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Matrix and Edge Effects on the Maintenance of Ecological Function in an Afromontane Protected Area

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MATRIX AND EDGE EFFECTS ON THE MAINTENANCE OF ECOLOGICAL FUNCTION IN AN AFROMONTANE PROTECTED AREA

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MATRIX AND EDGE EFFECTS ON THE MAINTENANCE OF ECOLOGICAL FUNCTION IN AN AFROMONTANE PROTECTED AREA

by

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BSc. University of Massachusetts, Amherst, MA, 1995

A dissertation submitted in partial fulfillment of the requirements for the degree of

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at

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DEDICATION

This dissertation is dedicated to the people, habitats, and wildlife of the Virunga Landscape, the place that ignited a passion in my heart and mind for the ecology and conservation of forested Africa.

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ABSTRACT

Land use type in the human dominated matrix surrounding tropical forest can influence edge effects at the forest-matrix interface. Edge effects can alter ecological processes and impact the function of forest edge ecosystems. A key ecological process that helps maintain tropical forest and is affected by forest disturbance is seed dispersal by large, fruit eating vertebrates (frugivores). This dissertation examines how the type of vegetation in the matrix, the ‘soft’ edge contrast of pine plantations and the ‘hard’ edge contrast of tea plantations, affect seed dispersal behavior of large frugivores, and the structure and composition of tree species, in forest edge habitat. Research was conducted in Nyungwe National Park, Rwanda, a protected area located in East and Central Africa. Focal tree observations were conducted from December 2011 to September 2012 in forest edges adjacent to two different matrix types and within the forest interior. I recorded visitation frequency and seed removal of frugivores at large-seeded trees. For analysis, seed dispersers were divided into two groups, birds and primates. The response to matrix type differed between disperser groups. Feeding visits by birds were less common in forest edges adjacent to a tea planation matrix, whereas feeding visits by primates were more common in edges adjacent to tea plantations. To explore the influence of matrix type and edge effects on tree species structure and composition, I sampled forest edges adjacent to the different matrix types and within the forest interior. The type of surrounding matrix influenced edge effects on forest structure and composition. I found evidence that a pine plantation matrix mitigated some of the adverse effects of edge on tree communities; tree communities in edges adjacent to tea plantations showed a stronger response to edge effects. Overall, this study shows evidence that land use type in the human dominated matrix can affect ecosystem function and the long-term persistence of some groups of species. The study provides new knowledge on the impact of matrix type on plants, animals, and plant-animal interactions in the edges of a large protected area and indicates the degree to which human disturbance may alter ecological function.

Key words: Land use, landscape change, matrix type, edge effects, seed dispersal, frugivore assembalges, large-seeded trees, protected areas, biodiversity conservation

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Chapter 1: Introduction

Tropical forest has experienced extensive loss, historically covering approximately 12 percent of global land area and today occupying less than 5 percent of the Earth's surface (Hansen et al. 2013). Tropical forests are the most biodiverse systems on Earth, supporting greater than 60% of all known species (Dirzo and Raven 2003), and providing ecosystem services worth twice the value of temperate forests (Brandon 2014, Costanza et al. 2014). Human driven forest loss and degradation and the resulting local extinction or decline of tropical forest biodiversity can cause dramatic changes in the biotic structure and composition of ecological communities (Hooper et al. 2005, 2012, Gardner et al. 2009). However, which species are affected and how they are affected can vary widely as some species are more vulnerable to forest loss and degradation than others (Gardner et al. 2009). The functional role of species, or the role species perform within an ecosystem, can be critical in maintaining biodiversity and ecosystem function (Hooper 2005). Loss of some functional forest species can have more severe consequences for the ecosystem than the loss of others. For instance, to maintain fitness, large-seeded trees in Tonga (Polynesia) are dependent on flying foxes to disperse their seeds (McConkey and Drake 2006). Although the seeds are handled by other animals they are unlikely to disperse as many seeds, or disperse seeds as far as flying foxes (McConkey and Drake 2006). In addition, flying foxes need to maintain a high population in order to function as effective seed dispersers (McConkey and Drake 2006). In this case, the decline or loss of these animals can affect the persistence of large-seeded trees on that island.

Seed dispersal by animals is one of the most critical processes within tropical forests because up to 90% of plant species depend on seed dispersal by animals for their natural regeneration (Howe and Smallwood 1982). Larger-bodied animals play a particularly important role in plant-animal interactions because they disperse the seeds of large-seeded canopy and emergent tree species (Fragoso et al. 2003, Blake et al. 2009). Recent research has shown that the local extinction of large fruit eating animals can drastically reduce seed dispersal and regeneration processes in large-seeded tree trees (Vanthomme et al. 2010, Campos-Arceiz and Blake 2011, Wotton and Kelly 2011). Human induced disturbance poses many threats to frugivores and causes declines and local extinctions of many seed disperser populations (McConkey et al. 2011). Though many of the threatening processes have been identified, there are still gaps in the research on the effects and mechanisms that impact frugivores populations.

The matrix is considered the dominant and most extensive component in the landscape and therefore plays a dominant role in landscape dynamics (Forman 1995). At forest edges, the interaction between the matrix and forest edge vegetation can cause alterations (known as edge effects) that influence animal activities in forest edge habitat, reducing or eliminating movement within forest edges and changing behaviors such as foraging (Murcia 1995). Forest edges can also disproportionately damage large emergent and canopy trees (Laurance et al. 2000). These changes can act independently or synergistically to affect tree regeneration processes with edge forest. Research shows that edge effects drive a shift in plant functional groups in forest edges of some tropical systems (Tabarelli et al. 2008), however, less is known about the changes in animal functional groups in forest edges (Restrepo et al. 1999, Galetti et al. 2003, Magrach et al. 2012, Menke et al. 2012, Vespa et al. 2014). Changes in species functional groups can cause biodiversity loss and have negative effects on ecosystem processes, resulting in a loss of ecological resilience, or the capacity of ecological systems to recover from disturbance (Pardini et al. 2010). Though much research has been conducted on the effects of edges, functional responses to edges can be variable and should be examined and interpreted within the context of the landscape matrix (Murphy and Lovett-Doust 2004, Fischer and Lindenmayer 2007, Lindenmayer et al. 2008, Campbell et al. 2011, Tscharntke et al. 2012). Biodiversity conservation in tropical forests should include knowledge about the ways in which landscape scale processes influence biodiversity patterns and processes within tropical forest edges.

The structure of the vegetation within the landscape matrix surrounding a forest patch can ameliorate some of the ecological effects of edges and support biodiversity and ecosystem function within the forest (Lindenmayer and Fischer 2006). Matrix vegetation that is more structurally similar to the forest can support forest species, facilitate movement within the landscape, and buffer the deleterious effects of edges (Gascon et al. 1999, 2000, Lindenmayer and Fischer 2006, Filloy et al. 2010, Zurita and Bellocq 2012). Matrix structure can draw frugivores to the forest edge and into the surrounding landscape. For example, some studies have shown that frugivorous bird species utilize plantation forest matrices more frequently and intensively than open matrix types in highly fragmented systems (Peh et al. 2006, Magrach et al. 2012, Zurita and Bellocq 2012). Primate use of the surrounding matrix has been correlated with the structural complex of the matrix vegetation (Mbora and Meikle 2004, Anderson et al. 2007, Boyle and Smith 2010). This suggests that the quality of the vegetation in the matrix can influence connectivity between patches of fragmented forest, and also throughout the forest patch. Animals that might otherwise avoid a hard or harsh contrast between the matrix and the forest edge are drawn to, and in some cases, through soft or low contrast edges.

Although it is recognized that the characteristics of the matrix matters to tropical forest ecosystem function and services (Kupfer et al. 2006, Franklin and Lindenmayer 2009, Tscharntke et al. 2012, Driscoll et al. 2013), the empirical evidence of matrix effects remains scarce (Driscoll et al. 2013). There is even less known about the effects of matrix types on the ecological function within forest edges of large intact tropical forests.

Dissertation overview

The goal of this dissertation research was two-fold: 1) to examine the influence of two different matrix types, high contrast tea plantations, and low contrast pine plantations, on the seed dispersal of two different large-seeded canopy tree species, and 2) evaluate the influence of edge and matrix effects on tree species structure and composition within forest edges adjacent to two different matrix types, tea plantations and pine plantations.

I conducted research in Nyungwe National Park (NNP), a montane tropical forest located in Albertine Rift, one of the most biodiverse places in Africa (Carr et al. 2013). The edge of the forest abuts several different matrix types, among them are intensively managed tea plantations and extensive pine plantations. Seed dispersal of large-seeded trees by large and medium-bodied birds and mammals contributes to the maintenance of the forest biodiversity in Nyungwe (Sun et al. 1997, Kaplin and Moermond 1998, 2000, Gross-Camp et al. 2009b). Several studies on seed dispersal processes in NNP have indicated the importance of fruit in the diets of fruit eating animals. For example, fruit accounts for 100% of the overall diet in the Great blue turaco (*Corythaeola cristata*) and nearly 50% of the diet of blue monkeys (*Cercopithecus mitis doggetti*) (Sun et al. 1997, Kaplin and Moermond 1998, 2000). Large-bodied chimpanzees (*Pan troglodytes*) also disperse the seeds of at least 37 different forest plants from 20 families, many of which are from large-seeded tree species (Gross-Camp et al. 2009a, Gross-Camp and Kaplin 2011). These frugivores play a crucial role in the regeneration of forest trees, but little is known about the effects of forest edges or the influence of the matrix on frugivores in NNP.

In chapter 2, matrix and edge effects on frugivorous vertebrate-plant mutualisms and implications for tropical forest regeneration, I review the literature on the edge effects and plant population dynamics, vertebrate frugivores and seed dispersal processes, focusing on the mechanisms driving changes in vegetation structure and composition. To highlight how edge affected habitat influences plant-frugivore interactions this chapter explores the literature on species responses to forest edges within a framework that links seed dispersal dynamics and different stages of plant recruitment. Given that edge effects are dependent upon landscape composition and configuration, I discuss how forest edges interface with the surrounding landscape matrix to ameliorate or exacerbate edge effects on seed dispersal processes in an effort to direct future research.

Chapter 3 explores the effects of landscape matrix type on the seed dispersal of two large-seeded canopy trees species in the forest edges of the national park and tests the hypothesis that matrix type influences the frequency of visitation and fruit removal at large-seeded trees within forest edges. I conducted observations on frugivore visitation and dispersal behavior at two different large-seeded tree species in forest edges adjacent to a low contrast pine plantation, a high contrast tea plantation, and within the forest interior. By evaluating regeneration stages beneath the focal trees I attempted to gain additional perspective on the removal and dispersal of seeds from trees in each matrix type. I focused on large-seeded canopy tree species because of the growing body of evidence that shows large-seeded trees are particularly susceptible to reduced dispersal and negatively impacted by edge effects. Not only are large-seeded trees susceptible to the negative effects of edges, but their seed dispersers are also known to be sensitive and vulnerable to the changes that occur at forest edges.

In chapter 4, I test the hypothesis that matrix type will affect the influence of edge effects on tree species structure and composition within forest edges. Less is known about edge effects and the role of different matrix types in larger, contiguous forest systems. In this study I sampled forest edges at different distances adjacent to high contrast tea plantations, low contrast pine plantations and within a forest interior control. I tested matrix effects and the depth of edge effects on the species richness and diversity of trees, seedlings, and saplings and quantified the proportion of species within regeneration categories.

Chapter 5 provides a brief synthesis of findings, implications of the research, and discusses directions for future research.

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CHAPTER 2: Matrix and edge effects on frugivorous vertebrate-plant mutualisms and implications for tropical forest regeneration

Introduction

The global decline of tropical primary forest due to deforestation and forest degradation presents one of the most critical threats to biodiversity (Fahrig 2003, Gibson et al. 2011). Primary forests have decreased by more than 40 million hectares since 2000 (FAO 2010). Agriculture is one of the primary drivers of deforestation and accounts for approximately 80% of forest loss worldwide (Kissinger and Herold 2012). Deforestation causes obvious losses in biodiversity and ecosystem function, yet primary forest degradation can also result in species loss and reduction in ecosystem function and services (Barlow et al. 2007, Thompson et al. 2013). In Africa, fuel wood collection and charcoal production are the most dominate drivers of degradation (Kissinger and Herold 2012). In Latin American and Asia, logging activities contribute to more than 70% of forest degradation (Kissinger and Herold 2012). Broadbent et al. (2008) reported that from 1999-2002 logging resulted in the creation of 38,000 km of new forest edges in the Brazilian Amazon.

Forest fragmentation is the subdivision of large forest into smaller forest fragments (Laurance 1997). Forest loss and fragmentation can alter many different ecological processes, change spatial patterns of vegetation cover, and influence individual species and assemblages of taxa (Lindenmayer and Fischer 2006, Fischer and Lindenmayer 2007). The increase in forest edge that results from forest fragmentation can play a large role in altering tropical forest dynamics

(Laurance 1997, Laurance et al. 2011). Edge effects refer to the diverse changes in biological and physical conditions that occur at ecological boundaries (Murcia 1995). Studies of edge related ecological changes are the most commonly studied phenomena in ecology (reviewed in: Ries and Sisk 2004, Ries et al. 2004, Harper et al. 2005). Edges are the ecological boundary between distinct patch types that identify the place of transition, contact, or separation between the contrasting elements of a mosaic (Cadenasso et al. 2003, Ries et al. 2004). These boundaries are critical features in the understanding of habitat heterogeneity (Wiens 1992) and influence both ecosystem structure and function through their roles as sites of exchange of energy, materials, and organisms between patches (Wiens et al. 1985). Determining the impact of fragmentation and associated edge creation on tropical forest biotas has been an important goal of conservation biology (Bierregaard Jr et al. 2001, Tscharntke et al. 2007). However, despite decades of research, much of the attention has been focused on the drivers of biodiversity loss in fragmented systems (Hobbs and Yates 2003) and less on edge-induced disruptions in species interactions and the consequences for ecological processes (Wirth et al. 2008, Santos-Heredia et al. 2011).

Seed dispersal by frugivorous animals is an essential process supporting tropical forest structure and function. Habitat disturbance and hunting has caused a decline in world-wide populations of frugivores (Redford 1992, Fa and Peres 2001, Peres 2001, Peres and Palacios 2007), yet the direct and indirect effects of these losses on tropical forests have only just started receiving scientific attention. The realization that human caused loss and decline of many medium and large-bodied species of fruit-eating vertebrates threatens tropical forest ecosystems has prompted a flurry of theoretical, empirical, and review articles on disruptions to seed dispersal processes and resulting consequences for tropical forest function (Dennis et al. 2007, McConkey et al. 2011, Farwig and Berens 2012, Markl et al. 2012). Much of the literature on the impacts of seed dispersal in human disturbed systems has focused on the consequences resulting from defaunation (the absence of mammal species as a result of exploitation such as hunting, (Dirzo and Miranda 1990)), logging, and decreased forest area and/or isolation from fragmentation (McConkey et al. 2011).

I review the literature on edge effects and plant population dynamics, focusing on the mechanisms driving changes in vegetation structure and composition in tropical forest. Next, I summarize the small body of literature on the impacts of edges on vertebrate frugivores and seed dispersal processes in tropical forest. To highlight how edge effects influence plant-frugivore interactions I explore the literature on species responses to forest edges within a framework that links seed dispersal dynamics and different stages of plant recruitment. I use this framework to look at the linkages between changes in plant-disperser mutualisms and changes in vegetation structure and composition in forest edges. Edge effects are dependent upon landscape composition and configuration. Therefore I discuss how forest edges interface with the surrounding landscape matrix to ameliorate or exacerbate edge effects on seed dispersal processes in an effort to direct future research.

The landscape context

Land-use systems in the matrix surrounding tropical forest play a critical role in the maintenance of ecological processes and in forest conservation (Lindenmayer and Fischer 2006, Franklin and Lindenmayer 2009, Driscoll et al. 2013). The contrast between forest edges and matrix land cover type (vegetation) can affect the magnitude of edge effects (Gascon et al. 1999, 2000, Harper et al. 2005, Lindenmayer and Fischer 2006). Matrix vegetation that is more structurally similar to the forest edge may attenuate edge effects, whereas less structure in the matrix (dissimilar to the forest edge) creates higher contrast between the forest edge and can increase disruptions within edge habitat (Gascon et al. 2000) and allow for greater penetration of edge effects. Counter to high contrast matrices, matrix types with low contrast and greater heterogeneity, such as low-intensity agroforestry, may support higher biodiversity and ecosystem function within forest edges and remnants (Tscharntke et al. 2007, 2012, Perfecto and Vandermeer 2008). The discussion of edge effects are linked to the surrounding landscape (Lindenmayer et al. 2008). Understanding the ways matrix type can maintain forest structure, function, and composition, and decrease threats associated with fragmentation and edge effects will help maintain seed dispersal interactions and conserve forest biodiversity in many tropical landscapes (Fahrig et al. 2011, McConkey et al. 2011, Mendenhall et al. 2014).

Plants at the Forest edge

Anthropogenic forest edges can affect plants at several or all stages of their life cycle. Large mature trees experience higher mortality and damage from edge effects (Laurance et al. 1998, 2000, 2011). In the fragmented forests of Central Amazonia large tree (>60 cm dbh) mortality was nearly three times higher within 300m of the forest edge (Laurance et al. 2000). Though vegetation responses can be site specific and highly dynamic, disproportionate effects of increased wind and illumination intensity on emergent and canopy trees along edges can contribute to significant changes in above ground biomass and alter canopy cover and vertical stratification at forest edges (Laurance et al. 1997, 2000). Forest edges also trigger changes in the microclimate which can adversely affect the distribution of plant and animal communities in edge habitat (Murcia 1995, Kapos et al. 1997, Williams-Linera et al. 1998, Newmark 2001, 2005). Microclimate plays an important role in maintaining many ecological processes, such as plant regeneration, leaf litter decomposition, and nutrient cycling, which help structure plant populations and communities (Chen et al. 1999). Habitat desiccation from declines in soil and air moisture and increases in solar radiation can also lead to reductions in seedling recruitment of shade-tolerant tree seedlings and increases in shade-intolerant pioneer tree species (Sizer and Tanner 1999, Benitez-Malvido and Martínez-Ramos 2003, Tabarelli et al. 2004). Some forest systems normally resistant to natural disturbances may not recover from the intensity of human caused disturbances resulting in long-term changes in the species composition of the vegetation cover (Lôbo et al. 2011, Tabarelli et al. 2012, Thompson et al. 2013).

Functional groups of tree species such as emergents (Oliveira et al. 2008) and large-seeded (Melo et al. 2006) trees are particularly sensitive to changes within forest edges. Oliveira et al. (2008) found that in forest edges large tree species (>10cm dbh) accounted for less than 15% of all stems compared to the forest interior where large trees represented greater than 25% of stems. Melo et al. (2006) documented a shift in the seed rain in forest edges. The percentage of large and very large seeds received in forest edges was ten times lower in forest edges than in forest interior and the number of species of seeds was three times lower in edge forest compared to the forest interior (Melo et al. 2006). Patterns of seedling distribution and abundance can be altered in forest edges. Changes in the attributes of seedling assemblages, such as lower species richness, were documented in small forest fragments (<100 ha) and forest edges up to 100 meters towards the forest interior (Benitez-Malvido 1998, Benitez-Malvido and Martínez-Ramos 2003). The studies suggest that changes in recruitment dynamics in these edges resulted from, reduced seed delivery by vertebrates, reduced seedling recruitment and establishment, and increased seedling mortality.

The combined effects of canopy tree species loss and reduced seedling establishment in edges can change the structural complexity of edge-affected forest and promote a persistent shift in composition towards a proliferation of short lived pioneer trees (Oliveira et al. 2004, 2008, Tabarelli et al. 2008) and a bias towards smaller seeded species (Melo et al. 2006, 2007). Forest edges can experience a 2-20 fold increases in the abundances of pioneer tree species (Tabarelli et al. 2012). Many edges receive seed rain from early-successional species in the adjacent modified habitat which further contributes to the regeneration of an assemblage of pioneer and secondary species at the expense of shade tolerant tree species (Laurance et al. 1998, Sizer and Tanner

1999, Melo et al. 2007). Trees in the highly fragmented Atlantic forests of Brazil demonstrate a particularly strong response to human created forest edge (Joly et al. 2014). In edge-affected Atlantic forest a complete absence of large tree species (>10cm dbh) which were present within the forest interior was recorded (Oliveira et al. 2008). The same study documented an approximately 30% structural shift towards smaller trees in forest edges compared to forest interior (Oliveira et al. 2008). This compositional shift in tree species corresponds with a loss in functional reproductive traits which can greatly influence ecosystem function (Hooper et al. 2005, Girão et al. 2007, Lopes et al. 2009).

Frugivores at the forest edge

While a large body of work exists on changes in animal abundances in forest edges (Fagan et al. 1999, Cadenasso et al. 2003, Ries et al. 2004, Ewers and Didham 2006), there has been less work focused on the responses to edges by vertebrate frugivores as a functional group (Restrepo et al. 1999, Galetti et al. 2003, Markl et al. 2012, Magrach et al. 2013, Martino et al. unpublished). By virtue of different microhabitat conditions and fruiting tree species, forest edges may attract different frugivores than the forest interior, thus influencing the abundance, richness, and behavior of frugivore assemblages (Restrepo and Gómez 1998, Bach and Kelly 2004, Delaval and Charles-Dominique 2006, Menke et al. 2012, Magrach et al. 2013, Martino et al. unpublished). In some instances, foraging and seed dispersal by opportunistic bird species increases along edges in response to the proportional change of bird-dispersed early successional trees and shrubs (Estrada et al. 1993, Gorchov et al. 1993, Silva et al. 1996, Galetti et al. 2003). Frugivorous bats that disperse early successional species may opportunistically use forest edges in areas where higher concentrations of these tree species are found, yet studies of bats in forest edges are few and results are variable (Delaval and Charles-Dominique 2006, Cortés-Delgado and Pérez-Torres 2011, Cortés-Delgado and Sosa 2014).

Animal-mediated seed dispersal processes in forest edges, particularly studies conducted in large forest edges which control for area affects (Banks-Leite et al. 2010), are poorly explored (Vespa et al. 2014). A recent network analysis in temperate forest edges shows a shift in avian frugivore assemblages at forest edges towards an increase in abundance of forest generalists (Albrecht et al. 2013). Generalist frugivores can introduce species from the surrounding landscape into forest edges (Cordeiro et al. 2004) and tend to be smaller (Howe 1993) and therefore, due to gape-limitation (Wheelwright 1985), dispersers of smaller seeded species. Menke et al (2012) found that forest visitors and small-bodied frugivores increased at forest edges, while large-bodied forest specialist species decreased in abundance. Edge-induced declines in specialist dispersers can reduce dispersal efficiency for some large-seeded species, perpetuating a more homogenized assemblage of small seeded plant species.

Although largely unexplored, frugivores in edge-affected habitat may employ different seed handling behaviors, switching from seed swallowers to seed predators or seed spitters, or they may consume less fruit overall (Kaplin and Moermond 1998, Ukizintambara 2010, Martino et al. unpublished), with implications for seed dispersal processes. Some fruit eating primates are attracted to forest edges (reviewed in: Ukizintambara 2010, Albert et al. 2014), but this can present increased threats (exposure to pathogens and predators) or mortality, creating an ecological trap (Schlaepfer et al. 2002, Battin 2004, Ukizintambara 2010). The effects of human disturbance on ecosystem processes can be mediated by changes in foraging behaviors and spatial movement of frugivores and the subsequent distribution and abundance of fruit resources (Garcia et al. 2010). Frugivore responses to habitat edges are likely to vary in diverse ways, and knowledge of the structure and function of assemblages as well as the local and landscape context is critical to understanding how edges disrupt plant-frugivore interactions.

Changes in patterns and processes

Human-induced tropical forest disturbances such as fragmentation and creation of edges results in direct and indirect negative effects on mutualisms between seed dispersers and their dependent plant species (Cordeiro and Howe 2001, 2003, Laurance et al. 2006, McConkey and Drake 2006, Wang et al. 2007, Nunez-Iturri et al. 2008, Cordeiro et al. 2009, Holbrook and Loiselle 2009, Sethi and Howe 2009, Herrera and García 2010, Herrera et al. 2011, Effiom et al. 2013). In Tanzania, the effects of disrupted plant-frugivore mutualisms in forest fragments, isolated by a high contrast agricultural matrix and deprived of large-bodied seed dispersers, resulted in less seeds removed from animal dispersed trees and more seedling and juvenile recruits beneath parent canopies than trees in continuous forest (Cordeiro and Howe 2003). It has been established that overhunting of medium to large bodied animals in tropical forests influences plant-frugivore interactions and the dynamics of forest regeneration with significant consequences for tropical forest plant communities (reviewed in Galetti and Dirzo 2013). Research in a forest in Borneo with severely depleted populations of frugivores found that over the past 15 years, trees reliant on fruit eating animals for dispersal have developed a more clustered pattern than those dispersed abiotically (Harrison et al. 2013). The effects of forest edges on plant-frugivore interactions are less straightforward, though the research on the effects of overhunting and fragmentation can be used as a guiding framework for understanding the potential influence of edge contrast on seed dispersal processes in forest edges. Edge-induced declines or absences in species can have similar influences on forest structure and composition in forest edge habitat as overhunting or reduced forest area, though few studies have explicitly connected declines in dispersers to changes in plant recruitment in edge-affected forest.

Recruitment limitation

Small fragment size, edge effects, and over exploitation of seed dispersers can limit plant recruitment through impacts on seed production, seed dispersal, and seedling establishment (Cordeiro and Howe 2001, Peres 2001, Benitez-Malvido and Martínez-Ramos 2003, Nunez-Avila et al. 2013). Reduced recruitment, or recruitment limitation in plants can occur through any or all of the following mechanisms: dissemination or dispersal limitation, which result from a change in how seeds are dispersed and can cause failure of seeds to reach suitable sites for establishment; source or seed limitation, which results when there is low seed availability and seeds do not arrive in all available sites for recruitment; and establishment limitation, where suitable sites are limited and can result when seeds arrive but do not establish due to an altered abiotic environment or to the failure of seeds to be dispersed to suitable recruitment sites (Nathan and Muller-Landau 2000, 2000, Schupp et al. 2002, Clark et al. 2007). In many habitats, these mechanisms often do not occur in isolation, but in disturbed habitat they can act synergistically with the potential for ecological cascades (Pardini et al. 2010, McConkey et al. 2011). For instance, shifts in large-seeded tree species within forest edges can influence the production of key fruit resources (source limitation) (Nunez-Avila et al. 2013), and changes in microclimate can alter seed and seedling establishment (establishment limitation) due to a decline in environmental conditions at deposition sites (Benitez-Malvido and Martínez-Ramos 2003).

Changes in the behavior of large-bodied seed disperser within forest edges can further limit seed dispersal of these species (Magrach et al. 2013). Other factors influencing recruitment limitation and seed dispersal processes in forest edges are seed and seedling predation and secondary dispersal (Donatti et al. 2009, Santos-Heredia et al. 2011). Though important to different trophic levels of plant recruitment, and affected by human disturbance and changing interactions, in this review I focus on primary dispersal and changes resulting from altered frugivore-plant mutualisms. The structural characteristics of the matrix can mitigate the decline of species and assemblages by maintaining interior conditions within forest edge and extending the habitat of small forest fragments. The matrix can promote connectivity by providing structural features dispersers can uses such as corridors, live fencing, and remnant trees, to facilitate movement between forest fragments and into forest edges (Tewksbury et al. 2002, Luck and Daily 2003, Harvey et al. 2005, 2006, Herrera and García 2009).

Dispersal limitation

The contribution a seed disperser makes to the regeneration of fruit-bearing plant species depends largely on how the seeds are removed and dispersed (Schupp 1993, Schupp et al. 2010). The quality of frugivore dispersal services can influence the probability of a seed establishing in several ways: by depositing the seed 1) in suitable habitat, 2) a certain distance away from the parent tree and 3) within a specific neighborhood or area that contains the right density and composition of plants (Schupp et al. 2010, Beckman and Rogers 2013). The seed dispersal effectiveness framework (SDE) provides a way to quantify the potential contribution different seed dispersers offer a plant (Schupp et al. 2010). The contribution of these factors can be affected by altered abundance, behavior, and movement patterns of seed dispersing animals all of which can be impacted by human activities.

Low numbers of frugivores can reduce the number of foraging visits made to fruit trees and fruit removal (Forget and Jansen 2007, Wang et al. 2007), two key components in ensuring that a frugivore provides effective dispersal services to a plant (Schupp et al. 2010). Studies on visitation and fruit removal in hunted forest versus non-hunted forest show that changes in the composition and abundance of seed dispersers reduce the numbers of seeds removed (Holbrook and Loiselle 2009, Sethi and Howe 2009). Trees in small forest fragments also experience reduced visitation by key dispersal agents, and consequently reduced seed removal (Cordeiro and Howe 2003, Cramer et al. 2007, Kirika et al. 2008, Cordeiro et al. 2009, Lehouck et al. 2009, Moran et al. 2009). The failure of seeds to be removed and dispersed from parent trees, and reduced dispersal distances, decreases seed survival as they fall in greater densities beneath the canopy making them more susceptible to predation and pathogens (Janzen 1970, Connell 1971, Schupp 1992, Terborgh 2013).

Changes in frugivore assemblages due to altered conditions in forest edges can alter natural seed dispersal by changing the number of seeds dispersed, the way seeds are handled (Martino et al. unpublished), the distance that seeds are dispersed (Magrach et al. 2013) and the spatial pattern of dispersal. Research in Nyungwe National Park, Rwanda showed that large-bodied birds made 26% fewer visits, spent 42% less time foraging, and removed 35% fewer fruits from large-seeded trees in forest edges next to a hard, or high contrast matrix compared to forest interior and low contrast matrix (Martino et al. unpublished). Conversely, primates made the most visits, spent the greatest time foraging and removed most fruit in the forest edges near a high contrast matrix of tea relative to low contrast pine and interior comparison sites.

In Chile, reduced canopy height and increased openness in forest edges affected removal of the mistletoe *Tristerix corymbosus* fruits by its exclusive marsupial disperser (*Dromiciops glirodies*) (Magrach et al. 2013). Fruit removal rates in this study increased more than 10-fold from the edge towards the interior of the forest (Magrach et al. 2013). Reduced populations of fruit trees in forest edges, especially large canopy trees with large crop sizes, changes the structure and composition of edges and can result in less intensive use of forest edges by key dispersers (Melo et al. 2006, 2007). This can change the disperser assemblage from large-bodied and wide ranging frugivores such as chimpanzees, elephants, tapirs, and hornbills that move seeds long distances creating geographically broad seed dispersal patterns (Holbrook and Loiselle 2009) towards smaller bodied birds that disperse many seeds near parent trees or in predictable locations based on the structure of the forest (Wenny and Levey 1998).

The structural quality and complexity of the matrix can be critical to maintaining movement throughout a large, contiguous forest landscape. Hard or high contrast forest edges such as those adjacent to an open matrix of low stature, such as pasture or tea can influence the movement of certain species throughout the forest landscape which can affect the dispersal of some populations of trees. For example in Nyungwe National Park, Rwanda, chimpanzees are important to the dispersal of many large seeded canopy trees (Gross-Camp et al. 2009) yet there is evidence that chimpanzees use forest edges adjacent to high contrast tea plantations less than forest edges adjacent to low contrast pine plantations (Kaplin et al unpublished). This can reduce dispersal of some large-seeded tree species within forest edges, such as *Chrysophyllum gorungosanum* that are reliant on large bodied fruigvores for dispersal (Martino et al. unpublished). Greater structural complexity and compositional heterogeneity within the matrix can help maintain higher levels of species richness within fragments and edge-affected habitat, increasing the ability of ecosystems to withstand disturbance (Loreau et al. 2001, Fahrig et al. 2011, Tscharntke et al. 2012).

Seed limitation and establishment limitation

The seed production of adult fruit bearing trees limits recruitment by affecting the amount of seeds available for dispersal to sites where they may germinate and mature (Clark et al. 1998, 1999). Seed availability can be affected when tree populations within small forest fragments and edge environments shift distribution, abundance, and size class towards smaller, early successional tree species. Smaller trees can be characterized by smaller fruit crops as basal area of a tree correlates with the crown size and fruit production (Chapman et al. 1992). Small fragments dominated by edge effects in Chile showed a reduction in density and basal area of a bird dispersed fleshy-fruited shade tolerant tree (Nunez-Avila et al. 2013). This led to lower seed yields and shorter fruiting periods, resulting in decreased visitation by avian dispersers (Nunez-Avila et al. 2013). Loss of key reproductive trees can alter seed rain and alter disperser behavior resulting in seed limitation and decreasing the probability of seeds reaching suitable recruitment sites (Terborgh 1986, Lindenmayer et al. 2013, Beckman and Rogers 2013)

Altered environmental conditions in forest edges can cause lower soil moisture and higher temperatures (Williams-Linera et al. 1998), favorable conditions for pathogens (Benítez-Malvido and Lemus-Albor 2005), and increased abundances of herbivores (Wirth et al. 2008), all of which can alter the chances of establishment and germination. Seeds that do arrive to potential germination sites within forest edges may be impeded by increased competition, which can be the case for large-seeded shade tolerant species when altered abiotic conditions promote a compositional dominance of functional groups in edges, such as early succession pioneer species (Muller-Landau et al. 2002).

The matrix can mediate some of these ecosystem changes buffering against edge effects, such as microclimate changes, at the local and landscape scale (Lindenmayer and Fischer 2007). Didham and Lawton (1999) showed that softer matrix vegetation, or vegetation with greater structural similarity as forest edges reduced edge effects on microclimate changes. This allows forest edges to maintain environmental conditions similar to the forest interior, with the opportunity to support an equally similar amount of suitable habitat for seed establishment. Matrix vegetation can also play a role in buffering some of the disturbance effects associated with edges on large canopy and emergent trees. Protecting these important trees from the high mortality frequently observed in forest edges can help maintain a key source of food for many frugivores (Laurance et al. 2011). Understanding how matrix structure and edge effects interact with seed dispersal processes has important implications for ecosystem function even in large, protected, tropical forest systems. By increasing biodiversity within forests and within the matrix, greater landscape heterogeneity has the potential to buffer the effects of human disturbances and help maintain plant-animal interactions.

Conservation implications

The roles species perform within ecosystems help maintain ecological processes vital to the functioning of the entire system (Chapin et al. 2000, Cardinale et al. 2002, 2006, Hooper et al. 2005). It has become progressively clear that ecosystem function benefits from high numbers of different species performing different functions within the ecosystem (Chapin et al. 2000, Hooper et al. 2005, Duffy et al. 2007, Duffy 2008, Thompson et al. 2013). Habitat disturbance and overhunting are reducing populations of large vertebrate frugivores, causing changes in the composition of many frugivore assemblages and significant alterations of seed dispersal for many species of plants with large animal-dispersed seeds (Galetti and Dirzo 2013). Edge driven changes in the structure of frugivore communities could cause ecological shifts affecting ecosystem functions and services and the maintenance of biodiversity (Duffy 2008, Gardner et al. 2009, Pardini et al. 2010).

As forest continues to be cleared and agriculture intensifies, there is an urgent need to increase knowledge on the ways human-modified landscapes impact biodiversity patterns and ecological function throughout the landscape (habitat and non-habitat) for more effective conservation approaches or strategies within the context of global land-use change. Recent articles have presented different conceptual frameworks illustrating the ways landscape composition and configuration influence the structure of ecological communities and ecosystem function (Lindenmayer et al. 2008, Gardner et al. 2009, Fahrig et al. 2011, Tscharntke et al. 2012). Other conceptual approaches have focused specifically on methods to evaluate the ecological mechanisms connecting protected areas to the surrounding landscape to mitigate impacts such as intensifying land use for agriculture and pressures from human population growth, and to improve protected area effectiveness (DeFries et al. 2005, 2007, 2010, Hansen and DeFries 2007). Landscape scale approaches have been a priority focus of biodiversity conservation initiatives since the 1980s (Sayer et al. 2013). Some landscape level approaches focused on improving the conservation value of large protected areas from the inside (i.e. building management capacity and conducting species inventories and monitoring plans) and improving the livelihoods of people living in close proximity to the protected areas. Less focus has been given to understanding the structural integrity of the surrounding landscape, or how the different land uses within the landscape matrix interact with the protected area biodiversity as a strategy to mitigate threats to the protected area.

Multifunctional landscape approaches that promote some of the fundamental concepts from landscape ecology and require an understanding of landscape structure, function, and change to support ecological systems (Wiens 1992, 2013), are becoming more widely embraced (Sayer et al. 2013) for protected area conservation and management. With that, greater recognition that landscape heterogeneity can influence animal movements, population persistence, and species interactions (Fahrig et al. 2011) can offer profound prospects for biodiversity conservation in human-modified landscapes (Gardner et al. 2009). Landscape scale conservation approaches that seek to mitigate the negative effects of the human dominated landscape on protected areas will be most effective if they integrate a scientific understanding of the ecological mechanisms driving degradation (Hansen and DeFries 2007).

Conclusion

Assessing differences in the structure of seed dispersal networks between disturbed versus undisturbed forest, such as overhunted and non-hunted areas or between forest edges and forest interior can lead to a better understanding of how human disturbance and structural complexity in the landscape impacts frugivore-plant interactions (Menke et al. 2012, Vidal et al. 2013). There are a wide range of mechanisms induced by forest edges that can limit the recruitment of plant species and impact plant-frugivore mutualisms. As large bodied frugivores disappear from small and medium sized fragments (Galetti and Dirzo 2013) it is necessary to understand how species respond to the spatial patterns and heterogeneity in the surrounding landscape of large fragments and intact contiguous forest. Further examination of the ways in which land use and land use change in the matrix influences the conditions in forest edges, and affect seed dispersal processes, is necessary to advance our understanding of strategies that can prevent long-term impacts of biodiversity loss throughout tropical landscapes.

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CHAPTER 3: Effects of Matrix Type on the Dispersal of Large-seeded Trees in Forest Edges of an Afromontane Protected Area

Abstract

The land use type in the matrix surrounding tropical forests can influence plant population dynamics in forest edge habitat. In tropical forests, the seeds of large-seeded trees rely on dispersal by animals, which contributes to the successful regeneration of these trees. To understand how two different matrix types – one presenting a hard edge and high structural contrast between the forest edge and a tea matrix, and the other a soft edge and low structural contrast between the forest edge and pine matrix – influences seed dispersal processes I studied the assemblage of frugivores at two large-seeded tree species in forest edges. Primates spent significantly more time foraging per tree (2.5±5.1 mins) and removed significantly more fruit (90%) in forest edges adjacent to the hard tea edge than time foraging per tree (1.1±4.0 mins) and removing fruit (5%) in edges adjacent to a soft pine edge; or foraging (0.2±1.2 mins) and removing fruit (5%) from trees within the forest interior. The opposite pattern was observed for birds. Large birds spent less time foraging per tree in hard tea edges (0.5±2.0 mins) compared to soft pine edges (2.8±7.7 mins) and the forest interior (2.9±11.3 mins). As a result large birds consumed a greater percentage of fruit in forest edges adjacent to pine (49%) and within the forest interior (36%), than edges adjacent to tea (14%). The differences found in the frugivore assemblage adjacent to tea suggest that large birds avoid trees in edges adjacent to a high contrast matrix and some primates are attracted to the high contrast, hard edge. I conclude that changes in the frugivore assemblage can have consequences for large-seeded trees in forest edges and lead to a potential decline in the seed dispersal services provided to these trees in some forest edges.

Introduction

Tropical deforestation and the fragmentation of native habitat cause declines in biodiversity and disruptions in ecological patterns and processes at many different scales (Millennium Ecosystem Assessment 2005, Hooper et al. 2012, Tscharntke et al. 2012). While direct disturbance and loss of species occurs when forest is cleared or reduced for agriculture expansion or urbanization, the remaining forest often faces less obvious but equally profound and irreversible ecological disturbances (Lindenmayer and Hobbs 2008, Brodie and Aslan 2012). Artificially created forest edges resulting from human landscape alteration are one of the most dominant drivers of change in tropical regions (Murcia 1995, Laurance et al. 2006, 2011). Responses to forest edges include changes in both abiotic and biotic conditions in forest edge habitat, with these alterations penetrating as far as 300 meters into the forest interior (Laurance et al. 2002, 2011) and in some cases 2-3 kilometers into the interior (Cochrane and Laurance 2002, 2008). The magnitude and extent of edge influence on forest remnants is affected by the type or quality of land-use activities in the non-habitat landscape, or matrix, surrounding the forest (Laurance 1997, Harper et al. 2005). The spatial pattern and composition of the human modified matrix can have acute impacts on edge biota.

While much fragmentation research has focused on the changes occurring within forest remnants and along edges (Bierregaard, 2001; Laurance, 1997; Tabarelli & Gascon, 2005), another more recent mounting body of research has focused on the relationship between matrix type and edge effects (Gascon et al. 2000, Kupfer et al. 2006, Lindenmayer and Fischer 2006, Driscoll et al. 2013). Over the past 15 years, studies on matrix effects have increased, focusing mainly on the influence of matrix quality on the diversity and abundance of species in remnant patches, and movement of individuals through the matrix (Prevedello and Vieira 2010). Structural characteristics of the landscape matrix have been shown to modulate some of the negative effects of fragmentation (Wiens 2009, Didham et al. 2012, Tscharntke et al. 2012b, Driscoll et al. 2013). A more structurally similar contrast between the matrix and the forest remnant has shown to reduce isolation by providing corridors for movement, in turn affecting patch colonization (Ricketts 2001), providing habitat that decreases area-effects (Prugh et al. 2008), and buffering forest edges against microclimate changes (Denyer et al. 2006). Edge responses are stronger when there is high contrast, or a "hard" edge between matrix and forest vegetation, and weaker when there is low contrast or a "soft" edge (Didham & Lawton, 1999, Fischer & Lindenmayer, 2007, Gascon et al. 2000, Laurance & Yensen, 1991, Mesquita et al. 1999, Murcia, 1995). The ecological edge that results from disturbance can depend on the intensity of the interaction with the adjacent environment.

Though ecological studies have demonstrated that certain matrix types can mitigate forest edge effects (Mesquita et al. 1999, Harper et al. 2005, Denyer et al. 2006), there is still little known about the influence of matrix type on ecological processes and species abundances in forest edge habitat (Franklin and Lindenmayer 2009). Seed dispersal by animals is an especially critical ecological process shaping tropical plant communities. Animal mediated seed dispersal allows seeds and seedlings a chance to escape high mortality near the parent tree (Connell 1971, Harms et al. 2000, Janzen 1970, Schupp, 1992) by providing opportunities for seeds to reach suitable sites for establishment (Muller-Landau et al. 2002). Animal dispersal agents can be sensitive to the quality of the surrounding landscape matrix which can influence the composition of the vertebrate disperser community in forest edges (Zurita et al. 2012, Menke et al. 2012, Magrach et al. 2013), and responses to forest edges can therefore vary depending on landscape context.

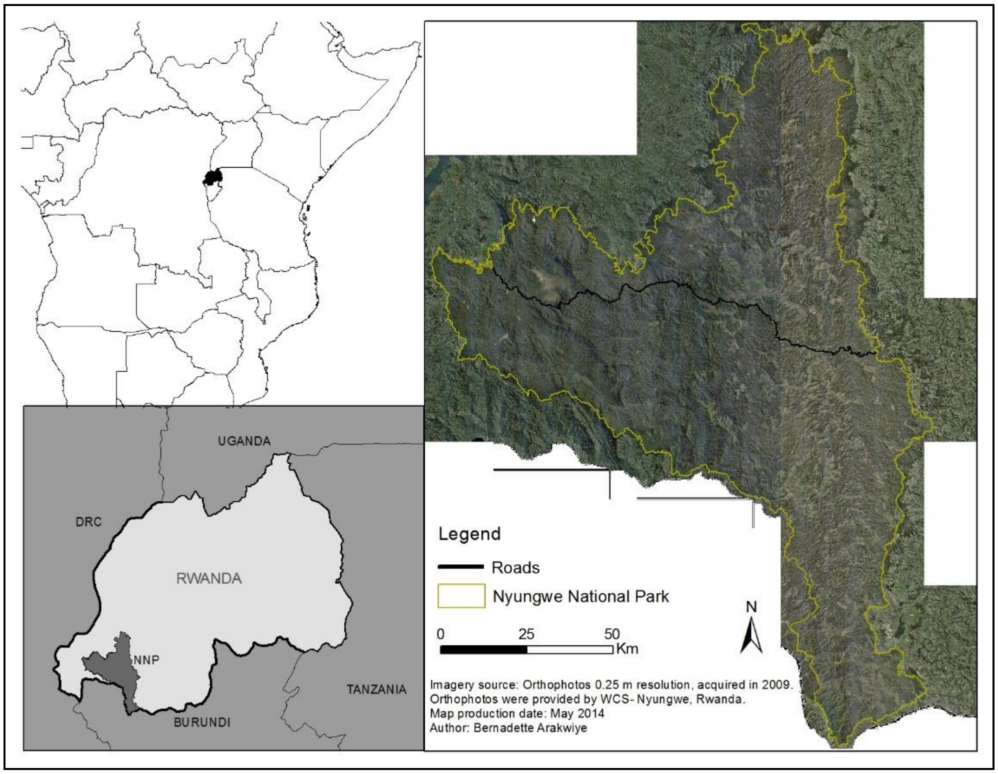
Subsequent changes in the composition or abundance of animal seed dispersers may alter seed removal and seed arrival patterns, affecting the distribution of plant populations and communities in edges (Wright and Duber 2001, Galetti and Dirzo 2013). Understanding how the surrounding landscape matrix affects seed dispersal processes in forest edges is integral to understanding human driven disruptions of key ecological processes in tropical forests.

The Albertine Rift (AR) region of East-Central Africa is world-renowned for supporting extraordinary biodiversity and a large human population (UNEP 2011, Carr et al. 2013). The region is also vulnerable to impacts from climate change, which is predicted to have a severe effect on the biodiversity and the ecosystem services in which people heavily rely (UNEP, 2011). Much work has been undertaken in the Albertine Rift to catalogue the diversity of species it contains, though less work has been conducted on the impacts of disturbance on species interactions and ecological processes (Carr et al. 2013). The Western portion of Rwanda falls within the Albertine Rift and contains the country's approximately 2 percent of remaining primary forest cover. There is intense pressure for agricultural land in Rwanda. The matrix of agricultural land use types in Rwanda can cause a variation in forest ecosystem level responses to landscape level processes.

I compared the effects of different land use types in the matrix surrounding a large, intact, afromontane forest on seed dispersal in forest edges. I examined frugivore visitation and dispersal behavior at two different large-seeded trees species in forest edges adjacent to a low contrast pine plantation, a high contrast tea plantation, and within the forest interior. High contrast matrices can perpetuate some of the ecological responses from edge effects including structural damage to vegetation, altered microclimate, and altered pollen and seed dispersal (Harper et al. 2005). Alternatively, low contrast matrices can buffer the effects of edge by extending habitat to support wildlife population and maintaining microclimate conditions (Harper et al. 2005). By evaluating regeneration stages beneath the focal trees I attempted to gain additional perspective on the successful removal and dispersal of seeds from trees in each matrix type. Low visitation combined with high seedling densities under tree crowns might indicate recruitment limitation from density-dependent mortality (Schupp 1992, Cordeiro and Howe 2003, Cordeiro et al. 2009). I focused on large-seeded canopy tree species because a growing body of evidence shows that large-seeded trees are particularly susceptible to reduced dispersal and negatively impacted by edge effects (Cramer et al. 2007, da Silva & Tabarelli 2000, Melo et al. 2007, Melo et al. 2010, Moran et al. 2009, Oliveira et al. 2008, Wotton & Kelly 2011). Ries and Sisk (2004) used a conceptual model to illustrate that different mechanism drive species responses to edge. The model predicted that animal species will respond to forest edges based on the distribution of food resources or on habitat preferences (Ries and Sisk, 2004). Edge avoidance is common with habitat-specific species, such as forest interior species (Ries and Sisk 2004, Magrach et al. 2013). I predicted that the behavior of seed dispersers (disperser arrival and seed removal) in forest edges adjacent to a low contrast matrix with structural characteristics similar to the forest interior, such as pine plantation, would be consistent with disperser behavior within the forest interior; and that forest edges adjacent to high contrast matrix, tea plantations, would experience less disperser activity and therefore reduced seed dispersal.

Methods

Study sites – Research was conducted in two forest edge sites, and within the forest interior of Nyungwe National Park (NNP), Rwanda (latitude 2° 15' and 2° 55'S, longitude 29° 00' and 29° 30'E). NNP is contiguous with Kibira National Park in Burundi and together this transboundary protected area covers 1,413 km² of Afromontane forest ranging between 1600-2900 meters in elevation. NNP is one of the most biologically important afromontane forests in Africa due to a richness of fauna which includes 13 species of primates, representing 20% of all African primates, 280 species of birds, 26 of which are Albertine Rift endemics and 11 are classified as either endangered, vulnerable, or near threatened, and approximately 47 local endemic species of flowering plants and about 280 Albertine Rift endemic plants (Fischer & Killman 2008, Plumptre et al. 2007). Nyungwe National Park is effectively isolated from other montane forest habitat, with the closet forest fragment, 300 ha, approximately 10 km away (Figure 1).



Imagery source: Orthophotos 0.25 m resolution, acquired in 2009.
Orthophotos were provided by WCS- Nyungwe, Rwanda.
Map production date: May 2014
Author: Bernadette Arakwiye

Figure 1.Location of Nyungwe National Park

Host to a population density of over 350 inhabitants per square kilometer, Rwanda is the most densely populated county in Africa (UNEP 2011). With 83% of the country residing in rural areas, the landscape around NNP, surrounded by a matrix of farmland, tea plantations, mixed agriculture, local woodlots, and buffer zones of pine and eucalyptus, supports much of the population (UNEP 2011). The buffer zone was established in 1969 under an agreement between the government of Rwanda and a Swiss Technical Agency (Bush and Ikirezi 2010). By 1979 nearly 17, 000 ha of natural forest was converted to predominantly pine and eucalyptus plantations, an area equivalent to approximately 15% of Nyungwe Forest (Bush and Ikirezi 2010). The primary goal of the buffer was to mark the boundaries of, at the time, Nyungwe Forest Reserve and prevent encroachment into the reserve by local communities (Gapusi 2007).

Another dominant land use surrounding NNP is tea plantations, which provide revenue at the local and national level (Bush and Ikirezi 2010, Masozera 2002). Preliminary data (Kaplin et al. 2009, 2011, Kaplin unpublished data) , as well as ecological theory, show that the pine buffer zone, as a low contrast or a “soft” edge, mitigates negative impacts of edge effects such as microclimate changes (Denyer et al. 2006) or increase tree mortality (Laurance et al. 2002). Preliminary data also show increased tree mortality in forest adjacent to tea plantations and reduced diversity and abundance of fruiting trees (Kaplin unpublished data).

To compare the effects of matrix type on seed dispersal in adjacent forest edge, one of my forest edge research sites was located in forest adjacent to tea plantations in Namashake district. The second forest edge site was located in forest adjacent to an approximately 25 year old pine plantation. Both edge sites and the forest interior were located in the western portion of the forest, an area of the forest shown to be highest in bird and mammal species richness (Plumptre et al. 2002). Each matrix type was homogenous and relatively static during the time of the study. Tea presented a very high and wide contrast between the forest and surrounding matrix along the edge, while pine presented a low and structurally similar contrast between the forest and surrounding matrix.

Sampling in forest adjacent to each matrix type was conducted within 0-70 meters of the edge, along approximately 1-3 km of forest edge length. Forest interior sampling was conducted > 500 meters from the forest edge. Sites were dominated by afromontane vegetation and located at an average elevation of 2018 m (±137m). I selected *Chrysophyllum gorungosanum* and *Syyzgium guineense* trees to sample effects of matrix type on seed dispersal of large-seeded trees. Both of these tree species are large-seeded (>1.0 cm), shade tolerant, emergent, canopy species that were present in each of my three treatments and in fruit during the research period. Previous studies in NNP show that both tree species are dispersed by large-bodied frugivores (Gross-Camp et al., 2009; Kaplin & Moermond, 1998; Sun et al., 1997).

Phenology data has been collected in Nyungwe since 1991 and meteorological data since 1988 (Sun et al. 1996a) with pauses in data collection and some loss of data during the genocide of 1994 (Plumptre 2012). The phenology data collection in NNP coincided with a larger fruit-frugivore dispersal study (Kaplin & Moermond 1998, Kaplin & Moermond 2000, Kaplin et al. 1998, Sun et al. 1996, 1997, Sun & Moermond 1997) and in 2002 Gross-Camp and Kaplin began examining the role of chimpanzees in seed dispersal (Gross-Camp and Kaplin 2005, 2011, Gross-Camp et al. 2009a, 2009b). Fruiting generally peaks during the major wet season in March-May and remains high during the major dry season in July-August (Sun et al. 1996a). Studies at NNP have indicated the importance of large-seeded fruits to the diets of large bodied frugivores and the importance of chimpanzees in the dispersal and regeneration of large-seeded fruiting trees (Sun and Moermond 1997, Kaplin and Moermond 2000, Gross-Camp et al. 2009b).

Study species – Chrysophyllum gorungosanum (Sapotactaceae) reaches up to 45 m in height and is characteristic of montane forest (Gapusi 1999, 2007). Fruits are brown or dark yellow when ripe with a reddish-brown pubescence containing latex and three seeds. Fruits in NNP measure 23.8±2.4 mm wide and 43.7±4.1 mm long (Sun et al. 1997). Seeds are dark brown or blackish, obliquely ellipsoid and up to 20.8 cm long and 11.6 mm wide (Sun et al. 1997). The relative density of *Chrysophyllum gorungosanum* is 0.03/ha (Kaplin et al. 1998). Dispersers of

Chrysophyllum gorungosanum in NNP include cercopithecines and chimpanzees (Kaplin et al. 1998, Gross-Camp et al. 2009a) and in other forests they are dispersed by gorillas and elephants (Cochrane 2001, Stanford and Nkurunungi 2003). *Chrysophyllum gorungosanum* usually fruits for 6 months in a non- synchronized pattern (Sun et al. 1996b). Ripe fruits occurred on our focal trees in April 2012 and fruiting lasted through July 2012.

Syyzgium guineense (Myrtaceae) is a common tree species throughout the montane forests of the Albertine Rift and is the most common tree species in NNP with a relative density of 12.81/ha (Kaplin et al. 1998). The tree reaches 30 m and fruits measure 13.6±2.2 mm width and 14.6±2.1mm length and seeds are 13.0±1.2 width (Sun et al. 1996b). *S. guineense* is used in traditional medicine by local people for the treatment of several diseases and research has shown it to have antibacterial value (Tsakala et al. 1996). Kaplin et al. (1998) reported *S. guineense* fruits as one of the top ten most frequently consumed plant species by blue monkeys (*Cercopithecus mitis doggetti*) in May, August and September of 1991 and July of 1992. *S. guineense* was the only large-seeded tree species Gross-Camp et al. (2009) found in both chimpanzee (*Pan troglodytes*) feces and orally discarded wadges. During the *S. guineense* fruiting period, chimpanzees were observed feeding almost exclusively on these fruits (Gross-Camp et al. 2009). During our study period *S. guineense* fruits began to ripen in December 2011 and fruiting lasted through September 2012.

A total of 24 *Chrysophyllum gorungosanum* trees and 24 *Syyzgium guineense* trees were identified, mapped and observed within each of the three sites. I was limited in the number of replicates I could locate for each treatment by what was naturally available at each of the three treatment sites. Each individual tree represented an independent experimental unit. For *C. gorungosanum* this resulted in eight trees within the forest interior, three trees within forest edges adjacent to pine and 13 trees within forest edges adjacent to tea. For *S. guineense*, we sampled 10 trees within the forest interior, five trees in edges adjacent to pine and nine trees in edges adjacent to tea

Focal tree observations - I conducted observations at the 24 fruiting individuals of *C. gorungosanum* and 24 *S. guineense* during fruiting periods from November 2011-September 2012. I rotated randomly between focal trees, observing trees in two hour intervals between 0600 – 1700 hours throughout the day. *C. gorungosanum* trees were observed for an average of 15.8±17.3 per tree for a total of 380 focal observation hours and *S. guineense* trees were observed for an average of 18.3±13.3 per tree for a total of 450 focal observation hours. Focal trees in forest adjacent to pine plantations received a greater number of observation hours because fewer individuals of both species were available. Watches were not conducted during periods of rain or at night, therefore results focus on diurnal activity. The tree canopy was scanned every 30 minutes to record all animals present in the tree, which provided an estimate of the number of visitors a tree received independent of foraging behavior. I used focal sampling to record the foraging time and handling behavior for a single fruit-eating animal. A focal observation began when an animal removed a fruit and the observation continued until the individual was no longer visible or present to observe, or until interruption for a 30 minute scan sample. Focal watch animals were identified, the time spent foraging, and fruit handling behavior – swallow, cheek pouch, drop, spit, regurgitate, defecate, leave with fruit – were recorded. For analysis, I defined fruit removed as the number of fruits swallowed and/or cheek pouched, and I calculated the number of fruits consumed by subtracting the number of fruits swallowed or cheek pouched by the number of seeds dropped. Foraging time was the number in minutes the animal spent feeding. The important variables in terms of dispersal are the number of fruits removed, dropped and spit, the number of foraging visits, and the time spent foraging.

Fruit abundance value – Following Sun et al. (1996) I estimated the size of the fruit crop for each focal tree by assigning a score to the percent of the crown containing fruit. A score between 0-4 (0=0%, 1=25%, 2=25-50%, 3=50-75%, 4=75-100%) was recorded at the beginning of each observation period. I used the diameter at breast height (dbh=1.4m) to correlate with the fruit crop score (Chapman et al., 1992; Kaplin et al., 1998). A fruit abundance value was calculated as the mean fruit score of each tree species multiplied by the basal area of that species. Because a given crop size can influence disperser visitation (Howe and Kerckhove 1979) I regressed the fruit abundance value against the number of disperser visits per treatment and the number of fruits consumed by dispersers per treatment to examine whether this was a factor in visitation.

Density of focal tree species – To characterize species richness and diversity in forest edges adjacent to pine plantations, tea plantations, and within the forest interior, circular plots with a 10 m radius were established in each habitat. Plots sampled within forest adjacent to each matrix type were set at different distance bands, parallel to the forest edge (Fig. 2), at 0-50 meters from the edge, 50-100 meters, and 100-150 meters from the edge, and plots within the forest interior were located >500m from the forest edge. The point along the forest edge to enter the forest and begin locating plots was randomly selected. In forest adjacent to pine plantations, 15 plots per distance band were sampled (i.e. 15 plots at 0-50, 50-100, and 100-150) for a total of 45 sample plots (1.4 hectares) within forest edges. In edges adjacent to the tea matrix, 13 plots per distance band were sampled, for a total of 39 plots (1.2 hectares) within forest edges. Within the forest interior, 26 plots (0.8 hectares) were sampled along randomly located transects. Within each plot, the dbh of all trees ≥ 10cm dbh (diameter at breast height) were measured and identified to species when possible.

Seedling and juvenile abundances – To further examine whether fruit removal differed in forest edges adjacent to tea and pine plantation I assessed seedling and juvenile regeneration under the canopies of *S. guineense* and *C. gorungosanum* focal tree species. The number of seedlings (<15 cm height) and juveniles (15-100 cm) was counted in 2m intervals within a 20° wedge extending 20 m from the base of each focal tree. The orientation of the wedge transects from the base of each focal tree was randomly selected and reoriented if the direction resulted in overlap with a neighboring fruiting conspecific. The number of trees sampled differed slightly from the number of focal trees observed because I could not sample beneath all focal trees due to saturated soil. Seven trees were sampled within the forest interior, four trees in edges adjacent to pine, and seven trees in edges adjacent to tea.

Statistical analysis –Data for fruit handling analyses did not meet assumptions of normality required by a one way analysis of variance (ANOVA) and standard transformations did not result in homogeneity. Therefore, I looked at differences in dispersal by each disperser group between all three treatments with a non-parametric ANOVA (Kruskall Wallis), with treatment (interior, pine, tea) as the independent variable and foraging behavior by all frugivores combined and separated by group, large birds, primates, as the dependent variable. If the Kruskall Wallis test was significant, a pairwise comparison of treatment groups was further tested using Mann-Whitney U tests. A non-parametric ANOVA was also used to test differences between the visit duration and number of visits per treatment using treatment as the independent variable and the visitation per two hour observation period by large birds or primates as the dependent.

I used chi-square tests to determine whether there was a difference between the three treatments in the counts of seedlings and saplings under (<10m) and away (>10m) from focal trees. A student's t-test was used to examine differences in the dbh of both species of focal trees per treatment and the dbh of *C. gorungosanum* and *S. guineense* trees sampled in 0-150 m vegetation plots at the forest edge sites and within the forest interior. I looked at density and basal area of focal trees to compare the distribution and abundance of focal trees (food resources) at each site. All analyses were performed using SPSS 20.0 or in the statistical software R (version 2.15.1 R Development Team 2011).

Results

Disperser assemblage - A total of five different diurnal species visited *C. gorungosanum* and14 different diurnal animal species visited *S. guineense* focal trees (Table 1). Of the five species of visitors to *C. gorungosanum*, three dispersed seeds: two primate species: *Cercopithicus mitis, Cercopithicus mona* and one large bird: *Tauraco schuetti.* The primary seed dispersers of *S. guineense* were primates (*Cercopithecinae*) and large birds/turacos (*Musophagidae*). Of the 14 visitors to *S. guineense*, seven were seed dispersers that swallowed, spit, or regurgitated seeds intact. Dispersers included four species of primates (*Cercopithecus l'hoesti, Cercopithicus mitis doggetti, Cercopithicus mona* and *Lophocebus albigena)* and three large fruit-eating birds (*Corythaeola cristata, Tauraco johnstoni, Tauraco schuetti).* Other species (e.g., small birds: *Andropadus nigriceps, Onychognathus walleri, Pycnonotus barbatus, Treron calva;* squirrels: *Paraxeus sp*; and black and white colobus monkeys *Colobus angolensis ruwenzori)* were observed pecking at fruit and chewing seeds.

Table 1. All species that visited focal trees in each sample site, interior, pine and tea. Includes foraging and non-foraging visits; Bl=large bird, Bs=small bird, P=primate, S=squirrel

Species	***Interior***	***Pine***	***Tea***
Tree: Chrysophyllum gorungosanum			
Birds			
Bycanistes subcylindricus		Bl	
Tauraco schuetti	Bl	Bl	Bl
Primates			
Cercopithecus mitis		P	P
Cercopithecus mona			P
Squirrel			
Paraxeus sp.		S	
Tree: Syzygium guineense			
Birds			
Andropadus nigriceps (SB)			Bs
Corythaeola cristata (LB)		Bl	Bl
Onychognathus walleri (SB)	Bs		
Pycnonotus barbatus (SB)			Bs
Tauraco Johnstoni (LB)	Bs	Bl	Bl
Tauraco schuetti (LB)	Bl	Bl	Bl
Treron calva (SB)	Bl		
Primates			
Cercopithecus l'hoesti	P		P
Cercopithecus mitis		P	P
Cercopithecus mona			P
Colobus angolensis ruwenzori		P	P
Lophocebus albigena			P
Squirrel			
Paraxeus sp.	S	S	S

Visit frequency and duration of foraging visit – Birds were observed visiting *S. guineense* focal trees adjacent to pine and within the interior more frequently than adjacent to tea while primates were observed visiting trees adjacent to tea more frequently than the other two sites. *S. guineense* focal trees were observed for a total of 450 hours (21.0±10.5 hrs per tree). Within the forest interior, *S. guineense* received a total of 22 foraging visits (21 large birds, one primate species). In forest edges adjacent to pine *S. guineense* received 36 foraging visits (24 large bird, 12 primate) and in edges adjacent to tea *S. guineense* received 51 foraging visits (9 large bird, 42 primate). *C. gorungosanum* received very few visitors for all three treatments during the total of 376 observation hours conducted (25.5±29.0 hrs per tree). Within the forest interior *C. gorungosanum* received one foraging visit (large bird only), forest edges adjacent to pine received three foraging visits (primate only), and within forest edges adjacent to tea, *C. gorungosanum* received three foraging visits (primate only). Given the small number of observations, *C. gorungosanum* was not included in the focal watch data analyses but visitation and foraging details are included in (Table 2).

Table 2. Visitation and fruit consumption at *Chrysophyllum gorungosanum* focal trees.

Species (no. observation hrs) no. of focal trees	**Total no. of foraging visits**	**Total time foraging (mins)**	**Mean time foraging**	**Mean fruits consumed per visit**	**Total number fruits consumed**
INTERIOR (118 hrs) N=8					
Tauraco schuetti	2	10	0.1±1.3	0.03±0.2	2
PINE (128 hrs) N=3					
Cercopithecus mitis	3	31	0.2±2.0	0.1±0.6	8
TEA (134 hrs) N=13					
Cercopithecus mitis	1	4	0.05±0.4	0.04±0.3	3
Cercopithecus mona	2	8	0.1±0.8	0.08±0.5	6

I found no statistical difference in the number of frugivore visits per tree between the three treatments (Kruskal-Wallis: H= 4.2, df=2, P>0.05). However, when separating data by large birds and primates, large birds made more visits to *S. guineense* trees within the forest interior (n=10 trees) contributing to 96% of visits and primates, 4% of visits. Large birds also made more visits to focal trees within forest edges adjacent to pine (Figure 2), accounting for 67% of all visits and primates 33% of visits. Primates were the main visitors to trees within forest adjacent to tea (Figure 3), making 82% of all visits and birds, 18% of visits. Differences in the number of foraging visits between treatments for large birds was not statistically significant

(H=1.9, df=2, P>0.05), while the number of foraging visits between treatments for primates was significant (H=7.9, df=2, P<0.05). Follow-up with Mann-Whitney tests showed a significant difference in the number of visits for primates between interior and pine (Z= -2.55, P=0.01) and interior and tea (Z= -2.50, P=0.01), with significantly more visits made to trees in edges near pine and near tea than trees in the interior, but not between tea and pine (Z= -0.13, P=0.89).

The mean duration of foraging visits per tree for large birds was longer in the forest interior (2.9 ± 11.3 mins) and in edges adjacent to pine (2.8 ± 7.7 mins) than edges adjacent to tea (0.5±2.0 mins), although these differences were not significant (H=2.7, df=2, P> 0.05) (Figure 4). The mean duration of foraging visits per tree for primates differed significantly between the interior (0.2±1.2 mins), pine (1.1±4.0 mins) and tea (2.5±5.1 mins) (Kruskal-Wallis test: H=6.5, df=2, P<0.05) (Figure 5). Post-hoc Mann-Whitney tests showed that the mean foraging visit differed significantly between the forest interior and the forest edge adjacent to pine (Z= -2.04, P=0.04), and the forest interior and the forest edge adjacent to tea (Z= -2.40, P=0.01), with more foraging visits to trees in forest edges adjacent to both pine and tea than within the forest interior. There was not a significant difference between mean foraging visits within pine forest edge and tea forest edge (Z= -0.47, P=0.63), though more mean visits were made within forest edges adjacent to tea.

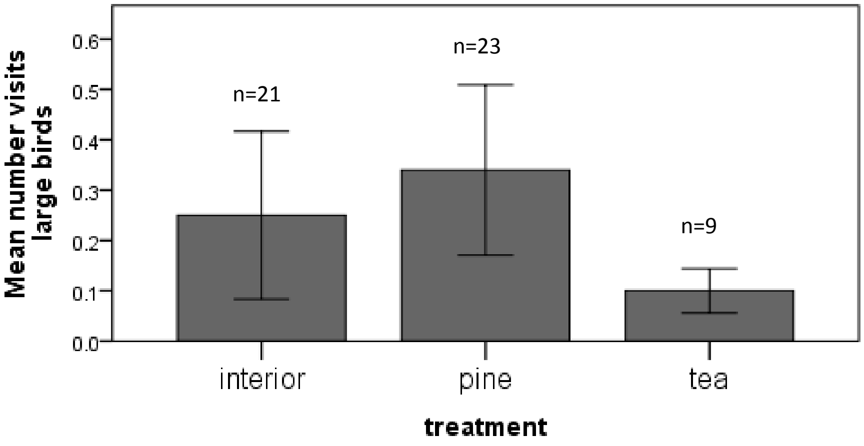


Figure 2. Mean (±SE) number of visits by large birds per tree made within each treatment: forest interior, forest edges adjacent to pine plantations and forest edges adjacent to tea plantations; n =total number of visits. Number of focal trees per treatment =10 interior, 5 pine, 9 tea.

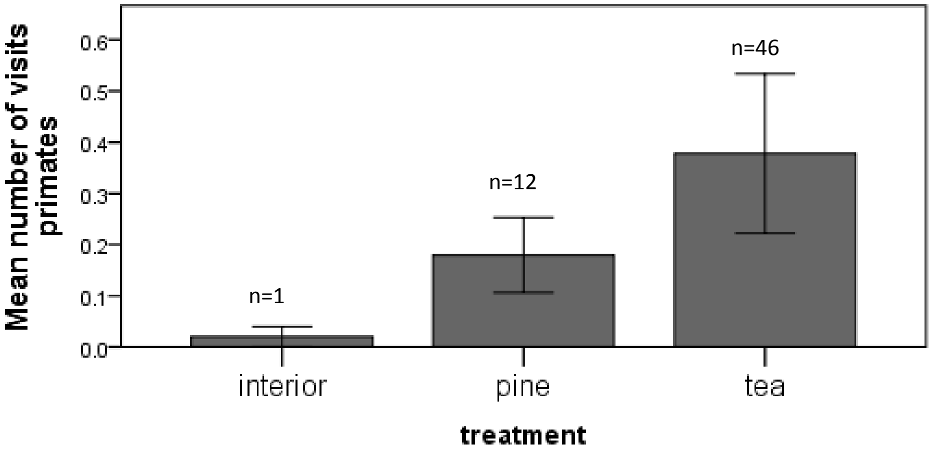


Figure 3. Mean (±SE) number of visits made by primates per tree within each treatment: forest interior, forest edges adjacent to pine plantations and forest edges adjacent to tea plantations; n=total number of visits. Number of focal trees per treatment =10 interior, 5 pine, 9 tea.

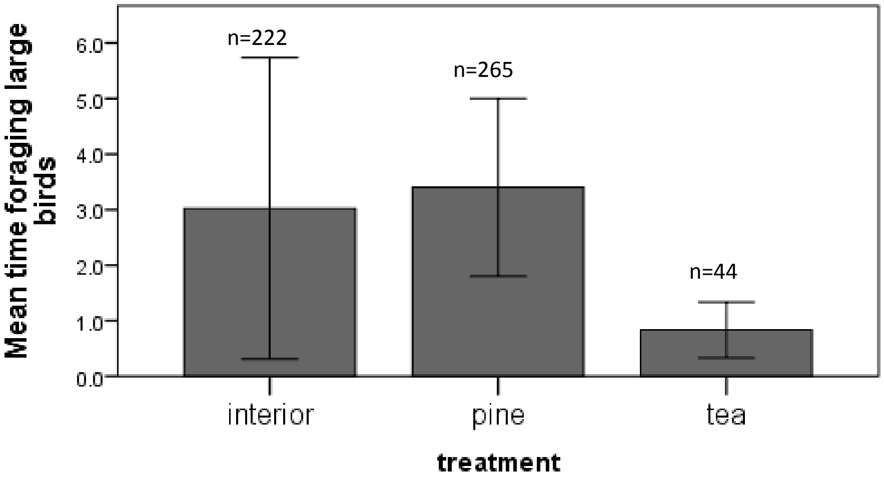


Figure 4. Mean (±SE) time large birds spent foraging per tree within each treatment: forest interior, forest edges adjacent to pine plantations and forest edges adjacent to tea plantations; n=total time minutes foraging. Number of focal trees per treatment =10 interior, 5 pine, 9 tea.

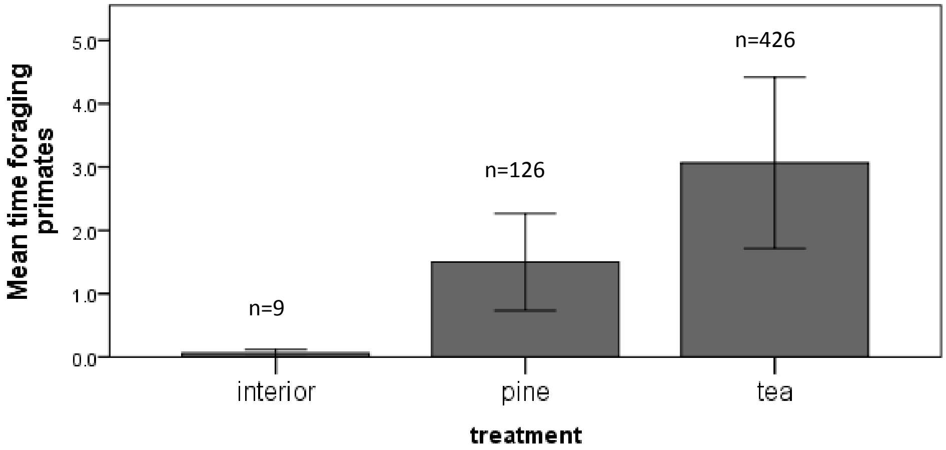


Figure 3. Mean (±SE) time primates spent foraging per tree within each treatment: forest interior, forest edges adjacent to pine plantations and forest edges adjacent to tea plantations; n= total minutes foraging. Number of focal trees per treatment =10 interior, 5 pine, 9 tea.

Handling behavior and fruit removal – The quantity of fruit consumed between disperser groups differed depending on the matrix or buffer zone type. Of the fruit observed consumed per tree by large birds, 36% (n=122) was in the forest interior, 49% (n=166) was within forest edges adjacent to pine and 16% (n=53) was within edges adjacent to tea (Figure 6). Observed fruit consumption per tree by primates showed an opposite pattern from birds, with 5% (n=49) consumed in the forest interior, 17% (n=175) in forest adjacent to pine and 78% (n=810) in forest adjacent to tea (Figure 7). The mean number of fruits consumed per tree by birds was higher in both the forest interior (1.6±3.5) and in forest edge adjacent to pine (1.7±4.1) than in forest adjacent to tea (1.0±4.3) although the difference was not statistically significant (Z=-0.71, P=0.47). There was a significant difference in the mean number of fruits consumed per tree for primates between interior (0.8±6.3), forest edges adjacent to tea (6.8±15.0) and forest adjacent to pine (1.8±6.4) (H=6.04, df=2, P=<0.04). Follow-up Mann-Whitney tests found no significant difference in the number of fruits consumed between interior forest and forest edges adjacent to pine by primates (Z= -1.72, P=0.08), or between tea and pine edges (Z= -1.02, P=0.30) but there was a significant difference in the number of fruits consumed by primates between forest interior and forest edges near tea (Z= -2.31, P=.02), with 90 times more fruit consumed in edges near tea.

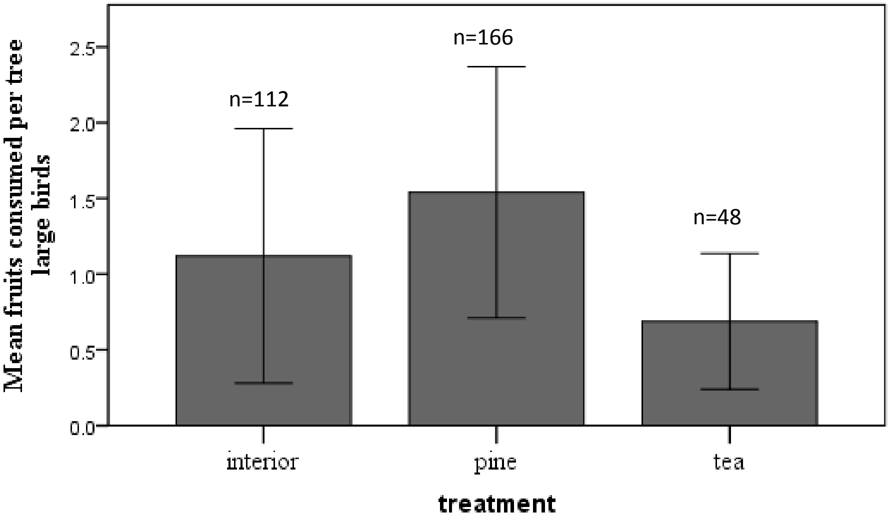


Figure 6. Mean (±SE) number of fruits consumed by birds per tree for each treatment: forest interior, forest edges adjacent to pine plantations and forest edges adjacent to tea plantations; n=total number of fruits consumed. Number of focal trees per treatment =10 interior, 5 pine, 9 tea.

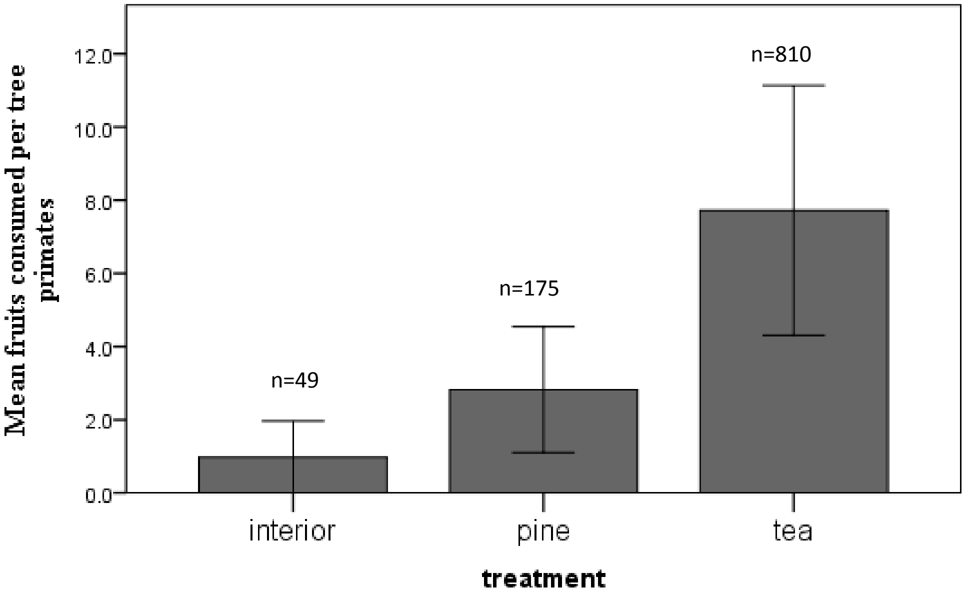


Figure 7. Mean (±SE) number of fruits consumed by primates per tree for each treatment: forest interior, forest edges adjacent to pine plantations and forest edges adjacent to tea plantations; n=total number of fruits consumed. Number of focal trees per treatment =10 interior, 5 pine, 9 tea.

Table 3: Overall visitation and fruit consumption by large birds and primates at all *Syzygium guineense* focal trees.

Species (no. observation hrs) no. of focal trees	Total no. foraging visits	Total time foraging (mins)	Mean time foraging	Mean fruits consumed per visit	% of fruits consumed (Total no. of fruits consumed)
INTERIOR (122 hrs) n=10					
Birds	**21**	**222**	**2.9±11.3**		**72%**
Tauraco johnstoni	7	76		4.7	18.6 (31)
Tauraco schuetti	14	146		20.9	53.7 (91)
Primates	**1**	**9**	**0.2±1.2**		**28%**
Cercopithecus l'hoesti	1	9		49.0	27.7 (49)
PINE (164 hrs) n=5					
Birds	**23**	**265**	**2.8±7.7**		**46%**
Corythaeola cristata	10	85		18.2	24.2 (84)
Tauraco johnstoni	1	10		5.0	1.3 (5)
Tauraco schuetti	12	170		18.6	20.8 (77)
Primates	**12**	**126**	**1.1±4.0**		**54%**
Cercopithecus mitis	12	126		45.6	53.7 (175)
TEA (164 hrs) n=9					
Birds	**9**	**44**	**0.5±2.0**		**5%**
Corythaeola cristata	1	1		8.0	0.9 (8)
Tauraco johnstoni	4	31		7.8	3.3 (23)
Tauraco schuetti	4	12		13.5	1.8 (17)
Primates	**46**	**426**	**2.5±5.1**		**95%**
Cercopithecus l'hoesti	8	60		191.5	31.4 (292)
Cercopithecus mitis	28	271		65.1	54.8 (446)
Cercopithecus mona	4	42		5.8	2.5 (23)
Lophocebus albigena	6	53		8.2	5.3 (49)

Focal tree dbh and fruit abundance value –I found no difference in the dbh of *S. guineense* focal trees between the three treatments. There was a significant difference between the dbh of *C. gorungosanum* focal watch trees within the forest interior (63.7±19.5) and focal watch trees in forest edges adjacent to tea (97.8±28.7); (t(18) = -2.79, p= 0.012). I found no difference in dbh of *C. gorungosanum* between the interior forest and forest edges near pine, or between forest edges near pine plantations and forest edges near tea plantations. For *S. guineense* I found no difference in the fruit abundance value among focal watch trees, calculated as the mean fruit score of each focal tree multiplied by the basal area of the focal tree species (Kaplin et al., 1998). There was a difference in the fruit abundance value for *C. gorungosanum* between the forest interior (0.44±0.30) and forest edges near tea (2.25±1.55) with a greater fruit abundance value in forest edges near tea, t(19) = -3.221, p = 0.004. *C. gorungosanum* showed no difference in fruit abundance between interior and pine edges or between pine edges and tea edges. However, given the few observations overall, I was unable to test whether the difference in fruit abundance influenced frugivore visitation.

S. guineense and C. gorungosanum density – To examine the distribution and abundance of food resources I compared the density of focal trees at each site sampled. Within the forest interior, *S. guineense* had the highest dominance, basal area per hectare, followed by forest edges adjacent to pine and then at edge adjacent to tea. *C. gorungosanum* had the greatest dominance in the forest edge adjacent to tea (Figure 8).

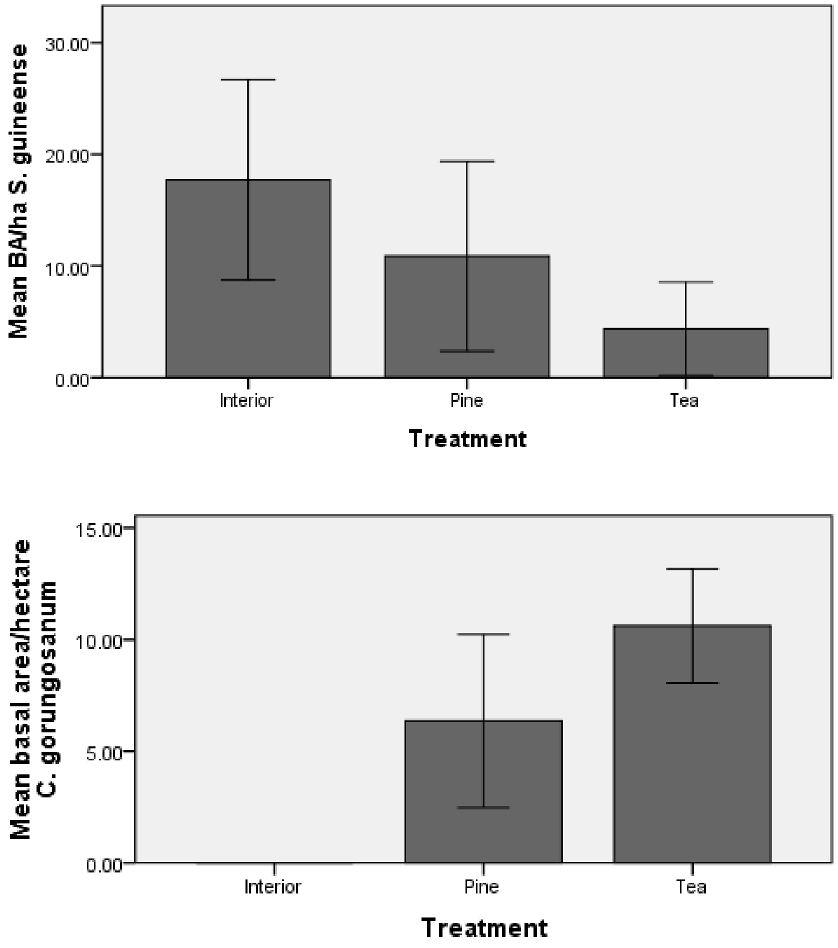


Figure 8. Mean and ±SE basal area per hectare for *S. guineense* and *C. gorungosanum* trees sampled in the forest interior, forest edges adjacent to pine plantation and forest edges adjacent to tea plantations.

Seedling and juvenile abundances –Seedling and juvenile counts of *S. guineense* were highest under (0-10m) the focal tree canopy and away (10-20m) from the focal tree canopy in forest edges adjacent to tea (χ^2 with a Yate's continuity correction = 29.54, df=1, P<0.00001) (Figure 8). Seedlings and juveniles were scarce in forest edges adjacent to pine, with counts of two or less in either distance category. The percentages of seedlings under (<10m) versus away from (>10m) the focal tree canopies was higher under the crowns of focal trees in forest edges near tea and under crowns within the forest interior (χ^2 =6.26, df=1, P=0.012). Although counts of juveniles were much higher under trees in tea edges than the forest interior, the numbers of juveniles in both the interior and in edges near tea were nearly even in distance categories (Figure 8).

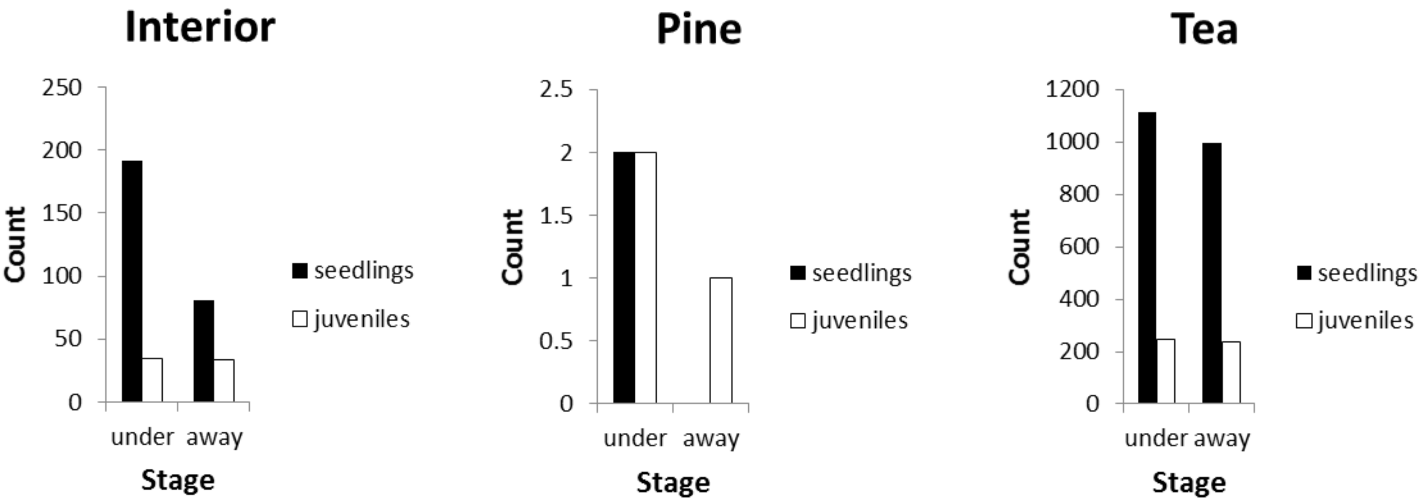


Figure 9. Abundances of *S. guineense* seedlings were greater under (<10m) and away (10-20m) in forest edges near tea than within the forest interior (χ^2 with a Yate's continuity correction = 29.54, df=1, $P<0.00001$). Juveniles were relatively even under and away in forest edges and forest interior.

I counted very few conspecific recruits beneath the canopy for *C. gorungosanum*. Within the forest interior I counted three juveniles away from (>10m) focal tree canopies and no seedlings in either distance category. I had similar results at the pine site, with two juveniles away (>10m) from the focal canopy and no counts for seedlings. In edges adjacent to tea, I counted one seedling under (<10m) the focal canopy, zero away and two juveniles away with none under.

Discussion

Frugivore species assemblage, visitation frequency and fruit removal differed in forest edges adjacent to the different matrix types sampled. I observed greater occurrence and greater fruit removal by primates in forest edges adjacent to tea than edges adjacent to pine or within the forest interior. The opposite pattern was observed for birds. Large birds showed decreased visitation and foraging to *S. guineense* at tea edges compared to the forest interior and pine edges. The percentage of visits and time spent foraging by large birds at focal trees within the forest interior and in edges adjacent to the pine matrix was relatively similar, and longer than time spent in trees adjacent to the tea matrix. Large birds consumed more fruit overall in forest edges adjacent to pine (49%) and within the forest interior (36%), than edges adjacent to tea (14%). I observed similar trends to those found in previous research at NNP on seed dispersal of large-seeded canopy trees conducted within the forest interior. Gross-Camp et al. (2009a) found large birds accounted for the greatest number of visits to focal trees (80% of visits), and *S. guineense* was the second most visited tree species.

These results are consistent with other studies that show forest edges affect plant-avian frugivore interactions (Restrepo and Gómez 1998, Restrepo et al. 1999, Galetti et al. 2003, Menke et al. 2012, Magrach et al. 2013). Land use change presents threats to tropical forest birds with certain functional traits (Bregman et al. 2014, Newbold et al. 2013, 2014, Sekercioglu 2012). Large, non-migratory, frugivorous, tropical bird species tend to be particularly sensitive to land use change and research shows they are less likely to occur and less abundant in habitats with more intensive use (Newbold et al. 2013, 2014). Large birds are critical to the dispersal of many large-seeded plants and local and regional declines can jeopardize the functional role these birds play within the plant community (Holbrook & Loiselle 2009, Sethi & Howe 2009). Much of the research on the anthropogenic impacts on different functional groups of birds has focused on fragmentation related area effects, and to a lesser extent, overhunting (Bregman et al. 2014, Sethi and Howe 2009, Holbrook and Loiselle 2009). However, edge effects maybe exerting a less pronounced but equally perturbing effect on the structure of avian frugivore assemblages.

This study is among the few that examined the effects of different matrix types on plant animal interactions in forest edges of a large, intact, isolated, tropical forest, thereby controlling for area effects and habitat loss. Studies on altered dispersal mutualisms in fragmented forests have generally occurred in forested systems that are dramatically disturbed and/or reduced in area, or as a comparison between continuous forest and small patches of remnant forest (Githiru et al. 2002, Cordeiro and Howe 2003, Cramer et al. 2007a, Lehouck et al. 2009a, Moran et al. 2009). Within this landscape context many studies correlate decreased frugivore visitation with decreased seed removal along a gradient of disturbance and reduced forest area (Cordeiro & Howe 2003, Githiru et al. 2002, Kirika et al. 2008, Lehouck et al. 2009). Lehouck et al. (2009a) showed that forest deterioration reduced avian visitation and seed removal rates independent of fragment size, and this was attributed to a loss or decline in abundance of the most effective avian seed dispersers, which were avian forest specialists. Fluctuations in bird densities in forest fragments and in forest edges may reflect interactions with the surrounding matrix (Luck and Daily 2003, Lehouck et al. 2009b). A higher quality matrix type comprised of food resources and/or greater structural heterogeneity can promote positive functional responses by frugivores in degraded landscapes.

Low contrast matrix structure can provide a buffering effect on the responses of some species to forest edges in forest fragments or contiguous forest (Renjifo 2001, Lindenmayer and Fischer 2006, Brockerhoff et al. 2008, Brady et al. 2009, Filloy et al. 2010, Campbell et al. 2011, Zurita et al. 2012). Campbell et al. (2011) reported that land use in the matrix surrounding a forest patch determined the edge response function of an invertebrate community in New Zealand. Their results demonstrated that compared to a matrix of high contrast pasture land, a low contrast plantation forest matrix effectively mitigated the disturbance effects across edges on invertebrate diversity and community composition (Cambell et al. 2011). A study in the Columbian Andes showed that greater structural complexity in the matrix from tree plantations influenced bird abundances in forest fragments; of the forest species declining in abundance with fragmentation, 20% were buffered by the tree plantation matrix (Renjifo 2001). These results suggest that matrix type and edge effects may drive changes in the community composition of frugivores in forest edges, reducing functional diversity and potentially altering seed dispersal processes (Lehouck et al. 2009, Menke et al. 2012, Restrepo et al. 1999, Restrepo & Gómez 1998). Studies comparing the recruitment of plant species in forest fragments experiencing a reduction in species, or a complete loss of species, suggest forest composition may change when vertebrates that mediate seed dispersal and seedling survival change (Bleher and Böhning-Gaese 2001, Cordeiro and Howe 2001, 2003). Structural features and contrast of the matrix may interact with forest edges and influence the fate of some plant populations.

Primates and large birds: functional redundancy or complementarity?

I observed nearly five times more visits to *S. guineense* focal trees by primates in forest edges adjacent to tea than the focal trees in forest edges adjacent to pine or within the forest interior.

Increased visitation coincided with fruit consumption; of all fruit consumed by primates, 78% was at focal trees in forest edges near tea, and the highest number of species (4) and individuals (46) were observed in edges adjacent to tea. Globally, fruit-eating primate species show a wide range of responses to forest disturbance (Marsh 2003, Benchimol and Peres 2014). In Kenya, Menke et al (2012) found a decrease in frugivorous primates at forest edges. In Amazonian and Atlantic forests, moderately frugivorous marmosets (genus *Mico*) tolerate, and in some instances prefer, forest edge habitat (Benchimol and Peres 2014). Researchers in Bwindi National Park, Uganda, found higher densities of L'Hoest's monkeys (*Cercopithicus lhoesti*) at the forest edge than within the forest interior (Butynski 1984, McNeilage et al. 2001).

Primates have been shown to be important and effective seed dispersers (Chapman & Onderdonk 1998, Chapman 1995, Garber & Lambert 1998, Gross-Camp & Kaplin 2011, Kaplin & Lambert 2002), yet their role in ecosystem function is still not entirely understood (Chapman & Russo 2007, Chapman et al. 2013, Garber & Lambert 1998). In NNP interior, chimpanzees (*Pan troglodytes*) were found to spit a large proportion of the *S. guineense* seeds from fruits they consumed, and despite close proximity to adult con-specifics, the seeds spat by chimpanzees resulted in a significantly higher germination rate than seeds deposited in chimpanzee feces, or seeds planted in germination trials (Gross-Camp & Kaplin, 2011). Though studies have shown decreased probabilities of germination under the canopy of conspecifics for some species (Howe et al. 1985), Lambert (2001) also found higher germination rates among seeds spat underneath conspecific trees by red tail monkeys (*Cercopithecus ascanius*) in Kibale forest, Uganda. In this study, the high concentration of time spent foraging and large number of fruit consumed by primates in forest edges near a tea matrix compared to edges near pine matrix and within the forest interior suggests that primates may play significant role in the dispersal of *S. guineense* in tea edge forest.

Like many tropical trees, *S. guineense* has a variety of frugivore species that disperse its seeds, potentially benefiting the plant by dispersing seeds widely throughout the habitat (Brodie et al. 2009, Clark et al. 2001, Howe & Smallwood 1982, Schupp et al. 2010). Empirical studies on dispersal by frugivores have shown differences in dispersal services within and between animal families (Holbrook and Smith 2000, Poulsen et al. 2002, Jordano et al. 2007). Although *S. guineense* may successfully recruit near to a conspecific adult, a heavier reliance on primates for seed dispersal in forest edges adjacent to tea could influence the quality of the seeds dispersed (Schupp et al. 2010, Schupp 1993), resulting in a largely uneven distribution of seeds throughout forest adjacent to high contrast matrices. Birds have been shown to disperse seeds widely, potentially 'out performing' primates in long distance dispersal (Holbrook et al. 2002, Sekercioglu 2006, Holbrook 2011, McConkey and Brockelman 2011). Birds are also known to deposit seeds in different areas of the forest than primates (Clark et al. 2001, 2005). However, virtually nothing is known about the role of seed dispersal by nocturnal animals in NNP. Though little is know about their behavior in forest edges, there is evidence that fruit bats consume the fruits of some large-seeded trees species within the forest interior (Martino, personal observation), and African fruit bats are known to move seeds long-distances dispersing them to potentially suitable habitat for establishment (Seltzer et al. 2013).

A greater species richness of frugivore dispersers can increase the chances that seeds will arrive in a greater variety of sites and at different distances (Kissling et al. 2012). Different species of birds have different foraging behaviors and movement patterns (Spiegel and Nathan 2007). This research suggests that the frugivore assemblage for *S. guineense* may be influenced by the structural characteristics of the surrounding matrix, and as a consequence, this could affect multiple aspects of seed dispersal in forest edges. The large birds in our study generally swallowed seeds whole, dropping very few beneath focal trees. Turacos in NNP are known to disperse over 80% of seeds consumed away from parent trees (Sun et al., 1997). Sun et al. (1997) showed that among the three species of turaco at NNP, each uses the habitat differently and generates different spatial patterns of dispersed seeds. The larger great blue turaco (*Corythaeola cristata*) may provide longer dispersal distances, having a 50-fold greater home range than the smaller turacos (*Tauraco johnstoni* and *Tauraco schuetti*) (Sun et al. 1997). Garcia and Martinez (2012) showed that avian frugivore abundance and richness had positive effects on the quantitative (number of seeds removed) and qualitative (spatial pattern of seed deposition) aspects of seed dispersal, but effects were proportionally more important for the qualitative component than the quantity of seeds being dispersed. With changes in the spatial behavior of frugivores edge effects may be driving changes in the frugivore assemblages in edge habitat, leading to a potential decline in seed dispersal function.

***Syzygium guineense*: a beacon for other large-seeded trees?**

It is predicted that greater species richness and diversity will maintain ecosystem function and resilience in the face of disturbance more effectively than systems that have encountered species loss and changes in community composition (Hooper et al. 2005, García and Martínez 2012, García et al. 2013). García et al. (2013) suggest that the diversity and functionality of an entire plant-frugivore assemblage promote seed dispersal services and the ability of ecosystems to maintain function after disturbance. Human related disturbance is creating shifts in the diversity of vertebrate communities. In many forests large and medium bodied seed dispersers are being replaced by smaller-bodied species (Dirzo and Miranda 1990, Galetti et al. 2009, Bueno et al. 2013, Galetti and Dirzo 2013, Harrison et al. 2013). A recent network analysis in Kakamega forest, Kenya, found a decrease in large bodied frugivores at forest edges (Menke et al. 2012). Niche complementarity between species was much lower at forest edges than within the forest interior, resulting in more specialized network interactions within the forest interior (Menke et al., 2012

As the most common tree in NNP, with a distribution spanning a wide variety of habitat types, *S. guineense* plays an important role in structuring the forest canopy and forest biomass. While the consequences of human disturbance driven changes in species composition on ecosystem processes differ, from a plant perspective, maintaining a suite of dispersal agents and a degree of ecological redundancy can buffer against non-random disturbance, preventing loss of essential ecosystem function and services (Brodie et al. 2009, Schupp et al. 2010, McConkey and Brockelman 2011, Wotton and Kelly 2011b, Harrison et al. 2013). These results may signal a shift in seed disperser functional groups at *S. guineense* in forest edges. Natural spatial variation in animal abundances (Chapman and Lambert, 2000) could be influencing the results, yet data from focal tree observations made by other seed dispersal researchers within the forest interior of NNP support the general pattern of visitation by large birds within the forest interior. Population density data are limited in NNP and frugivore abundance data for the three sites sampled would help produce a clearer picture of frugivore use of forest edges.

If a successful large-seeded tree such *S. guineense* experiences changes in its disperser assemblage in forest edges, what are the implications for other less common large-seeded tree species with a narrower assemblage of dispersers in edge-affected habitat? The limited dispersal observations at *C. gorungosanum* and the impoverished recruitment of seedlings and juveniles beneath the tree canopy of *C. gorungosanum* relative to *S. guineense,* suggests that this species could be encountering recruitment limitation. *C. gorungosanum* is a less common tree throughout the forest with a smaller disperser assemblage than *S. guineense*. Chimpanzee have been observed consuming *C. gorungosanum* within the forest interior (Kaplin 2005, Gross-Camp et al. 2009a). In Kibale National Park, Uganda, *C. gorungosanum* is a common canopy tree species, in some areas reaching a density of 65 trees/ha^{-1} (Chapman et al. 1999). Chimpanzees (*Pan troglodytes*) and elephants (*Loxodonta africana*) in Kibale have been found to provide high quality dispersal to *C. gorungosanum* (Wrangham et al. 1994, Dominy and Duncan 2005). Research on seed establishment at Kibale showed that 33% of *C. gorungosanum* seeds found within chimpanzee dung reached germination, while none of the seeds collected under parent trees germinated (Wrangham et al. 1994). Seeds of Amazonian trees in the same family as *C. gorungosanum* have also shown recruitment failure in the absence of seed cleaning services provided by vertebrate gut passage (Levi and Peres 2013). With the relatively recent extirpation of elephants from NNP (Plumptre et al. 2002), chimpanzees may be the most effective disperser of *C. gorungosanum* and critical to their dispersal. *C. gorungosanum* is a long-lived, large-seeded, vertebrate dispersed, forest species in the Sapotacaeae family; this family tends to be sensitive to disturbance and shows low occurrence in forest edges or secondary forests (Oliveira et al. 2004, Lima and Mariano-Neto 2014). More research is needed in NNP to understand if forest edges and matrix contrast affect the dispersal ecology and recruitment dynamics of *C.*

gorungosanum and other tree species that may generally have low visitation and high sensitivity to habitat disturbance.

Conclusions

The findings of this research suggest that high contrast matrices may influence seed dispersal by large birds and primates in forest edges. Large-bodied fruit eating birds were less common in forest edges adjacent to a high contrast matrix, suggesting possible ramifications for seed dispersal and regeneration in edge-affected habitat. The decline of large-bodied frugivores in other tropical forest has resulted in reduced recruitment of some tropical plant species (Galetti & Dirzo 2013, Galetti et al. 2006, Sethi & Howe 2009, Terborgh et al. 2008, Wotton & Kelly 2011b). These results call for more research on other large-seeded tree species, potentially those that receive lower visitation by dispersal agents, to determine whether these findings can be generalized across species. While I did assess the behaviors of dispersers, little is known about how matrix type impacts other steps in the seed dispersal process, such as seed deposition (Schupp 1993, 2010), and the abiotic environment which might influence microhabitat, germination probabilities, and recruitment in forest edges. My results indicate that large-bodied primates are more common along high-contrast matrix edges, making them more vulnerable to anthropogenic disturbances, and potentially putting the local population of primate species at risk.

Increasing our understanding of how matrix contrast surrounding NNP influences functional diversity in forest edges is critical to the effective management of the protected area. Higher complexity in the matrix, such as tree plantations, secondary forests and agroforestry can help maintain biodiversity, ecosystem function, and resilience (Fischer et al. 2006, 2008, Franklin and Lindenmayer 2009). The matrix can also serve to protect wildlife in the protected area from anthropogenic threats. In the Albertine Rift, and Rwanda particularly, where only approximately 20% of original forest is remaining, protected areas are critical to the conservation of biodiversity. Ensuring the effectiveness of Rwanda's protected areas is important not only for the persistence of native, and largely endemic biodiversity, but also to maintain important ecosystem services. If edge contrast and the type of human land use in the matrix surrounding large, intact protected areas impacts the behavior of large-bodied frugivores and consequently persistence of large-seeded tree species, then conservation strategies and calculations of protected area effectiveness will need to be adjusted.

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CHAPTER 4: Influence of matrix type and edge effects on tree species structure and composition in forest edges

Abstract

Land-use in the matrix surrounding tropical forest can play an important role in the maintenance of ecological processes within the forest edge. The type of matrix can amplify or ameliorate the physical and biotic changes that often occur within forest edges adjacent to human-modified landscapes, although this remains poorly explored. I investigated how matrix type influences the effects of edges on the structure and composition of trees in the Afromontane forest of Nyungwe National Park, Rwanda. I compared the species richness and diversity of trees, seedlings, and saplings within forest edges adjacent to pine plantations, and tea plantations, at different distance bands (0-50, 50-100 and 100-150 meters) from the forest edges and within a forest interior. Forest edges adjacent to tea plantations showed greater proportion of shade intolerant trees (65.8%) than shade tolerant (29.5%) trees throughout distance bands. Tea edges at 0-50 meters from the forest edge showed significantly higher stem density and basal area, attributed to the dominance of shade intolerant species, and significantly lower species richness and evenness compared to the forest interior. Edges adjacent to pine plantations showed dominant stem density and basal area of shade intolerant trees within 0-50 meters from the forest edge, though this declined as distance from the forest edge increased. These results suggest forest matrix type can influence the magnitude and distance of edge effects on forest habitat.

Introduction

Tropical forest biodiversity is closely linked to the matrix of human land-use practices in the surrounding landscape (Foley et al. 2005, Hansen and DeFries 2007, Gardner et al. 2009). In many tropical regions agricultural expansion and intensification drives deforestation and forest degradation and often leads to changes in biodiversity and ecological function within remaining fragmented forest (DeFries et al. 2007). The creation of new forest edges is the most dominant cause of ecological deterioration (Laurance et al. 2011) and among the many drivers of change in fragmented systems.

The ecological impact of artificially created forest edges on fragmented tropical forest has been extensively documented (Lovejoy et al. 1986, Murcia 1995, Didham 1997, Laurance et al. 1997, Didham and Lawton 1999, Bierregaard 2001, Ries et al. 2004, Tabarelli et al. 2004, Ewers et al. 2007, Ewers and Didham 2008). A range of abiotic and biotic changes can occur at the interface between existing native vegetation and the surrounding landscape (Murcia 1995). These changes at edges, or edge effects, can result in detectable differences in species composition, structure, or function as compared with the forest interior (Harper et al. 2005). The negative impacts of edge related changes on species can be diverse and vary widely depending on the habitat-species relationship. For example, some species of beetles (Didham et al. 1998, Ewers and Didham 2008), ants (Carvalho and Vasconcelos 1999), and birds (Watson et al. 2004) decline in abundance near forest edges, while other species of insects and birds increase in abundance, or show no effect at the forest edges (Laurance 2004, Wirth et al. 2007).

Like animals, many species of plants have been shown to increase or decrease in abundance at forest edges (Oliveira et al. 2004, Melo et al. 2007). Large canopy tree species are particularly vulnerable to the influence of forest edges. A growing body of empirical evidence indicates that edge effects drive old growth, shade-tolerant tree groups into decline (Lopes et al. 2009, Melo et al. 2007, Oliveira et al. 2008, Santos et al. 2008, Tabarelli et al. 2004, Tabarelli et al. 2008). The composition and arrangement of landscape features in the surrounding matrix can influence the ecological function within forest edges (Lindenmayer and Fischer 2006). A hard edge, creating high contrast between the forest edge habitat and the matrix of non-native vegetation (Murcia 1995), can severely modify forest edge microclimate (Kapos et al. 1997, Didham and Lawton 1999, Mesquita et al. 1999, Gascon et al. 2000). Conversely, soft forest edges, those that provide lower contrast and greater structural complexity between native forest and the surrounding matrix (Murcia 1995) can buffer the effects from edges (Gascon et al. 2000). Changes such as increased light and decreased humidity in edge microclimate can decrease regeneration of shade tolerant species (Melo et al. 2007), promote dominance of early successional, light demanding pioneer species (Oliveira et al. 2004) and the establishment of invasive non-forest species (Laurance 1997). Edge effects also cause high rates of adult mortality of large emergent trees due to uprooting and breakage from wind damage (Laurance et al. 2000, Tabarelli et al. 2004). The consequences of these changes can shift the abundance and composition of plant species in forest edges, causing changes in the floristic and vegetation structure along edge to interior gradients (Lovejoy et al. 1986, Tabarelli et al. 2012).

Shifts in plant guild structure in forest edges has been observed in the fragmented landscapes of the Amazon and Atlantic forests of Brazil (Oliveira et al. 2004, Laurance et al. 2006, Santos et al. 2008, Tabarelli et al. 2008, 2012, Lopes et al. 2009). These shifts coincide with a decline in large canopy tree species with fleshy fruits that are dispersed by large vertebrate frugivores (Tabarelli et al. 1999, Melo et al. 2007). As forest edges gradually shift towards a hyper-proliferation of pioneer species and an impoverished assemblage of large-seeded, shade-tolerant, tree species, ecological processes, such as fruit-frugivore interactions can be disrupted (Melo et al. 2007). Altered spatial recruitment of large-seeded shade tolerant trees and the concurrent or subsequent decline of their dispersers can jeopardize the persistence of biodiversity and functioning of ecosystems in some forested systems (Girão et al. 2007, Joly et al. 2014).

Human disturbance and land-use practices can dictate the extent and magnitude of edge related changes that lead to the modification and alteration of forest vegetation (Lindenmayer and Fischer 2006). Activities such as logging, fire, overhunting, or land-use type in the surrounding matrix can influence the breadth, depth, and intensity of edge effects (Harper et al. 2005, Tabarelli and Gascon 2005, Tabarelli et al. 2008). A soft matrix, characterized by vegetation elements that are similar to the natural forest, can ameliorate effects from edges by reducing changes in the microclimate at edges and thereby maintaining moisture and light levels similar to the forest interior (Didham and Lawton 1999, Cadenasso et al. 2003, Denyer et al. 2006). Different matrix types can provide an extension of the forest habitat, supporting the range and number of species more evenly throughout the forest (Gascon et al., 1999). For example, a comparison of the influence of cattle pasture and two different types of regenerating forest in the matrix on tree mortality at the forest edge, found that the regenerating forest provided a better buffering capacity than the open pasture (Mesquita et al. 1999).

The aim of this study was to investigate the role of matrix type on tree structure and composition in forest edges of a large, Afromontane protected area. Empirical evidence shows that edge effects can drive fragmented forest edge habitat toward a dominant assemblage of pioneer species, triggering a persistent early-successional system in edge-affected habitat (De Melo et al. 2006, Santos et al. 2008, 2010, Tabarelli et al. 2012). Less is known about edge effects and the role of different matrix types in larger, intact forest systems. In this study we sampled forest edges at different distances adjacent to high contrast tea plantations, low contrast pine plantations and within a forest interior control in a large, Afromontane forest known for its exceptional faunal and floral endemism. We tested matrix effects and the depth of edge effects on the species richness and diversity of trees, seedlings, and saplings and quantified the proportion of species within regeneration categories.

Methods

Study area – Research was conducted in two forest edge sites, and within the forest interior of Nyungwe National Park (hereafter NNP), Rwanda (latitude 2° 15' and 2° 55'S, longitude 29° 00' and 29° 30'E). NNP is approximately 970 km^2, and together with Kibira National Park in Burundi this contiguous transboundary protected area covers 1,413 km^2 of Afromontane forest ranging between 1600-2900 meters in elevation. NNP is one of the most biologically important Afromontane forests in Africa due to a richness of fauna which includes 13 species of primates, representing 20% of all African primates, 280 species of birds, 26 of which are Albertine Rift endemics and 11 of these endemics are classified as either endangered, vulnerable or near threatened (Plumptre et al. 2007). NNP is effectively isolated from other montane forest habitat, with the closest 3 km^2 forest fragment approximately 12 km^2 away.

Surrounded by a matrix of farmland, tea plantations, mixed agriculture, local woodlots, and buffer zones of pine and eucalyptus, NNP hosts a population density of approximately 430 people per square kilometer, one of the highest human population densities in Africa (World Bank 2010, UNEP 2011). A pine buffer zone was established in 1969 under an agreement between the government of Rwanda and a Swiss Technical Agency (Bush and Ikirezi 2010). By 1979 nearly 170 km^2 of natural forest was converted to predominantly pine and eucalyptus plantations, at the time, an area equivalent to approximately 15% of Nyungwe Forest (Bush and Ikirezi 2010). Apart from the role as a buffer to the natural forest edge, pine plantation buffer zones provide local communities with a source of fuel wood and building materials (Gapusi 2007). Another dominant land use surrounding NNP are tea plantations, which provide revenue at the local and national level (Bush and Ikirezi 2010, Masozera 2002). A proposal exists to expand tea plantations in some areas of the buffer zone (RDB Nyungwe National Park Management Plan 2012-2021). A recent contract to cut the pine buffer zone around NNP will change the surrounding matrix type, potentially affecting structural and functional aspects of the adjacent forest edge.

Nyungwe National Park is characterized by a cool, damp, climate typical of a tropical montane forest. The vegetation mosaic of NNP forms part of the montane forests of the Congo-Nile watershed and contain the eastern limit for plants from the Guineo-Congolian region (Fischer and Killmann 2008). Floristically, NNP is the richest forest remaining in Rwanda with more than 265 tree species belonging to 47 families (Plumptre et al. 2002). There is some floristic distinction in NNP between the western and eastern portions of the park, largely attributed to differences in rainfall, geology, and soil (Fischer and Killmann 2008).

The study compared forest edge sites located in forest adjacent to a tea plantation at the Gisakura Tea Factory, Namashake district, and two different pine plantations in Namashake district (Figure 10). Forest edge sites and the forest interior control sites were located in the western portion of the forest, an area of the forest shown to be highest in bird and mammal species richness (Plumptre et al 2002). Each matrix type – pine and tea - was homogenous and relatively unchanged during the period of the study. Tea presented a high contrast in comparison to the forest, while pine presented a low contrast and was more structurally similar to the natural forest. Forest interior control sites were also located in the western portion of the forest >500 meters from the edge of the forest. The research sites fell between the middle and lower altitude range of the park (2018 m ±137m). Dominant tree species in this region of the forest are *Carapa grandiflora, Newtonia buchanani, Macaranga kilimandscharica, Parinari excelsa,* and *Syzygium guineense* (Fischer and Killmann 2008).

Vegetation sampling - To characterize species richness and diversity in forest edges adjacent to pine plantations, tea plantations, and within the forest interior, circular plots with a 10 m radius were established in each habitat. Plots sampled within forest adjacent to each matrix type were set at different distance bands, parallel to the forest edge (Figure 11), at 0-50 meters from the edge, 50-100 meters, and 100-150 meters from the edge, and plots within the forest interior were located >500m from the forest edge. The point along the forest edge to enter the forest and begin locating plots was randomly selected. In forest adjacent to pine plantations, 15 plots per distance band were sampled (i.e. 15 plots at 0-50, 50-100, and 100-150) for a total of 45 sample plots (1.4 hectares) within forest edges. In edges adjacent to the tea matrix, 13 plots per distance band were sampled, for a total of 39 plots (1.2 hectares) within forest edges. Within the forest interior, 26 plots (0.8 hectares) were sampled along randomly located transects. Within each plot, the dbh of all trees ≥ 10cm dbh (diameter at breast height) were measured and identified to species when possible. Saplings (<5cm dbh) were enumerated in four 2 m^2 nested plots, and seedlings in five-1 m^2 plots. Canopy cover was estimated in the center of each plot in four different orientations using a *spherical convex densiometer (Ben Meadows No. 43887).* All plots were geo-referenced in UTM using a GPS (Garmin GPSMAP 60CSx).

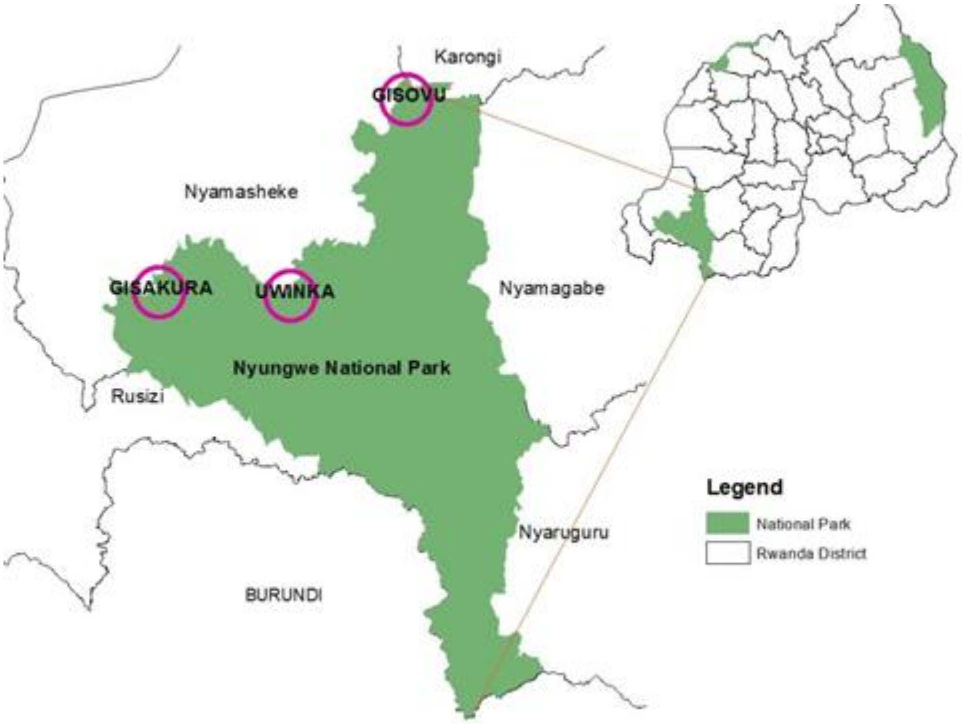


Figure 40. Location of Nyungwe National Park and vegetation sample sites. Gisovu and Uwinka are pine plantation sample sites, Gisakura is tea plantation.

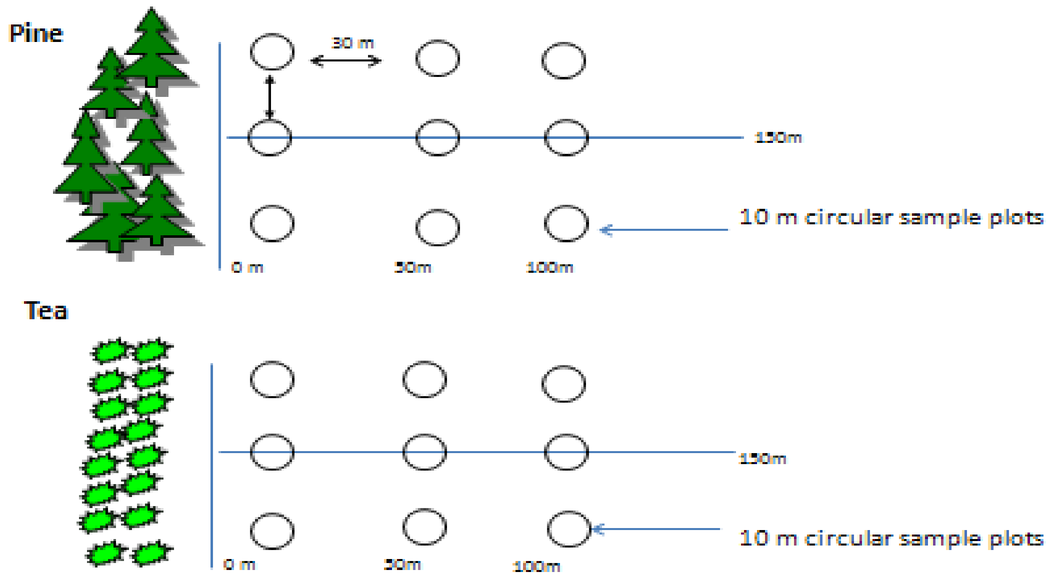


Figure 11. Vegetation sampling design replicated in forest adjacent to different matrix types.

Data Analysis – The vegetation plots in forest edges adjacent to pine plantations were located in edges adjacent to two different pine plantations. Tests to examine normality, homogeneity of variance, and independent-samples *t*-tests were conducted on data from the different independent replicates. Results indicated normality and equality of variances and the sample replicates were combined. These tests were also conducted on groups of interior vegetation plots that were separated by >500 meters which indicated these plots could also be combined for analyses.

I compared vegetation data from different distance bands (0-50m, 50-100m, and 100-150m) to evaluate the depth of edge effects adjacent to the two different matrix types. In each of the plots stem density (number of stems/ha) was calculated for seedlings, saplings, and trees. Basal area (BA/ha) per hectare was calculated for trees ≥ 10cm DBH and BA/ha per plot was compared between distances and treatments using a two-way ANOVA. Stem density/ha transformations did not result in normalized distributions requiring a non-parametric ANOVA Kruskal-Wallis to test differences for this measure.

Plant species diversity was calculated using Shannon-Wiener diversity index H', an index based on the number of species:

$$H' = - \sum p_i \ln p_i$$

where p_i equals the proportion of individuals of the *i*th species in a plot. A larger value of H' indicates a greater diversity of species.

Species abundance or evenness describes relative abundance of species. Evenness was evaluated using Smith and Wilson's (1996) evenness index:

$$Evar = 1 - 2 / (\pi \times \arctan(\sum_i \{ \log(n_i) - \sum_j \{ \log(n_j) \} \}^2 / S))$$

where n_i and n_j are the number of individuals in species i and j respectively, and S is the total number of species. This evenness index evaluates equitability among species abundances (Smith and Wilson, 1996).

Chi-square analyses and cross tabulations were conducted to examine the association between regeneration strategy and matrix type and regeneration strategy and distance band. Size class distributions by DBH category were generated and tested with non-parametric analyses for differences.

Results

Altogether 70 tree and shrub species belonging to 37 families were recorded in all vegetation plots. Shade tolerant tree species with the greatest basal area per hectare across all treatments included *Beilschmiedia rwandensis, Carapa grandiflora, Chrysophyllum gorungosanum, Chrysophyllum rwandense, Parinari excelsa, Strombosia scheffleri,* and *Syzygium guineense*; shade intolerant species with greatest basal area per hectare included: *Cleistanthus polystachyus, Macaranga kilimandscharica,* and *Newtonia buchananii.*

Trees

Basal area -

When comparing plots at different distance bands at forest edge sites, and interior plots with plots at different distance bands at forest edge sites, a two-way ANOVA revealed a significant difference (F6, 110) =2.22, p=.047). Multiple post-hoc tests revealed marginally significant differences between distance bands within forest edges near tea. Forest edges near tea at 0-50 meters showed the greatest mean BA/ha (58.46±26.31) (Figure 12). Tukey's HSD post hoc tests showed a marginally significant difference between the mean BA/ha at 0-50 meters from the edge near tea and the mean BA/ha at 50-100 (28.77±25.15) (p=.06). Post hoc tests also showed a difference between mean BA/ha at 0-50 and 100-150 (29.00± 19.86) meters from the edge (p=.06) (Table 4).

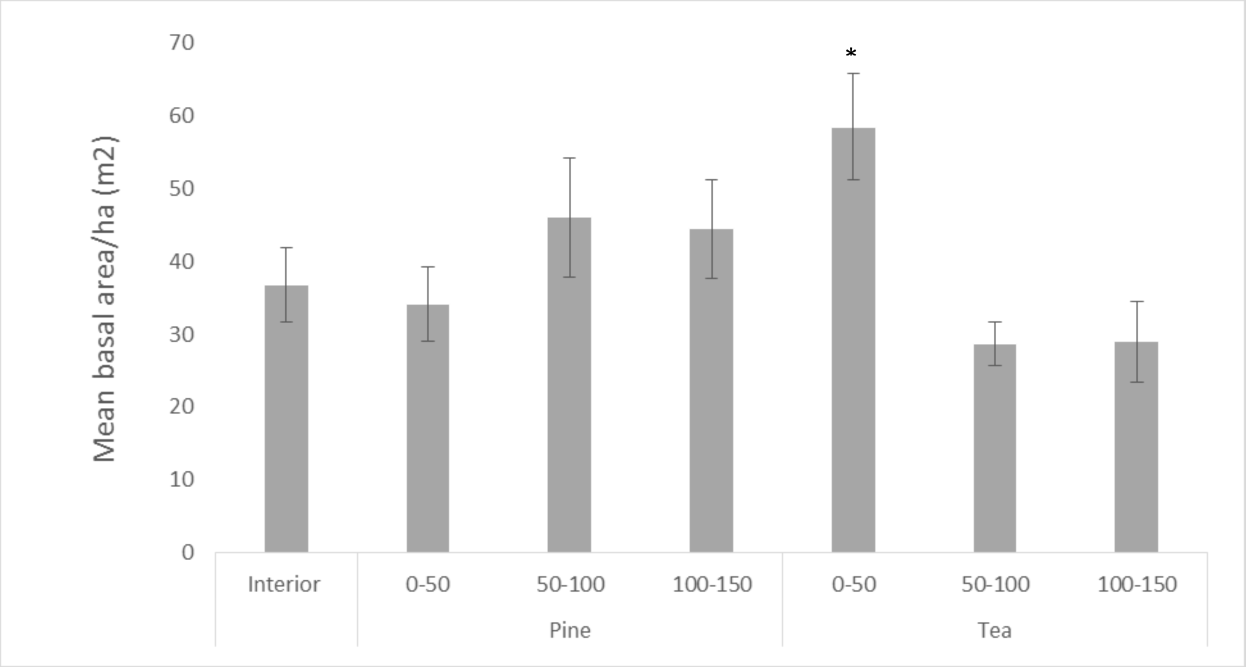


Figure 12. Mean and standard error of the basal area (BA) per hectare (m^2) within the forest interior and at each distance band within forest edges adjacent to pine plantations and tea cultivation. (*) indicates marginally significant difference between 0-50 m and both 50-100 m, 100-150 m.

The top four dominant species within the forest interior consisted of shade tolerant canopy species, *Syzygium guineense, Strombosia scheffleri, Carapa grandiflora* and *Beilschmiedia rwandensis*. Forest interior plots showed a mean BA/ha (39.76±28.23) with shade tolerant species accounting for more than 60% of the relative BA (Figure 13).

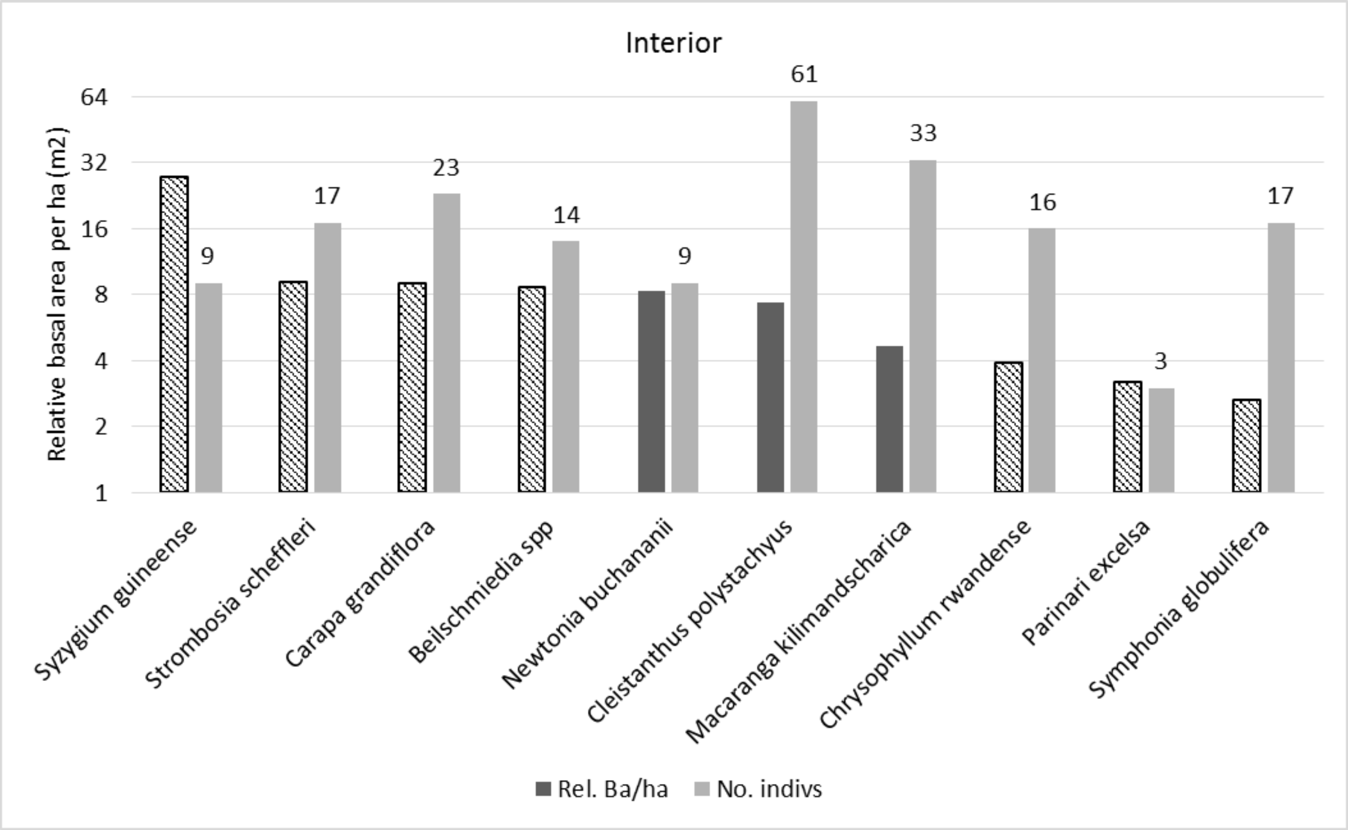
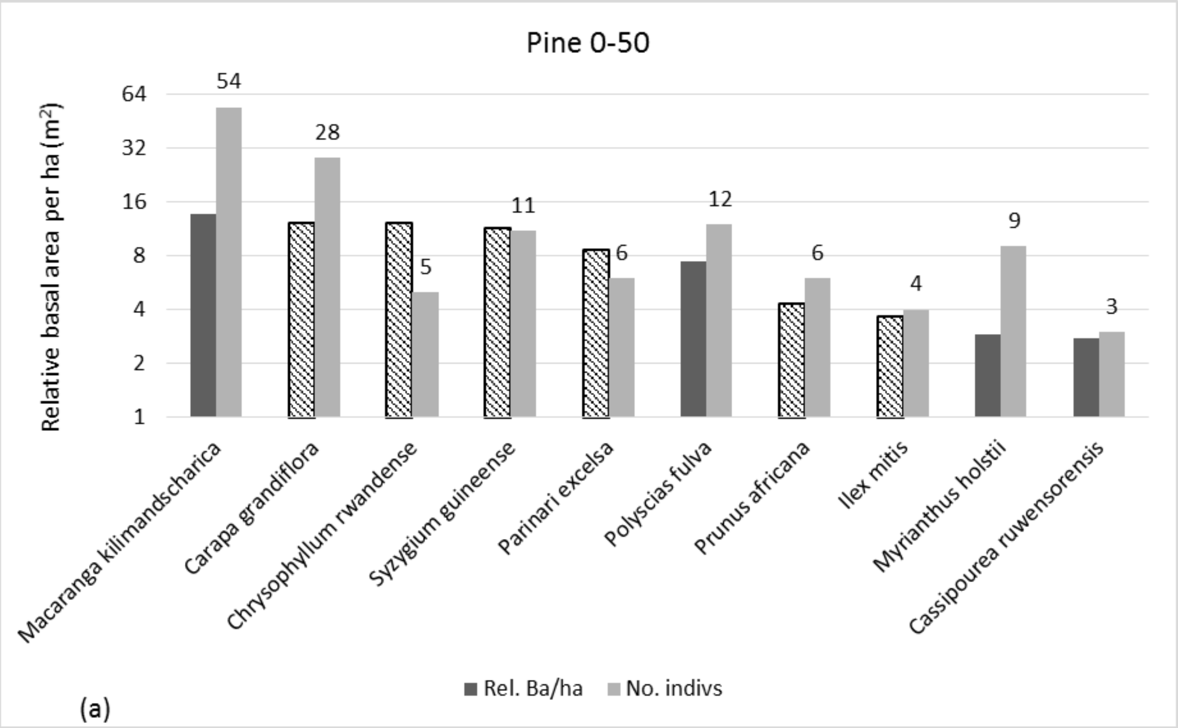
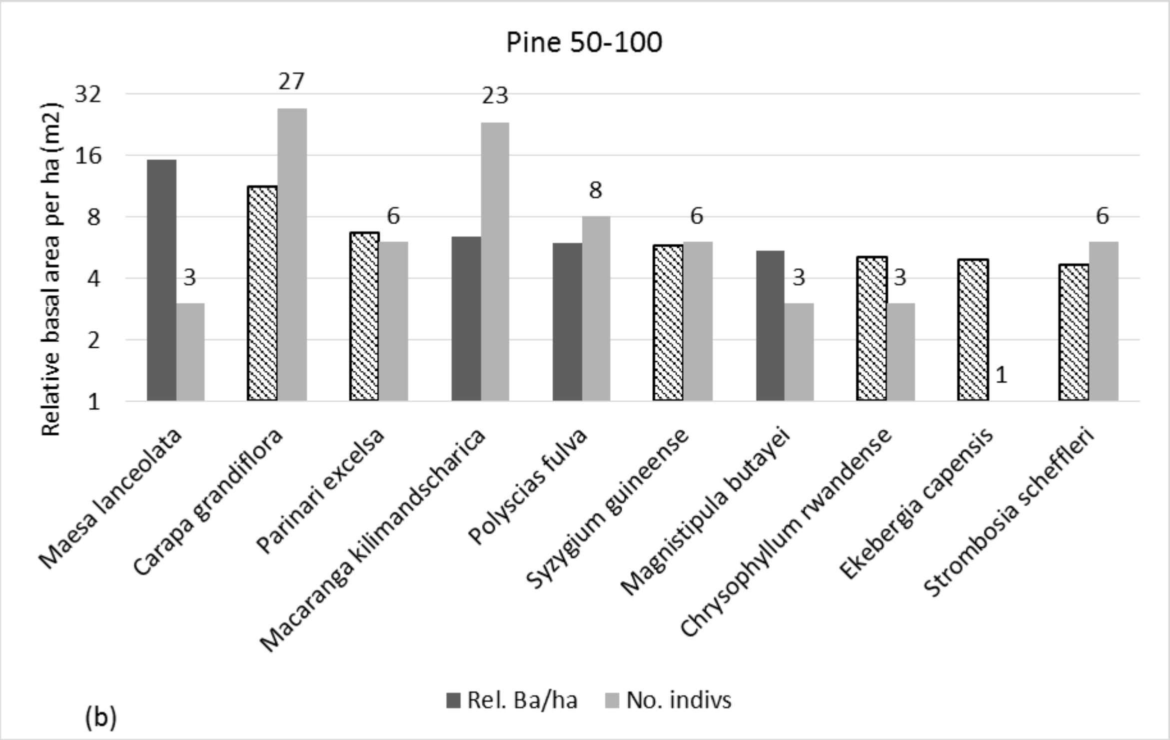


Figure 13. Interior forest log scale of relative basal area per hectare (m^2) of top ten dominant tree species, pattern filled bars denote shade tolerant tree species

Species composition within pine edges differed by distance band (Figure 14 (a-c)). Within edge adjacent to a pine matrix, BA/ha was reduced in 0-50m, compared 100-150m from the forest edge. The dominant species within plots at 100-150m of the forest edge near pine were large, shade tolerant, canopy trees species whereas shade intolerant pioneer species were dominant at 0-50m from the edge.


Pine 0-50
Relative basal area per ha (m^2)
64
32
16
8
4
2
1
54
28
5
11
6
12
6
4
9
3
Macaranga kilimandscharica
Carapa grandiflora
Chrysophyllum rwandense
Syzygium guineense
Parinari excelsa
Polyscias fulva
Prunus africana
Ilex mitis
Myrianthus holstii
Cassipourea ruwensorensis
Rel. Ba/ha
No. indivs
(a)


Pine 50-100
Relative basal area per ha (m2)
32
16
8
4
2
1
3
27
6
23
8
6
3
3
1
6
Maesa lanceolata
Carapa grandiflora
Parinari excelsa
Macaranga kilimandscharica
Polyscias fulva
Syzygium guineense
Magnistipula butayei
Chrysophyllum rwandense
Ekebergia capensis
Strombosia scheffleri
Rel. Ba/ha
No. indivs
(b)

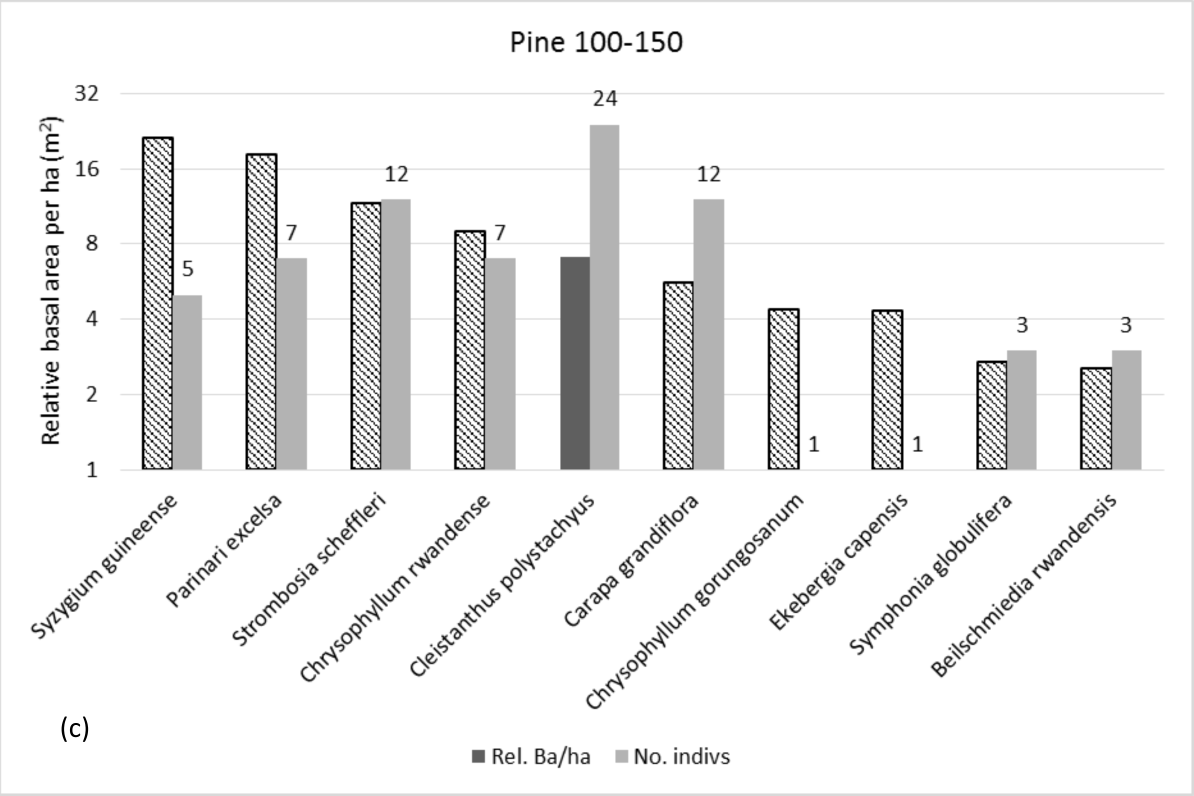
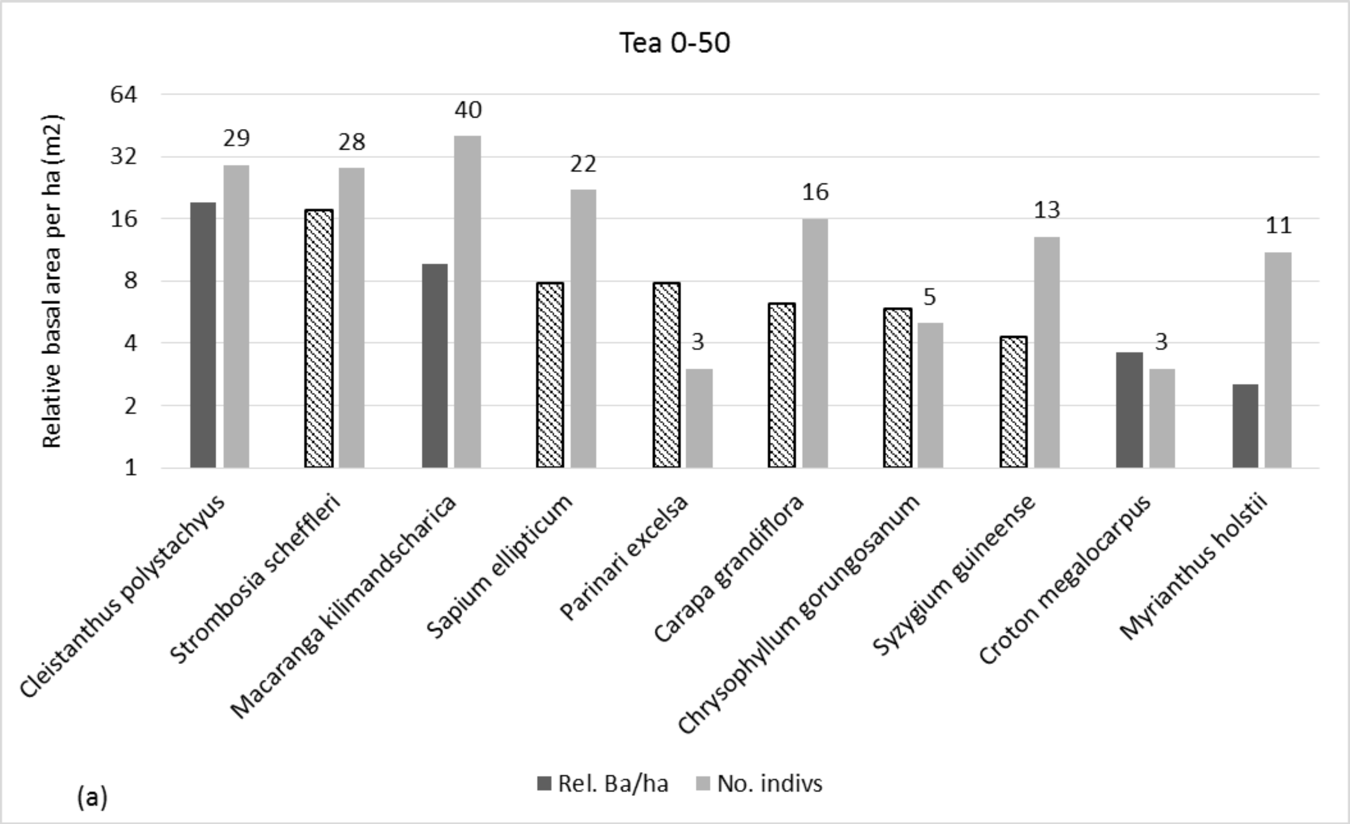
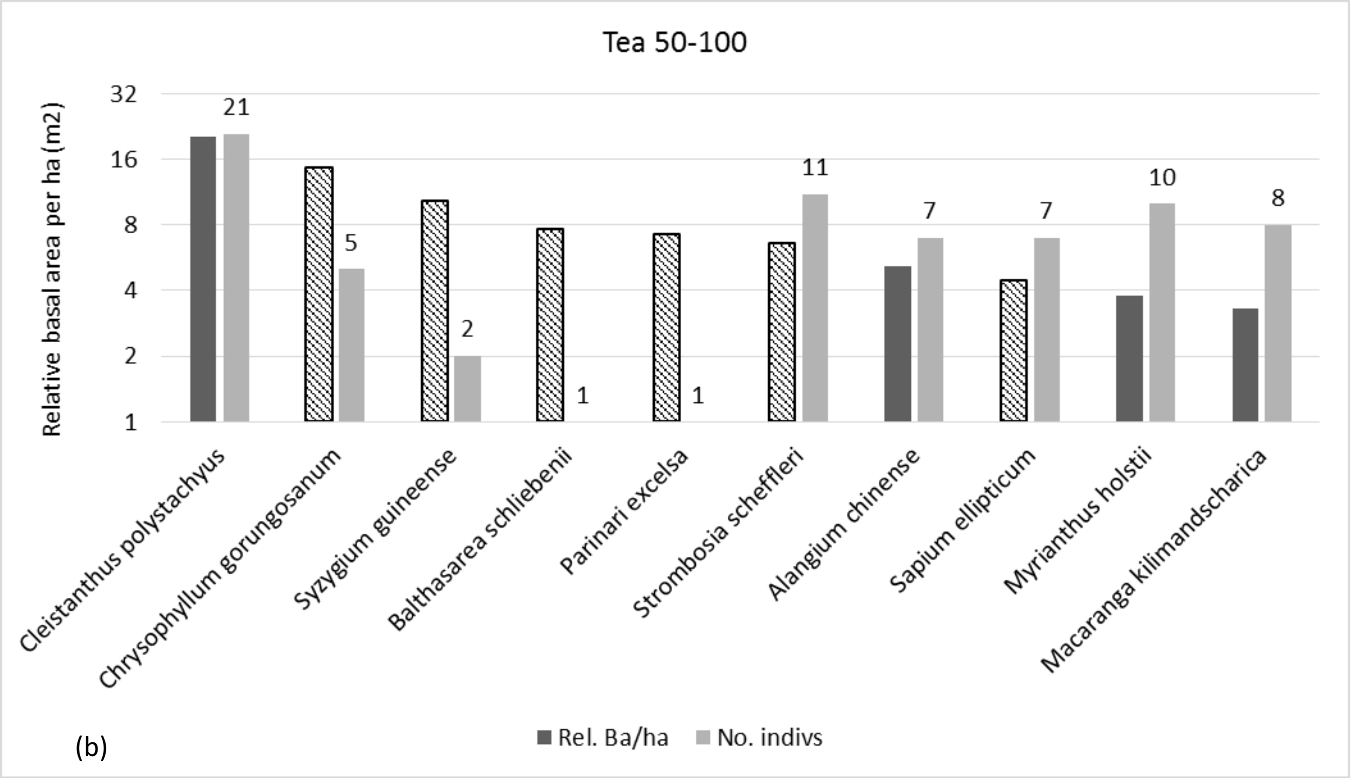


Figure 14 Pine matrix forest edge log scale relative basal area per ha (m^2) top ten dominant tree species per distance band, 0-50 (a), 50-100 (b), 100-150 (c). Pattern filled bars denote shade tolerant species.


Tea 0-50
Relative basal area per ha (m2)
64
32
16
8
4
2
1
29
28
40
22
3
16
5
13
3
11
Cleistanthus polystachyus
Strombosia scheffleri
Macaranga kilimandscharica
Sapium ellipticum
Parinari excelsa
Carapa grandiflora
Chrysophyllum gorungosanum
Syzygium guineense
Croton megalocarpus
Myrianthus holstii
Rel. Ba/ha
No. indivs
(a)


Tea 50-100
Relative basal area per ha (m2)
32
16
8
4
2
1
21
5
2
1
1
11
7
7
10
8
Cleistanthus polystachyus
Chrysophyllum gorungosanum
Syzygium guineense
Balthasarea schliebenii
Parinari excelsa
Strombosia scheffleri
Alangium chinense
Sapium ellipticum
Myrianthus holstii
Macaranga kilimandscharica
Rel. Ba/ha
No. indivs
(b)

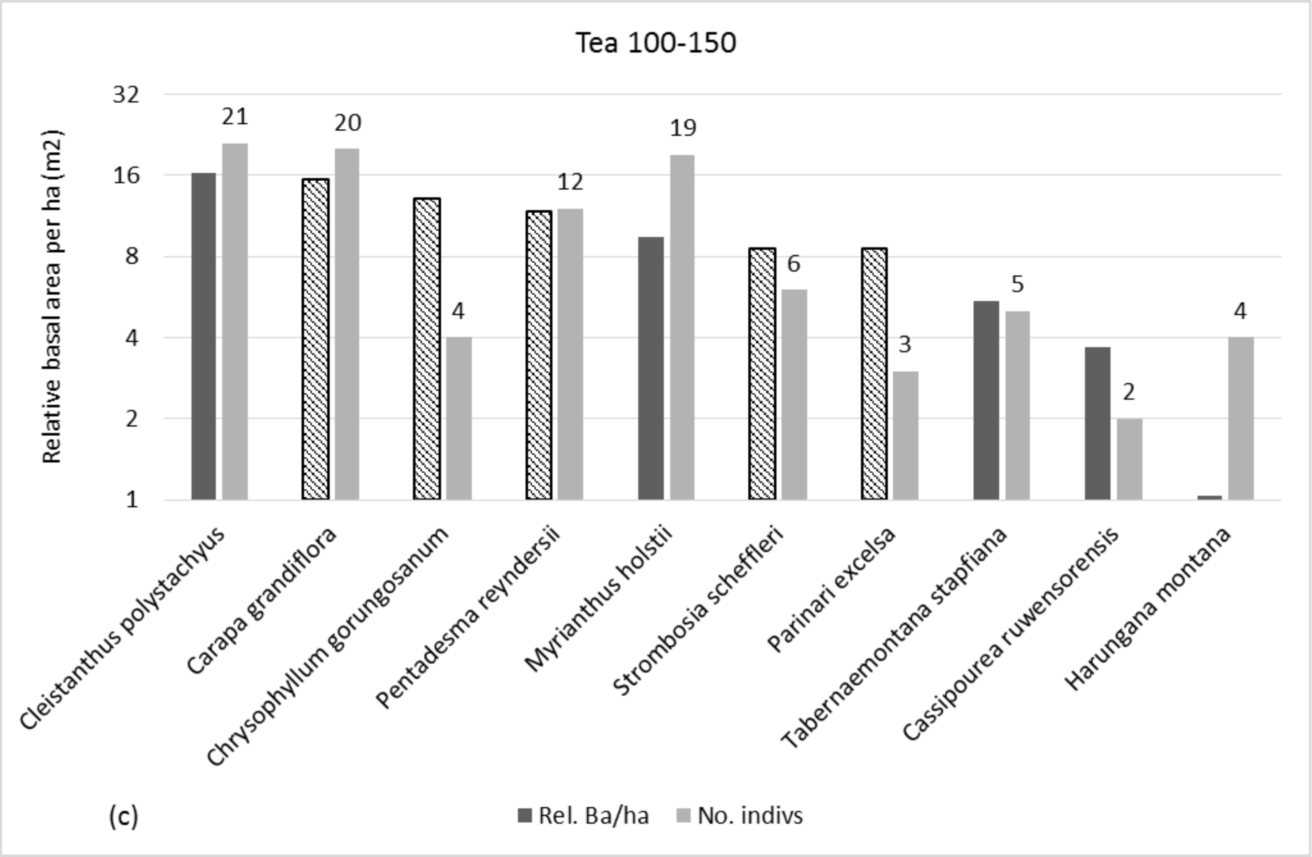


Figure 15. Tea matrix forest edge log scale relative basal area per ha (m^2) of top ten dominant tree species per distance band, 0-50 (a), 50-100 (b), 100-150 (b). Pattern filled bars denote shade tolerant species.

The early successional species *Cleistanthus polystachus* accounted for the greatest relative BA/ha throughout each distance within edges near a tea matrix.

Stem density-

With distances combined, there was a significant difference in stem density/ha between forest interior and edges near tea (Z=-1.97, p= .04), and between pine edges and tea edges (Z=-2.10, p=.03), but not between the forest interior and edges adjacent to pine (Z=-.28, p=.28). Different than the regeneration strategy of trees with the greatest mean BA/ha, tree species with greatest relative density/ha within the forest interior belonged to shade intolerant species, *Cleistanthus polystachus* (23%) and *Macaranga kilimandscharica* (13%).

Stem density in forest edges adjacent to pine showed no significant difference in stems/ha between distance bands (x^2=.15, df=2, p=.92) (Figure 16). The mean density of stems and standard error within 0-50m of forest edges adjacent to pine was 17.7±3.5, 50-100m from the edge, 15.8±2.3 and at 100-150m 16.4±3.5. Within pine edges, nearly 25% of stems at 0-50m were comprised of shade intolerant *Macaranga kilimandscharica*, at 50-100 m, *Carapa grandiflora* (15%) and *Macaranga kilimandscharica* (13%) represented the greatest relative density and *Cleistanthus polystachus* (18%) and *Neoboutonia macrocalyx* (10%) at 100-150m.

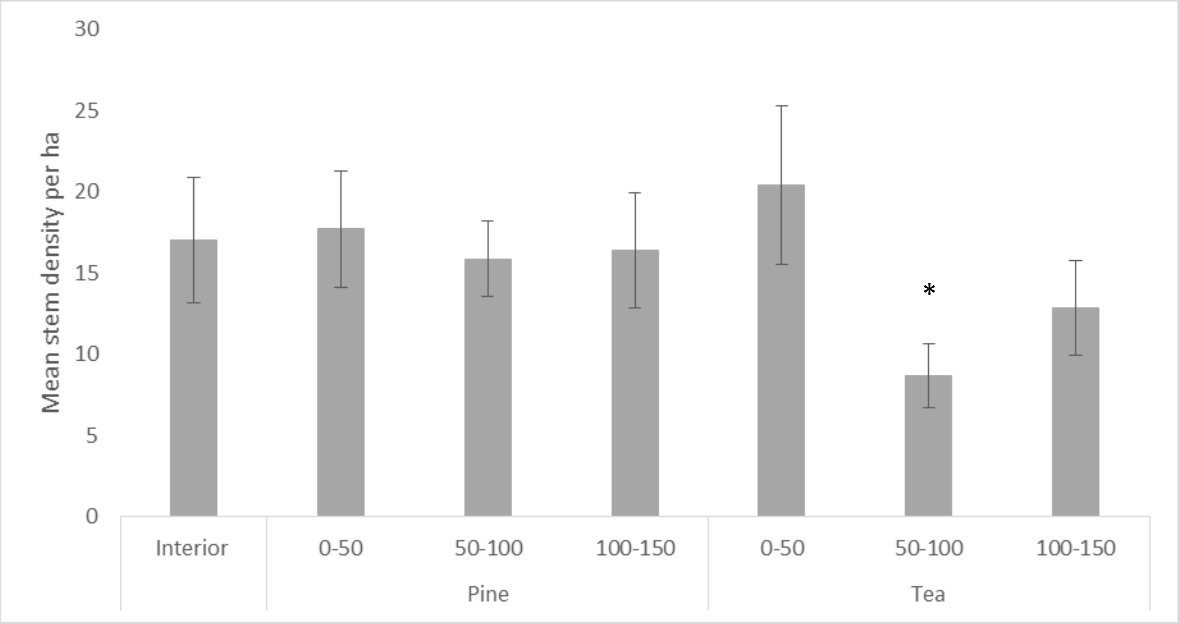
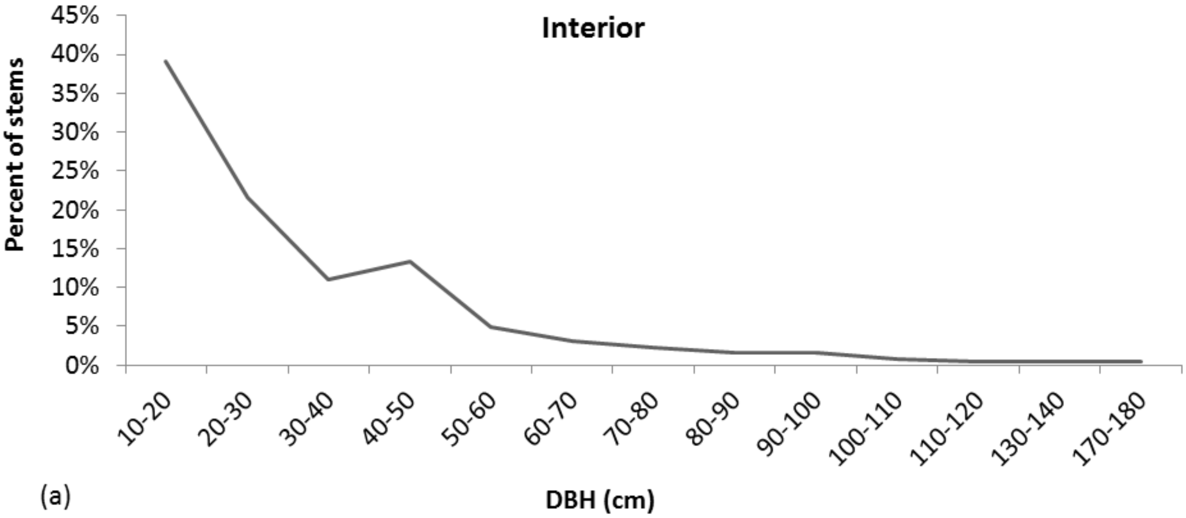


Figure 16. Mean and standard error of stems between different distance bands within forest edges adjacent to pine plantations, no difference between distances bands. (*) denotes a significant difference in stem density between 0-50 meters from the forest edge and 50-100 meters.

Stem density showed a significant difference in stem/ha between distance bands in forest adjacent to tea plantations (x^2=6.45, df=2, p=.04) (Figure 16). Within 0-50m of forest edges adjacent to tea mean stem density was 20.4±4.91 stems/ha. Mean stem density within 50-100m was 8.7±1.95 stems/ha and 12.8 ±2.8 stems/ha within 100-150m of the forest edge (Table 4). Post-hoc tests revealed a significant difference in stem/ha between 0-50m and 50-100 (Z=2.54, p=.01), but not a significant difference in stem/ha between 0-50 and 100-150 (Z=-1.52, p=.12) and 50-100 and 100-150 (Z=-.921, p=.35). The greatest relative stem density was attributed to shade intolerant *Cleistanthus polystachyus* and *Macaranga kilimandrscharica* within tea edges at each distance, comprising 20% of species at 0-50 m, 27% at 50-100 m and 16% at 100-150m from the edge.

Stem size class distribution-

For each edge treatment, the greatest percent of stems were between 10-20 DBH (cm) for all distance bands. Within edge adjacent to pine the largest percent of small stemmed trees occurred at 0-50m (55%), followed by 50-100m (42%) and 100-150m (39%) Within forest edge near tea the largest percent of smaller stemmed trees (10-20 cm) occurred within 100-150 m (51%) from the edge, followed by 50-100m (44%) and 0-50m (37%) (Figure 17 (a-c)).



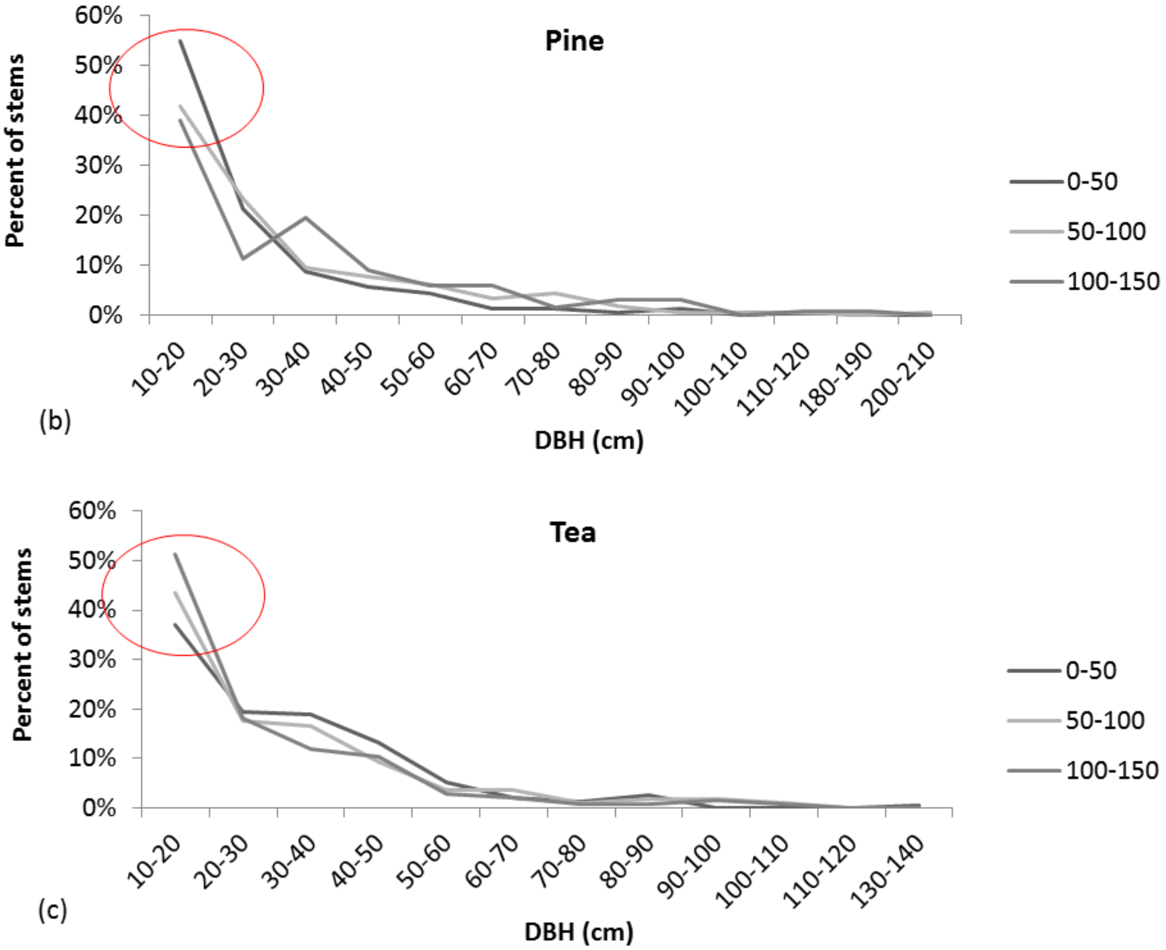


Figure 17. Stem class distribution in a) forest interior, b) forest edges adjacent to pine, and c) forest edges adjacent to tea

Canopy Cover - There was no significant difference in canopy cover between the three treatments with distances combined (F 2=2.19, p=.11), or between distances tested within or between treatments (F 6,81=1.52, p=.18).

Shannon-Wiener's diversity index (H')- No significant difference was found in Shannon-Wiener's diversity index with distances combined (interior 1.33±.61, pine 1.49±.48, tea 1.58±.52), (df=2, f=1.75, p=.17) (Table 4). No difference was found between interior plots and plots in edges near tea at different distances, or plots at different distances near pine. There were significant differences found in the diversity index between pine edge sites and tea edge sites within distance bands. Tea edges showed greater diversity at 0-50m than pine edges at 100-150m (ANOVA p=.018) and tea edges at 100-150m were more diverse than pine edges at 100-150m (ANOVA p=.040) (Table 4).

Smith-Wilson's Evenness A (Evar)- Evenness was significantly different between the three treatments with distances combined (df=2, f=4.131, p=.019, interior mean/SD 89±.02, pine .81±.13, and tea .81±.11) (Table 4). Post-hoc results showed a significant difference between interior and pine (p=.03) and interior and tea (p=.04) but not between pine and tea (p=.99). Species evenness was not significantly different between either distance from edge or treatment, with the exception of the forest interior which showed significantly more evenness that forest edge near tea at 0-50m (ANOVA p=.002) and with greater evenness at 50-100m (ANOVA p=.008) than 0-50m at tea edges (Table 4).

Table 4. Mean and stand error responses to selected parameters by sites and distance band. Area sampled per distance band and number of plots per distance band, number of species recorded per site by distance band, Shannon-Wiener diversity index H', Smith and Wilson's evenness index Evar, density and basal area per hectare.

Site	Area sampled (ha)	# species	H'	Evar	Density Stems/ha	Mean BA/ha
Interior	0.81 (n=26)	35	1.33±.61	.89±.02*	17.01±3.85	39.76±5.10
Pine	1.41		1.49±.48	.81±.13		
0-50	.47(n=15)	38	1.63±.39	.78±.03	17.72±3.56	34.20±5.08
50-100	.47	37	1.56±.60	.83±.03	15.88±2.31	46.05±8.17
100-150	.47	27	1.27±.36*	.81±.03	16.42±3.55	44.47±6.75
Tea	1.22		1.58±.52	.81±.11		
0-50	.41(n=13)	29	1.72±.30*	.72±.03*	20.43±4.91	58.46±7.30*
50-100	.41	32	1.31±.69	.89±.03	8.70±1.95*	28.77±6.97
100-150	.41	29	1.74±.35*	.81±.04*	12.85±2.89	34.27±4.99

Regeneration strategy- A significant difference was indicated between regeneration strategy, matrix type, and distance band, ($\chi(12) = 47.995$, $p < .001$). Area sampled differed between several sites so results are better considered within the sites. Interior forest plots showed a nearly proportionate mix of shade intolerant and shade tolerant tree species. Greater percentages of shade intolerant species were found in all edge treatments however, in forest adjacent to tea, greater than twice as many shade intolerant (65.8%) individuals than shade tolerant individuals (29.5%) were observed (Table 5).

Table 5. Proportion of species with shade tolerant and shade intolerant strategies by treatment with distance bands combined. Int = interior forest, Pine G = Gisovu pine site in the north of the forest, pine U= Uwinka pine site in the western portion of the forest, Tea = tea site in the west of the forest. Percent of trees within the strategy equals the percentage of trees in the regeneration strategy counted at each treatment. Percent within the treatment is the percentage of all trees counted by treatment in each strategy (includes small number of trees counted as shrubs, not shown in table).

Regeneration Strategy	INT (n=27)	Pine G (n=27)	Pine U (n=18)	Tea (n=39)
Shade intolerant				
Count	133	191	123	310
% within Strategy	17.6	25.2	16.2	41.0
% within Treatment	51.2	61.6	54.7	65.8
Shade tolerant				
Count	121	98	78	139
% within strategy	27.8	22.5	17.9	31.9
% within treatment	46.5	31.6	34.7	29.5

There was a significant difference between distance bands and regeneration strategy with distance bands from edge forest adjacent to both matrix types combined, ($\chi(12) = 42.915$, $p < .001$). Shade intolerant tree species (63.5%) comprise greater than two times the individuals than shade tolerant species (29.1%) within 0-50 meters from the forest edge. Results indicated an uneven distribution of shade intolerant versus shade tolerant species within 50-100m and 100-150m from the forest edge with a greater representation of shade intolerant species. However the dominance of shade intolerant species declined as distance from the edge increased towards the forest interior, showing a decreasing effect of edge with increasing distance towards the interior (Table 6).

Table 6. Proportion of species with shade tolerant and shade intolerant regeneration strategies by distance band sampled from the forest edge to interior.

Regeneration Strategy	0-50 (n=30)	50-100 (n=30)	100-150 (n=30)	INT (n=27)
Shade intolerant				
Count	292	180	152	133
% within Strategy	38.6	23.8	20.1	17.6
% within Distance Band	63.5	63.2	58.2	51.2
Shade tolerant				
Count	134	91	90	121
% within Strategy	30.7	20.9	20.6	27.8
% within Distance Band	29.1	31.9	34.5	46.5

Seedlings and saplings

There were greater seedlings per meter square within interior plots (0.75±0.83/m^2), followed by pine (0.55±0.56/m^2) and tea (0.44±0.65/m^2). A similar pattern was observed for saplings in plots adjacent to interior (0.37±0.41/m^2), followed by pine (0.27±0.28/m^2) and then tea (0.22±0.32/m^2). However, no significant difference was found in the density of seedlings/m^2 between each treatment ($F_{2, 110}$ =1.701, p=.18), or among distance bands ($F_{6, 110}$ =.994, p=.43); this was also true for density of saplings/m^2 between treatments ($F_{2, 100}$ = .737, p=.48) and distance bands ($F_{6, 110}$=.463, p=.83).

Discussion

The type of surrounding matrix influenced the magnitude and distance of edge effects on forest habitat. Our results suggest that matrix type can mediate the impact of edge effects on vegetation structure and composition. Within forest edges adjacent to a pine matrix the most significant effect of edge was observed within 0-50m from the forest edge and gradually decreased towards the forest interior. In edges adjacent to tea, edge effects could potentially be observed up to 150m from the forest edge towards the forest interior. The matrix type with more structural similarity, such as the low contrast of pine matrix, appeared to mitigate some of the adverse effects of edge on forest edge habitat.

Studies have emphasized how matrix effects might alter edge responses across forest boundaries (Harper et al 2005). The structural contrast between the forest and matrix can influence edge related alterations such as the changes in tree communities observed in edge affected forests in multiple Neotropical fragmented landscapes (Laurance et al. 2011, Tabarelli et al. 2012). In this study, forest edges adjacent to tea showed a significant increase in stem density within 0-50m of the edge. Tea edges overall contained greater abundances of shade intolerant tree species which contributed to a significantly greater density of stems and BA/ha particularly within 0-50m and at 100-150m from the forest edge. Basal area decreased significantly within 50-100m and 100-150m from the forest edge near tea yet these distance bands still showed higher stem density of smaller sized stems (>50%) than the same distance bands adjacent to pine (<40%).

Stem density was more evenly distributed throughout distance bands in forest adjacent to pine plantations, with a similar number of stems per hectare at each distance band adjacent to pine as within the forest interior, indicating the pine matrix may provide a buffer to some of the changes within these forest edges. Within pine edges, lower mean DBH in 0-50m, high overall stem density, and high shade intolerant stem density compared to 100-150m from the edge was indicative of disturbance in that distance band. Stem density decreased and basal area per ha increased with decreasing proportions of shade intolerant species at distances closer to the forest interior. The relative density of shade intolerant species was high at each treatment; and although there was high relative density of shade intolerant stems within the forest interior, the top five species with greatest relative basal area were all shade tolerant tree species.

The DBH size class distribution within pine edges generally followed a reverse J shaped curve, where stem frequencies decrease with increase in DBH, indicative of the natural distribution of a tropical rainforest (Mclaren et al 2005). Within tea forest edges we observed higher density and lower stem size throughout all of the edge distance bands, and DBH size class distribution showed less of a reverse J shape, though still directionally inverse. This is telling as diameter distributions can be used to detect disturbances effects within forests (Denslow 1995). Fashing et al (2004) found that a population of trees within intensely disturbed edge forest adjacent to tea fields failed to conform to the typical reverse J distribution. They suggested that in addition to edge disturbance, the area may be receiving pressure from local people exploiting the edge forest for small stems for building material (Fashing et al. 2004). Increased density of small stem trees is consistent with the literature reporting negative impacts from edge effects. Studies show that secondary structural responses to altered ecological processes can result in higher densities of pioneer species, higher basal areas, and woody stem densities near forest edges (Murcia 1995, Kapos et al. 1997, Laurance 1997, Laurance et al. 1998, 2006, Tabarelli et al. 1999, Oliveira et al. 2008, Santos et al. 2008). Laurance et al (2006) found that the population density of successional trees studied tripled within 100m of fragment edges, comprising 10-26% of all trees

>10cm dbh. Within forest edges adjacent to tea, plots sampled at 100-150 meters contained nearly 20% more small stemmed trees (10-20 dbh) than other distances bands adjacent to tea which could indicate an edge related disturbance in the successional trajectory.

As would be expected, shade intolerant species were common within 0-150 m of both edge treatments, accounting for the greatest percentage of trees within 0-50m and 50-100m, and slightly less, though still >50%, at 100-150 m at edges adjacent to tea. A forest wide vegetation survey of NNP found *Macaranga kilimandscharica* (Euphorbiaceae), a known disturbance adapted tree (Ewango 2001), was the second most common species of tree >30 cm dbh (Plumptre et al 2002). This species represented the greatest relative density within 0-50 m from the forest edge adjacent to both tea and pine matrices and second greatest relative density within the forest interior. These results show an increase in the relative basal area of large-seeded, shade tolerant canopy tree species beyond 50m from the forest edge within forest adjacent to pine and a consistently low basal area of large-seeded, shade tolerant canopy tree species throughout all plots adjacent to tea. Studies from the Brazilian Atlantic forest show human disturbance has produced a shift in the frequency and abundance of tree species which has impacted the structure of biological communities and ecosystem function at multiple scales (Joly et al 2014). These effects are most pronounced in edge-affected habitat and species most impacted are large emergent trees that bear large seeds or large fleshy fruits and are dispersed and pollinated by specialized animals (Girão et al. 2007, Santos et al. 2008, Tabarelli et al. 2012, Joly et al. 2014). Many of these edge-affected fragments exist within a harsh, open matrix which promote the persistence of a smaller functional group of biologically homogenous species (early successional pioneer species) and remain distinct from tree species assemblages found within undisturbed forest interior (Tabarelli et al. 2008, 2012, Joly et al. 2014).

It has become increasingly recognized that land use in the matrix can be managed to support biodiversity in many different landscapes (Kupfer et al. 2006, Lindenmayer and Fischer 2006, Franklin and Lindenmayer 2009). The results of this study indicate that matrices that reduce the contrast of the structural and biophysical conditions between the surrounding landscape and natural forest have the potential to buffer effects of edges and help maintain natural forest processes. If matrix type helps support the ecological processes in forest edges necessary to maintain forest interior conditions, it can shape the effective area of a protected forest. This research suggests that edge effects may be influencing forest structure within edge habitat, but knowledge is still lacking about the mechanisms driving the observed changes in NNP edges. Other factors that influence the structure of tree communities need to be assessed such as changes in the air temperature, humidity level, soil moisture, decomposition rates, and nutrient cycling in forest edges adjacent to different matrix contrast. The ecological impacts of edge effects and other human disturbances have the potential to alter the long term integrity of some primary forest, however land use practices within the matrix can be managed to promote conservation goals that support biodiversity and reduce forest degradation (Lindenmayer et al 2013, Laurance et al 2014, Putz and Romero 2014, Putz et al 2014).

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Chapter 5: Dissertation Conclusion

The studies in this dissertation indicate that forest edges adjacent to high contrast tea plantations experience a greater magnitude and intensity of edge effects. For large birds, mean fruit removal, foraging visits, and the duration of visit per large large-seeded focal trees declined in forest edges adjacent to tea in comparison to the forest interior and within forest edges adjacent to pine plantations. Conversely, primates were observed more frequently in forest edges adjacent to tea plantations than within the forest interior or edges adjacent to pine plantations. In general, there were nearly eight times more conspecific seedlings and juveniles both directly beneath and further away from focal tree crowns in the forest edges near tea plantations, compared to the forest interior; and virtually no seedling or juvenile conspecifics beneath crowns in edges near pine. The amount of seedlings and juveniles beneath and away from focal tree crowns in tea edges were nearly proportionate.

I observed primates feeding on large amounts of fruits in forest edges adjacent to tea plantations. Seed spitting is common when these species of primates feed on large-seeded fruits (Lambert 2002). The spatial distribution of seedlings and saplings may correspond with the handling behavior of the primates. The influence of forest edges on seed fate and dispersal distances are not known and seed handling behavior can vary among primates depending on a variety of different factors (Kaplin and Moermond 1998, Kaplin et al. 1998, Lambert 2002), but it may be predicted that more seeds from the focal trees are arriving nearby to conspecifics in forest edges adjacent to tea plantations than forest edges adjacent to pine plantations. This study suggests that matrix type might influence the frugivore assemblage within the forest edges and consequently may impact seedling distribution and regeneration.

Results from the observations of seed dispersal by frugivores in forest edge habitat suggests that the type of matrix may influence bird and primate mediated seed dispersal in different ways. Large, non-migratory, primarily frugivorous, forest interior birds are sensitive to human disturbances and less likely to occur in intensively used habitats (Sekercioglu and Sodhi 2007, Newbold et al. 2013). The observations in this study are consistent with these global patterns. Long distance dispersal plays an important role in the structure of tropical plants (Nathan 2006). Studies suggest that large bodied birds may move seeds farther distances than monkeys (Holbrook and Smith 2000, Poulsen et al. 2001, 2002, Holbrook et al. 2002), and estimates from research in this forest suggest that the largest of the turacos move seeds longer distances than the smaller bodied turacos, but further research is needed to understand differences in dispersal distance and if the environment in edges play a role. The findings that dispersers respond differently to land use in the matrix is important for understanding ecosystem functioning because species play different roles in their contribution to ecosystem processes (Hooper et al. 2005). The loss or declines of a disperser group might have implications for the recruitment of some tree species and have negative impacts on species diversity in edge-affected forest.

Overall, tree species within forest edges adjacent to tea showed an increased functional response to edge effects, with effects extending up to 150 meters from the forest edge, and potentially beyond. Within forest edges adjacent to pine plantations, tree species responded to edge effects most significantly within the first 0-50 meters from the forest edge. Results from forest edges near to tea plantations are consistent with the research that shows edge effects can alter forest structure between 0-400 meters, but up to 2000 meters from the forest edge (reviewed in

Broadbent et al. 2008). The results from edges adjacent to pine plantations are also consistent with research suggesting plantation forests can buffer natural forests from edge effects (reviewed by Brockerhoff et al. 2008). Research in edges of natural forest fragments bordering pine plantations in New Zealand found that microclimate changes across the forest edges abutting pine were half those that occurred across the natural forest and pasture edges (Denyer et al. 2006).

Changes in frugivore assemblages and densities of shade tolerant tree species, which generally bear fleshy, large-seeded fruits, within forest edges adjacent to high contrast tea matrix suggests an altered recruitment environment for large-seeded tree species. This could lead to dominance of shade intolerant tree species and an overall decline in species diversity in forest edges adjacent to hard, or high contrast matrices.

Future directions

This work creates opportunities for a range of additional research questions. All aspects of this study would benefit from a comparison of the microclimate along edge-interior gradients within forest edges adjacent to different matrix types. The seed dispersal cycle is a succession of processes (Wang and Smith 2002) and tremendous information would be gained by following seed cohorts through the cycle from dispersal through germination and recruitment in the different forest edges. Animal censuses in different edge habitat and within the forest interior will allow comparison of the species composition and relative abundances of frugivores, seed predators, and herbivores, this will help link seed dispersal and vegetation structure in different forest edges. Another insight on the role of animal dispersers would include seed dispersal by nocturnal species, or the wide ranging black-and-white casqued hornbill (Bycanistes subcylindricus), this information can offer an additional perspective on impacts of matrix effects on forest connectivity and the spatial pattern of seed dispersal in forest edges.

Tropical forest edges are critical to the conservation of protected areas, but have been largely unconsidered in the strategies to conserve biodiversity. Matrix vegetation can make an important contribution to the conservation of tropical forest protected areas. Decreasing the magnitude and the depth of edge influence on forest edges can help maintain functional habitat, with characteristics that are more similar to those found in the forest core, throughout the protected area (Hansen and DeFries 2007). This can help maintain large patches of protected forest with intact ecological processes and key components of biodiversity such as large, area sensitive species and keystone food trees (Fischer et al. 2006, Lindenmayer et al. 2013). This study indicates that seed dispersal, a key ecological process that helps to structure and maintain diversity, can be disrupted by the contrast between the forest and the matrix. Conservation of protected tropical forest should not focus solely on the preservation of the protected area. But examination of the matrix is required to fully realize how to keep ecological processes intact.

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