactions with terrestrial mammals, I drew vectors to originate in adults plots and end in corresponding

juvenile plots. This directionality should give a sense of inter-generational changes in tree composition due to plant-mammal interactions, specifically seed predation. Of course, tree communities may change between juvenile and adult stages of life even given constant mammal influences, though I would not expect inter-generational trajectories to differ greatly between two nearby forests of identical life zone.

I therefore concentrated on *relative* differences between sites in magnitude and direction of vectors, which may signify changing successional dynamics of woody-plant community composition at the recently defaunated site. Nevertheless, I detected no strong pattern of differentiation in vector magnitudes or directions between sites. This finding agrees well with patterns reported in chapter 2 of this thesis, evincing no discernible effect of large herbivores on medium- and large-seed predation at LA. One alternative hypothesis is that abundant agoutis at LCBS (*Dasyprocta punctate*) may be compensating for larger seed predator loss. Precaution should be taken in drawing conclusions here, given that my juvenile tree sampling may have been too limited to tease out potential shifts in successional dynamics.

I found no evidence that size-based imbalances in seed survival may translate into dominance of large-seeded species and lower diversity in future stages of regeneration, a potential implication of differential seed predation under mammalian defaunation (Dirzo *et al.* 2007, Wright *et al.* 2007). This meshes well with the lack of a contribution by large seed predators to site differences reported in chapter 2. I did, however, find interesting differences in adult tree communities between my sites, irrespective of defaunation considerations. There was considerable differentiation in adult community composition between sites, and LCBS had higher species richness and diversity (Shannon's H) than LA, despite similar numbers of

inventoried stems. I can only speculate as to the determinants of differing composition and diversity between sites.

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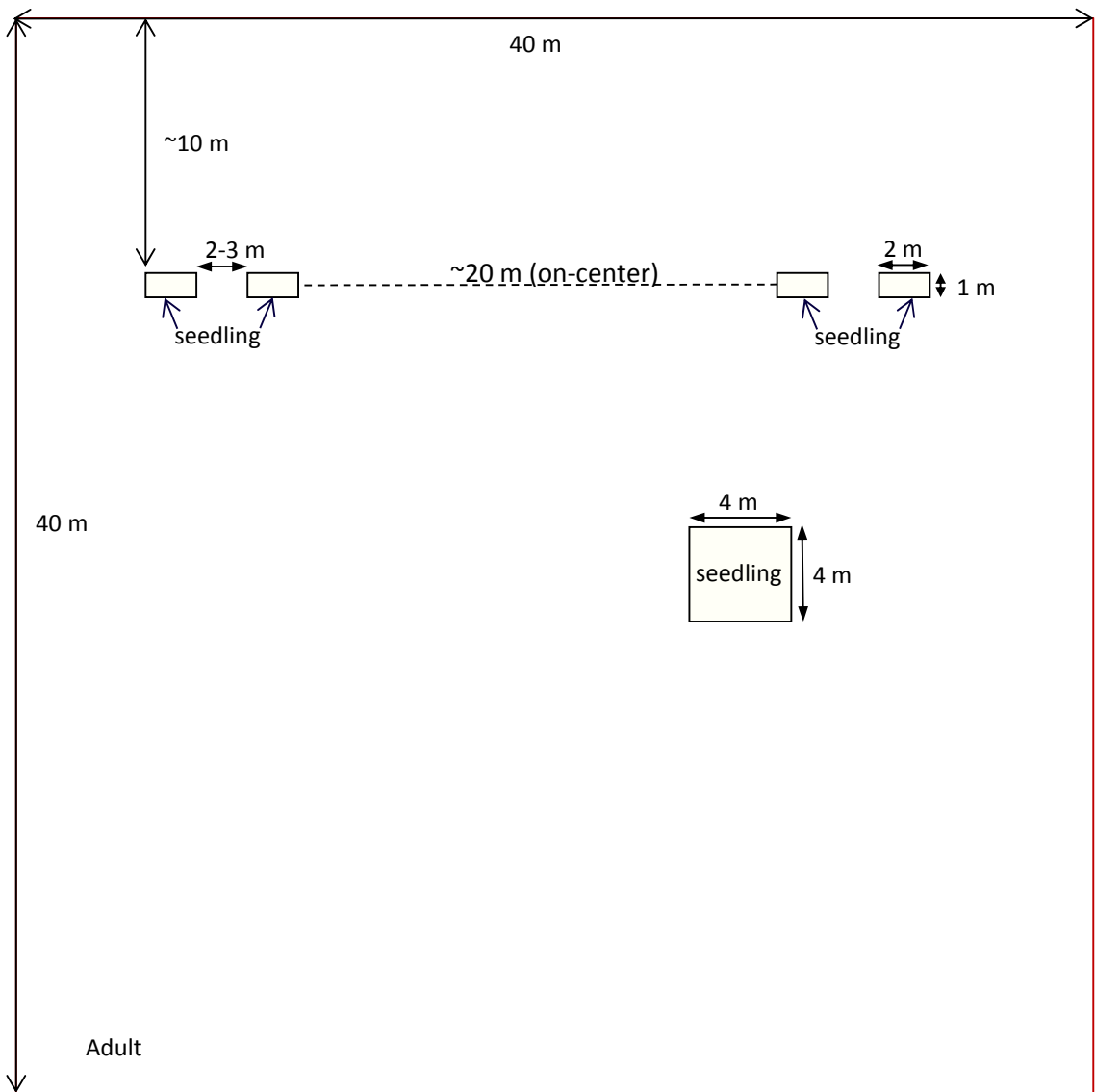


Figure 4.1: Layout of adult and juvenile tree plots within a block.

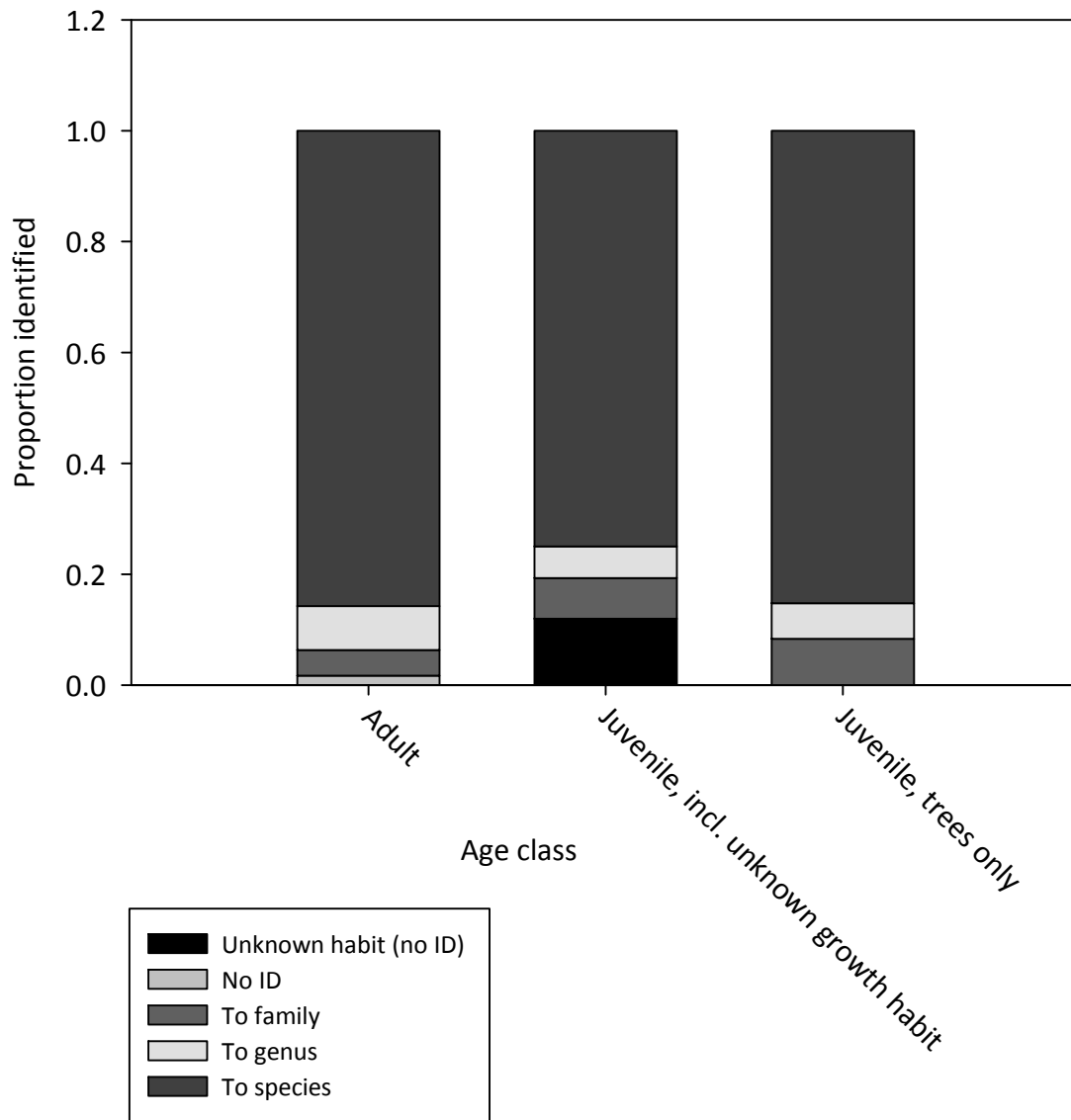


Figure 4.2: Identification precision for adult and juvenile trees.

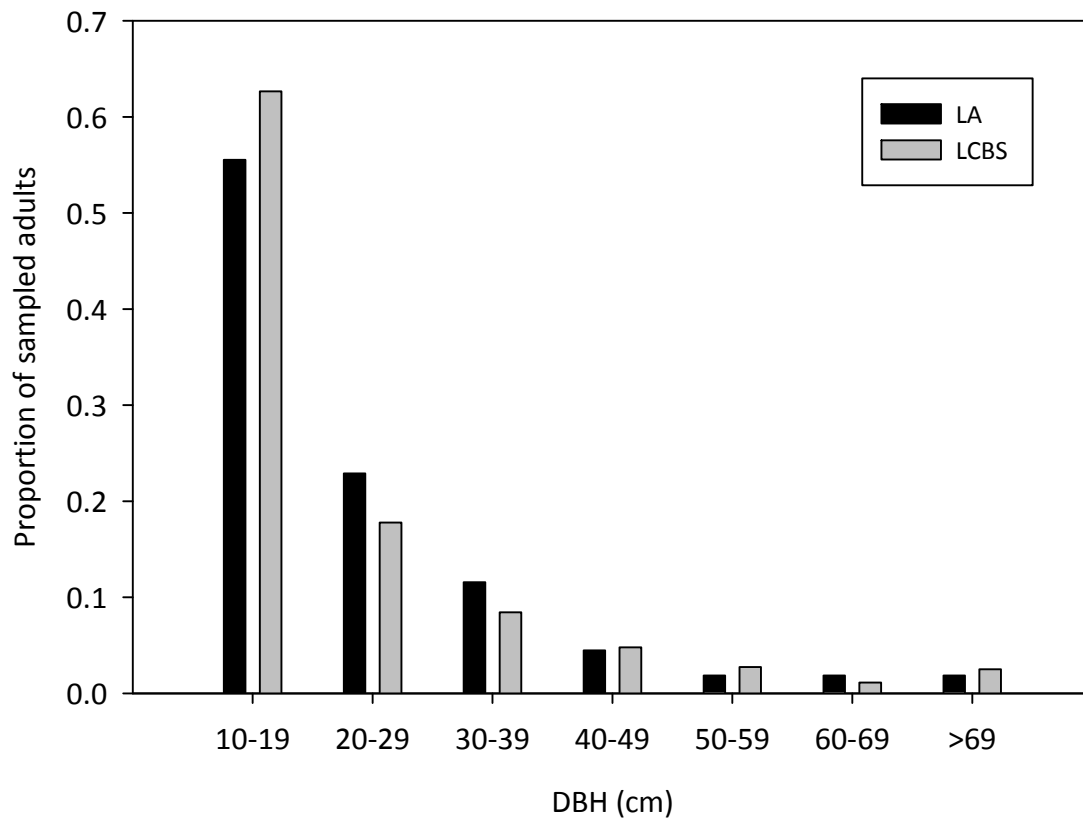


Figure 4.3: Size-distribution of adult trees, by dbh.

Table 4.1: Summary of abundances and diversity metrics for adult and juvenile tree plots.

Site	Size class	Sample level	No. stems	diversity metrics		
				Richness	Evenness	Shannon's H
LA	adults	pooled plots	380	93	0.859	3.892
	adults	per plot	95	40	0.900	3.303
	juveniles	per plot	31	18	0.939	2.686
LCBS	adults	pooled plots	442	92	0.876	3.961
	adults	per plot	111	46	0.917	3.504
	juveniles	per plot	35	19	0.926	2.703
LA&LCBS	adults	per plot	103	43	0.908	3.404
	juveniles	per plot	33	18	0.933	2.694

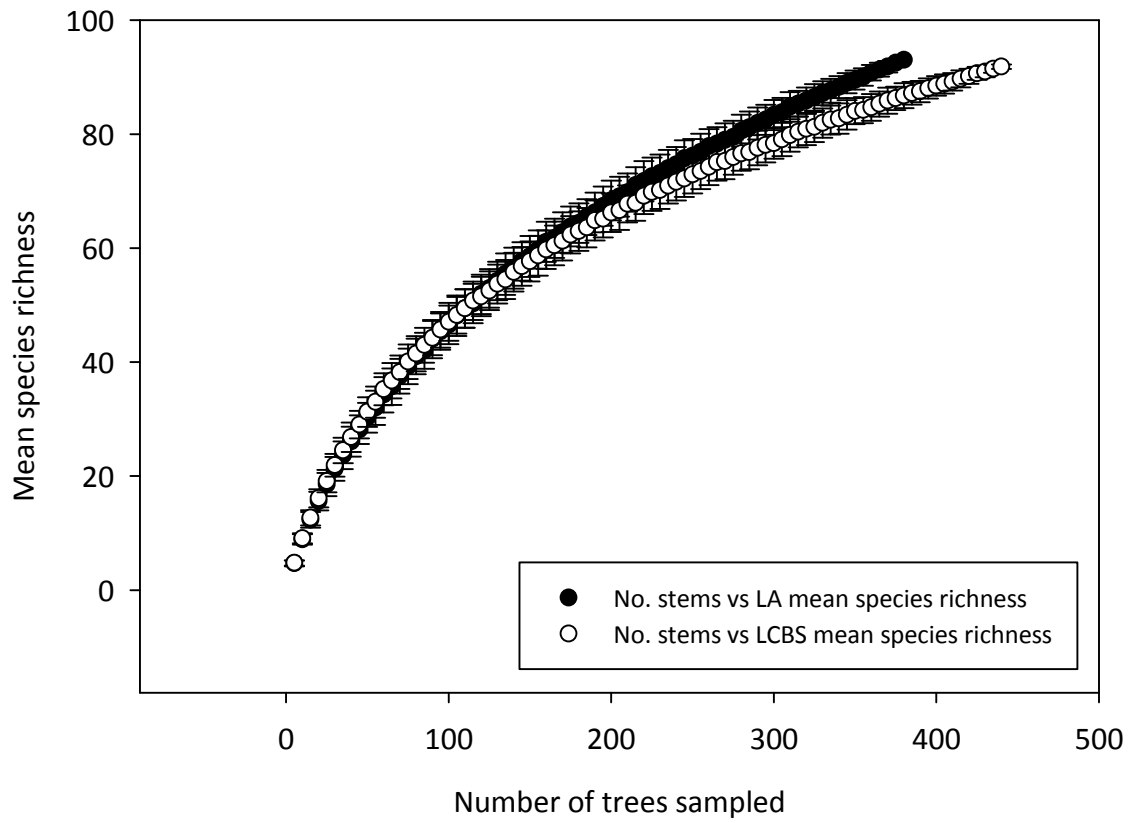
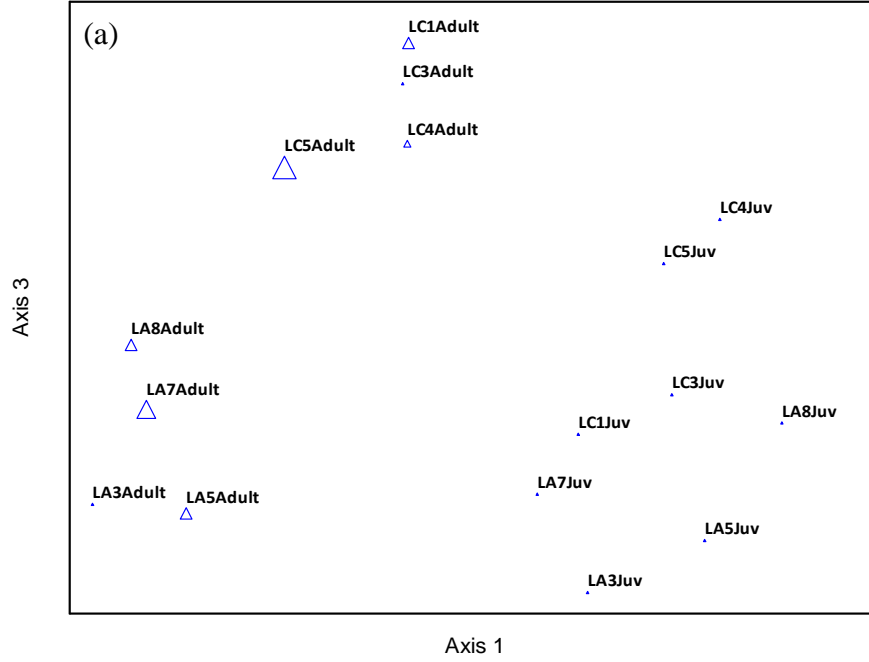


Figure 4.4: Stem-based species accumulation curves for adult trees. Error bars represent standard deviations.

Table 4.2: Ten most abundant families in adult tree plots at the two study sites.

LCBS				LA			
Rank	Family	No. stems	% stems	Rank	Family	No. stems	% stems
1	Clusiaceae	71	19	1	Lauraceae	43	10
2	Melastomataceae	34	9	2	Moraceae	42	10
3	Meliaceae	28	7	3	Myristicaceae	40	9
4	Moraceae	28	7	4	Euphorbiaceae	38	9
5	Lauraceae	26	7	5	Sabiaceae	34	8
6	Malvaceae	23	6	6	Malvaceae	28	6
7	Euphorbiaceae	21	6	7	Clusiaceae	26	6
8	Fabaceae	21	6	8	Myrtaceae	19	4
9	Sabiaceae	20	5	9	Meliaceae	14	3
10	Lacistemataceae	20	5	10	Fabaceae	13	3

NMS of adult and juvenile tree plots by species in two tropical forests



NMS of adult and juvenile tree plots by species in two tropical forests

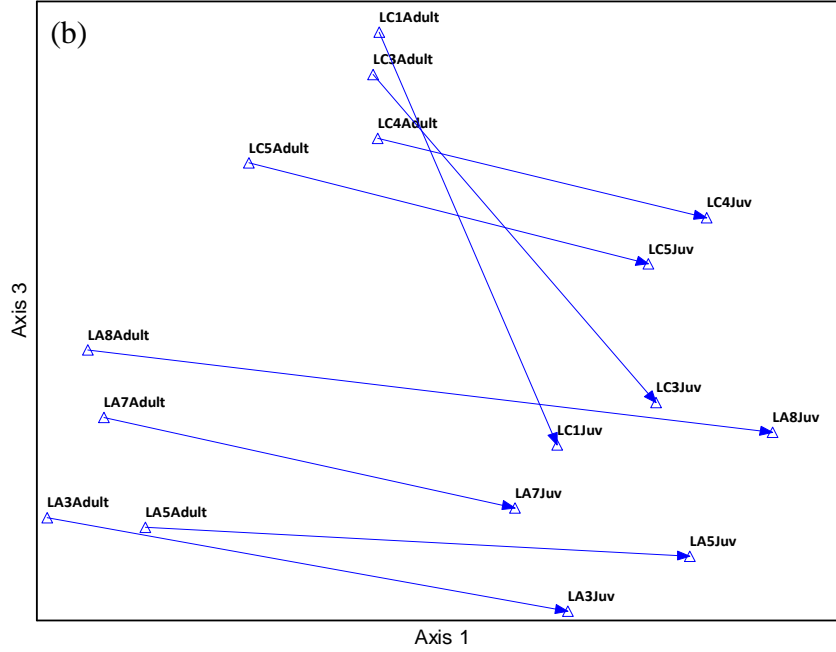


Figure 4.5: NMS plots of adult and juvenile tree plots.

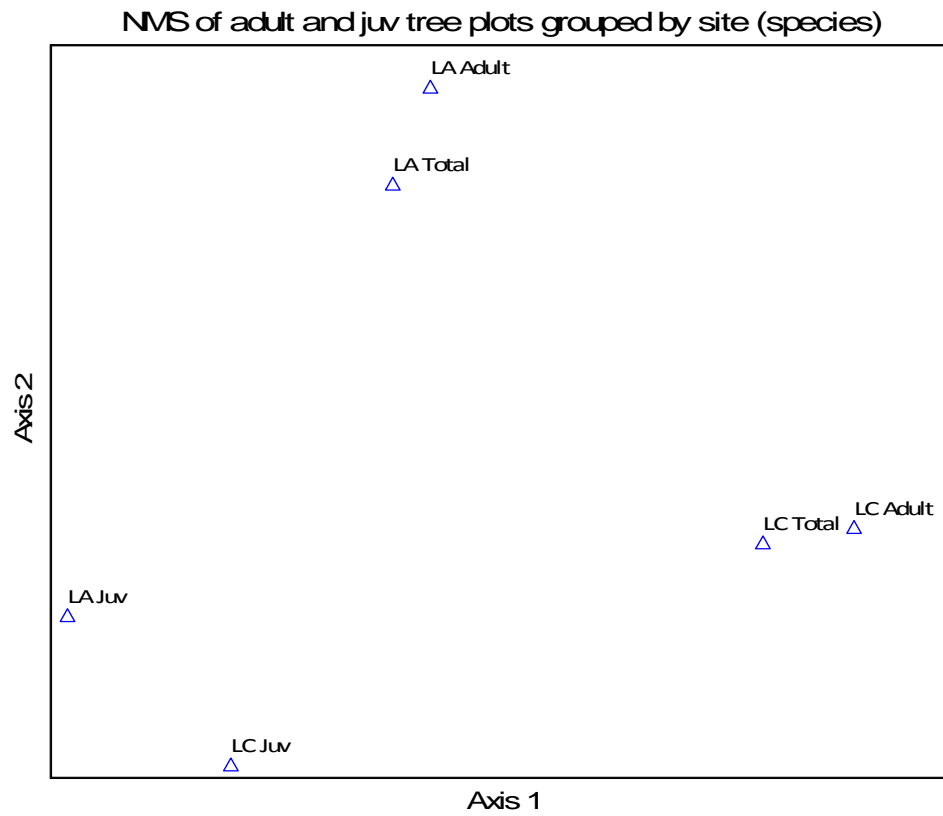


Figure 4.6: NMS plot of adult and juvenile tree plots pooled by site. "Total" plots are sums of adult and juvenile tree plots.

CHAPTER 5

CONCLUSIONS

My research investigated potential implications of mammalian defaunation for regeneration dynamics and community composition of tropical forest woody plants. I couched my studies in terms of two main filters that large mammalian herbivores apply to woody plant regeneration: seed predation (granivory) and foliar herbivory on juvenile plants. When large herbivores are expelled from a forest ecosystem, both these processes can be drastically altered. Further, changes to the seed predation regime of a system can ripple through to shifts in the community composition and diversity of young trees.

I reported the details of a two-season seed predation experiment in Chapter 2. In light of qualitative evidence from camera traps, I found that medium-sized mammals and ground birds may be the predominant predators of *isolated* groups of large seeds at both my sites, a finding that meshes well with the known role of dispersal away from the mother tree as an escape mechanism from predation by large mammals.

My seed predation study speaks especially to the need for temperance in drawing broad-stroke conclusions about the effects of mammalian defaunation. Small-seed predation appeared to be driving differences between sites, despite the salience of defaunation in the large herbivore class as the major difference between the two faunas. This may have been attributable to site idiosyncrasies, specifically at LCBS, where small rodent populations are thought to be surprisingly paltry.

Chapter 3 described an investigation into the possible effects of altered foliar herbivory regime at a defaunated tropical forest. Almost no mammalian herbivory of juvenile woody plants was recorded at either site, nor were changes to woody plant performance under large-mammal exclusion evident at either site. This came as a surprise, considering the nearly universal findings of previous research that seedling survival (Coley and Barone 1996) and densities (Terborgh and Wright 1994) in tropical forests increases when freed from large-mammal herbivory. However, the vast majority of such studies have concerned lowland tropical rainforests. Generally lower large-herbivore abundances may simply produce little evidence for juvenile plant herbivory during such a brief snapshot in time.

Finally, my chapter 4 study pursued a particular implication of differential seed predation under mammalian defaunation: size-based imbalances in seed survival may translate into dominance of large-seeded species and lower diversity in future stages of regeneration (Dirzo *et al.* 2007, Wright *et al.* 2007). I found no evidence of such a trend, which meshes well with the lack of a contribution by large seed predators to site differences reported in chapter 2. I did, however, find interesting differences in adult tree communities between my sites, irrespective of defaunation considerations. There was considerable differentiation in adult community composition between sites, and LA had higher species richness than LCBS. I can only speculate as to the determinants of differing composition and diversity between sites.

Indeed, given that my investigation was essentially a case study of two nearby tropical premontane forests, I draw many of my conclusions with a measure of caution. However, I believe it to be an important addition to a compendium of tropical defaunation papers dominated by lowland rainforest studies. Essentially, my sites were buffered to the differential

effects of large herbivore activity by idiosyncrasies of small rodent populations, scale-dependent ungulate behavior, and, perhaps, the novel climate of the study systems.

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