CONSERVING AND RESTORING BIODIVERSITY AND ECOSYSTEM SERVICES IN AFRICAN TROPICAL RAINFOREST

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THESIS ABSTRACT

African tropical rainforests, hotspots of species biodiversity and endemism, are often reduced to forest islands within a sea of some of the world's poorest, fastest growing, and most resource-dependent human populations. Logging and clearing land for agriculture destroy or degrade extensive areas of tropical rainforest, threatening flora, fauna, and the ecosystem services on which people depend. Natural resource managers are challenged to maintain multi-functional landscapes while balancing conflicting demands for resources, biodiversity conservation, and ecosystem services. Working in Kibale National Park, Uganda, I studied the legacies of land-use histories and restoration on spatial and temporal variation in rainforest tree communities, as well as on animal habitat suitability and the provision of ecosystem services. I compared unlogged forests with forests regenerating after logging, plantations of exotic timber, fire, and subsistence farming. I investigate the potential to restore native forest on abandoned farmland via remnant, exotic "*legacy*" trees that attract frugivorous seed-dispersers. Fruit legacy trees recruited large-seeded, late-successional forest tree species. I caution against removing legacy trees without weighing the risk of invasion against the benefit of restoring native forest. I also investigated spatial and temporal change in logged and unlogged forest over a 24 year period, finding that variation in tree assemblages was greater within than across years. Spatial heterogeneity in unlogged forest can be partially attributed to past disturbance factors, and in harvested forests had more to do with pre-logging conditions than logging intensity. Finally, I compared synergies and trade-offs among tree diversity, animal habitat suitability, and ecosystem services in areas with different land-use histories. I found consistent, positive relationships among tree diversity, primate and elephant foods, and provisioning, regulating, and cultural services. My results demonstrate that managing forest landscapes to maximize tree diversity can also maximize stocks of animal foods and ecosystem services. My results can be used to inform current policies in Kibale with respect to managing exotic species, tree planting, preventing fire, and resource access agreements with local communities.

RÉSUMÉ

Les forêts tropicales africaines sont un lieu de biodiversité et d'endémisme extrêmement élevés. Cependant, elles sont souvent fragmentées et réduites à de petits îlots au sein d'une mer humaine considérée comme étant une population des plus pauvres du monde, au taux de croissance le plus rapide, et aux dépendances les plus élevées aux les ressources naturelles. La coupe forestière et le défrichement des terres pour l'agriculture détruisent ou dégradent les vastes étendues de forêt tropicale, menaçant ainsi la flore, la faune et les services liés aux écosystèmes dont dépendent les gens. Les gestionnaires des ressources naturelles sont donc mis au défi de maintenir des zones à usage multiple qui doivent non seulement accommoder l'exploitation des ressources naturelles, mais aussi la conservation de la biodiversité et le maintien des services liés aux écosystèmes. Dans le Parc National de Kibale en Ouganda, j'ai étudié l'effet de l'aménagement et de la restauration sur la diversité des communautés d'arbres tropicaux, sur la qualité de l'habitat pour les animaux, et sur le maintien des services liés aux écosystèmes. J'ai comparé des forêts non-exploitées avec des forêts post-exploitation, des plantations de bois exotique, des forêts affectées par le feu et des aires d'agriculture de subsistance. J'ai étudié le potentiel de restauration de terres agricoles abandonnées en utilisant des arbres exotiques qui attirent les animaux frugivores qui dispersent des semences d'arbres. Mes résultats démontrent que ces anciens arbres fruitiers attirent des animaux porteurs d'essences forestières à grosse graine, qui arrivent tard dans le processus de succession. Je mets en garde contre la coupe des tels arbres sans évaluer les conséquences que pourraient entraîner leur disparition: l'invasion d'autres espèces d'arbres plutôt que la restauration d'une forêt naturelle. J'ai aussi étudié, sur une période de 24 ans, les changements au sein de forêts exploitées et non-exploitées sur une échelle temporelle et spatiale, démontrant que la variation au niveau de l'assemblage des arbres était supérieure au sein d'une même année plutôt qu'entre les années. L'hétérogénéité spatiale dans une forêt non-exploitée peut être partiellement attribuée à une perturbation antérieure et, dans les forêts exploitées, à l'état de la forêt avant exploitation plutôt qu'à l'intensité des activités d'exploitation forestière. Finalement, j'ai comparé les synergies et les compromis entre différentes espèces d'arbres, la qualité des habitats pour les animaux et les services liés aux écosystèmes dans des zones ayant des historiques d'utilisation des sols différents. J'ai trouvé des relations positives et constantes entre la diversité des arbres, les aliments utilisés par les primates et les éléphants et l'approvisionnement, la régulation et les services culturels. Mes résultats démontrent que la

gestion des forêts afin de maximiser la diversité des arbres peut également maximiser les stocks d'aliments pour les animaux sauvages ainsi que les services liés aux écosystèmes. Mes résultats peuvent aussi servir à informer les politiques actuelles du parc de Kibale en ce qui concerne la gestion des espèces exotiques, la reforestation, la prévention des feux de forêt, ainsi que les ententes avec les communautés locales afin qu’elles aient accès aux ressources naturelles.

For my mother, my first and most important teacher about Africa

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PREFACE

Thesis format and style

This thesis is written in a manuscript-based format. It consists of a set of three manuscripts on which I am lead author and that will be submitted for publication in peer-reviewed journals. The style of each chapter follows the scientific journal *Ecological Applications*. All chapters use data from fieldwork conducted in Kibale National Park in western Uganda.

As a whole, the thesis explores forest restoration in mid-altitude African tropical rainforest recovering from two major land-uses, agriculture and logging, and a number of management interventions. I used connecting statements to provide logical bridges between each data chapter (Chapters 2-4). Since each data chapter includes a brief introduction to the background literature relevant to that study, the general introduction (Chapter 1) expands on the overall theme of the thesis and provides additional background information about the study area, thereby creating a single cohesive text.

Each data chapter was prepared as a manuscript for publication in a peer-reviewed journal, generally one focused on applied ecology and conservation. The first paper (Chapter 2) explores a restoration strategy hitherto undervalued in Africa, namely the potential of exotic trees to accelerate the recovery of forest on abandoned farmland. These data were collected in an area of tall grassland with recolonizing forest that had been used for subsistence farming from 1971 until 1993. The second paper (Chapter 3) uses longitudinal data from 1989 to 2013 to explore spatial and temporal heterogeneity in unlogged forest and forest logged at different intensities. The third paper (Chapter 4) explores the synergies and trade-offs between tree biodiversity, the availability of animal foods, and ecosystem services. These data were collected from 2008-2010 in twelve sites spread throughout Kibale.

Contributions of co-authors

This thesis consists of three manuscripts in preparation for submission to peer-reviewed journals. During my studies at McGill University, I received valuable guidance and assistance from a number of collaborators who contributed to the development of the thesis through academic mentorship, providing funding and equipment, and offering advice on the manuscript-based chapters. I was, however, the primary person deciding the research questions, organizing the recent rounds of data collection, analyzing and interpreting the data, and writing the manuscripts. I had local assistants helping me to collect data in Kibale National Park as well as others helping to enter and process data at McGill University.

Chapter 2: This manuscript will be co-authored with M. J. Lechowicz and C. A. Chapman, who were both valuable intellectual contributors. I conceived of the research project, developed sampling methodology, and supervised the initial data collection, aided by input and essential logistical support from Colin Chapman and his Ugandan collaborators. Martin Lechowicz provided advice on statistical analyses and several rounds of editorial comments as the manuscript was in various stages of preparation.

Chapter 3: This manuscript will be co-authored with M. J. Lechowicz, K. T. Martins, and C. A. Chapman. Colin Chapman generously shared his long-term tree data from permanent sampling plots in Kibale. Kyle Martins played a significant role in the conceptual development of this chapter, and provided both valuable guidance in the statistical analyses and comments on the manuscript. Martin Lechowicz provided advice on statistical analyses and assisted with manuscript development.

Chapter 4: This manuscript will be co-authored with M. J. Lechowicz and C. A. Chapman. Colin Chapman assisted with sampling design and provided essential logistical support in the field. Martin Lechowicz played a significant role in developing and interpreting the statistical analyses, and assisted with manuscript development.

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For permission to conduct fieldwork in Kibale National Park, I thank the Office of the President, Uganda Wildlife Authority, the Uganda National Council of Science and Technology, and the Makerere University Biological Field Station. While conducting this research, I was supported by scholarships and awards from the Natural Sciences and Engineering Research Council, the Canadian Federation of University Women, McGill University and the McGill Biology Department, Primate Conservation Inc., and the Quebec Centre for Biodiversity Science through the Fonds québécois de la recherche sur la nature et les technologies.

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“The advance of forests rarely takes place steadily on a broad front, but follows the principles of modern warfare; infiltrating along the valleys, surrounding successive areas of grassland, cutting them off from their supply of fire and then rapidly mopping them up.”

– H. A. Osmaston (1959)

“Two of the most important truths about rainforest are that more research is needed to establish the facts; and that it will be impossible to wait for the facts before acting.”

– C. Caulfield (1982)

“Here is the means to end the great extinction spasm. The next century will, I believe, be the era of restoration in ecology.”

– E. O. Wilson (1992)

1 INTRODUCTION

Tropical forests, which contain between half to two-thirds of global terrestrial biodiversity, provide humanity with a myriad of ecosystem services (Gardner et al. 2009). More than 800 million people live in or near tropical forests (Chomitz 2007) most of whom directly depend on forests for their drinking water, fuelwood, and animal protein (Wright 2010). Consequently, more than half of the world's tropical and subtropical forests have been "*substantially altered*" by people through land conversion, wood extraction, and hunting (Wright 2010, Laurance et al. 2014). These alterations almost inevitably reduce biodiversity (Gibson et al. 2011), affecting both protected areas and the surrounding landscape (DeFries et al. 2005, Laurance et al. 2012).

Forests can be degraded through commercial logging and subsistence level harvest (Asner et al. 2009), or lost entirely through deforestation driven by demand for farmland (DeFries et al. 2010, Gibbs et al. 2010, Kissinger et al. 2012). Urbanization can drive the abandonment of recently cleared and cultivated land, and yet further increase forest degradation and deforestation by creating urban markets for natural resources (Rey Benayas et al. 2007, DeFries et al. 2010). In this context, my thesis considers the consequences of a variety of land-use histories for the conservation and restoration of African tropical rainforest. In particular, I focus on the legacies left by agriculture and logging in forest restoration, and the trade-offs between managing forest for biodiversity conservation and the provision of ecosystem services.

Issues related to forest restoration are critical in Africa, which has close to 675 million ha of forest (FAO 2012). This equates to 17% of the world's total and 21% of the global carbon stock. Compared to the rest of the world, Africa has insufficient levels of protection, conservation, social service, and multiple use policies for forest (FAO 2012). The estimated net forest change in tropical Africa from 1980-1990 and from 1990-2000 was -3.9 million and -5.2 million hectares per year (Ramankutty et al. 2007). Between 1980 and 2000, 95% of all new land cleared for agriculture in Africa came from forested or formerly forested land (Gibbs et al. 2010). Today, only 10% of forest in sub-Saharan Africa is considered *primary forest* where 1) there are no clearly visible indicators of human activities, 2) the ecological processes are not significantly disturbed, and 3) forest stands are pre-dominantly composed of self-sown native trees (FAO 2012). More than 80% of forest in sub-Saharan Africa is *secondary/modified natural* *forest* – forest that 1) is composed of naturally regenerated native tree species but where there are visible indications of human activities (*e.g.,* logging, abandoned farms) and 2) displays a major difference in forest structure and/or canopy species composition compared to primary forests on similar sites (FAO 2012). In summary, sub-Saharan Africa has the highest levels of forest loss and lowest levels of forest protection in the world, compounded by poor and marginalized people with the world's highest levels of population growth, urbanization and dependence on natural resources (Ahrends et al. 2010, Palm et al. 2010, FAO 2012, World Bank 2012).

1.1 Perspectives on management of tropical forests

To maintain both ecological integrity and biodiversity, management and conservation strategies must consider the nature of *disturbance*. Disturbance can be defined as "*relatively discrete events in time that disrupt the ecosystem, community, or population structure and bring about a change in resources, substrate availability, or the physical environment*" (White and Pickett 1985 in Mori 2011). A *disturbance regime* is characterized by its intensity, frequency and spatial extent. Disturbances can be manipulated by managers to achieve a conservation goal. For instance, a natural disturbance regime may be reduced, or enhanced to the advantage of the biodiversity in a protected area. However these strategies must consider the consequences of altering natural regimes. For instance, some ecosystems are frequently and repeatedly disturbed, such as fire-prone savanna-woodland complexes. Removing the disturbance, fire, also removes one of the most important ecological processes structuring the ecosystem. This could have detrimental, potentially cascading, effects on species composition and diversity, as well as ecosystem function and services. As a result, managers must acknowledge the intrinsically dynamic nature of disturbance processes including the interaction between disturbance regimes and the spatial structure of the affected landscapes.

1.1.1 Ecological restoration and restoration ecology

In systems where a particular disturbance is considered detrimental, management often involves *ecological restoration*, "*the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed*" (SER 2004). Restoration involves initiating, assisting, or accelerating the recovery of ecosystems with respect to their health, integrity and sustainability. The end goal of ecological restoration is returning the restored system to its historic, pre-disturbance trajectory in a pre-determined *reference state*. This reference state is an actual ecosystem (or its conceptual model) used to set goals and evaluate the trajectory and outcomes of restoration activities. Characteristics of the reference state can be gleaned from historical records (*e.g.,* aerial photographs, traditional knowledge), ecological descriptions, species lists, and herbaria or museum collections, amongst other sources (SER 2004).

Restoration ecology is the scientific application of ecological theory to the practice of ecological restoration (SER 2004). Restoration has been called the "*acid-test of ecological theory*", whereby restoration ecologists predict and test how ecological communities develop and function in restored sites (Bradshaw 1987). Restoration ecology has its roots in, and is sometimes considered a sub-discipline of, conservation biology (Young 2000). However, the two disciplines differ in their philosophical approach and scale to study of the same problem. Conservation biology is predicated on the preservation and maintenance of existing habitat and biodiversity. This discipline generally focuses on individual species and genetic- and population-level dynamics. Restoration ecology assumes that habitats and biodiversity are threatened or in decline because of certain processes, and that to some degree these processes are reversible. Consequently, restoration ecology focuses on ecosystem organization and interaction with the goal rebuilding functioning ecosystems. The activities and practice of restoration ecology are therefore a complementary approach to conservation with the over-arching goal of preserving and enhancing biodiversity at local and global levels.

1.1.2 Approaches to forest recovery and restoration

A full review of current silvicultural practices (Günter et al. 2011) and the international regulatory framework (ITTO http://www. itto. int/) associated with timber harvests in tropical rainforests is beyond the scope of this thesis, which is focused on recovery and restoration in only a few particular sites harvested in the 1960s (Bonnell et al. 2011). In general the recovery of tropical forests after timber harvest depends on both the methods and intensity of harvest (Günter et al. 2011). In Africa, the detrimental impacts of 1960s era harvest methods on recovery still persist (Picard et al. 2012). Compared to commercial timber harvests, the traditional cutting of a few trees by pit-sawyers has negligible impacts on the forest and sets in motion recovery processes not inherently different from those following the natural death of a canopy tree. In contrast, commercial harvests remove greater numbers of trees of selected species (Picard et al. 2012), and hence qualitatively altering community composition. Furthermore, secondary damage associated with undirected felling and hauling of cut timbers from the forest is on a scale far greater than traditional harvesting. Post-logging treatments such as using arboricide to manage regrowth can further disrupt natural recovery processes. This thesis provides a comparison of forest recovery and forest restoration across a variety of land-use histories that include logged and unlogged forest as well as reforestation on land formerly used in agriculture.

Abandoned farmland sites, including cleared tropical forests and grassland, are often target sites for re/afforestation. Because biodiversity hotspots often overlap with densely-populated human settlements, which drive cycles of agricultural encroachment, abandoned farmland can be a particularly important part of tropical forest conservation (Luck et al. 2004, Cordeiro et al. 2007, Fisher and Christopher 2007, Luck 2007). Here, establishing native forest cover requires removing factors inhibiting the dispersal and establishment of tree species, such as harsh microclimates, lack of seed sources, high seed predation, and competition from aggressive shrubs or grasses (Somarriba 1988, Rhoades et al. 1998). Methods to develop forest on abandoned agricultural land range from relatively hands-off, passive approaches to active, labour intensive approaches. *Passive restoration* involves removing or preventing factors that damage or degrade ecosystems, such as fire or logging, and allowing natural ecological succession to occur. *Active restoration* involves physical change including reforesting or re-vegetating areas, removing ecological barriers such as invasive exotic species, or reintroducing extirpated native species. By and large, restoration managers will chose to use passive or active methods according to the local context while considering the type, intensity, and time since disturbance as well as the desired outcomes of rehabilitation or restoration, and any financial or logistic constraints.

Both biodiversity and ecosystem services can be enhanced through forest restoration, though restored systems rarely, if ever, entirely replicate the reference system (Rey Benayas et al. 2009). Animal species richness recovers fairly quickly (Dunn 2004), although it can take well over a century for animal species composition to approach undisturbed forest (Dent and Wright 2009). Plant community recovery seems to take longer: across the Neotropics, less than half the number of undisturbed forest species were present in 80 year-old secondary forest (Chazdon et al. 2009).

Carbon stocks recover faster than tropical forest biodiversity, and aboveground biomass recovers faster than belowground biomass (Martin et al. 2013). Whether managing or restoring ecosystem services positively or negatively affects biodiversity conservation is the subject of heated debate (Bullock et al. 2011, Kareiva and Marvier 2012, Reyers et al. 2012, Noss et al. 2013, Soule 2013). Conflicts exist when restoration projects focus on single elements to the exclusion of ancillary concerns (Bullock et al. 2011). The ecological success of forest restoration depends on the type and intensity of past and present land use, time since abandonment, landscape composition and configuration, and the dispersal abilities of forest plants and animals (Lugo and Helmer 2004, Lamb et al. 2005, Bowen et al. 2007, Rey Benayas et al. 2007, Chazdon 2008, Hobbs et al. 2009, Rey Benayas and Bullock 2012). Practically, success also depends on the feasibility of the desired outcome itself, as well as the time and resources available; maximizing the efficiency of any expensive, slow, or labour intensive interventions is generally critical to success.

1.1.2.1 Nodal forest recovery

Nodal forest recovery or *applied nucleation* (Corbin and Holl 2012) involves using isolated trees left after cutting natural forest or as a legacy from some other land use to restore forest. The individual trees – nodes – are referred to as *biological legacies* or *regeneration nuclei* (Guevara et al. 1986, Elmqvist et al. 2002), or *recruitment, regeneration,* and *dispersal foci* (McDonnell and Stiles 1983, Slocum 2001, Clark et al. 2004, Berens et al. 2008). Nodal forest recovery applies in both active and passive restoration strategies. It makes use of isolated native trees, or ‘remnant’ trees, which are sometimes left standing when the forest is cleared for cultivation, pasture, or logging (Guevara et al. 1986), as well as exotic trees, or ‘legacy’ trees, which have been planted by farmers for fruit or wood. Isolated trees be recruitment foci by attracting seed dispersers (Guevara et al. 1986, Uhl 1987, Duncan and Chapman 1999, Slocum 2001, Guevara et al. 2004) and by creating favorable microclimates for seedlings (Uhl et al. 1982, Guevara et al. 1986, Guevara et al. 1992, Belsky et al. 1993, Carrière et al. 2002, Clark et al. 2004, Guevara et al. 2004, Berens et al. 2008, Cole et al. 2010, Zahawi et al. 2013). Isolated trees also increase structural complexity and habitat connectivity at local and landscape scales, and therefore, are often considered to be ‘keystone structure ecosystems’ (Tews et al. 2004, Manning et al. 2006).

With intensified agricultural management and natural mortality, most isolated trees are predicted to disappear from many agricultural landscapes within the next two centuries (Gibbons et al. 2008). Losing such recruitment foci will make restoring forest cover on these lands more difficult. Restoration strategies must be aware that the use of recruitment foci will attract seed dispersers, which will likely transport seeds of various tree species and help reduce compositional differences between the restored and original forests (Lamb et al. 2005). For instance, managers might target the establishment of mid- or late-successional, rare, or keystone trees (*e.g.,* figs *Ficus* spp., the marula tree *Sclerocarya birrea* subsp. *caffra* and African baobab *Adansonia digitata*), or trees with limited dispersal ability (Cochrane 2003, Babweteera et al. 2007) or that provide staple or fallback foods for animals (Terborgh 1986, Wrangham et al. 1993). In the absence of mature isolated trees, similar processes operate with other ‘nurse’ foci including rocks, logs and patches of shrubs (Slocum 2000, Carlucci et al. 2011, Corbin and Holl 2012). Although isolated trees can facilitate restoration of native forest cover, some species have negative effects on nutrient cycles, soil or light conditions, and suppress natural vegetation (Struhsaker et al. 1989, D'Antonio and Meyerson 2002). Thus, species-specific traits, such as height, canopy size and density, fruit type, leaf chemistry, nitrogen-fixing ability, and frequency, predictability, and duration of phenological cycles may determine the effectiveness of an isolated tree as a regeneration nucleus.

1.1.2.2 Reforestation and afforestation

A widely used method of restoring tropical forest cover on intensively used land is planting native or non-native tree species on non-treed land. Whereas *reforestation* refers to establishing tree cover on formerly forested land, *afforestation* refers to land that was either never forest or has not had forest cover for a very long time. In active agricultural systems, tree planting often takes the form of *agroforestry,* which involves deliberately growing woody perennials on the same unit of land as agricultural crops or animals where there is a significant positive (or negative) ecological or economic interaction between the woody and non-woody components of the system (Nair 1993). In abandoned or severely degraded agricultural land, or intensively harvested forest, tree planting becomes akin to *plantation forestry,* where a small number of tree species are planted in a regular spatial pattern. With the added potential economic benefits of timber and fuelwood production and/or carbon storage, plantation forestry has become particularly attractive to both small- and large-scale land-holders and managers (but see Jacob et al. 2014b for caution against large-scale application in non-plantation forests). Plantation forestry based on exotic species is unusually popular in Africa. In most of the world, 75% of planted forests are composed of native species and only 25% are introduced species (FAO 2010). In contrast, 40% of planted forests in Africa are introduced species. There is a large body of evidence suggesting that these non-native plantations can accelerate restoration of native tropical forest (Chapman and Chapman 1996, Lugo 1997, Lamb 1998, Duncan and Chapman 2003). However, there is also potential for the detrimental effects on neighbouring intact forest through altered soil chemistry or fungi (Struhsaker et al. 1989), and there can be considerable damage to regenerating native forest if the plantation is harvested.

Ideally, choosing an appropriate restoration strategy would rely on detailed knowledge of land-use history at the site, a clearly defined reference system and restoration goals, no change in biotic or abiotic conditions during restoration, access to native seed sources and dispersers, and unlimited time, funding, and human resources to implement, monitor, and adapt management. In reality, managers are constrained by limited information, the competing needs of multiple stakeholders, and uncertain future conditions, amongst other factors. Ultimately, the restoration strategy or strategies used in a particular area may mean making the best of a bad situation: maximizing possible rewards while minimizing adverse outcomes where possible.

1.2 Localization and characterization of the study area

I conducted research in Kibale National Park, one of the most important medium-altitude moist tropical rainforests remaining in the Albertine Rift region of East Africa (Kasenene 1987, Struhsaker 1997). The Albertine Rift runs along the borders of five countries in Central Africa: the Democratic Republic of Congo, Uganda, Rwanda, Burundi, and Tanzania (Appendix 1). There is great need for forest conservation and restoration in this area, where some of the continent's highest levels of species richness and endemism coincide among the densest, fastest growing, and poorest rural human populations (Burgess et al. 2004, Cordeiro et al. 2007, Plumptre et al. 2007, Hartter et al. 2012). In the 1960s, the savannah areas of this landscape had the highest biomass density of large mammals in the world; today, it has more threatened species than any other region in Africa (Plumptre et al. 2008). Areas of the Albertine Rift have been repeatedly identified as global priority areas for biodiversity conservation by major international conservation NGOs (a Biodiversity Hotspot by Conservation International, a World Heritage Site by UNESCO, a Ramsar site by the Ramsar Convention on Wetlands, a critically endangered Priority Eco-region by the Worldwide Fund for Nature, and an Endemic Bird Area by Birdlife International) and researchers (Brooks et al. 2001, Olson and Dinerstein 2002, Plumptre et al. 2007).

Pressure on forests to provide natural resources and land for agriculture has resulted in the fragmentation of regional forest cover. Between 2000 and 2009, Uganda lost more forest *area* than any other of 12 East African countries (4,608 km2, compared to 36.3% relative background forest loss; Pfeifer et al. 2012). In addition, Uganda's population of 33.4M people is young (50% under 14 years old), growing rapidly (annual population growth rate of 3.3%), and poor (nearly 40% of Ugandans live at or below the global poverty line of $1.25 USD/day) (FAO 2012). It is estimated that the gross contribution of the natural resources to Uganda's economy is US$63.9 billion/year; however the costs of environmental degradation have been "*conservatively*" estimated at 4-12% of its gross national product (Moyini et al. 2002).

Land-use of forested and formerly forested land in western Uganda presently runs the gamut from ostensibly full protection in national parks to subsistence and commercial agriculture, fallows, burning to improve grazing, commercial logging, exotic plantations for timber and fuelwood, and reforestation to sequester carbon. With the anticipated return of internally displaced people, immigration for the perceived benefits of tourism and oil extraction, increased market demand from urban areas, and the weak capacity and coherence of civil society organizations, government, and infrastructure in the region, pressure on natural resources will only increase (Kaggwa et al. 2009a, MacKenzie and Hartter 2013, Van Alstine et al. In Press). An unfortunate consequence of this situation is that access to land and natural resources are significant factors in sparking and sustaining violent conflict in the region, from household to national levels (Huggins et al. 2005). Effective strategies to manage tropical forest diversity in the Albertine Rift are much needed, but not easily achieved.

1.2.1 Kibale National Park, Uganda

Kibale National Park lies north of the equator and 30 km from the border with the Democratic Republic of Congo (0˚13' - 0˚41' N and 30˚19' - 30˚32' E; Appendix 1, Figure 7-1). Kibale is a 795 km^2 "island" of forest within a "sea" of humanity, part of a set of forest fragments isolated in an intensely deforested landscape. Forests in the vicinity were once extensive and connected such that elephants moved seasonally throughout the landscape (Wing and Buss 1970) and forest elephants interbred with savanna elephants (Blanc 2007; Sameul Wasser, personal communication). Today, these forests are broken into fragments under varying degrees of protection and management: the Queen Elizabeth, Kibale, Semuliki, and Rwenzori Mountains National Parks and Itwara Central Forest Reserve and Toro-Semuliki Wildlife Reserve in Uganda, and the Ituri forest in eastern Democratic Republic of Congo (Appendix 1, Figure 7-2). Human pressure on natural resources and land throughout the region rapidly intensify the adverse effects of forest fragmentation. Forest cover within a five km radius of Kibale National Park has decreased by half and agriculture has nearly doubled since 1984 (Jacob et al. 2014a). In the 1950s local people had sufficient fuelwood and construction materials in their communities (Osmaston 1959), but people now report shortages of such wood products and increasingly turn to illegal extraction from the park (Kakudidi 2007, MacKenzie et al. 2012). Despite, or perhaps because of, these adverse trends, Kibale National Park offers a favorable venue for investigating various approaches to the conservation of regional forest biodiversity.

There are at least six advantages to conducting conservation research in Kibale:

1. The park has a multi-functional mandate, existing to "... *protect the remarkable biodiversity and biophysical elements… and to preserve both tangible and intangible benefits from the protected environment including sustainable supplies of traditional forest products for local people, now and in the future"* (UWA 2003).
2. Land cover in Kibale has been affected by a wide range of disturbances, including elephant damage, natural and human-caused fire, selective logging, subsistence agriculture, and planting of native and non-native trees. This creates the opportunity to investigate the roles of disturbance and forest restoration and the synergies and trade-offs between biodiversity and ecosystem services.

3. Human pressure on natural resources in and around Kibale is intense and rapidly increasing (MacKenzie et al. 2012, Jacob et al. 2014a).
4. For over forty years researchers have intensely studied how the legacies of human disturbance has affected both tree assemblages (Kasenene and Murphy 1991, Struhsaker 1997, Chapman et al. 2002c, Lwanga 2003, Omeja et al. 2009, Bonnell et al. 2011, Duclos et al. 2013) and animals (Kasenene 1984, Skorupa 1986, Weisenseel et al. 1993, McCoy 1995, Struhsaker et al. 1996, Struhsaker 1997, Dranzoa 1998, Gillespie et al. 2005, Massimino et al. 2008, Chapman et al. 2010b).
5. Researchers have recently begun to study local peoples' perceptions, attitudes and dependence on ecosystem services from Kibale and neighbouring fragmented natural areas (Hartter 2010, Naughton-Treves et al. 2011, MacKenzie 2012a). These services include the provision of non-timber forest products such as wild coffee and honey, medicinal plants, dead or fallen wood for fuel, thatching grass, and fishing.
6. Research has been initiated on the efficacy of actively restoring forest on degraded farmland for carbon sequestration (Klomp 2009, Omeja et al. 2011), and passively restoring forest on grasslands by preventing fire (Lwanga 2003).

In this thesis I try to leverage these advantages, maximizing insights into tropical rainforest conservation that can be gained from my study in Kibale, and more generally in tropical regions.

1.2.2 Physical geography

Kibale National Park lies on a plateau with elevation ranging from 1590 m in the northwest to 900 m in the southwest with drainage south into Lake George through the Mpanga and Dura Rivers. The south-eastern boundary of the park follows an escarpment that naturally separates the rainforest from savannah woodland at lower elevation on the floor of the Rift Valley. The region around the park is underlain by pre-Cambrian, strongly metamorphosed sedimentary rocks of the Toro System subjected to considerable rifting and volcanic eruptions 4,000-6,000 years BP (Taylor et al. 1999). Much of northern Kibale has red ferralitic soils, which are deeply weathered, shallow, and stony with relatively low fertility; southwestern Kibale and hilltops within the northern forest have more fertile soils derived from volcanic ash with a high mineral content (Osmaston 1959, Lang Brown and Harrop 1962, Langdale-Brown et al. 1964, Kasenene

1987). Upland soils are generally well-drained sandy loams and sandy clay loams with some local variation associated with topography (Wing and Buss 1970). There can be a marked soil catena with increasing fertility from valley-bottom to hill-top, and high phosphorous content on hilltops ascribed either to a history of cultivation or volcanic tuff (Lang Brown and Harrop 1962; but see Struhsaker 1997, Kingston 1967). A relatively low concentrations of chemical compounds for plant defense in the vegetation and the high biomass of folivorous primates suggest that soils in parts of Kibale may be more fertile than many tropical rainforest soils (McKey et al. 1978, Gartlan et al. 1980, Struhsaker 1997).

Kibale also tends to be cooler and drier than other tropical rainforests, with a high-to-low north-to-south gradient in rainfall and vegetation gradients that follow elevation (Struhsaker 1997). Mean daily minimum and maximum temperatures from 1970-2010 were 15 °C and 23 °C (T. T. Struhsaker and C. A. Chapman, unpublished data). Mean annual rainfall from 1968-2010 was 1654 mm (Hartter et al. 2012), falling in two rainy seasons from March-May and September-November (Struhsaker 1997). Inter-monthly variations in both rainfall and temperature are greater during El Nino years. Long-term climate records from 1903-2005 indicate that the region has become gradually wetter with less frequent droughts and greater variability in temperatures (Struhsaker 1997, Chapman et al. 2005a).

1.2.3 Vegetation: past and present

Kibale lies between the Afro-montane and Afro-alpine phytogeographical regions and the lowland forests of the Guineo-Congolian region (Hamilton 1974). It is classified as a moist evergreen and semi-deciduous tropical rainforest, transitional between montane and lowland forest (Langdale-Brown et al. 1964, Howard 1991). Up to 351 species of trees and woody shrubs have been identified in Kibale (Howard et al. 1996), including 209 species of trees, half of Uganda's total (Howard 1991). Foresters working in Kibale during the 1950s reported evidence that "*refute[d] any concept of these as virgin, unchanging, or primeval forests*", although they thought the forests were "*of some antiquity*" (Osmaston 1959).

Humans have occupied and manipulated African tropical forests for many thousands of years (van Gemerden et al. 2003, Olson 2004, Brncic et al. 2007, Bayon et al. 2012, Yasuoka 2013). Interactions between climate, technology, conflict, and disease have contributed to the dynamic nature of forest-grassland change in western Uganda in the last 2000 years (Taylor et al. 1999, Taylor et al. 2000, Ssemmanda et al. 2005, Lejju 2009). Around 500 BC, people in western Uganda began forging iron, and by 1000 AD there had been major reduction in the extent of forests (Taylor et al. 2000). Over the last thousand years there were several periods of aridity when people sought new land and any regenerating forest was open woodland dominated by *Olea* species followed by wetter periods when people moved back to the area and regenerating forest was dominated by *Celtis* species (Taylor et al. 2000) (Ssemmanda et al. 2005). Rainforests in the region were one of East Africa's principal biotic refugia during climatic fluctuations in the Pleistocene (Rodgers et al. 1982); their repeated fragmentation and reconnection may contribute to the high regional biodiversity today (Taylor et al. 1999).

European and Arab traders first explored Uganda in the early 1800s, and by 1894 Uganda had become a British Protectorate (Mugisha 2002, Turyahabwe and Banana 2008). Although all written records document a mosaic of grassland and forest in the Kibale landscape, early researchers found fossil leaves even in areas now dominated by grassland (Osmaston 1959, Wing and Buss 1970). They concluded that Kibale used to be part of a continuous block of forest with the Rwenzori and Itwara forests (Appendix 1) until large areas were destroyed by volcanic eruptions within the last 1000-10,000 years. This speculation is supported by pollen core analyses in Rift Valley lakes adjacent to Kibale and throughout the region, which show widespread forest cover 6,800 years ago (Hamilton et al. 1986). Some of the earliest written descriptions of the area clearly describe a interconnectedness among forest in western Uganda: "*a magnificent stretch of typically West African forest extend[ing] almost uninterruptedly from the vicinity of the Victoria Nile… through eastern Toro, parallel with the Ruwenzori range but not joining with it, into northern Ankole*" (Johnston 1902). Furthermore, the "*tropical luxuriance*" of such forest "*surpass[es] in splendour of vegetation and in loftiness of trees the finest forest effects I have seen on the Congo, the Cameroons, in the Niger Delta, and in Liberia*" (Johnston 1902). The crater lake area west of Kibale was described as having scenery "*so extravagantly beautiful that I feel that – coupled with the fact that they are in a country possessing a very healthy climate and few inhabitants – they may sometime become the seats of small European settlements*" (Johnston 1902).

Prior to colonialisation, many parts of Uganda had well-developed monarchies, including the Kingdom of Toro where Kibale is located. Within the kingdom, forests adjacent to settlements were collectively owned by that community, used for timber and non-timber forest products, and managed through informal means and traditional, culturally transmitted taboos against over-exploitation (Turyahabwe and Banana 2008). People of the local Batoro tribe farmed grassy hilltops inside what is now Kibale National Park, and used the forest for hunting and sanctuary during tribal wars (Lang Brown and Harrop 1962). Explorers in the late 1880s came across a "*considerable [human] population*" in the area (Osmaston 1959). Hilltop grasslands within the forest matrix were inhabited and farmed under shifting cultivation practices (Kingston 1967; Lang Brown & Harrop 1962). There is evidence in Kibale of harvesting timber to produce charcoal and supply a nearby iron smelting industry up to the 1920s (Osmaston 1959). Pit-sawing for local timber consumption has occurred in Kibale since at least 1900, with most timber cut near the main road (Osmaston 1959). However, many people left the Kibale area during 1900-1950 as a result of tribal war, drought-induced government resettlement policies, the livestock disease rinderpest, and the human diseases malaria and sleeping sickness (Osmaston 1959, Mugisha 2002). This rural depopulation set up a positive feedback loop, whereby "*remaining inhabitants were no longer able to repel*" crop raids and livestock losses from wild animals (Osmaston 1959), leading to another round of forest regeneration and expansion. Thus despite a long history of human occupation in and around Kibale, some parts of the forest appear to have been disturbed relatively little by humans for several hundred years (Struhsaker 1975).

Events in the latter half of the 20th century inside Kibale created a complex mosaic of mature forest interspersed with habitats regenerating after a variety of recent human disturbances. As late as the 1940s, what is now Kibale National Park was extensively covered by mature forest interspersed with various types of grassland, woodland-thicket, and patches of successional forest. A former game corridor connecting Kibale to the Queen Elizabeth National Park to the south was 61% grassland and 31%forest (Ryan and Harter 2012) (Appendix 2). The former forest reserve sector within Kibale was only 60% forested due to past harvest practice and land clearing (Wing & Buss 1970) (Appendix 2). Forest succession over the last half-century shows a progressive loss of grassland and increase in native forest, primarily from efforts to prevent fire and intensive reforestation (Jacob et al. 2014a). Today, land cover in Kibale National

Park is 74% unlogged and regenerating forest, 15% bare ground and short grasses, 6% tall grasses, 4% wetland, and 1% shrubs (Jacob et al. 2014a).

In most places, the canopy in mature forest is of irregular height between 30-45 m tall (Kingston 1967). Forest in northern and central Kibale is moist evergreen, while forest in the warmer and drier parts of southern Kibale tend towards semi-deciduous (Wing and Buss 1970, Oates 1974). In general, many tree species co-occur in various combinations or mixtures, but some areas are noticeably dominated by species such as *Piptadeniastrum africanum* or *Cynometra alexandri* (Lang Brown and Harrop 1962, Kingston 1967, Wing and Buss 1970). Mixed species *Parinari* forest types such as *Parinari-Carapa-Strombosia* and *Parinari-Olea* are predominant in northern Kibale; *Celtis-Chrysophyullum* forest is more common elsewhere in the park with *Diospyros abyssinica* and *Markhamia lutea* become abundant towards the east. Southeastern Kibale contains *Pterygota mildbraedii* forest with *Olea welwitschii* and *Cynometra alexandri* abundant in the valleys (Osmaston 1959, Langdale-Brown et al. 1964) (Appendix 3). Considerable uncertainty exists about what, if anything, can be called a 'climax forest' in the region. *Parinari* forest (at least between between 1370-1525 m; Eggeling 1947, Osmaston 1959), *Celtis-Chrysophyllum* forest (Langdale-Brown et al. 1964), and *Cynometra* forest (Laws 1970) have all been suggested as possibilities. Successional forest colonizing grassland tends to be low-growing and scrubby with species such as *Millettia dura, Securinega virosa,* and *Vernonia amygdalina* common. Grasslands themselves have few trees, save fire-adapted species like *Erythrina* and *Acacia*, and are dominated by the grasses *Pennisetum purpureum, Hyparrhenia* spp. , and *Cymbopogon afronardus*.

1.2.3.1 History of management

The origin of Kibale as a protected area lies in the Toro Agreement of 1900 between the British Protectorate Government and the king of the Toro, which stipulated that all forests in the Toro Kingdom would become the property of the Crown (Osmaston 1959). The Protectorate Government established its Forest Department around this time with the aim of harvesting forest products, including wild rubber (*Funtumia elastica*) and commercially valuable trees such as mahogany (*Khaya* and *Entandrophragma* spp.) and African teak (*Milicia excelsa*) (Webster and Osmaston 2003). The Kibale area was inspected by a botanist in 1905, and by a forester in 1914 who considered Kibale to be the "*largest and reported best forest*" in the Toro kingdom

(Osmaston 1959). The first forestry enumeration, conducted in northern Kibale in 1915, noted a mosaic of forest and large grassy areas (Osmaston 1959). In 1926, the Protectorate Government designated the southwestern part of what would later become Kibale National Park as a 206.5 km^2 Game Corridor (Appendix 2) managed for controlled hunting and to promote the movement of large animals, notably elephants (Ryan and Hartter 2012). In 1993, the Kibale Central Forest Reserve and Game Corridor were joined and status upgraded to become Kibale National Park (Struhsaker 1997, Ryan and Hartter 2012).

1.2.3.2 Commercial timber harvest

The first official Uganda Forest Policy was adopted in 1929, with an emphasis on managing forests for environmental protection (Webster and Osmaston 2003, Turyahabwe and Banana 2008). Later revisions also recognized the non-market benefits of forests, including regulating climate, protecting water supplies, and minimizing soil erosion, and determined that the Uganda Protectorate would benefit from increased forest cover and protection (Turyahabwe and Banana 2008). In 1932, the northern, central, and southeastern parts of what would later become Kibale National Park were designated as a 560 km^2 Forest Reserve (Osmaston 1959) with two specific sectors designated as Nature Reserves and protected from logging. The primary management objective of Kibale outside these protected sectors, however, was to maximize yields of hardwood timber from natural forests and of softwood timber plantations (*Cupressus lusitanica*, *Pinus patula*, *P. carribea*) in grasslands (Kingston 1967). Kibale forest had mainly general purpose timber species with few high-value species such as *Entandrophragma* spp. **(**mahogany) (Kingston 1967). Secondary management objectives included producing wild coffee and fuelwood for local needs, so long as they did not conflict with the primary objective.

The three parts of the Forest Reserve to be harvested were divided by the Kampala-Fort Portal and Fort Portal-Kamwenge roads and called the North, Central, and South Blocks (Appendix 2). The North Block was selectively harvested between 1948-56 and the northwestern part of the Central Block between 1956 and the early 1970s; the South Block remains unlogged (Wing and Buss 1970). Initial harvests were planned on a polycyclic felling cycle of 200 years; beginning in 1948 sawmills were contracted to cut 9-26 species (Appendix 4) of merchantable trees over 48.5 cm diameter-at-breast-height (DBH) and removed 25-50% of the basal area. Other tree species and sizes could be cut at the mill's discretion.

Between 1954-56, the Uganda Forest Department used a combination of aerial photography and extensive ground work to map forest types throughout the Forest Reserve (Appendix 3) (Osmaston 1959). The survey was a 1% enumeration covering two-thirds of the forest (259 km^2), and requiring over 130 km of transect lines (Webster and Osmaston 2003). The forest enumeration in 1954-56 "*… is the first time that a vegetational classification of tropical high forest has been attempted on this scale in Africa using quantitative data*" (Kingston 1967). Thirteen forest types were identified and a 1:50,000 map created (Osmaston 1959, Uganda Forest Department 1960). During these inventories in the 1950s, the highest standing volume of commercial timber species was found in the *Parinari* forests of northern Kibale (forest types K1 and K2; Appendix 3) (Osmaston 1959).

In 1957, polycyclic harvest on a 200 year rotation was rejected in favour of a uniform, intensive harvest "*as near to clear felling as is economically possible*", followed by intensive elephant control and treating undesirable tree species with arboricide (2,4,5-T, a component of DDT) (Osmaston 1959, Hamilton 1984, Webster and Osmaston 2003). This was intended to convert the existing uneven-aged natural forest to optimal regeneration of 20-40 high-quality timber trees per acre (each on average ~80 cm DBH), ready for a 70 year felling rotation (Kingston 1967, Kasenene 1987). The North and Central Blocks were split into management units approximately 1 sq. mi. (2.6 km^2) in size, roughly following natural features such as rivers and ridgelines (Osmaston 1959). By 1969 approximately 35% of the northern sector of the park had been harvested under this new management plan (Struhsaker 1997). A lack of sufficiently trained personnel unfortunately meant that it was difficult to enforce policies on directional felling, removal of compulsory species, retention of seed trees, placement of skid trails, and treating with arboricide. Therefore, the effects of harvest vary both among and within compartments. Harvested areas were left to regenerate naturally. Attempts were made to exclude elephants from regenerating areas via patrols and scare-shooting (Wing and Buss 1970).

Since harvest in the 1950s and 1960s, forest regeneration in the logged areas has ranged from relatively good in areas with low-intensity harvest to very slow or stopped altogether in areas with high-intensity harvest, especially in those treated with arboricide (Struhsaker 1997, Paul et al. 2004). Regeneration appears to be related to the degree of damage during logging, specifically the creation of large gaps in heavily logged areas (upwards of 7000 m2, Kasenene 1987) (Paul et al. 2004). Such large gaps allow rapid growth of aggressive herbaceous vegetation, particularly *Acanthus pubescens*, creating dense growth of shrubs and vines that suppresses forest succession (Struhsaker 1997). Elephants are attracted to these areas and through browsing damage saplings and seedlings, which further prevents forest regeneration (Struhsaker *et al.* 1996b; Lawes & Chapman 2006). Detailed descriptions of the effects of logging on Kibale forest can be found in Kasenene (1987), Skorupa (1988), and Struhsaker (1997). Many of the study sites in this thesis originated as a result of this 1959 forest management plan (Osmaston 1959) (Appendix 2 and Appendix 3).

1.2.3.3 Exotic timber plantations

While timber harvest was planned in Kibale forest, experiments were conducted in Kibale grasslands to test softwood timber plantations (Kingston 1967). In the late 1950s, foresters noted that "*estimates of future consumption indicate that by 2000 AD the natural forests will be quite inadequate to supply the timber required in Uganda*" (Kingston 1967). It was determined that the national forest estate would need to quadruple in size to meet projected need, and that this gap would be filled by extensive, fast-growing plantations (Turyahabwe and Banana 2008). In particular, there was high demand for timber in western Uganda because it was not yet connected by rail to the rest of East Africa (Kingston 1967). Between 1953 and 1977, managers planted many grasslands within the forest reserve with fast-growing exotic softwoods, mainly *Cupressus lusitanica, Pinus patula* and *P. caribaea* (Chapman and Chapman 1996, Struhsaker 1997, Omeja et al. 2009). Preventing elephant damage to the growing plantations was a top management priority and considerable effort was put into discouraging elephants through scare-shooting, electric fences, and trenches, but with little effect (Kingston 1967).

In 1993, when the Kibale Central Forest Reserve and Kibale Game Corridor were combined and upgraded to national park status, the protected areas managers (Uganda Wildlife Authority) decided to harvest the mature conifer plantations. By this time, a considerable amount and diversity of native forest had regenerated in the understory (Struhsaker 1997). Harvest methods included both saw-milling and pit-sawing. Although regulations were established to reduce damage to regenerating native forest, harvest was poorly supervised and there was extensive damage to surrounding forest (Kasenene 2007). As in the logged native forest, harvest damaged naturally regenerating trees and created very large gaps. Regeneration of these softwood plantations has been repeatedly monitored. Kasenene (2007) found that pit-sawn areas had higher stem density than saw-milled areas, and that there was better regeneration in terms of species richness and density in the harvested timber plantation than in neighbouring grassland. Omeja et al. (2009) compared enrichment planting to natural regeneration, concluding that planting indigenous trees was not necessary to ensure the beginnings of native forest regeneration in the harvested plantation. However, concern was raised the plantation might adversely affect native forest. Specifically, Struhsaker et al. (1989) concluded that downslope proximity to the plantation was responsible for considerable dieback in neighbouring forest, up to 100% mortality in one species. Furthermore, a striking increase in the number of snares and incidents of bushmeat hunting in the forest were noted during the period of plantation harvest (Omeja et al. 2012).

1.2.3.4 Grasslands

The hilltop and hillside grasslands in Kibale were likely created and maintained through a combination of volcanic action, fire, and/or long-term cultivation and livestock grazing by subsistence agriculturalists (Lang Brown and Harrop 1962, Kingston 1967). The earliest, and most thorough, classification of grasslands in Kibale identified tall, hilltop tall, and poor grassland types as well as a grassland-forest ecotone (Lang Brown and Harrop 1962). Three different types of grasslands were recognized: Tall Grass on lower slopes with deep, dark red loam soils (dominated by *Hyparrhenia* spp. and on lower slopes with *Pennisetum purpureum*), Poor Grass on upper steep slopes with very thin soils (dominated by *Cymbopogon afronardus* and often associated with *Imperata cylindrica*), and Hilltop Tall Grass on level summits with deep laterite-covered soils (dominated by *Beckeropsis uniseta*, similar to the Tall Grass type bit with richer flora) (Lang Brown and Harrop 1962). Forest colonizing the ecotonal grasslands was bushy and about 3-7 m high, including primarily *Millettia dura, Securinega virosa* and *Vernonia amygdalina*.

Grasslands in Kibale are important habitat for wildlife including grassland-specialist or restricted-range bird and butterfly species (Howard et al. 1996) and large mammals, especially bulk grazers such as African buffalo (*Syncerus caffer*) and elephant (Wanyama et al. 2010; Jacob and Chapman, unpublished data). Even though elephants in Kibale spend a great deal of time in forest, stomach content analyses reveal that upwards of 90% of their diet is grass (Buss 1961). Since the 1970s, grasslands in Kibale have gradually converted to forest due to fire prevention efforts, including intentionally cutting of fire-breaks (that also serve as vehicle tracks) and the unintentional effect of the presence of researchers that deters illegal fires started by bush-meat hunters. Forest succession occurs naturally if grassland is consistently protected from fire, with animals playing a large role in dispersing the seeds of forest tree species (Lwanga 2003, Omeja 2009, Omeja et al. 2009, Majid et al. 2011, Omeja et al. 2011).

1.2.3.5 Agricultural encroachment

The widespread civil unrest and violence which occurred during the regime of Idi Amin in the 1970s halted forest management activities throughout Uganda's protected area system. There was extensive deforestation and land use change outside protected areas, as well as encroachment by people into all Ugandan forest reserves with the stated objective to "*capture*" economic returns to the nation by using the remaining forests (Howard 1991). Deforestation in the Kibale Forest Reserve was started by Bakiga immigrants in 1971 or 1972 (Hamilton 1984); settling in the Kibale Game Corridor may have begun some years earlier. Aerial counts conducted in and around Uganda's protected areas in 1982 showed that most reserves were heavily encroached and settled with permanent buildings. Estimates vary widely, but upwards of 50,000 people settled illegally in Kibale, mostly in the Game Corridor but also affecting the Forest Reserve. Many areas of the Forest Reserve were so heavily deforested and settled that they were deemed "*irretrievably lost*" (Van Orsdol 1983). In total, encroachment negatively affected over 140 km^2 of grassland and forest, about 19% of the park (Van Orsdol 1986, Chapman and Lambert 2000). When civil conflict in Uganda finally drew to a close, a new more stable government was formed and attention returned to managing protected areas. In 1992, the settlers were evicted from Kibale; this eviction has led to sustained resentment in many local communities (Ryan and Hartter 2012).

In association with ending the illegal settlements in the Forest Reserve, the new government created Kibale National Park in 1993 by joining the Central Forest Reserve with the adjacent Game Corridor (Appendix 2). With the designation of national park status, access to forest resources by local people was curtailed. Where it was allowed, harvest was to be more strictly regulated through individual- and village-level permits. Restoring "*natural forest cover*" on the encroached area has been a high priority for the Uganda Wildlife Authority (UWA) ever since (UWA 2003). Two complementary approaches have been used to restore forest in the previously encroached areas: passive forest regeneration by cutting fire-breaks in the tall grass (Lwanga 2003) and re/afforestation by planting native tree species (Omeja et al. 2011). Since current park policy aims to remove non-native species (UWA 2003), the tree planting project mainly plants five tree species: *Albizia* spp. *, Bridelia micrantha, Shirakiopsis elliptica, Celtis gomphophylla,* and *Warburgia ugandensis* (Omeja et al. 2011). Previous research found an additional 39 tree species naturally regenerating in the restored area, with indications that birds and mammals were using the area (Omeja et al. 2011). Unfortunately, there are some indications that levels of illegal resource extraction (*e.g.,* timber harvest, animal snares) are higher in areas where more people are employed by the tree planting program (MacKenzie et al. 2012).

1.2.4 Wildlife

With its mosaic of natural habitats, it is no surprise that Kibale has an abundant and diverse faunal community. The park ranks fifth in species richness and sixth in overall biodiversity importance among all Ugandan forests (Howard et al. 1997): it has 115 mammal, 327 bird, and 532 plant species (Plumptre et al. 2007). Kibale also ranks within the top five in terms of globally threatened plants and mammals for 38 protected and unprotected areas in the Albertine Rift (Plumptre et al. 2007). This exceptional faunistic diversity should and does figure centrally in discussions of conservation strategy in Kibale.

Kibale is internationally renowned for its exceptionally high primate numbers and species diversity (Chapman and Lambert 2000). Twelve primate species are found in Kibale: chimpanzees (*Pan troglodytes* ssp. *schweinfurthii*), olive baboons (*Papio anubis*), grey-cheeked mangabeys (*Lophocebus ugandae*), black-and-white colobus (*Colobus guereza*), red colobus (*Procolobus rufromitratus* ssp. *tephrosceles*), l'Hoest's monkeys (*Cercopithecus l'hoesti*), blue monkeys (*Cercopithecus mitis* ssp. *stuhlmanni*), red-tail monkeys (*Cercopithecus ascanius* ssp. *schmidti*), dwarf bushbaby (*Galago demidovi*), Inustus bushbaby (*Galago inustus*), potto (*Perodicicus potto*), and possibly occasional vervet monkeys (*Cercopithecus aethiops*) (Struhsaker 1997). The park has the largest population of chimpanzees and the only viable population of red colobus monkeys in Uganda (Struhsaker 1997).

The park is also notable for its elephant population, which are believed to be hybrids between the savannah elephant (*Loxodonta africana africana*) and the forest elephant (*Loxodonta africana cyclotis*) (Blanc 2007; Samuel Wasser, personal communication). Kibale elephants are remnant of a larger population that was systematically culled in the first half of the 20th century, and then isolated by forest fragmentation and changing land use in the second half. In the early 1900s, the Game Department of Uganda reported that "*this small Protectorate [Uganda] is still literally over-run with elephants – big, dangerous, destructive beasts – if we are to afford the inhabitants of this fertile land the measure of protection which is their due, an annual slaughter of elephants on a large scale is not only necessary but imperative*" (1924). Extensive elephant control measures were enacted throughout the country to create separate areas for people and wildlife; during 1927-1958, over 40,000 elephants were shot, reducing the area of the country occupied by elephants from 70% to 17%. Thirty percent of these were from western Uganda around Kibale, reflecting their relative abundance (Brooks and Buss 1962). During Uganda's civil unrest, elephant populations throughout the country decreased by a further 90%. Today, elephants in Kibale are confined to the park apart from crop-raiding neighbouring farms; human-elephant conflict remains one of the highest priority concerns for local people.

1.3 Structure of the thesis

In the broad context summarized in preceding sections, my thesis uses Kibale as a platform from which I explore the conservation and restoration of African tropical rainforest stemming from a variety of land-use and disturbance histories. In particular, I focus on the legacies of agriculture and logging in forest recovery and restoration, and the trade-offs in managing forest to both conserve plant and animal biodiversity while providing ecosystem services relevant to people. The body of the thesis consists of three manuscripts to be submitted for publication, each serving as a chapter addressing topics related to developing effective management strategies for Kibale and contributing to a larger discussion about conserving tropical rainforest more generally.

1.3.1 Focus on tree assemblages

I focus my data collection and analysis on tree assemblages in Kibale for several reasons. First, trees define the physical structure of forest ecosystems, are the basis of the park's designation and management, and canopy-level individuals are the only components visible to remote sensing. Thus, trees provide a logical framework to study and manage tropical rainforests. Second, many animal species within Kibale use trees for shelter and sustenance, including some of high conservation concern such chimpanzees and red colobus monkeys. Third, since forest resources are becoming even more limited in the region, particularly fuelwood and construction material, people are increasingly turning to illegal resource extraction from the park (MacKenzie et al. 2012). This increases competition with, and opportunities to hunt, forest-dependent wildlife. Fourth, forest restoration is a high priority for land managers including the Uganda Wildlife Authority that is in charge of national parks (UWA 2003) and the National Forest Authority in charge of Central Forest Reserves. Finally, my emphasis on trees reflects the paucity of information about other plant life-forms. While I had access to several excellent field guides for trees in Uganda (Eggeling and Dale 1951, Hamilton 1981, Katende et al. 1995) and tropical Africa (Letouzey 1986, Keller 1996), only one source for common species of ground-layer vegetation was available (Lind and Tallantire 1962). Furthermore, the efficiency of botanical fieldwork in Kibale is greatly enhanced by the extensive knowledge that local field assistants have of the tree community. Aspects of the results would perhaps change if I had included a comprehensive survey of ground vegetation (*e.g.,* herbs, sedges, grasses, non-vascular plants), but this would naturally have limited the areal extent I could survey within the time allowed. For these reasons, I opted to limit my data analysis to trees and woody shrubs.

1.3.2 Chapter 2: Legacy trees

Since 1) subsistence agriculture is the single largest cause of forest degradation globally, 2) Africa has the highest urbanization rate in the world and land abandonment is steadily increasing, and 3) financial and human resources for conservation are limited, there is pressing need to develop efficient methods to restore forest on degraded, formerly forested land. In Chapter 2, I explore a method of restoring forests on abandoned farmland that is too often overlooked in Africa: nodal forest recovery, also called applied nucleation. I investigated whether legacy trees were acting as regeneration foci on abandoned farmland in Kibale.

Understanding how legacy trees affect the early-stage recruitment of native trees during forest succession and recovery can be used to assess the effectiveness of nodal forest recovery as a conservation tool. My goal in this chapter was to determine to what extent the presence of legacy trees could complement existing management activities and help restore forest.

In this chapter, I address four research questions:

1. How is the establishment of native forest trees on abandoned farmland influenced by *proximity* to a legacy tree?
2. How is the establishment of native forest trees on abandoned farmland influenced by the *species* of legacy tree?
3. How is the establishment of native forest trees on abandoned farmland influenced by the *dispersal mechanism* of the forest tree?
4. How do tree assemblages associated with legacy trees resemble or differ from those in nearby forests?

1.3.3 Chapter 3: Heterogeneity and logging

Although deforestation for the purposes of agriculture can be the death knell for primary tropical forest, forests are usually first degraded through unsustainable timber and wood harvest. In Chapter 3, I investigate spatial and temporal heterogeneity in logged and unlogged forests. Forest management generally is organized at the level of fairly large cut-blocks, and thus research on logging effects tends to report aggregated impacts summarized across large spatial scales. However, disturbances during timber harvest generally occur at smaller spatial scales associated with selectively felled trees and skid trails associated with timber removal. Hence the trajectories of forest recovery can be complicated by small-scale variation in forest species composition and structure. I examined the influence of spatial variation in both pre-logging forest conditions and in response to different levels of logging intensity in Kibale. I used published results and older unpublished documentation and longitudinal data on forest composition collected in permanent study plots during 1989–2013 to explore patterns of small-scale spatial and temporal heterogeneity. Understanding spatial heterogeneity in forest compositional patterns and dynamics can help target sampling designs for data necessary to evaluate and improve conservation and management of tropical forests.

In this chapter, I address two research questions:

1. How do patterns of temporal heterogeneity and spatial heterogeneity differ among tree assemblages in lightly, moderately, and heavily logged forest, and unlogged forest?
2. What is the relative importance of natural and human disturbance in creating and maintaining forest heterogeneity?

1.3.4 Chapter 4: Synergies and trade-offs

A major challenge facing conservation biologists, restoration ecologists, and protected areas managers is to balance the needs of biodiversity conservation with pressures from local people for access to resources. In Chapter 4, I investigate how land-use and disturbance history affects synergies and trade-offs between tree diversity, animal habitat, and ecosystem services in regenerating and intact forests in Kibale. I collected data in sites with eight different disturbance histories: unlogged forest, forest regenerating after arboricide and/or a range of logging intensities, fire, and on harvested exotic timber plantations and abandoned farmland either planted or not planted with native tree species. Using data on animal diet preferences and human uses for different trees, I quantified and compared tree species diversity and the availability of animal food and ecosystem services in these sites.

In this chapter, I address four research questions:

1. How does tree species diversity vary in parts of Kibale with different land use histories?
2. How does the availability of primary and secondary foods for chimpanzees, elephants, and folivorous and frugivorous arboreal monkeys vary in parts of Kibale with different land use histories?
3. How does the availability of provisioning, cultural, and regulating ecosystem service indicators vary in parts of Kibale with different land use histories?
4. What are the synergies and trade-offs amongst these variables across differing land-use histories and degrees of disturbance?

The questions I address in my thesis fall within topics identified among the top 200 research questions in biodiversity conservation and ecology (Sutherland et al. 2009, 2013). It is my hope that this work will prove useful to managers responsible for Kibale National Park in Uganda, and may also hold some lessons of wider interest in biodiversity conservation and ecology.

2 EXOTIC LEGACY TREES FACILITATE NATIVE FOREST RECOVERY ON ABANDONED FARMLAND IN UGANDA

2.1 Abstract

Restoring forest on abandoned, formerly-forested farmland is an important factor in conserving tropical biodiversity. Abandoned farmland often contains isolated exotic trees that were planted by farmers for fruit or wood. Conservation and management plans often require removing these ‘legacy’ trees. However, exotic legacy trees might attract seed dispersers and/or create micro-climates favourable for establishment of native seedlings; therefore removing legacy trees could be unintentionally counterproductive to forest recovery.

I worked in abandoned farmland in Kibale National Park, Uganda, to evaluate the effects of non-native legacy trees on native forest regeneration. I measured the number, diversity, and dominance of native trees that regenerated directly under and near (20-50 m distance) avocado, mango, and eucalyptus trees, and compared these tree assemblages to those in unlogged native rainforests throughout the park. Plots under legacy trees, particularly fruit trees, had significantly more total stems and higher species richness than plots near legacy trees. Cumulative basal area of regenerating stems was also higher under fruit trees than under eucalyptus trees or near legacy trees. When compared to unlogged forests, tree assemblages under avocado trees were most similar to tree assemblages in *Parinari*-forest.

Overall, fruit legacy trees, particularly avocado, were important to recruitment of rare native tree species that are large-seeded, shade-tolerant, and animal-dispersed. Results of this study demonstrate that exotic legacy trees can act as recruitment foci for native tree species, and facilitate recovery of native forest on abandoned farmland. This process complements existing management strategies for restoration of forest cover in Kibale, such as tree planting and fire prevention. I caution against removing exotic trees from abandoned farmland without consideration of their effects on long-term regeneration of native forest.

Keywords: abandoned agriculture; applied nucleation; Kibale National Park; native trees; recruitment; regeneration; remnant trees; restoration; tropical rainforest

2.2 Introduction

Urbanization and agriculture are major drivers of tropical deforestation (DeFries et al. 2010, Gibbs et al. 2010, Kissinger et al. 2012), but the same factors drive the abandonment of recently cleared and cultivated land (Rey Benayas et al. 2007). The abandonment of farmland, a phenomenon projected to increase in the future (DeFries et al. 2010), is linked to unpredictable changes in landscape heterogeneity, biodiversity, ecosystem services, and fire frequency (Kappelle et al. 1995, Dunn 2004, Rey Benayas et al. 2007). Some view abandoned land as an opportunity to restore forest cover, conserve biodiversity, and enhance ecosystem services (Lamb et al. 2005, Navarro and Pereira 2012), potentially helping to alleviate poverty (Kettle 2012a). Because biodiversity hotspots often overlap with areas of high human population density (Luck et al. 2004, Cordeiro et al. 2007, Fisher and Christopher 2007, Luck 2007), restoring forest on abandoned farmland is a particularly important part of conservation.

The success of forest restoration depends on the type and intensity of past and present land use, timing since abandonment, landscape composition and configuration, and dispersal abilities of forest plants and animals (Lugo and Helmer 2004, Bowen et al. 2007, Rey Benayas et al. 2007, Chazdon 2008, Hobbs et al. 2009, Rey Benayas and Bullock 2012). Restoration of native forest requires removing factors that inhibit dispersal and establishment of tree species, such as harsh microclimates, high seed predation, and competition with aggressive shrubs or grasses (Somarriba 1988, Rhoades et al. 1998). Success also depends on maximizing the efficiency of expensive, slow, or labour intensive restoration activities (Lamb et al. 2005, Chazdon 2008).

The use of landscape features, such as isolated trees, as nodes of forest recovery is one strategy to increase restoration efficiency. Nodal forest recovery is also referred to as applied nucleation (Corbin and Holl 2012), and the nodes are referred to as biological legacies or regeneration nuclei (Guevara et al. 1986, Elmqvist et al. 2002), or recruitment, regeneration, and dispersal foci (McDonnell and Stiles 1983, Slocum 2001, Clark et al. 2004, Berens et al. 2008). Nodal forest recovery can make use of isolated native trees, or ‘remnant’ trees, which are sometimes left standing when the forest is cleared (‘remnant trees’, usually native; Guevara et al. 1986), as well as exotic trees, or ‘legacy’ trees, which are subsequently planted by farmers for fruit or wood. The majority of tropical forest tree species are animal-dispersed (Howe and

Smallwood 1982), and since isolated trees can provide safe perches, shade, and attractive sources of food (particularly trees with large fleshy fruits) for a variety of frugivorous birds and mammals (Harvey and Haber 1998, Tews et al. 2004), they have more frequent and longer visits by fruit dispersers, leading to elevated levels of seed rain under isolated forest trees. Hence isolated trees can act as recruitment foci by attracting seed dispersers (Guevara et al. 1986, Uhl 1987, Duncan and Chapman 1999, Slocum 2001, Guevara et al. 2004). Although the arrival of seeds does not necessarily lead to the germination and establishment of trees (Holl 1998, Reid and Holl 2012), the microclimate under isolated trees generally favours seedling germination and establishment more than the surrounding matrix (Uhl et al. 1982, Guevara et al. 1986, Guevara et al. 1992, Belsky et al. 1993, Carrière et al. 2002, Clark et al. 2004, Guevara et al. 2004, Berens et al. 2008, Cole et al. 2010, Zahawi et al. 2013), although some species may suppress regeneration (Struhsaker et al. 1989, D'Antonio and Meyerson 2002). Isolated trees also increase structural complexity and habitat connectivity at local and landscape scales; the effect isolated trees have on ecosystem functioning is much larger than the area and biomass of any single tree, leading to their identification as ‘keystone structure ecosystems’ (Tews et al. 2004, Manning et al. 2006).

Nodal forest recovery has been studied throughout the tropics in abandoned pastures (Guevara et al. 2004, Zahawi et al. 2013) and farmland (Eshiamwata et al. 2006, Berens et al. 2008), savannas (Belsky et al. 1993), and damaged rainforest (Elmqvist et al. 2002). However, most research on applied nucleation has been carried out in the Neotropics, and relatively little has been done in Africa with the exception of isolated trees in African savannah (Belsky et al. 1993, Tews et al. 2004), remnant trees in slash-and-burn agriculture in West Africa (Carrière et al. 2002), and legacy guava trees in Kenyan farmland (Berens et al. 2008)). Because Africa is the continent with the highest urbanization rate (Maseland et al. 2010), where population is projected to quadruple by 2100 (United Nations 2013), and where deforestation and forest degradation are predominantly driven by subsistence (Hosonuma et al. 2012, Kissinger et al. 2012), nodal forest recovery could be an especially valuable approach to restoration of African forests. Although nodal forest recovery has promise, we have little direct knowledge of how effective this restoration strategy might be over the long term either in Africa or elsewhere. Restoring forest structure and floral and faunal species composition can take decades or even centuries (Guariguata and Ostertag 2001, Chazdon 2003, Chazdon et al. 2009, Martin et al. 2013). One way to begin to assess long term efficacy of this restoration strategy is to compare the tree community regenerating beneath a legacy tree to that of nearby mature forest, assessing the trajectory of changes and focusing on tree species of particular interest.

I carried out such a study in Kibale National Park in western Uganda, which has both mature tropical rainforest and deforested areas that were in subsistence agriculture but are now abandoned (Struhsaker 1997, Chapman and Lambert 2000). During the 1970s and 1980s, upwards of 55,000 people illegally settled inside Kibale, cultivating and degrading over 140 km^2 of grassland and forest (19% of the park) until they were evicted in 1992 (Van Orsdol 1986, Chapman and Lambert 2000). Most of this former farmland is now tall grassland, much of which is being planted with native trees to sequester carbon (Face the Future; Omeja et al. 2011). Exotic trees remain in some areas, but the current policy of the Uganda Wildlife Authority (UWA) is to remove all exotic species, including the legacy trees, as part of its attempt to "*restore natural forest cover*" (UWA 2003). Studying nodal forest recovery in this situation provides a useful contrast with the efficacy of the tree planting project that may lead to a more diversified and cost-effective management strategy. Toward that end, I investigated the potential of avocado, mango, and eucalyptus legacy trees to serve as regeneration foci.

My research addressed four questions: How is the establishment of native forest trees on abandoned farmland influenced by 1) proximity to a legacy tree, 2) the species of legacy tree, 3) the dispersal mechanism of the forest tree, and 4) How do tree assemblages associated with legacy trees resemble or differ from those in nearby forests? Understanding how legacy trees affect recruitment of native trees, as an early stage in forest succession and recovery, is important to determining the effectiveness of nodal forest recovery as a conservation tool.

2.3 Methods

2.3.1 Study area

Kibale National Park (795 km^2) is a mid-altitude moist tropical rainforest in western Uganda (0˚13'–0˚41'N, 30˚19'–30˚32'E; Figure 2-1). There is a north-to-south gradient from high to low elevation, temperature, and rainfall, which is reflected in the change from evergreen and semi-deciduous forest in the north and center, to grasslands and woodlands in the southwest (Struhsaker 1997). Kibale lies within the Albertine Rift, a global biodiversity hotspot (Cordeiro et al. 2007) and one of the most densely human-populated areas in sub-Saharan Africa (Plumptre et al. 2004). Agricultural pressure around the park is the second highest of all protected areas in Uganda (Hartley et al. 2010). Most farms in the region are small (< 5 ha) and grow a variety of subsistence crops (*e.g.,* bananas, beans, cassava, groundnuts, maize, yams) and some exotic fruits such as avocado, mango, guava, and papaya. *Eucalyptus* species are the most common locally grown source of firewood and timber (personal observation).

In the early 1900s, a combination of tribal conflict, disease, and livestock depredation caused people to abandon homesteads on grassy hills in Kibale (Osmaston 1959, Lang Brown and Harrop 1962). In 1926, the British Protectorate Government designated the southwestern part of Kibale as a Game Corridor managed for controlled hunting (Ryan and Hartter 2012). In 1932, the northern, central, and southeastern parts of Kibale were designated as a Forest Reserve, and managed for commercial timber extraction. Land cover in the game corridor was estimated as 61% grassland and 39% forest (Ryan and Hartter 2012); the forest reserve was estimated as 60% forest, interspersed with grassland, woodland-thicket, and recolonizing forest (Wing and Buss 1970). The game corridor and forest reserve were joined when Kibale was upgraded to national park status in 1993. Over time, the park has had a progressive loss of grassland and an increase in native forest, primarily due to fire prevention (Chapman and Lambert 2000) and intensive reforestation (Omeja et al. 2011). At present, the park is 74% unlogged and regenerating forest, 15% bare and short grasses, 6% tall grasses, 4% wetland, and 1% shrubs (Jacob et al. 2014a).

The present study was conducted in a five km^2 of abandoned farmland in west-central Kibale (average elevation, 1450 m a.s.l.; Figures 2-1 and 2-2), where grassy hilltops and hillsides were cultivated, and forested valleys were degraded from the early 1970s until 1992 (Hamilton 1984, Chapman and Lambert 2000). Intermittent fire prevention has allowed native forest to start re-colonizing some of the grassy areas adjacent to forest. Dominant grasses include *Pennisetum purpureum* (elephant grass)*, Imperata cylindrica,* and *Cymbopogon afronardus.* The most common medium to large native grassland trees are fire-resistant *Acacia sieberana* and *Erythrina abyssinica*.

2.3.2 Legacy trees

The most common legacy trees in the study area are *Persea americana* (avocado), *Mangifera indica* (mango), and species of *Eucalyptus*. Avocado and mango are large-fruited, large-seeded trees native to Mexico and India, respectively. Avocado was introduced to East Africa in the 1800s and mango likely several centuries before. In Kibale, their seeds are dispersed by people and large animals, including chimpanzees and elephants. Eucalyptus seeds are held in woody capsules that have no special dispersal mechanisms (Calviño-Cancela and Rubido-Bará 2013). Mango and eucalyptus have an allelopathic effect on some plants (Sahoo et al. 2010, Dessie and Erkossa 2011), although subsistence farmers in Africa also use mango leaves for mulch (Musvoto et al. 2000, Orwa et al. 2009).

2.3.3 Data collection

From July 2010 to December 2011 and during follow-up work in April 2013, we located avocado (n = 11), mango (n = 9), and eucalyptus (n = 15) legacy trees on abandoned farmland in the study area. Sampling was limited to trees ≥ 15 cm diameter at ground height (DGH), based on local reports that this was the minimum size capable of producing fruit (A. Jacob unpublished data). The location of each legacy tree was mapped using a handheld GPS. The height of each legacy tree was estimated, and diameters at breast and ground height (DBH and DGH, with DBH measured at 1.2 m above the ground) were measured.

Seedling recruitment was determined in 10 m radius circular plots around each legacy tree ("legacy plots"). Legacy plots with multiple legacy trees of the same species were included in the sample, but legacy plots with mixed species ≥ 15 cm DGH were excluded. Legacy plots around recently cut legacy trees were included, as long as species identification and diameter measurements were still possible. All live seedlings, saplings, and trees (hereafter called "regenerating stems") within each legacy plot were identified to species level, where possible (Hamilton 1981, Katende et al. 1995). Voucher specimens of unknown species were identified by the Makerere University Herbarium in Kampala. Height, DGH, and DBH (where regenerating tree was tall enough) were measured or estimated for all regenerating stems. To assess how legacy trees affect nearby recruitment, regenerating stems were also sampled in paired "near-legacy" plots, located at a random compass bearing and distance, between 20 and 50 m from each legacy tree. Near-legacy plots were excluded if they contained fruit or eucalyptus legacy trees ≥ 15 cm DGH, or if the center of the plot was within 20 m of another legacy tree.

Tree assemblages in legacy and near-legacy plots were compared to assemblages at three unlogged forest sites spread throughout Kibale, locally known as Dura, K30, and Mainaro and located approximately 5, 10, and 12 km from the legacy tree study area (Figure 2-1). These sites have canopies > 30 m high with several subcanopy levels (Hamilton 1984), with similar topography and soils (Lang Brown and Harrop 1962). K30 (1500 m a. s. l) is a forestry compartment that was set aside from logging as a nature reserve in 1973 (Struhsaker 1997). This forestry compartment contains forest dominated by *Parinari excelsa* Sabine (forest type K2 unknown subtypes; Appendix 3) (Osmaston 1959, Hamilton 1984). K30 is often considered mature, old-growth, or pristine forest (Osmaston 1959, Hamilton 1984, Struhsaker 1997, Chapman and Lambert 2000), although a localized disturbance might have occurred in part of the compartment in the last several hundred years (see Chapter 2 and Chapman et al. 2010a). Dura (1250 m a. s. l.) contains mixed *Celtis-Chrysophyllum* forest (forest type K3) and *Pterygota* forest (forest type K4) (Osmaston 1959, Uganda Forest Department 1960, Hamilton 1984). Mainaro (1200 m a. s. l.) contains *Pterygota* forest (forest type K4) and *Cynometra* forest (forest type K6) Local pit-sawyers removed a few large trees from each site prior to 1970 (1-4 trees/km^2), but had little effect on the forest (Struhsaker 1997, Chapman and Lambert 2000).

I searched published literature to determined dispersal mechanism, successional status, guild, and habitat affinity for all trees in the legacy study area and unlogged forest, with specific focus on reports from Kibale, within Uganda, or elsewhere in Africa (Eggeling and Dale 1951, Hamilton 1981, Synnott 1985, Hawthorne 1995, Katende et al. 1995, Lwanga 1996, Maundu and Tengnäs 2005, Orwa et al. 2009, Beentje 2012, Lemmens et al. 2012) (Table 2-2). Native forest species were those identified by Lwanga (1996) as *forest-dependent* (occurring in the forest interior, forest edge, dry forest, and/or riverine/lakeshore forest) and or *forest non-dependent* (occurring in at least one of the above forest habitats as well as at least one non-forest habitat: woodland, grassland, rocky places, bush/thickets, dry scrub, swamp, and/or moorland). I restricted my analysis to species that occur only in forest, excluding the non-dependent species because their occurrence in grassland and scrub might be a poor indicator of long term trends favouring restoration of rainforest. For the same reason I also removed six exotic species of regenerating stems from the analysis.

2.3.4 Data analysis

I used the packages `BiodiversityR` (Kindt and Coe 2005) and `vegan` (Oksanen et al. 2013) in the software R (R Development Core Team 2013) to calculate five variables for regenerating stems in each plot: stem frequency, cumulative basal area, species richness (S), Shannon index (Shannon-Wiener index, H'). I also used these packages to calculate Chao diversity and create rarefied species accumulation curves for each treatment category (*i.e.,* legacy and non-legacy plots, fruit and non-fruit plots, etc.). Although species richness remains the most common measure of success in restoring or conserving degraded ecosystems (Gotelli and Colwell 2011), it does not include other aspects of biodiversity such as species composition and abundance. These are important characteristics of any community, which affect intra- and inter-specific interactions and ecosystem function (Zhang et al. 2012). Furthermore, it is difficult to accurately estimate species richness in complex systems with high diversity such as tropical rainforest (Gotelli and Colwell 2001). However, although the Shannon index take species abundances into account (giving more weight to rare than common species, Magurran 2004), this measure is actually an entropy and not a true measure of diversity (Jost 2006, Ellison 2010). I therefore used the 'effective number of species' (also called 'equivalent number of species' or Hill number) to compare species diversity among plots. Effective numbers represent the number of species present if all were equally common (Jost 2006). I calculated the effective number of species based on Shannon entropy as $HE=\exp(H')$ (Jost 2006).

Mean and standard deviation were calculated for each variable. I used non-parametric Kruskal-Wallis tests and multiple comparison post-hoc tests in the R package `pgirmess` (Giraudoux 2008) to determine if tree regeneration was significantly affected by proximity to a legacy tree (legacy plots vs. near-legacy plots), legacy tree type (fruit tree vs. wood tree), or legacy tree species (avocado vs. mango vs. eucalyptus). The same tests were run using regenerating tree data divided by seed-dispersal mechanism: non-animal (*e.g.,* wind, gravity, ballistic) vs. animal (*e.g.,* birds, primates, elephants). Statistical significance of differences was accepted at $p < 0.05$, but results with $p < 0.10$ were considered to be biologically relevant.

I used individual-based rarefaction curves to estimate the average rate of species accumulation in legacy and near-legacy tree plots (Gotelli and Colwell 2001). Rarefaction is useful for datasets with unequal sampling effort, as it allows the user to investigate the expected species richness of a community in a random, equal-sized sample of individuals or samples (Magurran 2004). The evenness of distribution of species in communities can be evaluated by comparing the steepness of the curve, where steeper curves indicate higher heterogeneity. To understand how species relative abundance and dominance are affected by proximity to, and type of, legacy tree, I created rank/abundance curves for the regenerating tree communities in fruit, wood, and respective near-legacy plots (Magurran 2004). I plotted the abundance of each species on a log scale versus the species rank, ordered from the most to the least abundant.

I tallied the presence or absence of forest tree species regenerating in legacy and near-legacy plots and compared it to those of the three unlogged forests. Presence-absence data emphasizes species' identity which allows infrequent species to play a significant role in the comparison. I used the Sørensen similarity index (Magurran 2004) to assess the similarity of tree communities in the legacy and near-legacy plots compared to the three unlogged forests. All similarity indices measure variations of three parameters: the species composition in each of two sites, and the number of species shared between the two sites. The Sørensen index weights all species equally and measures the proportion of species shared between two sites, using the equation: $2ab/(a + b)$ where a is the number of species found at site A, b is the number of species found at site B, and ab is the number of shared species (Magurran 2004). Similarity values close to 1 indicate few differences between sites.

2.4 Results

2.4.1 Proximity to and differences between legacy tree species

After excluding unidentified, exotic, and non-forest tree species, the dataset contained 3808 stems of 63 species of regenerating stems (Table 2-1). Legacy plots had 50% more regenerating stems than near-legacy plots (H=4.93, df=1, *p*=0.026), and around 50% more species, although the difference was not significant (H=3.16, df=1, *p*=0.075) (Table 2-2, Figure 2-3). Species richness and cumulative basal area were significantly higher in fruit legacy plots than in eucalyptus plots (H=7.88, df=3, *p*=0.048 and H=12.53, df=3, p=0.006, respectively). Both variables were highest in avocado and lowest in near-eucalyptus plots. The effective number of species and Chao diversity were also highest in avocado plots.

Both individual-based and sample-based rarefaction curves showed higher rates of species accumulation in fruit plots than in near-fruit, eucalyptus, or near-eucalyptus plots (Figure 2-4). Rank-abundance curves indicated few abundant and many rare species in the samples, especially for fruit legacy plots (Figure 2-5). Dominance patterns were fairly consistent among fruit, eucalyptus, and near-legacy plots (Table 2-3): the five overall dominant species (*Shirakiopsis elliptica, Ficus asperifolia, Prunus africana, Clausena anisata*, and *Alibizia glaberrima*) were among the eight most-dominant species in each plot type. However, patterns of rare species differed among plot types: 14 species, including one pioneer species, occurred only in fruit plots; two species (no pioneer species) occurred in eucalyptus and near-eucalyptus plots; no species occurred only in near-fruit plots (Table 2-1). Many of these rare species included saplings up to 7 cm DBH, *i.e.,* were well established.

I found many avocado, relatively few mango, and no eucalyptus regenerating stems in the study area (n=710). Of these, 81% were in avocado (n=576), 9% in mango (n=67), <1% in eucalyptus legacy plots (n=6). Only 9% were found in near-avocado, near-mango, and near-eucalyptus plots (n=25, n=9, and n=27). I found far fewer mango seedlings (n=51). Of these, 86% were in mango legacy plots (n=44 in mango, n=6 in avocado, and n=1 in non-legacy plots).

2.4.2 Effects of seed dispersal mechanism on regenerating stems in legacy and near-legacy plots

The five wind-dispersed, forest-dependent tree species (Table 2-1) regenerated equally well in legacy and near-legacy plots. However, 79–90% of the species in legacy plots were animal-dispersed, especially in fruit legacy plots (avocado, 85%; mango, 90%). In near-legacy plots, the highest numbers of stems and species of animal-dispersed trees occurred near avocado legacy trees, and fewest near eucalyptus legacy trees (H=13.7, df=5, p=0.017, and H=12.3, df=5, p=0.031, respectively). Legacy plots had four times more trees dispersed by elephants than non-legacy plots, and seven times more trees dispersed by black-and-white casqued hornbills (*Bycanistes subcylindricus subquadratus*) (Kalina 1988). Tree species with fruits eaten by hornbills accounted for 21% and 18% of total stems in avocado and mango legacy plots, respectively, but only 10% and 4% in the respective near-legacy plots. Eucalyptus and near-eucalyptus plots showed the opposite pattern – lower in legacy than in near-legacy plots (10% and 17%, respectively).

Stems of *Ficus* spp. were twice as frequent in legacy plots as in near-legacy plots (415 vs. 250). The size of regenerating *Ficus* trees did not differ between fruit and near-fruit plots, but stems ≥ 1.0 cm DBH were twice as frequent in eucalyptus as in near-eucalyptus plots, perhaps suggesting that allelopathy from eucalyptus does not affect the growth of young fig trees. *Ficus asperifolia*, a shade-bearing species whose fruits are commonly eaten by primates and birds in Kibale, was the most common regenerating tree in fruit legacy plots, second most common in near-fruit legacy plots, and sixth most common in eucalyptus and near-eucalyptus plots.

2.4.3 Similarity to unlogged forest

Of the three unlogged forest areas, Dura is closest to the legacy study area while K30 and Mainaro are likely the youngest and oldest forests (see Appendix 3 for forest types). Previous research on adult trees shows that Mainaro has the lowest tree species richness and stem density (Chapman et al. 1997). Overall, I found 23 species in the three unlogged forests that were not found in legacy or near-legacy plots, and 12 species recorded in legacy or near-legacy plots were not found in the three unlogged forests (Table 2-1). Twenty-four tree species that occurred in K30 were not found in either Dura or Mainaro. Eight of these species occurred in avocado and/or mango plots, but not in eucalyptus plots or any near-legacy plots. The tree assemblage in K30 was most similar to that in Dura, and the assemblage in Dura was most similar to that in Mainaro (Table 2-4).

Pooled assemblages in legacy and near-legacy plots were more similar to each other than to those in the three unlogged forests. However, when compared to the unlogged forests, pooled assemblages of legacy and near-legacy plots were most similar to K30 and least similar to Dura. Assemblages pooled for the three unlogged forests were most similar to assemblages in avocado plots and least similar to eucalyptus plots. For avocado and mango, legacy plots were more similar to unlogged forest than near-legacy plots. For eucalyptus, near-legacy plots were more similar to unlogged forest than legacy plots.

2.5 Discussion

The overall results of the present study demonstrate that exotic legacy trees, especially fruit trees, can facilitate restoration of native rainforest trees on abandoned farmland in Africa. Although most legacy trees are relatively far from the edge of intact forest, they attract frugivorous animals, which disperse the seeds of native trees into the impacted area. Microclimatic conditions under the legacy trees can then provide suitable growing conditions. These effects are particularly important for large-seeded, shade-tolerant species. Similarity between sapling assemblages, particularly in avocado plots, and unlogged forest suggest that succession in legacy plots will eventually lead to tree assemblages similar to native forest. These overall results suggest that the nucleation effects often studied on abandoned pasture and farmland in Neotropical forests (Guevara et al. 2004, Eshiamwata et al. 2006, Berens et al. 2008, Zahawi et al. 2013) may apply more generally in Africa, where the topic has received comparatively little study (but see Belsky et al. 1993, Tews et al. 2004 for effects of isolated trees in savannah). That said, there is a rich level of site-specific detail in the results that needs to be considered in deciding management strategies for both forest restoration and wildlife management in Kibale.

2.5.1 Legacy effects in Kibale National Park

There were significantly more regenerating tree stems, species, and diversity in legacy plots, especially avocado and mango plots, than in near-legacy plots. Legacy plots also had more stems and species of animal-dispersed trees, and this partly explains the overall positive influence of legacy trees. The high fat content of avocado fruits make them attractive to specialized frugivores (Gautier-Hion et al. 1985, Guevara et al. 1986), which could account for the relatively high frequency of elephant- and hornbill-dispersed seeds in avocado plots. [High sugar content of some fruits, including mango, might also be a factor in attracting frugivores (Gautier-Hion et al. 1985, Levey 1987). However, high sugar content also increases the susceptibility of fruit to insect and microbial attack, thereby reducing seed viability. Furthermore, it is unlikely that any animal but elephants, and perhaps chimpanzees, is large enough to effectively disperse mango seeds.] All but one of the fourteen species found exclusively in fruit legacy plots were late successional species, and several had very large seeds (≥ 20 mm) that could only be dispersed by animals. This result, and a number of species-specific examples, demonstrate the interaction between fruit legacy trees and animal seed-dispersers critical for recruiting large-seeded and late-successional tree species. For example, *Balanites wilsoniana* is a large-seeded, late successional tree that depends on elephants for dispersal (Cochrane 2003, Babweteera et al. 2007) and was only found in mango legacy plots. *Coffea* spp. and *Chionanthus africanus* are both shade-tolerant species dispersed by frugivorous birds and primates (Table 2-1) and were only found in fruit plots. So too were seedlings of *Pterygota mildbraedii* (a shade-tolerant, wind-dispersed species that is an important food for chimpanzees). The dense shade under avocado and mango trees could perhaps encourage the growth of these four species. More *Kigelia africana, Cola gigantea,* and *Monodora myristica* (all large-seeded, animal-dispersed species, the latter two shade-tolerant) were found in fruit than in near-fruit plots. The highest number of *Celtis gomphophylla* stems was found in avocado plots; this species is arguably the most important food tree for primates in Kibale and is eaten by at least seven diurnal primates (chimpanzee, baboon, black-and-white colobus, red colobus, blue monkey, grey-cheeked mangabey, and red-tailed monkey, as well as birds) and makes up more than 4% of the diet of the five arboreal monkeys (C. Chapman, unpublished data). Finding 90% of *C. gomphophylla* stems in legacy plots (n=116; mainly in avocado plots), a third of which had grown to at least 1.0 cm DBH, points to higher visitation from frugivores (birds and/or primates) as well as survival past the seedling stage.

My results support some results of previous work on the role of isolated trees in native forest regeneration in Kibale. Working in grasslands in central Kibale near Ngogo (Appendix 2), Majid et al. (2011) studied regenerating stems under and near the canopies of the native, fire-resistant trees *Erythrina abyssinica* and *Acacia sieberiana* (Majid et al. 2011). They too found greater species number, diversity, and abundance under nurse trees than nearby, that one nurse species (*Acacia*) was a better recruiter than the other (*Erythrina*), and that vertebrate seed dispersers played a large role in this regeneration.

2.5.2 Legacy effects as a function of proximity to intact forest

It seems reasonable to expect more seeds of forest tree species dispersed close to intact forest than in neighbouring treeless areas, and thus higher number of stems and species, but empirical support for this is mixed (Guevara et al. 1986, Duncan and Chapman 1999, Holl 1999, Slocum and Horvitz 2000, Cubiña and Aide 2001, Majid et al. 2011). I found a weak, though significant relationship between the species richness and stem frequency of plots and the distance to intact forest at the approximate time of abandonment (land cover data from Uganda Forest Department

2002). Frugivores in my study area differ in the distance or time of day they will venture away from forest. Elephants travel unimpeded throughout the study area at day and night. Large, fairly terrestrial primates like chimpanzees and baboons range widely throughout grassland and are regularly seen in the abandoned farmland (A. Jacob, personal observation) but return to the forest at night to sleep. Since small, more arboreal monkeys will only travel short distances on the ground, I do not expect them to disperse seeds far from the forest edge. I assume local fruit-eating bats (*i.e., Hypsignathus monstrosus* and *Epomops franqueti*) visit the avocado and mango legacy trees to feed on fruit, but disperse only small seeds (mainly Ficus spp., Duncan and Chapman 1999). Given that the average legacy tree is 600 m from forest, the vector of seed dispersal, and thus the community of regenerating stems, likely changes across the landscape.

Some of my results contrast with Majid et al. 's (2011) research on isolated grassland trees. However, they determined that crown size of nurse trees had a greater influence than distance to forest. At least two reasons might account for differences between our two studies. First, frugivorous seed dispersers reap greater nutritional rewards from visiting fruit legacy trees compared *Erythrina* or *Acacia* (see Eshiamwata et al. 2006, and Berens et al. 2008 for discussion how figs (Ficus spp.) and guava (Psidium spp.) trees attract frugivorous forest birds into Kenyan farmland). Second, since legacy trees are significantly taller than *Erythrina* or *Acacia* (each grows to a maximum height of 12 m though generally much shorter), they are more visible emerging above tall grassland and therefore more attractive as perches. Together, our studies provide compelling reasons for researchers and managers to focus more attention on the roles isolated trees play in restoring forest.

2.5.3 Composition of legacy sites with unlogged forests

Comparing tree assemblages regenerating under or near legacy trees to assemblages in unlogged forest allows evaluation of the success of forest restoration. Effective restoration strategies requires monitoring and comparing ecosystem recovery to a quantifiable endpoint (a 'reference state', SER 2004), enabling adaptive management. My comparison indicated that the trajectories of forest recovery in avocado plots and near-avocado plots were most similar to the assemblage at K30. A third of the tree species found in K30 – but neither Dura nor Mainaro – were found in fruit plots, but neither eucalyptus nor near-fruit plots. Of the three forests, one might have reasonably expected the Dura tree community to be most similar to the legacy plots since it is the closest (six km, Figure 2-1). However, K30 is not only at more similar elevation (a proxy for rainfall) to the legacy plots, but evidence on tree density, species diversity, and population dynamics (Chapman et al. 1997, Chapman et al. 2010a) indicates it has a more recent disturbance history (also see Chapter 3). Thus, the tree assemblage in K30 is perhaps at an earlier successional stage than Dura or Mainaro. Although some gap specialist tree species have declined at K30 during the past 18 years (notably C. gomphophylla, Chapman et al. 2010a) seven of the ten most abundant gap specialist species Chapman et al. (2010) identified in K30 are among the ten most abundant species identified in my fruit legacy plots. Although forest recovery likely takes many decades or centuries, if the patterns of seed dispersal and germination I observed continue and are combined with consistent fire prevention, I anticipate the assemblage of forest tree species in fruit plots will become increasingly similar to K30.

2.5.4 Potentially adverse legacy effects

Although it is clear that legacy trees can facilitate recruitment, and possibly survival and growth, of forest trees, legacy plots also accumulate seedlings of the exotic legacy species. I found many avocado, few mango, and no eucalyptus seedlings in the study area; the majority of such seedlings were in conspecific legacy plots (likely the parent tree). Mango trees are shade-intolerant (Thompson et al. 2007), and their seedlings might not survive well in the heavy shade of the parent tree. I did not find any eucalyptus seedlings. Thus, mango and eucalyptus recruitment appears to have little influence on local forest regeneration. Avocado trees have slow maturation time (Gardener et al. 2013) and seeds do not have long dormancy periods (Itow 2003). Seeds are capable of germinating in both shade and sun (Itow 2003), and, although seedlings are shade tolerant (Itow 2003), they may require light to for maximal growth, flowering, and fruit production (Wolstenholme and Whiley 1999). Although avocado seedlings were numerous under conspecific trees, light under the dense canopy might be insufficient for seedlings to recruit into larger size classes and reproduce (Itow 2003). It is unclear if removal of mature avocado trees could unintentionally increase avocado seedling growth and survival. On the other hand, increased light following legacy tree removal might allow aggressive grasses, like *P. purpureum,* to out-compete both legacy and native seedlings.

However, given some experiences with non-native species in other locations, it is understandable that removing legacy trees from the encroached area has been identified as a near-term restoration goal for Kibale managers (UWA 2003). For instance, non-native species are reportedly the second greatest threat to native species in the United States (Ewel and Putz 2004). More specific to tropical forest restoration, in Puerto Rico invasive alien tree species can form mono-dominant stands on degraded and abandoned land, effectively preventing colonization by native tree species for several decades (Lugo 2004). However, the presence of non-native plants is not necessarily antithetical to ecosystem restoration. In situations where non-native species have benign effects, funds and energy dedicated to their removal might be redirected to other conservation activities. In situations where non-native species actually benefit ecosystem restoration, as may be the case with the legacy trees in this study, their removal may be counter-productive (Ewel and Putz 2004). Further research is needed to determine the effects of legacy tree removal on local tree assemblages. In particular, future work should focus on the longer-term growth and survival of the regenerating stems, particularly avocados and late-successional native tree species, with and without removal of legacy trees. Since 91% of regenerating stems of legacy trees were found in legacy plots, logistics required to study of growth and survival of legacy tree seedlings and saplings would not be prohibitive. A cost-benefit analysis of removing legacy trees must weigh the ecological risks of immediate or delayed action versus inaction, including both the probability and magnitude of facilitating or hindering native forest regeneration at local and landscape levels (Ewel and Putz 2004, Lugo 2004).

2.5.5 Legacy effects compared to alternative management strategies

Developing low-cost alternative strategies to increase forest cover is a current management priority for Kibale park managers (UWA 2003). Three approaches have been or are currently used: 1) preventing fire by clearing large swaths of vegetation in grasslands, and planting fast-growing 2) native and 3) non-native tree species (Lwanga 2003, Omeja et al. 2011, Omeja et al. 2012). Since Kibale was upgraded to national park status in 1993, only native tree species are used in restoration planting (UWA 2003).

When Kibale grasslands were consistently protected from fire, they accumulated high diversity of woody species and high aboveground biomass (Lwanga 2003, Omeja et al. 2011). In fact, woody biomass was twice as high in grassland protected from fire for 32 years than in abandoned farmland planted with native trees 10-15 years prior (Omeja et al. 2011). The cost is around \$500/km^2/yr for fire prevention, and at least US\$120,000/km^2/yr for planting and maintaining trees (Omeja et al. 2012). Although a considerable body of research exists on the role of isolated trees in tropical forest regeneration (Guevara et al. 1986, Rhoades et al. 1998, Toh et al. 1999, Slocum 2001, Carrière et al. 2002, Elmqvist et al. 2002, Berens et al. 2008, Corbin and Holl 2012), including work in Kibale (Majid et al. 2011), current Kibale park policy requires removal of non-native species, including "*all exotic species left from the encroachment*" (UWA 2003). However, leaving legacy fruit trees as regeneration foci may complement existing strategies to restore forest on the abandoned farmland, especially if fire prevention efforts were focused around clusters of legacy trees. Not only do the results demonstrate that legacy trees can facilitate native forest regeneration on former farmlands, but isolated trees have been shown to have a disproportionately large effect on forest restoration in grasslands in Kibale (Majid et al. 2011). Legacy trees accelerate forest restoration by increasing biodiversity and facilitating the recruitment of diverse functional groups – species associated with early and late successional stages, species with small- and large-seeded fruits, species with fleshy and non-fleshy fruits, etc. These effects accelerate the recovery of ecosystem processes and function (Montoya et al. 2012, Verdú et al. 2012).

Intensified agricultural management and natural mortality are predicted to cause most isolated trees to disappear from many agricultural landscapes within the next 200 years (Gibbons et al. 2008). In Kibale, removal of rapidly spreading invasive legacy trees, such as *Senna spectabilis*, is certainly prudent (UWA 2003), but the role of legacy trees in forest restoration demonstrated by the present study argues against a blanket approach to their management (Ewel and Putz 2004). If the UWA ultimately decides to remove all legacy trees, restoration managers should consider using recruitment foci as a strategy. Such foci might include logs (Slocum 2000), rocks (Carlucci et al. 2011), termite mounds (Støen et al. 2013), patches of shrubs (Corbin and Holl 2012) and tree islands (Cole et al. 2010). Tall native trees with high-quality and fleshy fruits that are particularly attractive to frugivorous seed dispersers likely to bring seeds of native tree species would also serve as effective regeneration foci. In places where enrichment planting is desired, for instance far from forest or where land was badly degraded, it is suggested that managers first plant dominant tree species of key functional groups and then increase ecological redundancy by adding species that vary in traits (Montoya et al. 2012). In addition, there is some evidence that increased differences in life-form and phylogenetic distance between the focal/nurse tree and the regenerating/facilitated trees will increase restoration success (Verdú et al. 2012). Maximizing the effect of existing, natural successional processes will free scarce financial and logistical resources to be concentrated on fire prevention and tree planting to increase habitat connectivity. Based on these results, management strategies for restoration of impacted farmland in Africa should incorporate maintenance of at least some species of legacy trees.

2.6 Tables and figures

2.6.1 Table captions

Table 2-1. Forest tree species regenerating in legacy and near-legacy plots and three unlogged forests.

Table 2-2. Forest structure and diversity measures in legacy and near-legacy plots. Values are the mean for each category with standard errors in parentheses. Trees in the analyses are native, forest-dependent species regenerating in the respective plots.

Table 2-3. Rank abundance of regenerating tree species in legacy and near-legacy plots.

Table 2-4. Similarity of tree assemblages among three unlogged forests and legacy and near-legacy plots. The Sørenson similarity index weights all species equally and measures the proportion of species shared between pairs of sites. Similarity values close to 1 indicate a high degree of similarity (*i.e.,* few differences) between sites.

Table 2-1. Forest tree species regenerating in legacy plots, near-legacy plots, and three unlogged forests

						Unlogged forest			Legacy and near-legacy plots					
Species	Family	Habitat affinity[a]	Forest depend. [b]	Guild[c]	Dispersal[d]	K30	Dura	Mainaro	Avo	Near avo	Mango	Near mango	Euc	Near euc
Albizia glaberimma	LEGU	F	FF	npld	w				yes	yes	yes	yes	yes	yes
Albizia grandibracteata	LEGU	F,r,g,f	Fn	npld	w			yes	yes	yes			yes	
Albizia gummifera	LEGU	F,f,r	FF	npld	w				yes	yes			yes	yes
Alangium chinense	CORN	f	FF	p	bi				yes		yes		yes	
Allophylus spp.	SAPI	F	FF/Fn	sb	bi								yes	
Antiaris toxicaria	MORA	F,wo,r	Fn	npld	ba, bi, oa, p	yes			yes	yes			yes	yes
Balanites wilsoniana	ZYGO	F	FF	npld	e		yes				yes			
Beilschmiedia ugandensis	LAUR	F,sw,r	Fn	sb	ba, bi	yes								
Blighia unijugata	SAPI	f	FF	sb	bi, e, p	yes			yes	yes	yes	yes	yes	yes
Baphiopsis parviflora	LEGU	F,sw	Fn	sb	p		yes	yes						
Bersama abyssinica	MELI	F,wo,g,t,r	Fn	p	bi				yes	yes	yes	yes	yes	yes
Craibia brownii	LEGU	F,r	FF	sb	w		yes	yes						
Cordia spp.	BORG	F, f, t, wo	FF/Fn	p	u	yes								
Celtis africana	CANN	F,df,r	FF	p	ba, bi, p	yes		yes	yes	yes	yes	yes	yes	yes
Celtis gomphophylla	CANN	F	FF	npld	bi, e, p	yes	yes	yes	yes	yes	yes	yes	yes	yes
Celtis mildbraedii	CANN	F	FF	sb	bi, p			yes						
Coffea spp.	RUBI	F	FF	sb	bi, g, p	yes			yes		yes			
Chaetachme aristata	ULMA	f,r	FF	p	bi, e, p	yes	yes		yes		yes			yes
Chionanthus africanus	OLEA	F	FF	sb	p	yes	yes	yes	yes		yes			
Clausena anisata	RUTA	f,t,wo	Fn	p	bi				yes	yes	yes	yes	yes	yes
Croton spp.	EUPH	F, f, ro	FF	npld	p			yes	yes	yes	yes		yes	yes
Cola gigantea	MALV	F	FF	sb	bi, p		yes		yes	yes			yes	yes
Cassipourea ruwensorensis	RHIZ	F	FF	sb	bi, p	yes	yes	yes	yes					
Chrysophyllum spp.	SAPO	F	FF	sb	ba, bi, e, p	yes	yes	yes	yes					
Casearia spp.	SALI	F	FF	p	p			yes						
Citropsis articulata	RUTA	F	FF	sb	bi	yes								
Cynometra alexandri	LEGU	Ud[b]	Ud	sb	w			yes						
Dasylepis eggelingii	ACHA	F	FF	sb	e, p	yes	yes	yes	yes					
Dombeya mukole	MALV	f	FF	npld	w				yes			yes	yes	
Diospyros abyssinica	EBEN	F,f,df	FF	p	bi, p, e	yes	yes	yes	yes	yes	yes	yes	yes	yes

						Unlogged forest			Legacy and near-legacy plots					
Species	Family	Habitat affinity^{a}	Forest depend. ^{b}	Guild^{c}	Dispersal^{d}	K30	Dura	Mainaro	Avo	Near avo	Mango	Near mango	Euc	Near euc
Dracaena spp.	ASPA	F, f	FF	sb	bi				yes					
Dovyalis spp.	SALI	F, df, wo,	Fn	npld	p	yes			yes		yes	yes		
Drypetes gerrardii	PUTR	F,r,ro	Fn	sb	ba, bi, p	yes	yes							
Ehretia cymosa	BORA	F,t,g	Fn	p	bi, p				yes					
Englerophytum oblanceolatum	SAPO	F	FF	sb	bi, p		yes	yes						
Fagaropsis angolensis	RUTA	F,df,f	FF	npld	bi	yes	yes							
Ficus asperifolia	MORA	F,wo,f,r	Fn	sb	bi, p	yes			yes	yes	yes	yes	yes	yes
Ficus conraui	MORA	F	FF	npld	bi, p	yes								
Ficus exasperata	MORA	F,f,ro,r	Fn	p	p	yes								
Ficus natalensis	MORA	F,r,wo	Fn	npld	ba, bi, e, oa, p							yes	yes	
Ficus sansibarica	MORA	F,r	FF	sb	bi, p						yes			
Ficus sp.	MORA	-^{e}	FF/Fn	-^{e}	u (likely p)						yes	yes		
Ficus saussureana	MORA	F,f,r	FF	sw	bi, p			yes						
Ficus sur	MORA	F,r,wo	Fn	p	ba, bi, p			yes	yes		yes	yes	yes	yes
Ficus thonningii	MORA	F,wo,r,ro	Fn	npld	bi, oa, p						yes			yes
Funtumia africana	APOC	F	FF	npld	w	yes	yes	yes	yes	yes	yes	yes	yes	yes
Harrisonia abyssinica	RUTA	F	FF	npld	bi, p		yes	yes						
Ilex mitis	AQUI	F,df,t	Fn	npld	bi	yes								
Kigelia africana	BIGN	F,sw,wo	Fn	npld	e, p	yes			yes	yes	yes			yes
Leptonychia mildbraedii	MALV	F	FF	sb	bi	yes	yes	yes						
Lindackeria spp.	ACHA	F,f	FF	sb	bi, p	yes								
Lovoa spp.	MELI	F, ro	FF	sb	w	yes	yes	yes		yes				yes
Lepisanthes senegalensis	SAPI	Ud^{e}	Ud	sb	e, p	yes	yes	yes	yes	yes	yes	yes	yes	yes
Lychnodiscus cerospermus	SAPI	F	FF	sb	bi, u	yes	yes	yes						
Macaranga schweinfurthii	EUPH	F,r	FF	p	bi, p, w						yes			
Millettia dura	LEGU	f	FF	npld	w	yes			yes	yes	yes	yes	yes	yes
Mimusops bagshawei	ACAN	F	FF	sb	bi, e, oa, p	yes	yes	yes			yes	yes	yes	
Monodora myristica	ANNO	F,r	FF	sb	bi, e, p, ua	yes	yes		yes	yes	yes	yes	yes	yes
Margaritaria discoidea	PHYL	F,f,wo,t	Fn	p	bi, p	yes								
Maesopsis eminii	RHAM	F	FF	p	ba, bi, oa, p	yes								
Morus mesozygia	MORA	F	FF	p	bi, p				yes					
Neoboutonia spp.	EUP	F, f, r	FF	npld	p				yes				yes	

						Unlogged forest			Legacy and near-legacy plots					
Species	Family	Habitat affinity[a]	Forest depend. [b]	Guild[c]	Dispersal[d]	K30	Dura	Mainaro	Avo	Near avo	Mango	Near mango	Euc	Near euc
Newtonia buchananii	LEGU	F,r	FF	sb	w	yes	yes		yes					
Olea welwitschii	OLEA	F,df	FF	p	bi, p	yes								
Oncoba routledgei	SALI	F,r	FF	npld	e, p									yes
Oxyanthus speciosus	RUBI	F	FF	sb	u	yes	yes	yes	yes	yes				
Pancovia pedicellaris	BRAC	F	FF	sb	p	yes	yes							
Pittosporum spp.	PITT	F, f, r	Fn	p	bi									yes
Pleiocarpa pycnantha	APOC	F	FF	sw	bi	yes	yes	yes						
Premna angolensis	LAMI	f	Fn	p	bi			yes	yes	yes		yes		yes
Podocarpus spp.	PODO	F	FF [e]	-[e]	ba, bi	yes								
Pouteria altissima	SAPO	F,r	FF	npld	ba, p	yes								
Parinari excelsa	CHRY	F,r	FF	npld	ba, bi, e, p	yes								
Pseudospondias microcarpa	ANAC	f,r,sw	Fn	sw	bi, e, oa, p	yes	yes	yes	yes	yes	yes	yes	yes	yes
Pterygota mildbraedii	MALV	f	FF	npld	w	yes			yes		yes			
Prunus africana	ROSA	F,wo	Fn	p	bi, e, p				yes	yes	yes	yes	yes	yes
Polyscias fulva	ARAL	F,r,g	Fn	npld	bi, p	yes			yes	yes	yes	yes	yes	yes
Rothmannia urcelliformis	RUBI	F	FF	sb	e, p	yes	yes	yes	yes	yes				yes
Rauvolfia spp.	APOC	f	FF	p	bi		yes		yes		yes		yes	
Scolopia rhaniphylla	SALI	F,df,t,r	Fn	sb	bi	yes				yes	yes			yes
Shirakiopsis elliptica	EUPH	f,r	FF	p	bi, p				yes	yes	yes	yes	yes	yes
Symphonia globulifera	CLUS	F,r	FF	sb	p	yes								
Spathodea campanulata	BIGN	f	FF	p	w					yes	yes	yes	yes	yes
Strychnos mitis	LOGA	F,r	FF	sb	ba, bi, e, p	yes	yes							
Strombosia scheffleri	OLAC	F	FF	sb	ba, bi, p	yes	yes							
Tabernaemontana pachysiphon	APOC	F	FF	sb	bi, p	yes	yes		yes	yes	yes		yes	yes
Treculia africana	MORA	F,r	FF	npld	e, p		yes							
Trichilia dregeana	MELI	F	FF	npld	bi, p				yes					
Trilepsium madagascarensis	MORA	F,r	FF	npld	ba, bi, p	yes	yes	yes						
Trema orientalis	CANN	f,r	FF	npld	bi, p								yes	
Tarenna pavettoides	RUBI	f,t,wo	Fn	sb	bi, p		yes							
Uvariopsis congensis	ANNO	F	FF	sb	bi, e, p	yes	yes	yes	yes	yes	yes	yes	yes	yes
Vangueria apiculata	RUBI	f	FF	p	bi, p	yes	yes	yes	yes	yes	yes	yes		yes

						Unlogged forest			Legacy and near-legacy plots					
Species	Family	Habitat affinity[a]	Forest depend. [b]	Guild[c]	Dispersal[d]	K30	Dura	Mainaro	Avo	Near avo	Mango	Near mango	Euc	Near euc
Vepris nobilis	RUTA	F,r,wo	Fn	sb	bi, e, p	yes	yes	yes	yes	yes	yes	yes	yes	yes
Warburgia ugandensis	CANE	F,df,f	FF	npld	e, p						yes	yes		
Zanthoxylum spp.	RUTA	F	FF	p	bi, p	yes	yes		yes	yes	yes		yes	yes

[a] df=dry forest, F=forest interior, f=forest edge, g=grassland, r=riverine/lakeshore, ro=rocky places, sw=swamp, t=bush/thickets, wo=woodland

[b] FF=forest dependent, Fn= forest non-dependent, Ud=undetermined

[c] npld = non-pioneer light demander, p=pioneer, sb= shade-bearer, sw=swamp as defined by Hawthorne (1995); dash indicates unknown.

[d] bi=bird, ba= bat, e=elephant, g=gravity, hb=hornbill, oa=other animal, p=primate, ua= unknown animal, u=unknown, w=wind.

[e] Habitat affinity or forest dependence not given in Lwanga (1996) but inferred from other sources if possible. Habitat affinities and guild for *Ficus* sp. are too varied to generalize.

Table 2-2. Forest structure and species diversity measures in legacy and near-legacy plots

	Stem frequency	Cumulative basal area (m^2)	Species richness	Shannon diversity	Effective no. species	Chao diversity[a]
Overall	54.4 (5.1)	0.079 (0.02)	9.71 (0.7)	1.63 (0.1)	5.1 (1.1)	72.4 (6.8)
Treatment						
Legacy	65.4 (7.8)	0.085 (0.03)	10.89 (0.9)	1.69 (0.1)	5.4 (1.1)	76.1 (10.3)
Near-legacy	43.4 (6.1)	0.074 (0.03)	8.54 (0.9)	1.57 (0.1)	4.8 (1.1)	49.1 (4.43)
Legacy tree type or species						
Fruit[b]	73.9 (11.9)	0.135 (0.05)	12.45 (1.4)	1.81 (0.2)	6.1 (1.2)	73.4 (9.9)
Near-fruit[b]	47.0 (6.8)	0.086 (0.04)	9.30 (1.0)	1.68 (0.1)	5.4 (1.1)	54.1 (10.4)
Avocado	76.8 (15.0)	0.144 (0.06)	14.46 (1.7)	2.07 (0.2)	7.9 (1.2)	82.3 (20.1)
Near-avocado	44.5 (5.5)	0.109 (0.06)	10.46 (1.4)	1.86 (0.2)	6.4 (1.2)	54.1 (11.0)
Mango	70.3 (20.1)	0.124 (0.08)	10.00 (2.2)	1.49 (0.3)	4.4 (1.3)	52.5 (9.2)
Near-mango	50.1 (14.0)	0.627 (0.03)	7.89 (1.2)	1.46 (0.2)	4.3 (1.2)	61.0 (33.4)
Eucalyptus	38.6 (8.5)	0.018 (0.01)	8.80 (0.9)	1.42 (0.1)	4.1 (1.1)	56.1 (16.4)
Near-eucalyptus	54.1 (11.2)	0.058 (0.04)	7.53 (1.6)	1.53 (0.2)	4.6 (1.2)	46.6 (7.7)

[a] Chao diversity is not calculated as an average per plot, but rather for the group as a whole (*e.g.,* tree species diversity across all plots in each treatment or type: legacy, all near-legacy, all fruit, all near-fruit, etc.).

[b] Fruit and near-fruit are pooled results of mango and avocado legacy and near-legacy plots, respectively.

Table 2-3. Rank abundance of regenerating tree species in legacy and near-legacy plots

Rank	Fruit plots	Near-fruit plots	Wood plots	Near-wood plots
1	*Ficus asperifolia*	*Shirakiopsis elliptica*	*Shirakiopsis elliptica*	*Shirakiopsis elliptica*
2	*Shirakiopsis elliptica*	*Ficus asperifolia*	*Prunus africana*	*Clausena anisata*
3	*Prunus africana*	*Albizia glaberrima*	*Clausena anisata*	*Diospyros abyssinica*
4	*Funtumia africana*	*Clausena anisata*	*Albizia glaberrima*	*Prunus africana*
5	*Clausena anisata*	*Prunus africana*	*Celtis africana*	*Albizia glaberrima*
6	*Albizia glaberrima*	*Funtumia africana*	*Ficus asperifolia*	*Ficus asperifolia*
7	*Celtis africana*	*Celtis africana*	*Blighia unijugata*	*Funtumia africana*
8	*Celtis gomphophylla*	*Monodora myristica*	*Diospyros abyssinica*	*Monodora myristica*
9	*Diospyros abyssinica*	*Millettia dura*	*Funtumia africana*	*Celtis africana*
10	*Millettia dura*	*Uvariopsis congensis*	*Celtis gomphophylla*	*Vepris nobilis*
11	*Monodora myristica*	*Ficus sur*	*Tabernaemontana pachysiphon*	*Uvariopsis congensis*
12	*Uvariopsis congensis*	*Dombeya mukole*	*Millettia dura*	*Tabernaemontana pachysiphon*
13	*Tabernaemontana pachysiphon*	*Pseudospondias microcarpa*	*Antiaris toxicaria*	*Chaetachme aristata*
14	*Lepisanthes senegalensis*	*Vepris nobilis*	*Monodora myristica*	*Millettia dura*
15	*Vepris nobilis*	*Tabernaemontana pachysiphon*	*Polyscias fulva*	*Celtis gomphophylla*
16	*Pseudospondias microcarpa*	*Albizia grandibracteata*	*Albizia gummifera*	*Rothmannia urcelliformis*
17	*Chrysophyllum spp.*	*Bersama abyssinica*	*Spathodea campanulata*	*Pseudospondias microcarpa*
18	*Mimusops bagshawei*	*Diospyros abyssinica*	*Pseudospondias microcarpa*	*Albizia gummifera*
19	*Albizia grandibracteata*	*Blighia unijugata*	*Vepris nobilis*	*Bersama abyssinica*
20	*Blighia unijugata*	*Spathodea campanulata*	*Zanthoxylum spp.*	*Blighia unijugata*
21	*Dovyalis spp.*	*Celtis gomphophylla*	*Croton spp.*	*Polyscias fulva*
22	*Polyscias fulva*	*Premna angolensis*	*Dombeya mukole*	*Spathodea campanulata*
23	*Kigelia africana*	*Vangueria apiculata*	*Lepisanthes senegalensis*	*Antiaris toxicaria*
24	*Zanthoxylum spp.*	*Ficus sp.*	*Albizia grandibracteata*	*Kigelia africana*
25	*Cola gigantea*	*Lepisanthes senegalensis*	*Bersama abyssinica*	*Vangueria apiculata*
26	*Ficus sp.*	*Mimusops bagshawei*	*Ficus sur*	*Ficus thonningii*
27	*Macaranga schweinfurthii*	*Antiaris toxicaria*	*Rauvolfia spp.*	*Lepisanthes senegalensis*
28	*Rothmannia urcelliformis*	*Rothmannia urcelliformis*	*Alangium chinense*	*Oncoba routledgei*
29	*Vangueria apiculata*	*Albizia gummifera*	*Allophylus spp.*	*Zanthoxylum spp.*

Rank	Fruit plots	Near-fruit plots	Wood plots	Near-wood plots
30	*Bersama abyssinica*	*Cola gigantea*	*Cola gigantea*	*Cola gigantea*
31	*Dracaena spp.*	*Kigelia africana*	*Ficus natalensis*	*Croton spp.*
32	*Albizia gummifera*	*Polyscias fulva*	*Mimusops bagshawei*	*Ficus sur*
33	*Chionanthus africanus*	*Croton spp.*	*Neoboutonia spp.*	*Lovoa spp.*
34	*Pterygota mildbraedii*	*Dovyalis spp.*	*Trema orientalis*	*Pittosporum spp.*
35	*Spathodea campanulata*	*Ficus natalensis*	*Uvariopsis congensis*	*Premna angolensis*
36	*Alangium chinense*	*Lovoa spp.*		*Scolopia rhaniphylla*
37	*Antiaris toxicaria*	*Oxyceros longiflorus*		
38	*Chaetachme aristata*	*Scolopia rhaniphylla*		
39	*Ficus sur*	*Warburgia ugandensis*		
40	*Ficus thonningii*	*Zanthoxylum spp.*		
41	*Oxyceros longiflorus*			
42	*Coffea spp.*			
43	*Croton spp.*			
44	*Dasylepis eggelingii*			
45	*Rauvolfia spp.*			
46	*Trichilia dregeana*			
47	*Balanites wilsoniana*			
48	*Cassipourea ruwensorensis*			
49	*Dombeya mukole*			
50	*Ehretia cymosa*			
51	*Ficus sansibarica*			
52	*Morus mesozygia*			
53	*Neoboutonia spp.*			
54	*Newtonia buchananii*			
55	*Premna angolensis*			
56	*Scolopia rhaniphylla*			
57	*Warburgia ugandensis*			

Table 2-4. Similarity of tree assemblages among three unlogged forests and legacy and near-legacy plots.

	K30	Dura	Mainaro	Avo	Near-avo	Mango	Near-mango	Euc	Near-euc
K30	-	-	-	-	-	-	-	-	-
Dura	0.638	-	-	-	-	-	-	-	-
Mainaro	0.477	0.667	-	-	-	-	-	-	-
Avo	0.563	0.483	0.469	-	-	-	-	-	-
Near-avo	0.500	0.417	0.515	0.851	-	-	-	-	-
Mango	0.505	0.380	0.356	0.682	0.767	-	-	-	-
Near-mango	0.386	0.269	0.361	0.579	0.754	0.647	-	-	-
Euc	0.378	0.351	0.353	0.723	0.853	0.667	0.689	-	-
Near-euc	0.484	0.400	0.406	0.714	0.928	0.737	0.656	0.732	-

2.6.2 Figure captions

Figure 2-1. Map of legacy tree and forest study areas. a) Location of Kibale National Park within Uganda. b) Location of legacy study area and unlogged forests K30, Dura, and Mainaro within Kibale. c) Land covers classed from satellite images taken in the early 1990s, the approximate time that subsistence farmland inside the park was abandoned. Note that this is a different land cover classification than Appendix 3.

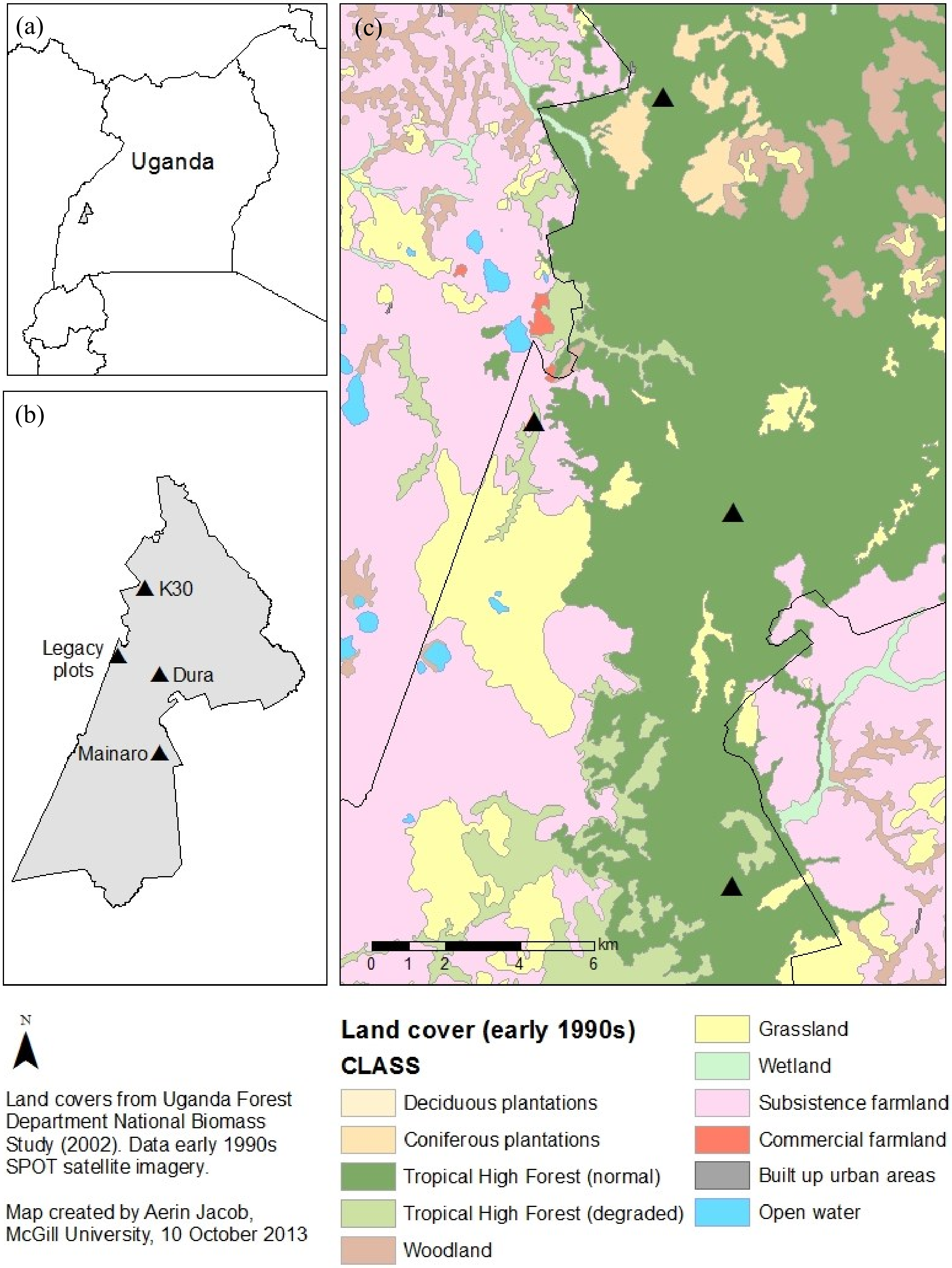
Figure 2-2. Photographs of legacy tree study area. a) Legacy plot study area on abandoned farmland in Kibale National Park, looking westward towards the Rwenzori Mountains. The forested valley in lower right corner is the patch of degraded tropical high forest near the legacy study area visible in Figure 2-1. Farms in the middle distance on the right are outside the park. b) Grassland (largely *Pennisetum purpureum*) and recolonizing forest on abandoned farmland, with eucalyptus legacy trees on the right and ridgeline. Photographs by A. L. Jacob.

Figure 2-3. Results of non-parametric Kruskal-Wallis tests among types of legacy trees. Boxplots of a) stem frequency in legacy and near-legacy plots; b) species richness and c) cumulative basal area in fruit and wood legacy and near-legacy plots; d) species richness, cumulative basal area, and f) effective numbers of species for avocado, mango, and eucalyptus legacy and near-legacy plots.

Figure 2-4. Species accumulation curves. Curves show rarefied species richness based on number of a) individuals and b) samples for fruit and wood legacy and near-legacy plots.

Figure 2-5. Log abundance curves. Abundance versus rank (from most to least abundant) for tree species in fruit and wood legacy and near-legacy plots.

Figure 2-1. Map of study areas



Land covers from Uganda Forest Department National Biomass Study (2002). Data early 1990s SPOT satellite imagery.

Map created by Aerin Jacob, McGill University, 10 October 2013

Figure 2-2. Photographs of study area

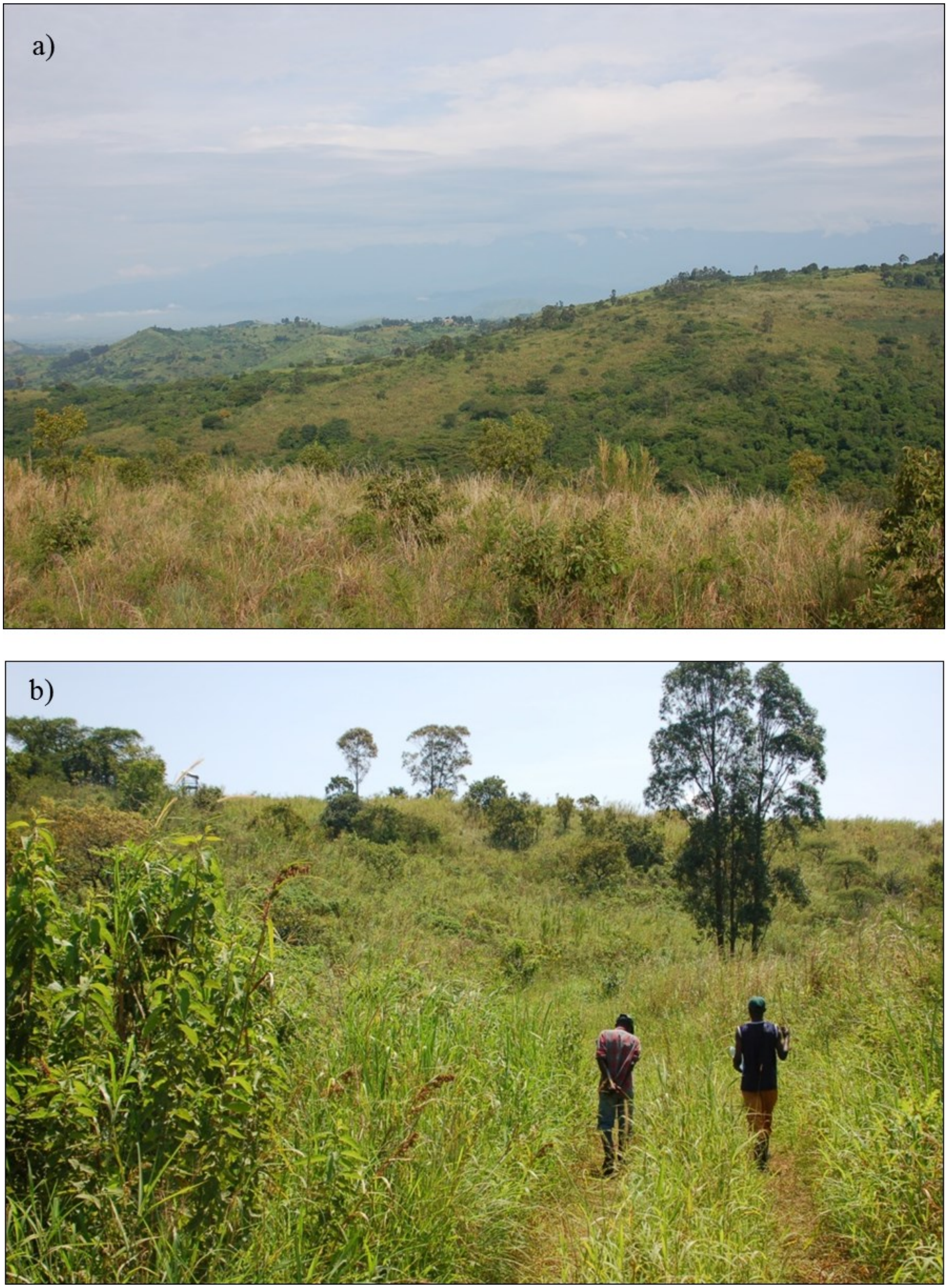


Figure 2-3. Results of non-parametric Kruskal-Wallis tests among types of legacy trees

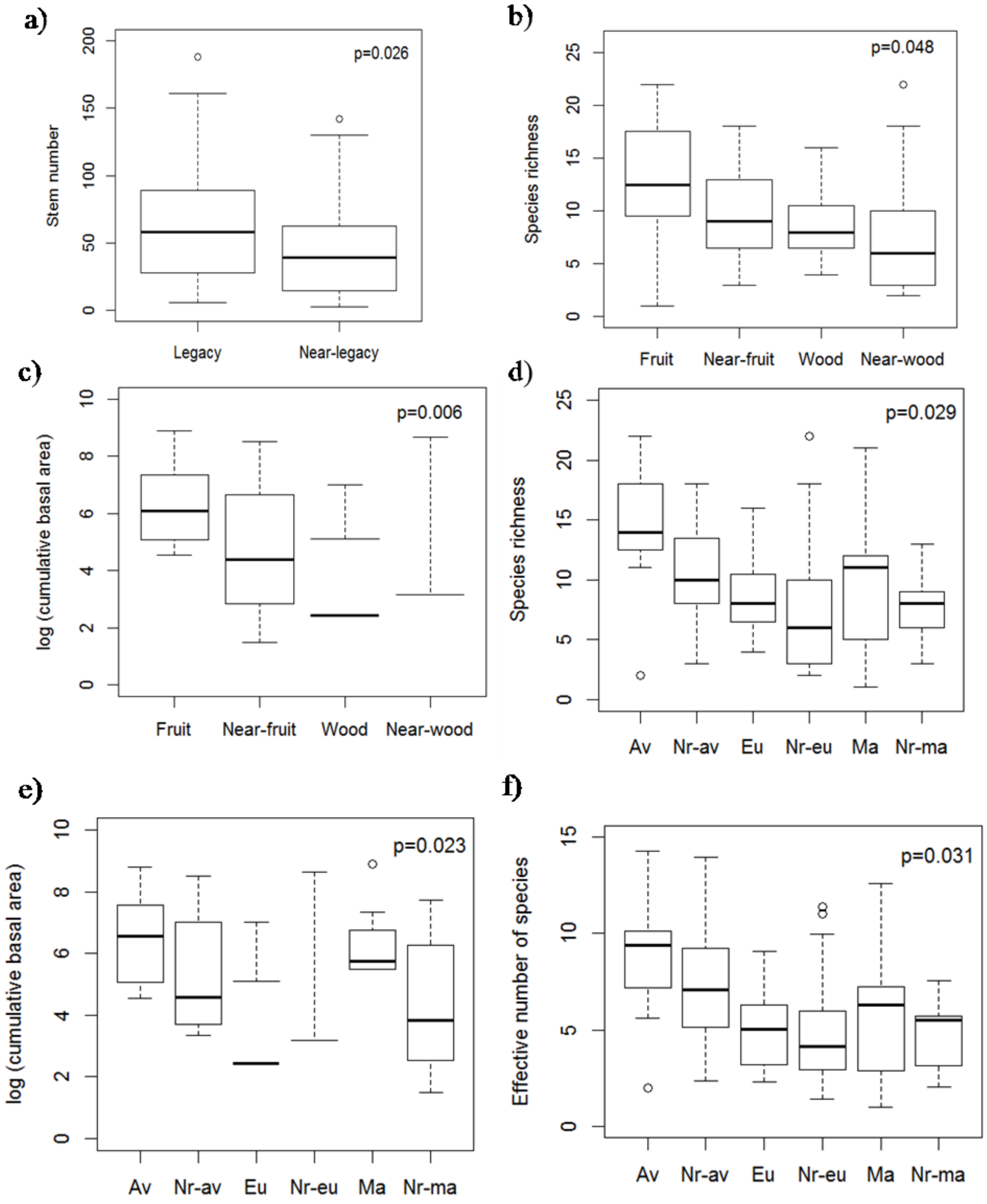


Figure 2-4. Species accumulation curves

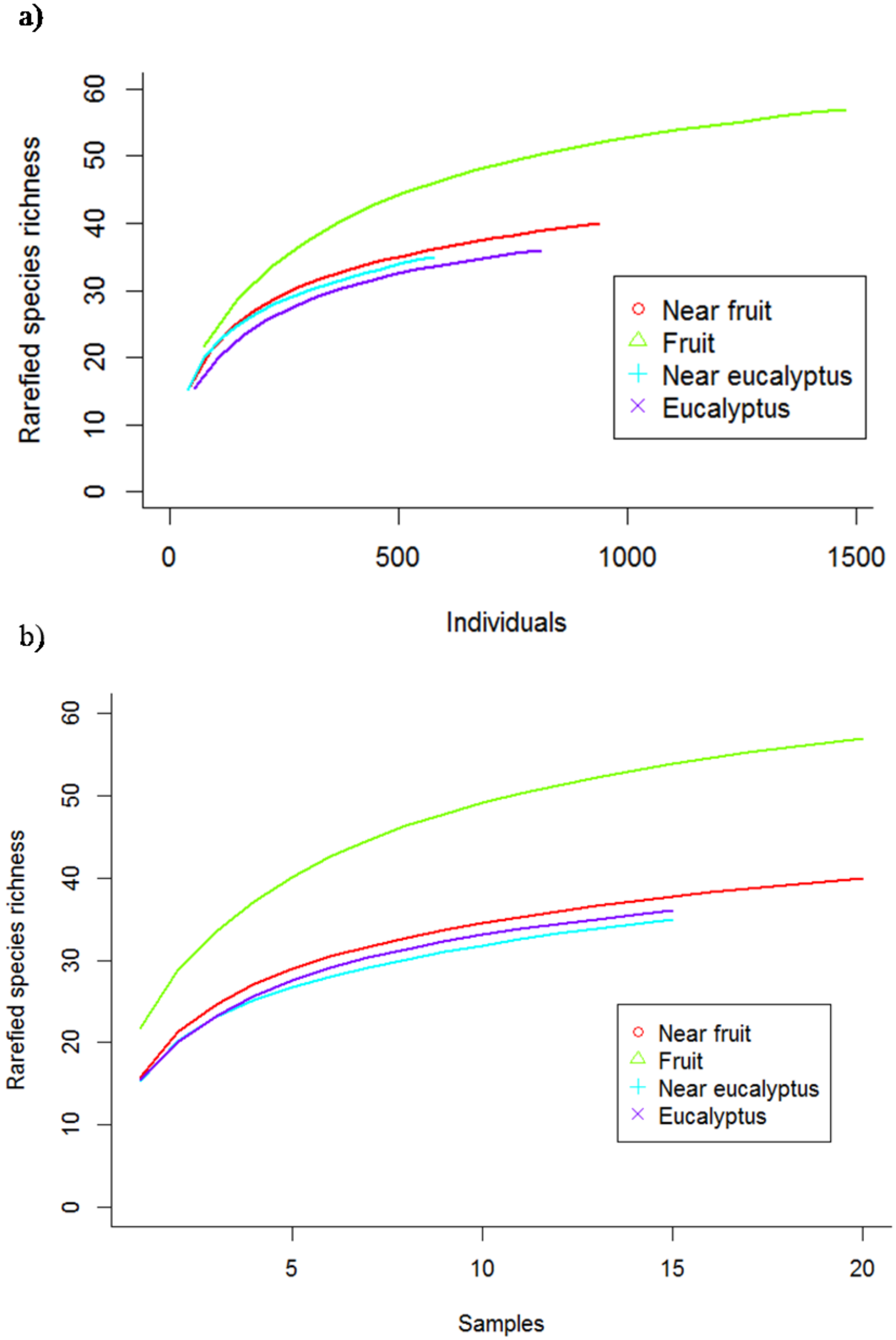
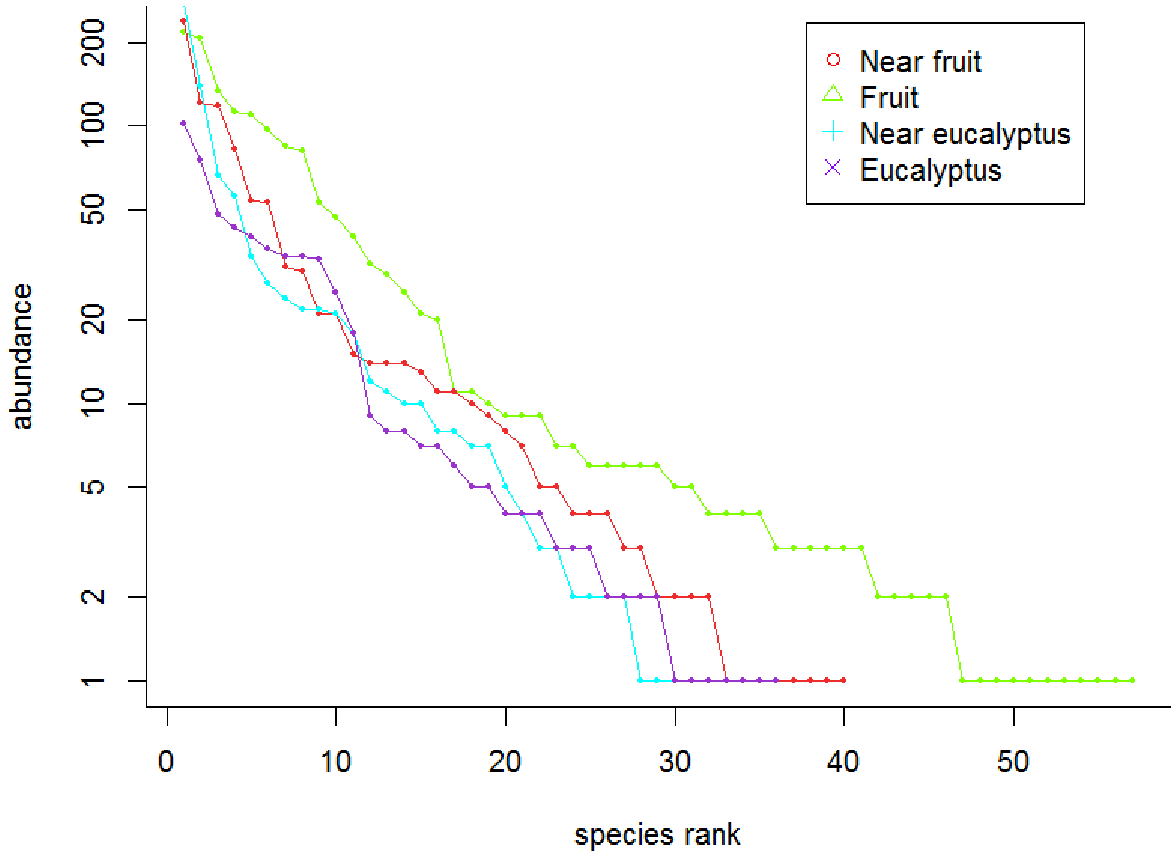


Figure 2-5. Log abundance curves



Linking Statement 1

Chapter 1 showed that nodal forest recovery has promise in restoration of rainforest species in grasslands that developed when agricultural land on formerly deforested sites is abandoned. This result could stimulate useful discussions about management plans about when and where the existing tree planting program could be complemented using nodal forest recovery mechanisms. Both of these restoration programs involve spatially restricted action: passive nucleation around single legacy trees scattered across the landscape or active planting of single seedlings. Hence both restoration strategies will leave distinct, localized spatial signatures for many years in rainforest at the site. Similarly, logging at different intensities and by different methods inevitably introduces some degree of spatial heterogeneity that persists through the successional recovery of the forest. On reflection, spatial heterogeneity arising in restoration and logging programs may have some analogy to regeneration patterns in mature forest in which the natural death of trees individually or in localized disturbance events creates distinctive spatial structure. The specific spatial patterns in natural forest may be more random than those arising in human interventions, but some degree of spatial heterogeneity in forest composition occurs even in mature rainforest. Chapter 3 considers data recorded over the course of 24 years on tree species composition and structure across a range of logging intensities in the Kanyawara region of Kibale. I use these data to assess the degree to which spatial heterogeneity at the plot level within sites might obscure or confound comparisons among sites differing in land use history.

3 SPATIOTEMPORAL HETEROGENEITY ACROSS A RANGE OF LOGGING INTENSITY IN AFRICAN TROPICAL RAINFOREST

3.1 Abstract

Tropical forests are complex environments in which tree assemblages vary widely over small spatial scales. Multiple factors interact to produce such heterogeneity, including historical conditions, abiotic and biotic factors acting in both natural and anthropogenic disturbances. Characterizing such heterogeneity and understanding its causes is challenging, but not identifying or accounting for it can confound botanical and zoological research and management.

I investigated spatial and temporal heterogeneity of tree assemblages in mid-altitude tropical rainforest in Kibale National Park, Uganda. Unlogged forest was compared to adjacent forest areas that were logged at various intensities in 1969. In four surveys between 1989 and 2013, trees were identified, counted, and measured in permanent study plots within forest compartments that were either unlogged or logged lightly, moderately or heavily. Results of Ward's hierarchical clustering of individual plots indicated that spatial heterogeneity was more closely related to pre-logging conditions than to logging intensity. These plot-based results run counter to those in the traditional approach of comparing compartments.

This strong influence of pre-logging conditions has important implications for research and management. Studies designed to examine effects of disturbance usually assume that pre-disturbance conditions in each treatment were equivalent. Since research and management are often conducted at relatively large spatial scales on the basis of shared management or land-use history, it is important to use sampling and statistical methods that minimize the impacts of small-scale heterogeneity resulting from pre-disturbance variation.

Keywords: Kibale National Park; logging; multiple factor analysis; spatial and temporal heterogeneity; tropical rainforest; Uganda; Ward's hierarchical clustering

3.2 Introduction

It is well recognized that spatial and temporal heterogeneity exists in tropical forests, influencing and being influenced by ecological processes at multiple scales (Connell 1978, Hubbell 1979, Denslow 1987, Huston 1999, Rees et al. 2001, Condit et al. 2002, Chave et al. 2003, Chazdon 2003, Brown et al. 2013). Vegetation can vary spatially over fine scales within a site and over coarse scales among sites, as well as temporally in the short-term (*e.g.*, seasonality) and long-term (*e.g.,* succession). Sources of heterogeneity can be abiotic or biotic, historical or recent, and act in additive or multiplicative ways. Substrate, rainfall, and temperature are major sources of floristic heterogeneity in tropical forests, as is environmental disturbance (Hamilton 1974, Hart et al. 1989). Natural disturbances include broad-scale events, such as earthquakes, cyclones, floods, volcanic eruptions, and forest fires, which affect entire landscapes (sometimes patchily), and fine-scale events, such as wind-throw, lightning, and elephant damage that affect individual or small numbers of trees (Denslow 1987, Forman 1995, Everham and Brokaw 1996, Foster et al. 1998, Peterson et al. 1998). Most historical disturbances in Africa have been small, frequently repeated events (Lewis et al. 2009), although climate change and drought have had significant broad-scale effects in some parts of Africa (Parmentier et al. 2007; but see Maley 2002 and van Gemerden et al. 2003 for effects of historic climate change and drought). People have lived in African forests for millennia, and the finer-scale disturbances often have human origins (Brncic et al. 2007). Historically, shifting agriculture (van Gemerden et al. 2003) and household waste (Yasuoka 2013) have been two major sources of anthropogenic disturbance in African forests (White and Oates 1999). Today, however, extracting timber and gathering fuelwood are the major sources of forest disturbance and degradation in Africa (Hosonuma et al. 2012, Kissinger et al. 2012).

Regardless of whether the source is environmental or human-induced, all disturbances have the potential to alter forest composite on and structure. Some disturbances affect species indiscriminately, such as volcanic eruptions and clearing land for agriculture; other disturbances are species-specific and affect forest composition and structure in different ways. For example, drought selects for drought-tolerant species, and humans plant or harvest trees that are useful. Many previous studies in disturbed forests used structural measures such as basal area, aboveground biomass, tree height, stem density, canopy structure, frequency and size of canopy gaps, and light availability to monitor recovery from disturbance (Kasenene and Murphy 1991, Everham and Brokaw 1996, Turner et al. 1998, Aide et al. 2000, Hall et al. 2003, Chazdon et al. 2007, Bonnell et al. 2011). However, changes in plant species composition can occur independently of changes in structure, and show longer-lasting effects of disturbance (Chazdon 2003, Chazdon et al. 2009). Some disturbed tropical forests quickly regain their former species diversity, if extinction is local and immigration is possible, or if disturbance affects only the canopy (Chazdon 2003, Wills et al. 2006). In cases where disturbance affects soils or drastically alters species composition, recovery can take decades or even centuries (Guariguata and Ostertag 2001, Chazdon 2003, Martin et al. 2013).

The multiple effects of disturbance and ecological interactions result in complex environments and high levels of biodiversity, making it difficult to distinguish the causes of observed vegetation patterns. The study of temporal change in forests is particularly challenging, because trees can live for hundreds or even thousands of years (Condit 1995, Rees et al. 2001) and intervening disturbances can obscure recovery from the disturbance of primary interest (Laufer et al. 2013). Although the responses of African tropical tree communities to selective logging have been extensively studied (e.g., White 1992, Struhsaker 1997, Hall et al. 2003, Brown and Gurevitch 2004, Fashing et al. 2004, Makana and Thomas 2006, Poulsen 2009, Bonnell et al. 2011, Hawthorne et al. 2011, Asase et al. 2012, Gourlet-Fleury et al. 2013), few studies extended for more than thirty years after the logging event (Plumptre 1996, Sheil et al. 2000, Hall et al. 2003, Taylor et al. 2008, Bonnell et al. 2011, Newbery et al. 2013). Furthermore, studies of selective logging have been plagued by problems, including failure to establish baseline conditions and intensity of harvest, poor spatial and temporal resolution in the sampling design, pseudoreplication (Ramage et al. 2012), and disparate field and analytical methods (Sheil 1995, Laufer et al. 2013) making it difficult to generalize logging effects.

Closely examining long-term data from well-studied sites allows researchers to assess spatial and temporal variation due to disturbance. The present study used 24 years of data from logged and unlogged areas of Kibale National Park, a mid-altitude tropical rainforest in western Uganda, to examine causes of spatial and temporal heterogeneity. Kibale was originally protected as a forest reserve in 1932 to provide a sustainable supply of timber. Mechanized, commercial harvest began in the 1940s until 1970s. In 1993 Kibale was upgraded to a National Park. The forest management compartments set out in the 1950s and subsequently logged at differing intensities in the 1960s have influenced the spatial organization of subsequent research in everything from primate ecology to plantation forestry (Kingston 1967, Struhsaker 1997). Researchers have used the northwestern area of Kibale to study how logging intensity affects tree growth and mortality (Kasenene 1987, Kasenene and Murphy 1991, Chapman and Chapman 1997, Mucunguzi et al. 2007, Bonnell et al. 2011); leaf chemistry (Gogarten et al. 2012); size and persistence of forest gaps (Skorupa and Kasenene 1984, Kasenene 1987, Paul et al. 2004); parasites and diseases (Gillespie et al. 2005, Chapman et al. 2012); and the population biology and ecology of insects (Nummelin and Hanski 1989, Nummelin 1998, Nummelin and Zilihona 2004, Nyafwono et al. 2014), birds (Dranzoa 1998, Sekercioglu 2002), rodents (Kasenene 1984, Basuta and Kasenene 1987), prosimians (Weisenseel et al. 1993), monkeys (Waser and Floody 1974, Struhsaker 1975, Skorupa 1988, Olupot 2000, Chapman et al. 2010b, Milich et al. 2013), chimpanzees (Chapman et al. 1995, Malenky et al. 1996, Potts 2011), duikers (Nummelin 1990, McCoy 1995), bush-pigs (Nummelin 1990), and elephants (Nummelin 1990, Omeja et al. Accepted). Many of these studies compared forest areas logged at different intensities with adjacent unlogged forest, assuming that pre-logging conditions were equivalent or that, if they varied, the variation was less important than effects of logging disturbance.

The present study examined the influence of variation in pre-logging conditions and of differences in subsequent logging intensity on spatiotemporal heterogeneity of tree assemblages. Published results and older unpublished documentation from Kibale National Park were examined, and longitudinal data on forest composition, collected in permanent study plots during 1989–2013, were analyzed using multivariate statistics to investigate patterns in fine-scale spatial and temporal heterogeneity. I specifically addressed the following research questions: 1) How do patterns in temporal heterogeneity and spatial heterogeneity differ among tree assemblages in lightly, moderately, and heavily logged forest, and unlogged forest? 2) What is the relative importance of natural and human disturbances in creating and maintaining forest heterogeneity?

3.3 Methods

3.3.1 Study area

Kibale National Park (795 km^2) is a medium-altitude, moist tropical rainforest in western Uganda, just north of the equator and 30 km from the border with the Democratic Republic of Congo (0˚11' - 0˚41' N and 30˚12' - 30˚32' E; Figure 3-1). Kibale lies within the Albertine Rift, a biodiversity hotspot where Africa's highest levels of species richness and endemism coincide with some of its densest, fastest growing, and poorest human populations (Burgess et al. 2004, Cordeiro et al. 2007, Plumptre et al. 2007, Hartter et al. 2012). Historically, people lived, practiced shifting cultivation, and grazed livestock on grassy hilltops and hillsides within Kibale forest. However, a combination of tribal conflict, disease (rinderpest and sleeping sickness), and livestock depredation caused people to abandon homesteads in the early 1900s (Osmaston 1959, Lang Brown and Harrop 1962). Large parts of Kibale forest have been disturbed relatively little by humans for at least 200-300 years (Struhsaker 1975). In 1932, the British Protectorate Government designated 560 km^2 of northern, central, and southeastern Kibale as a Forest Reserve, which was managed for commercial timber extraction from the late 1940s until the early 1970s (Struhsaker 1997). In 1993, the forest reserve was joined with the adjacent Kibale Game Corridor and upgraded to national park status (Figure 3-1).

The park lies on a plateau tilted slightly to the south ranging from 1618 m in the northwest to 904 m in the southwest, draining into Lake George through the Mpanga and Dura Rivers. The region is underlain by pre-Cambrian, strongly metamorphosed sedimentary rocks of the Toro System (Taylor et al. 1999). No detailed soil analyses exist for Kibale at the landscape scale. In general, Kibale soil has higher quality and fertility than most tropical rainforests, perhaps resulting in lower concentrations of chemical plant defense compounds and exceptionally high biomass of folivorous primates (McKey et al. 1978, Gartlan et al. 1980, Struhsaker 1997). While there is considerable variation from site to site, soils tend to be well-drained, dark grey to red, consisting of sandy loams and sandy clay loams (Lang Brown and Harrop 1962, Wing and Buss 1970, Struhsaker 1997). Kibale tends to be cooler and drier than most tropical rainforests, with a high-to-low north-to-south gradient in rainfall and vegetation that follows elevation (Struhsaker 1997). Mean daily minimum and maximum temperatures from 1970-2010 were 15 °C and 23 °C (T. T. Struhsaker and C. A. Chapman, unpublished data).

Mean annual rainfall from 1968-2010 was 1654 mm (Hartter et al. 2012), falling in two rainy seasons from March-May and September-November (Struhsaker 1997).

Kibale lies within a transitional range of altitudes for Ugandan vegetation (1500-2000 m; Hamilton 1975, Skorupa 1988) having affinity with both montane tropical rainforest and mixed tropical deciduous forest (Kingston 1967). The earliest land cover classification was based on aerial photography and extensive ground surveys in the mid-1950s to determine the forest reserve's potential for commercial timber harvest (Osmaston 1959, Uganda Forest Department 1960) (Appendix 3). Forest in northern and central Kibale is evergreen, while warmer and drier southern Kibale tends towards semi-deciduous (Wing and Buss 1970, Oates 1974). Broadly speaking, forests in the northern part of the park are dominated by *Parinari excelsa*, in the middle by mixed *Diospyros-Markhamia-Strombosia-Newtonia* forest, and in the south by *Pterygota mildbraedii* or *Cynometra alexandri* (Langdale-Brown et al. 1964). There has been a progressive increase in forest cover over the last half-century as a result of fire prevention efforts (Chapman and Lambert 2000); today, the former forest reserve contains 90% unlogged and regenerating forest, 5% bare ground and short grasses, 3% wetland, 1% tall grasses, and 1% shrubs (Jacob et al. 2014a).

Kibale forest had mainly general purpose timber species with few high-value species such as *Entandrophragma* spp. (mahogany) (Kingston 1967). Mature natural forest is over 30 m tall with closed canopies and stratified tree crowns, and many tree species grow in different combinations (Lang Brown and Harrop 1962, Wing and Buss 1970). Starting in 1950, sawmills were contracted to cut 29 species of merchantable trees over 5' (1.52 m) girth-at-breast-height (48.5 cm DBH); other tree species and sizes could be cut at the mill's discretion (Kingston 1967). By 1957, the original polycyclic felling cycle of 200 years was rejected in favour of a uniform, intensive harvest intended to convert the existing uneven-aged natural forest to optimal regeneration for 70 year felling cycle (Kingston 1967, Kasenene 1987). By 1969 approximately 35% of the northern sector of the park had been selectively harvested (Struhsaker 1997). Lack of personnel meant that it was difficult to enforce policies on directional felling, removal of compulsory species, retention of seed trees, and treatment with arboricide; therefore, the effects of harvest vary between areas. Detailed descriptions of the effects of logging on Kibale forest can be found in Kasenene (1987), Skorupa (1988), and Struhsaker (1997).

3.3.2 Study sites

I studied forest dynamics in northwestern Kibale, in an area locally known as Kanyawara (0°33'36"N, 30°21'47" E) (Tables 3-1 and 3-2; Figure 3-1). This is *Parinari* forest and thought to represent the climax state between 1370 and 1525 m a.s.l. (Eggeling 1947, Osmaston 1959, Skorupa 1988); under UN Food and Agriculture Organization (FAO) guidelines, it would all have been classified as frontier forest having a "*very high degree of naturalness*" (category n8, FAO 2005). Oates (1974) described unlogged *Parinari* forest in Kanyawara as heterogeneous, varying in species composition on a local geographic scale and in composition and structure between valley-bottom and hill-top (maximum 150 m elevation rise). I specifically studied three adjacent logging compartments varying in harvest intensity. Although the three compartments contained different combinations of forest types (Figure 3-1, Table 3-2), studies in the 1980s decided they were well-matched in terms of their vegetative affinities, topography, and climate (Skorupa and Kasenene 1984).

Unlogged: Compartment K30 (360 ha) was set aside from logging in 1948, first protected as part of a 'Nature Reserve Working Circle' and then as a 'Research Plot' (Osmaston 1959, Howard 1991, Olupot et al. 1994). Forest gaps in K30 are the result of natural tree deaths and wind throws, with natural tree-fall rate being approximately 3 stems/ha/yr (Kasenene 1987). Although pit-sawyers removed 3-4 stems/km^2 prior to 1970, this low level of extraction was believed to have had little effect on forest composition and structure (Skorupa 1988). K30 has frequently been used as a reference site to compare the effects of timber harvest on adjacent stands (e.g., Bonnell et al. 2011).

Lightly logged: Compartment K14 (410 ha) was selectively logged from May to December 1969. Prior to logging, land cover in K14 was estimated as 59% forest, 31% grassland, and 10% swamp (Appendix 28 in Kingston 1967). Logs of 23 species were removed from K14, but nine species made up more than 94% of total timber out-take (Skorupa 1988) (Table 3-1; Appendix 4). Canopy coverage in K14 was reduced by 25% from logging and incidental damage, including non-directional felling and damage by heavy machinery (Struhsaker 1997). Harvest intensity varied throughout K14, focusing on the mid-slopes of hills rich in desirable timber species (Kasenene 1987) and removing an average of 14 m^3/ha or 3.0-5.1 stems/ha (Struhsaker 1997) (Table 3-1). Recognizing this, some researchers have split this compartment into two areas: the 'lightly logged' K14 *sensu stricto* and 'moderately logged' Mikana (e.g., Chapman and Chapman 1997, Bonnell et al. 2011). I follow this convention.

Heavily logged: Compartment K15 (281 ha) was selectively logged from September 1968 to April 1969. Prior to logging, land cover in K15 was estimated as 91% forest, 1% grassland, and 8% swamp (Appendix 28 in Kingston 1967). Logs of 18 species were removed from K15, but nine species made up more than 95% of the total timber out-take (Skorupa 1988) (Table 3-1; Appendix 4). The high number of desirable timber species, particularly *Olea welwitschii* (Knobl.) Gilg & G. Schellenb., led to "*excessive*" harvest in K15 (Kasenene 1987) and resulted in many clear-cut areas interspersed with remnant patches of mature forest. Between 50-66% of the original stand was destroyed by logging and incidental damage (Skorupa 1988). Harvest intensity averaged 21 m^3/ha or 7.4-8.6 stems/ha (Struhsaker 1997).

3.3.3 Field methods

From December 1989 to January 1990, C. A. Chapman established 26 permanent sampling plots in Kanyawara to monitor forest phenology (Figure 1; Table 3-3) (Chapman et al. 1994). Each 200 m x 10 m plot (0.2 ha) was randomly located along the existing grid-like trail system, stratified by logging history: 11 plots in unlogged compartment K30, 10 in moderately logged compartment K14 *sensu lato* (six in K14 *sensu stricto* and four in Mikana), and five in heavily logged compartment K15. The plots are spread over an area of 7 km^2, with a maximum distance between plots of 4.75 km. Within each plot, every tree ≥ 10 cm diameter-at-breast-height (DBH, measured at 1.2 m) within five meters on either side of the central trail was marked with a numbered aluminum tag, identified to species-level (Eggeling and Dale 1951, Hamilton 1981), and measured for DBH. If the tree was on uneven ground, DBH was measured from the downhill side. If the tree had large buttresses (*e.g.,* large *Olea welwitschii*), DBH was measured by mounting a meter stick on a pole and having a second observer read the diameter at the top of the buttress. If a tree branched into two stems below 1.2 m, each stem was measured individually. Chapman and Chapman (1997) determined that, when the plots were established, there was no difference between compartments in terms of slope, amount of light reaching near to the ground, or density of ground vegetation (trees, herbs, shrubs, grasses). Plots were re-surveyed in May 1999, November-December 2006, and January-May 2013. During each re-survey, all marked trees were re-located and measured, cause of death determined where possible, and new trees recruiting into the ≥10 cm DBH size class were identified, counted, measured, and marked.

3.3.4 Mapping

Between 1954-56, the Uganda Forest Department used a combination of aerial photography and extensive ground work to survey and map forest types throughout the Kibale Forest Reserve (Figure 3-1) (Osmaston 1959). Thirteen forest types were identified and mapped (Osmaston 1959, Uganda Forest Department 1960). I digitized this map using ArcMap 10.1 (ESRI 2012) (Appendix 3). I also digitized the logging compartment boundaries following descriptions in the original management plans (Osmaston 1959, Kingston 1967) and Struhsaker (1997), and sketches made by T. T. Struhsaker on a map of northern Kibale (Uganda Department of Lands and Surveys 1965, available upon request to A.L. Jacob). I used the digitized layer in a GIS to calculate the area of each forest type in each of the three study compartments circa 1955. I used GPS coordinates at the beginning and end of each of the 26 permanent plots to identify which forest type(s) they fell in circa 1955 (Table 3-1).

3.3.5 Statistical methods

I assessed the spatial heterogeneity of forest composition in permanent sampling plots measured four times between 1989 and 2013. My overall goal was to compare community composition over time and space (*i.e.,* variance explained across sites) and identify indicator species. My statistical methods followed three main steps: 1) identifying the ecological importance of each tree species in each plot (relative dominance ratio (RDR), explained further below), 2) identifying ecologically meaningful groups of plots *post hoc* based on a clustering algorithm of RDR (clusters) and comparing these groups to the traditional *a priori* grouping by logging history (compartments), and 3) determining which tree species indicated the groupings by cluster versus logging compartment (indicator species). All statistical analyses were performed using the software R (R Development Core Team 2013).

I excluded one plot (Plot 12) because confusion over the boundary between K14 and K30 led to accidental felling of trees in this general part of K30, and thus the logging history of this plot could not be precisely determined (Figure 7 in Oates 1974; J.F. Oates and T.T. Struhsaker, pers. comm.). I pruned the dataset using suggestions from Sheil (1995), retaining free-standing fig species (*i.e., Ficus exasperata, F. mucuso, F. sur,* and *F. vallis-choudae*) but excluding stranglers (*i.e., Ficus asperifolia, F. conraui, F. natalensis, F. sansibarica, F. saussureana,* and *F. thonningii*; identified using Eggeling and Dale 1951, Hamilton 1981, Hawthorne 1995, Katende et al. 1995).

3.3.5.1 Relative Dominance Ratio

I created two site x species matrices for each of the four survey years (1989, 1999, 2006, 2013): one based on the frequency (stem count) and one based on the dominance (cumulative DBH: the sum of DBH of each tree in the sample unit) of each species. Each matrix had 25 rows (s) and 87 columns (species). For each year, I combined the two matrices into a single matrix using the relative dominance ratio (RDR) (Curtis and McIntosh 1951) which is the sum of the relative frequency and relative dominance (*e.g.,* cumulative DBH, basal area, biomass) for each species in a given transect divided by two. Since RDR incorporates the number of stems and dominance of each species, it provides a more representative measure of how each species contributes to the forest community than either stem frequency or dominance alone (Magurran 1988, Laurance et al. 2006, Prasad et al. 2006). The frequency (stem count), dominance (cumulative DBH) and RDR were calculated for each species *i* by following the formulae: Frequency = $(N_i/N)*100$; Dominance = $(S_i/S)*100$; RDR = (Frequency+Dominance)/2, where N_i is number of the individuals in *i*th tree species, N is the total number of individuals of all the tree species in the plot; S_i is total DBH of the trunk of a tree species, S is total DBH of the trunks of all tree species in the plot. It should be noted that a very large, infrequent species could have the same RDR as a small, widespread species.

3.3.5.2 Clustering

Identifying relatively homogenous clusters of plots is a complex task due to changes in tree species composition, frequency, and size over space and time throughout the study. My first step was to test for inter-year variance in community composition (*i.e.,* the site x species RDR matrices) with a permutational multivariate analysis of variance (PERMANOVA, also called a non-parametric MANOVA) of distance matrices, using the function adonis in the R package vegan (Oksanen et al. 2013). The effect of survey year was not significant, so I focused all subsequent analyses on identifying ecologically meaningful clusters of plots across space. I used a multiple factor analysis (MFA) to create the best compromise across years. MFA is a useful way of analyzing multiple sets of variables measured on the same individuals or objects at different points in time (*i.e.,* data were collected on the same plots, and very often on the same trees, in multiple survey years) because it balances the influence of the groups (survey years) when computing distances between plots (*i.e.,* combining several data tables into one analysis) (Bécue-Bertaut and Pagès 2008, Abdi et al. 2013). I used four primary plot x species RDR response matrices, one for each survey year (*i.e.,* 1989, 1999, 2006, 2013), and standardized them according to the eigenvalues of their first principle component, which equalizes the weight of each survey year in the final solution and makes it possible to simultaneously analyze data from the four surveys in a meaningful way. The four matrices were concatenated and subjected to a global PCA using the R package FactoMineR (Lê et al. 2008). This approach allowed me to normalize data from each of the survey years, studying the covariance of site objects in multivariate space.

I then extracted the principal coordinates for each plot from the dimensions accounting for the majority of the variance of the MFA (as determined from a screeplot) to create a Euclidean dissimilarity matrix of the principal components. This focuses on the information most likely to yield stable clusters in hierarchical agglomerative clustering (Lê et al. 2008, Husson et al. 2011). This analysis initially considers each plot as a single cluster. The agglomerative algorithm progressively joins clusters with the lowest dissimilarity; this process requires specifying a *distance measure* (that determines how similarity/dissimilarity between clusters is calculated) and a *linkage rule* (which determines how the hierarchy is built). I used the Euclidean distance measure because I wanted to preserve the distances between site coordinates in the MFA and thus the compromise across the four survey years. I used Ward's method as the linkage rule to find the best clustering hierarchy, using the function agnes in R package stats (Murtagh and Legendre 2011, Legendre and Legendre 2012). The Ward criterion is generally viewed as very efficient: it is based on both multidimensional variance and principle component methods, and minimizes the within-cluster variance and maximizes the between-cluster variance each time clusters are joined (Husson et al. 2010). The result of the hierarchal clustering is represented by a dendrogram, which shows how plots – each initially considered single clusters – are successively joined together until all plots are in a single cluster. The dendrogram is indexed by the change of within-group variance with each subsequent partition. The optimal grouping structure (*i.e.,* the number of clusters, Q, where the tree should be 'cut') is determined qualitatively on the appearance of the dendrogram and the ecological interpretability of the clusters, and quantitatively on the decrease of within-clusters variance (inertia) according to the number of clusters. I used a cut-off rule for the number of clusters between three and 10 (as suggested by Husson et al. 2010) where the increase in between-group variance between Q-1 and Q clusters was much greater than that between Q and Q+1 clusters (Murtagh and Legendre 2011).

In determining the optimal number of clusters, I considered both changes in between group variance per partition and whether groupings led to ecologically meaningful clusters. I then used PERMANOVA to evaluate how well grouping the plots by these clusters explained the variance in the Euclidean distance matrix, compared to grouping the plots by historic logging intensity (*i.e.,* by compartment). Multivariate homogeneity of group dispersion was verified following each PERMANOVA. I visually compared the clustering scenarios with a Principal Components Analysis (PCA) of the Euclidean distance matrix in order to compare their representation on a biplot. I then depicted the two clustering scenarios as different placements of groups on a map of the study area to better understand underlying ecological reasons for clustering. I calculated the distances between each plot and the centroids of their respective cluster to identify which plots were 1) the most representative of their cluster (*i.e.,* plots closest to the center of their cluster), and 2) the most unlike the other two clusters (*i.e.,* plots farthest from the center of the other clusters) (Husson et al. 2010).

3.3.5.3 Indicator species

To further explore the ecological differences in grouping plots by clusters as opposed to logging intensity, I identified indicator species or combinations of species (hereafter 'indicators') that characterized both grouping scenarios (De Cáceres et al. 2012, De Cáceres and Jansen 2013). The ideal indicator is both found exclusively in its cluster of plots (*i.e.,* not in other clusters) and occurs in all sample plots within the cluster. It should be noted that species combinations are not requisite species associations: the former is a group of species that, as a whole, indicates a group of sites, while the latter is a group of highly correlated species. Sometimes specific combinations of species that co-occur have better indicator value for a group than the occurrence of individual species.

I conducted this indicator species analysis in four steps. First, for each cluster I restricted the analysis to choose only species that occurred in at least ten plots (40% of the total number of plots). Second, I built a combined species matrix consisting of all species combinations from single species to a maximum of three species. Third, I used the function indicators in the R package indicspecies to identify and quantify two important aspects of the validity of indicators: i) positive predictive value (A, sometimes called specificity, a measure of how indicative that indicator is of its group) and ii) sensitivity (B, sometimes called fidelity, the probability of finding that indicator in the target group of sites) (De Cáceres et al. 2012, De Cáceres and Jansen 2013). Species with high values of both A and B are likely to be good indicators for a particular group of sites. I used an A threshold of 0.5 and a B threshold of 0.2, and calculated confidence intervals around A and B using 999 permutations. Fourth, I pruned the indicator list using three selection criteria (and the same A and B thresholds): i) I selected indicators with valid positive predictive values, sensitivity and indicator values, according to the input thresholds (in the case of confidence intervals, the lower bound was used to select valid indicators); ii) I discarded valid indicators whose occurrence pattern was nested within other valid indicators; and iii) I evaluated the coverage (proportion of sites of a given site group where the indicator is found) of the remaining set of indicators and explored subsets of increasing number of indicators, until the same coverage and set of indicators was attained. If the maximum allowed members was attained, then the set of indicators with maximum coverage was returned. This is the preferred method when the factor used in the indicator species analysis is derived from the response matrix. The alternative, calculating p-values for the indicator species values, is only valid if the factor is derived independently from the response matrix.

3.4 Results

The final dataset included 87 species from 81 genera and 42 families (Table 3-4). Most genera had only a single species in the dataset (with a few exceptions, *e.g., Albizia, Cordia, Celtis,* and *Ficus* spp.). The family Rubiaceae was the most species-rich with nine species, followed by Apocynaceae, Leguminosae, and Moraceae each with five species; 22 families each had only one species.

3.4.1 Mapping

The historical map of pre-logging forest types showed considerable forest heterogeneity within and among the three logging compartments and study plots (Tables 2 and 3, Figure 1; Uganda Forest Department 1960). Before logging, the northern half of the study area was *Parinari-Pouteria (*formerly *Aningeria)* forest (type K1) while the southern half was mixed *Parinari* forest (type K2 unidentified subtypes). This distribution corresponds reasonably well with logging intensity: timber harvest was heaviest in the north (compartment K15 and Mikana), lighter in the center (compartment K14 *sensu stricto*), and non-existent in the south (compartment K30). Ten plots fell in each of *Parinari-Pouteria* forest and mixed *Parinari* forest (Table 3-3, Figure 3-1). Two plots fell in the transition zone between these two forest types. The remaining two plots fell in a small patch of early colonizing forest (type K10) in southern compartment K30. The origin of this patch is unknown; at 9.7 ha, it is nearly 150 times larger than the largest tree-fall gaps in K30, and 13 times larger than the largest gaps in in K15, as measured twenty years after logging (Kasenene 1987) (Table 3-1).

3.4.2 Clustering

The first PERMANOVA showed that no survey year was significantly different from the others (R^2=0.01, p=0.99), but there were strong differences among plots (R^2=0.92, p<0.001). This means that species composition (RDR) in plots varies more across space (*i.e.,* comparing different plots within the same survey year) than across time (*i.e.,* comparing the same plot in different survey years). The first nine dimensions from the MFA principal components analysis explained 87% of the variance amongst the four survey years.

After examining the dendrogram produced by cluster analysis (Figure 3-2) and comparing different cut-off levels to topographic, historical, and botanical information about the study area, I chose the result with three clusters (Table 3-3). When the Euclidean distance matrix was ordinated, and the clustering scenarios tested for goodness of fit, these clusters showed very distinct groups of plots (goodness of fit test r^2=0.71, p<0.001). Conversely, grouping plots by logging compartments showed a great deal of variation within the unlogged plots and overlap between groups (goodness of fit test r^2:0.31, p<0.01) (Figure 3-2). Clusters showed different spatial arrangements than logging compartments when mapped onto the study area (Figure 3-4):

all four plots in compartment K15 and three of the four plots in Mikana are in Cluster 2; nine of the 11 plots in compartment K30 align in two spatially distinct groups: Cluster 1 in the north and Cluster 3 in the south; and plots in compartment K14 are divided between all three clusters. The three most representative plots of Cluster 1 and Cluster 2 were from three different logging treatments (Cluster 1: moderately, lightly, and unlogged forest; Cluster 2: heavily, unlogged, and moderately logged forest), while the three most representative of Cluster 3 were all from unlogged forest (Table 3-6).

That the Ward clusters better explains variation in the tree community than grouping by logging intensity (*i.e.,* compartments) is supported by the fact that the former represent distinct groups along the first two axes of the PCA, whereas grouping by logging histories shows a great deal of overlap in the ordinal space. Note that the dispersion of the unlogged group is very large and this group overlaps almost entirely with the lightly and moderately logged groups (Figure 3-4). Together, this means that the heterogeneity in community composition of the unlogged compartment is very high and it should not be considered a valid basis for forest classification.

Discrepancies between the Ward clusters and the logging compartments can in part be explained by the historical legacies of pre-logging conditions. For instance, Plots 04 and 05 are unusual in that they are among the most representative of Cluster 2 (Table 3-2, Figure 3-3) but occur in the south of unlogged compartment K30; on the other hand, all other Cluster 2 plots occur in the heavily and moderately logged areas. This is because both Plots 04 and 05 lie in a small patch of colonizing forest (9.7 ha) within compartment K30, as revealed by the pre-logging map (Figure 3-1). Without having considered the pre-logging forest type of these plots, I would have been unable to explain why these two plots clustered as they did. Knowledge of local habitat heterogeneity can even be used to explain why some plots are more representatives that others for a given cluster of the Ward classification. For example, Plot 07 was the least representative of Cluster 1 because unlike other plots in this cluster it lies near the Nyakagera River and would thus be subject to unique soil and moisture conditions (Figure 3-1). Understanding of pre-logging conditions thus provided useful insights on past and present patterns of forest community composition.

3.4.3 Indicator species analysis

The indicator species analysis identified indicator species or combinations of species that characterize each Ward cluster and logging compartment, as well as the associated positive predictive (A) and fidelity (B) values, and respective confidence intervals for each indicator (Table 3-6). On average, grouping plots by Ward clusters had higher positive predictor and fidelity values and smaller confidence intervals than grouping plots by logging history. This reinforces the observation that grouping plots by logging compartments had more internal heterogeneity than grouping by Ward clustering.

3.4.3.1 Indicators of clusters

One indicator was selected for Cluster 1: *Strombosia scheffleri* Engl. (Olacaceae), a tall (30 m) shade-bearing tree with seeds dispersed by birds, primates, and bats. It was harvested from Kibale (Osmaston 1959, Kingston 1967) but at extremely low levels from K14 (0.01 m3/ha) and not at all from K15 (Skorupa 1988). *Strombosia* was found in every plot in Cluster 1 (A=1.00; Table 3-6). All but one Cluster 1 plots were found in compartments K30 and K14 (the other was the southernmost in Mikana; Figure 3-1). The Cluster 1 plots in K30 fell in mixed *Parinari* forest (type K2) while Cluster 1 plots in K14 fell in both mixed *Parinari* forest and, to a lesser degree, *Parinari-Pouteria* forest (type K1; Figure 3-1). My result of *Strombosia* indicating Cluster 1 confirms pre-logging records showing that it was twice as abundant throughout mixed *Parinari* forest (type K2) than in *Parinari-Pouteria* forest (type K1), specifically in the *Parinari-Carapa-Strombosia* subtype (K2a) where basal area and stem density were six and ten times higher (Appendices 17 and 18 in Kingston 1967).

Three indicators were identified for Cluster 2: *Euadenia eminens,* the combination of *Celtis africana + Neoboutonia macrocalyx,* and *Cassipourea ruwensorensis. Euadenia eminens* (Capparaceae) is a short (5 m), shade-tolerant, non-timber species dispersed by birds and primates. *Euadenia* was a good predictor of Cluster 2 but was not found in every Cluster 2 plot (Table 3-6). *Celtis africana* (Cannabaceae) is a tall (35 m) shade-bearing tree with seeds dispersed by many small and large animals; it was harvested in Kibale including from compartments K14 and K15 (Skorupa 1988). Before logging, the stem density and basal area and of *C. africana* in mixed *Parinari* forest were three and four times higher than in *Parinari-*

Pouteria forest, particularly in the *Parinari-Carapa-Strombosia* subtype (Appendices 17 and 18 in Kingston 1967). Harvest records reflect this, with more than ten times the volume of *C. africana* removed from K14 (mostly mixed *Parinari* forest) than K15 (*Parinari-Pouteria* forest) (Skorupa 1988). Therefore, while most Cluster 2 plots are in *Parinari-Pouteria* forest, and there was more *C. africana* in mixed *Parinari* forest before logging, the fact that *C. africana* still emerges as an indicator of Cluster 2 may reflect that it was removed from the Cluster 2 plots in compartment K14 *sensu lato* and not from compartment K15. That *C. africana* is part of the indicator species combination with *N. macrocalyx* is interesting; it does not mean that the two species are necessarily associated, but rather that together they indicate Cluster 2 plots. *Neoboutonia macrcalyx* (Euphorbiaceae) is a medium-sized non-timber tree with unusually low wood density (0.33 g/cm3 oven dry mass/fresh volume; Chave et al. 2009, Zanne et al. 2009). It is a non-pioneer light demander frequently associated with waterlogged soil or the edges of swamps in Kibale (Oates 1974, Struhsaker 1975). *Neoboutonia* was not found in the two Cluster 2 plots in K30 (Plots 04 and 05). Of the three indicators for Cluster 2, the *Celtis africana* + *Neoboutonia macrocalyx* combination has the lowest fidelity value, meaning it was not found in every Cluster 2 plot. Finally, *Cassipourea ruwensorensis* (Rhizophoraceae) is a medium-sized (12 m) non-timber, shade-bearing species with average value fidelity to Cluster 2 plots.

Only one indicator was selected for Cluster 3: *Uvariopsis congensis* (Annonaceae). *Uvariopsis congensis* is a short, non-timber shade-bearing tree with synchronous fruiting. Previous work found it to be the most abundant forest species in Kibale (60.4 trees ha−1), throughout the park except in the far north and with a strongly clumped (patchy) distribution (Dominy and Duncan 2002, Chapman et al. 2005a). There was unusually high mortality of *Uvariopsis* in K15 between 1989 and 1999 (Chapman and Chapman 2004). *Uvariopsis* was an unusually good indicator for Cluster 3, having high positive predictive and fidelity values (Table 3-6).

3.4.3.2 Indicators of logging compartments

The two indicators selected for the unlogged compartment K30 were *Leptonychia mildbraedii* (Malvaceae) and *Ilex mitis* (Aquifoliaceae). *Leptonychia mildbraedii* is a short (10 m), non-timber shade-bearing tree. *Ilex mitis* is a tall (24 m) non-timber species that is a non-pioneer light demander (NPLD). Neither was a particularly good predictor, nor particularly faithful, to compartment K30 (Table 3-6).

The sole indicator selected for the lightly logged area K14 *sensu stricto* was *Vepris* (*Teclea*) *nobilis* (Rutaceae). *Vepris nobilis* is a short, shade-bearing non-timber tree. It was very faithful (*i.e.,* restricted) to compartment K14, but not a particularly good predictor (Table 3-6).

The two indicators selected for the moderately logged area Mikana were the two-species combination of *Albizia grandibracteata* + *N. macrocalyx*, and the three-species combination of *Blighia unijugata* + *Chaetachme aristata* + *C. ruwensorensis*. The number of indicators reflects the heterogeneous species composition of Mikana plots. *Albizia grandebracteata* (Leguminosae) is a tall non-pioneer light demanding tree (Sheil et al. 2000, Poorter et al. 2004), recorded as harvested in Kibale but not in compartments K14 or K15 (Table 2.1 in Skorupa 1988). Pre-logging records indicate that *A. grandibracteata* was only present in *Parinari-Olea* forest (subtype K2c) and at low density (Appendix 18 in Kingston 1967). *Blighia unijugata* (Sapindaceae) is a tall (25 m) timber tree but harvested at very low levels from compartments K14 and K15 (<0.1 m3/ha, Table 2.1 in Skorupa 1988). Historical records show low density of *B. unijugata* trees in both *Parinari-Pouteria* and mixed *Parinari* forest before logging (Appendix 18 in Kingston 1967). *Chaetachme aristata* (Ulmaceae) is a short (10 m), non-timber, understory tree. Overall, the *B. unijugata* + *C. aristata* + *C. ruwensorensis* indicator was a poorer predictor and less faithful to Mikana than the other indicator (Table 3-6). Overall, the *A. grandibracteata* + *N. macrocalyx* indicator was the best predictor of its compartment, but it was not found in all Mikana plots (Table 3-6).

The indicators selected for the heavily logged compartment K15 were *Cordia africana*, and *Cassipourea ruwensorensis* + *Myrianthus arboreus*. *Cordia africana* (Boraginaceae) is a medium-sized (15 m), non-pioneer light-demander, non-timber species. *Myrianthus arboreus* (Urticaceae) is a medium-sized (15 m) non-timber tree found in swamps and swamp forest. Both were average indicators for, and had low fidelity to, compartment K15 (Table 3-6).

3.4.3.3 Characterizing clusters

Using data on species composition, the indicator species analysis, and information on baseline conditions, I interpret forest in the clusters as follows. I call Cluster 1 the '*Trilepisium* cluster': most plots in Cluster 1 likely consist of *Parinari-Carapa-Strombosia* forest (subtype K2a) and are influenced by the dominance of *Trilepisium madagascernsis* (Figure 3-5). I call Cluster 2 the 'heavily disturbed cluster': most plots fall in the moderately or heavily logged *Parinari-Pouteria* forest (type K1). I call Cluster 3 the '*Uvariopsis* cluster': most plots are composed of an unknown subtype of mixed *Parinari* forest (type K2) and heavily influenced by the dominance of *Uvariopsis congensis* (Figure 3-5).

3.5 Discussion

My analysis showed that variation in the tree community over the 24-year study period (temporal heterogeneity) paled by comparison to variation across the 7 km^2 study area (spatial heterogeneity). Furthermore, the geographic resolution of this spatial heterogeneity is finer than the scale of the forestry compartments. In effect, each forestry compartment was composed of multiple coherent patches of forest such that tree communities within compartments cannot be considered internally homogenous. I was not surprised to find similar tree communities within the heavily (compartment K15) and moderately (Mikana) logged areas, commensurate with previous research in Kibale (Chapman and Chapman 1997, Bonnell et al. 2011). Nor was I surprised to find heterogeneity within the lightly logged area, since timber harvest in compartment K14 was quite patchy (Oates 1974, Kasenene 1987, Chapman and Chapman 1997, Struhsaker 1997). But I did not expect to find the greatest spatial variation in tree communities within the unlogged area. Indeed, differences within the unlogged compartment K30 were i) greater than across the other three disturbed areas combined, and b) greatest across a short distance (i.e., Plots 04 and 05 vs. Plots 02, 03, and 06, Figure 3-2). Studies designed to test the effects of disturbance often assume that pre-disturbance conditions in each treatment were equivalent (Willott 1999, Barlow and Peres 2004, Potts 2008, Stokes et al. 2010, Potts 2011, Laufer et al. 2013). My analysis shows that this assumption is not always valid, even in an area as well-studied as the northwestern part of Kibale National Park.

3.5.1 Predominance of spatial heterogeneity at local scales

Kibale researchers design comparative research studies within the logging compartment framework because this was the basis for historical timber harvest (Kingston 1967). Although many historical records were destroyed during Uganda's civil war, differences in harvest volume, post-harvest damage and recovery have been documented for a number of compartments (Kasenene 1987, Skorupa 1988, Struhsaker 1997; Table 3-1). There are also summary data available on baseline forest conditions, which is useful for studying forest recovery after differing logging intensities. During 1954-56 (prior to logging), aerial and exhaustive ground surveys measured and mapped the distribution of forest types throughout what was then the Kibale Central Forest Reserve. This work also defined the compartment boundaries compartments and recorded variation in the number and size of 29 commercially harvested species among different forest types (Osmaston 1959, Uganda Forest Department 1960, Kingston 1967) (Tables 3-2 and 3-3, Figure 3-1). These surveys reported four unequivocally distinct kinds of forest in northwestern Kibale: *Parinari-Pouteria* (type K1), *Parinari-Carapa-Strombosia* (type K2 subtype a), *Parinari-Olea* (type K2 subtype b), and *Parinari*-Mixed (type K2 subtype c) forest (Figure 3-1). Total stem density was three-quarters higher, and basal area twice as high, in *Parinari-Carapa-Strombosia* forest than in the other three types; this was particularly so for the dominant species *Parinari excelsa, Pouteria altissima, Strombosia scheffleri, Carapa procera,* and *Olea welwitschii* (Appendices 12 and 17 in Kingston 1967). These records parallel my finding that Cluster 2 forests – predominantly in the northern part of compartment K30 – were indicated by *S. scheffleri* (Table 3-6, Figure 3-1), meaning that this area is likely forest type *Parinari-Carapa-Strombosia* (type K2 subtype a).

In addition to pre-logging records, early Kibale researchers reported significant variation in tree species composition and size, canopy height, and thickness of the understory of unlogged forest around Kanyawara (i.e., compartment K30; Waser and Floody 1974, Struhsaker 1975, Oates 1977). Most agreed that such heterogeneity reflected local differences in topography, drainage patterns, edge effects, successional stage, and history of small-scale pit-sawing as well as large-scale commercial felling (Waser 1974, Rudran 1977, Skorupa 1988), although some felt the effect of logging outweighed the other factors (Kasenene 1987).

This initial, detailed appreciation of the nature of the unlogged forests in northwestern Kibale has somewhat faded over time, perhaps because access to historical documents is limited (i.e., Osmaston 1959, Uganda Forest Department 1960, Kingston 1967). Some researchers acknowledge the difficulty of verifying differences between the unlogged and logged areas prior to logging and i) assume the differences are primarily due to logging (Chapman and Chapman 2004), or ii) that there would have been only minor variation in pre-logging forest structure because the compartments are adjacent, and because there are few discernible physiogeographic differences over the relatively small area (e.g., Chapman et al. 2010b). But generally, when pre-logging conditions are reported for Kanyawara, researchers cite these same early management plans (i.e., Osmaston 1959, Kingston 1967) as attesting that the different types or subtypes of *Parinari* forest were very similar (±5%) in composite measures of forest structure such as stem density, basal area, canopy cover (Skorupa and Kasenene 1984, Skorupa 1986, Skorupa 1988, Chapman and Chapman 1997, Sekercioglu 2002, Bonnell et al. 2011) and species diversity (Kasenene 1987, Mucunguzi 2007). For this reason, some authors contend that composite structural measures can be validly compared between compartments K14, K15, and K30 (Skorupa 1988, Bonnell et al. 2011). Skorupa (1988) cautioned that such comparison would be invalid if focused on individual or combinations of a few species. Still other reserachers emphasize the importance of investigating the extent of natural variation within unlogged forest, and using it to account for measured differences between logged ‘treatment’ and unlogged ‘control’ site, but acknowledge that obtaining baseline data on pre-logging conditions can be difficult (Potts 2011). My results demonstrate strong spatial patterns in tree heterogeneity within compartments, specifically in unlogged compartment K30. Combined with the abovementioned information on forest distribution and composition before logging, this questions the assumption of compartment comparability prior to logging. Furthermore, the method I used demonstrates that, while baseline information is necessary to interpret observed differences in vegetation, it is not required to identify differences. Furthermore, unlike the pre-logging records restricted to commercially harvested species, my analysis is more sensitive to the high degree of variability found in many tropical rainforests, where many species are rare and localized, small-scale disturbances can be frequent.

The spatial heterogeneity found in the unlogged parts of northwestern Kibale is on par with information on species distributions in other tropical rainforests. Tropical rainforests commonly have non-random distributions of trees because of edaphic gradients and environmental or topographic conditions that include gaps, soil moisture, canopy height, and soil fertility (Clark et al. 1998, Condit et al. 2000), as well as the influence of animal seed dispersal (Janzen 1970, Seidler and Plotkin 2006). The high degree of small-scale spatial heterogeneity I document in northwestern Kibale is similar to patterns found in central, unlogged Kibale (Potts 2008), and other rainforests in Africa (Hart et al. 1989, Lovett et al. 2000, Newbery et al. 2013), the Neotropics (DeVries et al. 1997, Clark et al. 1998) and Asia (Webb and Peart 2000); notable exceptions in the region include mono-dominant forests in Uganda and Democratic Republic of Congo (Eggeling 1947, Hart et al. 1989, Pitman et al. 2005). Across four protected forests in western Uganda, including Kibale, most tree species have large geographic ranges and broad habitat affinity. Nonetheless, there is considerable local variation within a given forest (Eilu et al. 2004b). Thus, the spatial scale of sampling design and data analysis is important: although there is high landscape homogeneity, forests exhibit high local heterogeneity.

It is well known that small- and large-scale heterogeneity affects population dynamics, community structure, and ecosystem function and processes in forest systems (Turner 1989, Pickett and Cadenasso 1995, Fortin and Dale 2005, Haas et al. 2011, Turner et al. 2013). Arguably, forests with more heterogeneous structure better conserve biodiversity (Tews et al. 2004), although the distinction should be made between forest-specialist and -generalist species as greater species richness might not be the management goal. Local environmental factors, most notably soil pH, and regional environmental factors like rainfall, elevation, and temperature, play an important role in determining forest composition (Eilu et al. 2004a). Across Kibale, there are recorded and correlated differences in elevation, rainfall, and temperature between the long-term field sites: it tends to be higher, cooler, and wetter at Kanyawara where this study was conducted than at Ngogo, which is approximately 10 km away in the center of the park (Appendix 2) (Lwanga 2003). Human disturbance interacts with these abiotic factors at small and large spatial and temporal scales. For example, the mosaic pattern of evergreen and deciduous trees in Central African forest is thought to reflect historical climate change, with lower rainfall favouring deciduous species while higher rainfall favored evergreen species (Maley 2002). Variation in forest composition at another long-term study site in Uganda, the Mpanga Central Forest Reserve, is also thought to reflect pit-sawing in the first half of the 20th century (Taylor et al. 2008). In addition to edaphic and topographic differences, possible sources of small-scale heterogeneity in this part of Kibale National Park include natural disturbances like gaps created by wind-throw (Kasenene 1987, Zanne and Chapman 2005), pathogens and rot (Kingston 1967), feeding behaviour of elephants (Wing and Buss 1970, Struhsaker et al. 1996), limited seed dispersal (e.g., clumped distribution of Balanites wilsoniana, Cochrane 2003), differential survival with intra- and inter-species competition (Clark 2010), and human disturbances such as negative effects of exotic plantations on adjacent forest (Struhsaker et al. 1989), legal and illegal timber harvest (Struhsaker 1997, MacKenzie et al. 2012), and positive or negative interactions therein.

Local variability in forest is important for both social and ecological reasons. The reason that so much valuable timber is found in Kibale and other western Ugandan forests is likely a reflection of forest expansion and contraction as a result of small- and large-scale disturbances over the past few centuries; climax forest, reached in the absence of frequent disturbance, contains relatively less valuable timber (Howard 1991). Furthermore, climax forest does not provide diverse or rich food for elephants, themselves a disturbance agent responsible for considerable local heterogeneity in tropical rainforest (Wing and Buss 1970). In Kibale, the frequency of small-scale disturbances has decreased over the last few decades. Preventing fire has resulted in marked forest regeneration in the grasslands (Lwanga 2003, Omeja et al. 2011); although we can speculate, we do not yet know what effect the reduced elephant populations has and will continue to have on forest (estimates of 400-600 in the early 1960s, approximately 100 in 1988, and approximately 400 in 2005: Wing and Buss 1970, Struhsaker et al. 1989, Wanyama et al. 2010). In the current study, it is not possible to attribute the heterogeneity we found to any specific set of factors aside from logging. But, whatever the sources of heterogeneity in the tree community, there is no doubt that variation at the local scale (sub-compartment) predominates in northwestern Kibale. This variation needs to be acknowledged in designing and interpreting observational studies, or ecologists risk masking or misinterpreting true population and community dynamics of logged and unlogged forests.

3.5.2 Accounting for local heterogeneity in observational studies

Before we can fully characterize and understand the ecological implications of environmental heterogeneity, sampling and analytical procedures must enable researchers to identify and separate it from other factors. Ideally, spatial heterogeneity should be explicitly considered in the sampling design (Willott 1999, Barlow and Peres 2004, Stokes et al. 2010, Potts 2011, Laufer et al. 2013). This is difficult because landscape research and management are frequently conducted at scales larger than patches, in units based on human constructs (*e.g.,* forestry cut-blocks or agricultural fields), and without knowledge of baseline conditions. This is particularly the case for ecological restoration, which must consider the scales at which ecological processes operate both temporally (*e.g.,* disturbance regimes) and spatially (*e.g.,* at the level of ecosystems and landscapes) (Callicott 2002). However, failing to acknowledge and account for spatial heterogeneity can lead researchers to misinterpret the results of observational studies.

It is especially important to design studies to account for local spatial variability in heterogeneous habitats, such as tropical forests. One way that researchers can take this variability into account is by carefully choosing and defining the scale of their analysis - distinguishing patchiness at local scales from trends at larger scales depends on a number of factors including the extent of the study area, and the size (grain), number, and shape of the sampling units as well as their spatial arrangement (Fortin and Dale 2005). Choosing the size of a study area should be decided relative to the ecological process of interest: a phenomenon could look homogenous or heterogeneous depending on whether it is studied at a spatial scale too small or too large to detect the underlying ecological pattern (*i.e.,* one forest patch vs. a mosaic of forest patches). Similarly, sampling units that are too small will contain too much variability for meaningful comparison, whereas ones that are too large will reduce variability and be unable to detect interesting patterns. In general, smaller sampling units would be preferred as they can be nested within larger ones (Fortin and Dale 2005), and small sampling units will tend to be within a habitat patch while large sampling units will tend to contain multiple patches (Forman 1995). The choice about the number of sampling units is often a decision based on logistical constraints (time, money, ease of access), but must be sufficient to detect spatial patterns (Fortin and Dale 2005). Any sampling design meant for long-term data collection should be periodically assessed and modified to ensure it meets the objectives of the study (Stokes et al. 2010).

In this study, the decision of where to locate study plots was based on the extensive trail system in Kanyawara. The trail system itself is a 50 m x 50 m grid running along NW-SE and NE-SW compass bearings; it tends to avoid some areas such as very swampy valley bottoms (Chapman and Chapman 1997). It was designed to follow and observe primates in thick vegetation – early descriptions of fieldwork in Kanyawara before the trail system describe that it was "*impossible to move unrestrictedly through the vegetation*" and that the trail system allowed researchers to "*follow monkeys without creating undue noise… and map positions of monkeys, vegetation, and physical features of the environment*" (Oates 1974). Although my study plots were placed randomly along the trail system, the regular nature of the grid imposes structure that can influence the results when sampling vegetation. In addition, comparing treatments between study sites requires testing for homogeneity. If environments are heterogeneous, confounding environmental factors may be identified and controlled for whenever possible, such as geography (*e.g.,* slope, aspect, and elevation) and seasonality (*e.g.,* phenology). However, logged areas are generally not selected from forest at random but instead more often are on flatter areas with high concentrations of commercially valuable species (Laufer et al. 2013). Similarly, areas are sometimes selected for conservation based not only on their ecological attributes, but also on their degree of accessibility or usefulness to people (Joppa and Pfaff 2009). In Kibale, compartment K30 was set aside as a nature reserve to be representative of the forest (Osmaston 1959, Howard 1991), but perhaps this decision was also influenced by K30's rugged terrain, compared to flatter terrain of the heavily logged compartment K15 (Dranzoa 1998) .

The problematic effects of not acknowledging or accounting for heterogeneity in vegetation can be magnified when applied to animal studies, since temporal and spatial variation in habitat affects the structure and behaviour of animal communities (Potts 2008, Louys et al. 2011). In Kibale, tree communities sampled along the 25 plots in this study are not only used to assess forest recovery following logging, but also to assess changes in phenology (Chapman et al. 1999), the availability of primate foods, and subsequent implications for primate populations (Chapman et al. 2010b, Bonnell et al. 2011). However, in some compartments there is more overlap in the trails used to count primates (census trails) and those used to estimate primate foods (the 25 tree plots in this study) (Figure 5.9 in Struhsaker 1997). There is good overlap between census trail and tree plots in the two logged compartments (K14 *sensu lato* and K15). However, the census trail used in the unlogged compartment K30 skirts the southernmost tree plots: most of Cluster 3 and the 9.7 ha patch of early colonizing forest (Figure 3-1). While the distance between these plots and the nearest point on the census trail is not large (100-400 m), that area contains two of the most disparate parts of K30. Without acknowledging the spatial heterogeneity within a single logging compartment, we risk drawing spurious conclusions about how changes in food supply over the whole compartment will affect primates surveyed in only part of the compartment (Chapman et al. 2010b). Heterogeneity cannot be ignored without significant risk, so we need to allow for it during sampling and/or analyses.

Fortunately, statistical methods exist that allow us to account for spatial heterogeneity after sampling, including spatial statistics (Fortin and Dale 2005) and canonical analyses. Whereas non-spatial statistics describe and summarize a large set of data values, or explore how representative the sample is of a larger population, spatial statistics are designed to be used with geographic data (*e.g.,* location). Spatial statistical methods allow us to measure, test, and predict spatial patterns, structures, and relationships among variables (Legendre and Legendre 2012). On the other hand, canonical analyses are useful when we want to preserve the original sampling structure (*i.e.,* group plots by logging history), since they work to minimize the differences within a group and maximize the difference between groups (McGarigal et al. 2000). Said another way, if groups with different treatments contain internal heterogeneity (*i.e.,* compartments have different logging histories but contain multiple clusters of different tree assemblages), canonical methods allow the user to shrink the difference within treatments (clusters) and instead examine the signal between treatments (logging).

In this chapter I identified considerable heterogeneity, including discrete patches, in tree assemblages across a relatively small area. Contrary to the assumptions of previous research, I found more heterogeneity within the unlogged area, more so than within or among all the other treatments combined. Such heterogeneity was based on features of the tree assemblages such as species composition and size, rather than on treatment differences in logging disturbance. I used historical information on baseline conditions to interpret the heterogeneity but not to identify it. The type of forest variation that I identified has always been present in tropical forests like Kibale, but it exists on spatial scales smaller than typical management units. Research designed to examine effects of disturbance on flora and fauna will be confounded by this heterogeneity unless researchers use sampling or statistical techniques to account for it. Without identifying the intra-compartment variation, we focus on the forest but miss variation between the trees.

3.6 Tables and figures

3.6.1 Table captions

Table 3-1. Physical description and logging history in the three study compartments in Kibale National Park, Uganda.

Table 3-2.Coverage of forest types in logging compartments before harvest. Note that Mikana is not a clearly defined physical area, and thus cannot be separated from compartment K14 *sensu lato* in logging records. See Appendix 3 for details on baseline data.

Table 3-3. Plots grouped by Ward clustering vs logging compartment. Pre-logging forest type was determined from aerial photographs and extensive timber enumeration surveys conducted from 1954-56 (Osmaston 1959, Uganda Forest Department 1960, Kingston 1967). Plot 12 was removed from the dataset as its logging history could not be precisely determined.

Table 3-4. List of tree species recorded over the course of this study. Stem frequency, mean and maximum diameter-at-breast-height (DBH, at 1.2 m) are from the 2013 survey of 25 0.2-ha permanent sampling plots (total area=5.0 ha). Plant nomenclature follows The Plant List (2013).

Table 3-5. Results of the Principal Components Analysis of the Euclidean distance matrix. The Euclidean distance matrix was based on relative dominance ratio of species in each plot. The results show which five plots are most representative of their cluster (*i.e.,* have the shortest distance to the center of their cluster in the PCA), and which five plots are most unlike the other clusters (*i.e.,* have the largest distance to the center of other clusters in the PCA). Plots most representative of their cluster Plots least like other clusters.

Table 3-6. Results of the indicator species analysis. Indicators (species and combinations of species) were derived based on grouping the plots either by clusters derived from Ward's hierarchical agglomerative clustering (based on a Euclidean dissimilarity matrix of the relative dominance ratios for each species) or by logging histories. A=positive predictive value (a measure of how indicative that species is of its group), B = fidelity (the probability of finding that species in the target group of sites). UL=unlogged, LL=lightly logged, ML=moderately logged, HL=heavily logged.

Table 3-1. Description and logging history of study compartments in Kibale National Park, Uganda

							No. commercial stems/ha removed based on:		% reduction in canopy		
Site	Area[a] (ha)	Elevation range (m)	Logging intensity	Date logged	No. tree species removed[b]	Volume harvested (m^3/ha)	Volume conversion	Stump count	All species	Commercial species	Mean gap size (range)[c] (m^2)
K30	360	1397-1562	Unlogged	-	-	-	-	-		-	256 (100-663)
K14[d]	410	1454-1559	Light[e]	05-12/1969	23	14	5.1	3.0	25	49.5	467 (75-1800)
K15	282	1440-1510	Heavy	09/1968-04/1969	18	21	7.4	8.6	47	59.7	1307 (73-7100)

Adapted from Kasenene 1987, Skorupa 1988, and Table 3.1 in Struhsaker 1997.

[a] Area estimates based on digitizing logging compartment boundaries (Appendix 3)

[b] Nine species made up >90% of total out-take: *Celtis africana, Chrysophyllum gorungosanum, Fagaropsis angolensis, Newtonia buchananii, Olea welwitschii, Parinari excelsa, Pouteria (Aningeria) altissima, Prunus africana (Pygeum africanum),* and *Zanthoxylum leprieurii (Fagara angolensis)* (Table 2.1, Skorupa 1988)

[c] Gap sizes measured in 1989, twenty years after logging (Kasenene 1987)

[d] Including Mikana (K14 *sensu lato*)

[e] Harvest estimates are for the compartment as a whole (*i.e.,* K14 *sensu lato*)

Table 3-2. Coverage of forest types in logging compartments before harvest

Compartment [a]	Forest type	Area (ha)	% of compartment
K30 (UL)	K2 mixed *Parinari* subtypes	347.3	96.4
	K10 Colonizing forest stage 2	9.7	2.7
	Scrub	3.2	0.9
K14 (LL) [b]	K1 *Parinari-Pouteria*	243.8	59.5
	Scrub	72.4	17.6
	K2 mixed *Parinari* subtypes [c]	43.2	10.5
	Papyrus swamp	35.1	8.6
	Swamp forest	11.7	2.8
	Uncategorized forest	3.8	0.9
K15 (HL)	K1 *Parinari-Pouteria*	220.2	78.4
	Uncategorized forest	25.1	8.9
	Swamp forest	23.2	8.3
	K10 Colonizing forest stage 2	7.7	2.7
	K2 mixed *Parinari* subtypes	4.7	1.7

Sources: (Osmaston 1959, Uganda Forest Department 1960, Uganda Department of Lands and Surveys 1965)

[a] LL= lightly logged, HL=Heavily logged, UL=Unlogged

[b] Including Mikana (K14 *sensu lato*)

[c] Forest type K2 includes three subtypes: K2(a) *Parinari-Carapa-Strombosia*, K2(b) *Parinari-Olea*, and K2(c) *Parinari*-Mixed

Table 3-3. Plots grouped by Ward clustering versus logging compartment

	Grouped by			
Plot	Cluster	Compartment	Logging intensity [a]	Pre-logging forest type [b]
07	1	K30	unlogged	K2 mixed *Parinari* subtypes
08	1	K30	unlogged	K2 mixed *Parinari* subtypes
09	1	K30	unlogged	K2 mixed *Parinari* subtypes
10	1	K30	unlogged	K2 mixed *Parinari* subtypes
11	1	K30	unlogged	K2 mixed *Parinari* subtypes
14	1	K14	light	K1 *Parinari-Pouteria* & K2 mixed *Parinari* subtypes
15	1	K14	light	K1 *Parinari-Pouteria*& K2 mixed *Parinari* subtypes
18	1	Mikana	moderate	K1 *Parinari-Pouteria*
04	2	K30	unlogged	K10 Colonizing forest type 2
05	2	K30	unlogged	K10 Colonizing forest type 2 & K2 mixed *Parinari* subtypes
13	2	K14	light	K2 mixed *Parinari* subtypes
17	2	K14	light	K2 mixed *Parinari* subtypes
19	2	Mikana	moderate	K1 *Parinari-Pouteria*
20	2	Mikana	moderate	K1 *Parinari-Pouteria*
21	2	Mikana	moderate	K1 *Parinari-Pouteria*
22	2	K15	heavy	K1 *Parinari-Pouteria*
23	2	K15	heavy	K1 *Parinari-Pouteria*
24	2	K15	heavy	K1 *Parinari-Pouteria*
25	2	K15	heavy	K1 *Parinari-Pouteria*
26	2	K15	heavy	K1 *Parinari-Pouteria*
01	3	K30	unlogged	K2 mixed *Parinari* subtypes
02	3	K30	unlogged	K2 mixed *Parinari* subtypes
03	3	K30	unlogged	K2 mixed *Parinari* subtypes
06	3	K30	unlogged	K2 mixed *Parinari* subtypes
16	3	K14	light	K1 *Parinari-Pouteria*

[a] UL=unlogged, LL=lightly logged, ML=moderately logged, HL=heavily logged

[b] Forest type K2 includes three subtypes: K2a *Parinari-Carapa-Strombosia*, K2b *Parinari-Olea*, K2c *Parinari*-Mixed. *Pouteria altissima* was formerly called *Aningeria altissima.*

Table 3-4. List of tree species recorded over the course of this study

Species	Family	Stem density (stems/ha)	Mean DBH (±Std Dev) (cm)	Max DBH (cm)
Albizia grandibracteata Taub.	Leguminosae	5.2	24.1 (10.7)	43.0
Albizia gummifera (J. F. Gmel.) C. A. Sm.	Leguminosae	0.2	10.4 (N/A)*	10.4
Antiaris toxicaria Lesch.	Moraceae	2.0	14.3 (4.3)	25.7
Apodytes dimidiata E. Mey. ex Arn.	Icacinaceae	0.4	25.3 (4.6)	28.5
Balanites wilsoniana Dawe & Sprague	Zygophyllaceae	0.4	75.0 (76.4)	129.0
Beilschmiedia ugandensis Rendle	Lauraceae	0.4	14.8 (1.1)	15.5
Bersama abyssinica Fresen.	Melianthaceae	0.4	29.0 (8.5)	35.0
Blighia unijugata Baker	Sapindaceae	3.2	19.6 (21.3)	97.4
Bridelia micrantha (Hochst.) Baill. †	Phyllanthaceae	-	-	-
Casearia battiscombei R. E. Fr.	Salicaceae	2.2	21.2 (8.0)	41.2
Cassine aethiopica Thunb.	Celastraceae	1.8	49.4 (25.3)	90.5
Cassipourea ruwensorensis (Engl.) Alston	Rhizophoraceae	5.4	13.4 (2.6)	20.7
Celtis africana Burm. f.	Cannabaceae	13.6	25.8 (15.0)	86.3
Celtis gomphophylla Baker	Cannabaceae	45.2	33.3 (19.1)	119.5
Celtis mildbraedii Engl.	Cannabaceae	0.2	22.0 (N/A)	22.0
Chaetachme aristata Planch.	Ulmaceae	13.2	18.4 (9.0)	61.0
Chionanthus africanus (Knobl.) Stearn	Oleaceae	2.2	21.4 (9.6)	43.4
Chrysophyllum spp.	Sapotaceae	2.2	49.4 (84.6)	296.8
Clausena anisata (Willd.) Hook. f. ex Benth.	Rutaceae	0.2	10.8 (N/A)	10.8
Coffea canephora Pierre ex A. Froehner	Rubiaceae	0.4	12.5 (1.3)	13.4
Cordia africana Lam.	Boraginaceae	2.4	45.8 (16.5)	92.0
Cordia millenii Baker	Boraginaceae	0.4	18.7 (8.2)	24.5
Craterispermum laurinum (Poir.) Benth.	Rubiaceae	0.6	12.9 (0.7)	13.7
Croton spp.	Euphorbiaceae	0.8	26.7 (7.2)	33.0
Dasylepis eggelingii J. B. Gillett	Achariaceae	2.0	12.8 (2.4)	17.2
Dictyandra arborescens Welw. ex Hook. f.	Rubiaceae	0.6	15.9 (7.3)	24.3
Diospyros abyssinica (Hiern) F. White	Ebenaceae	38.6	29.0 (13.6)	76.5
Dombeya mukole Mast.	Malvaceae	5.8	35.7 (13.7)	63.5

Species	Family	Stem density (stems/ha)	Mean DBH (±Std Dev) (cm)	Max DBH (cm)
Dovyalis abyssinica (A. Rich.) Warb.	Salicaceae	0.2	11.6 (N/A)	11.6
Ehretia cymosa Thonn.	Boraginaceae	1.8	28.5 (18.7)	62.0
Erythrina abyssinica DC. *	Leguminosae	-	- (N/A)	-
Euadenia eminens Hook. f.	Capparaceae	3.2	18.9 (6.4)	31.0
Fagaropsis angolensis (Engl.) H. M. Gardner	Rutaceae	3.2	21.4 (17.2)	82.0
Ficus exasperata Vahl	Moraceae	3.2	40.4 (33.0)	110.0
Ficus sur Thunb. *	Moraceae	-	-	-
Fleroya rubrostipulata (K. Schum.) Y. F. Deng	Rubiaceae	0.4	28.6 (16.4)	40.2
Funtumia africana (Benth.) Stapf	Apocynaceae	44.4	28.9 (13.3)	69.0
Harungana madagascariensis Lam. ex Poir.	Hyperiaceae	0.2	35.5 (N/A)	35.5
Ilex mitis (L.) Radlk.	Aquifoliaceae	3.4	14.6 (3.4)	24.5
Kigelia africana (Lam.) Benth.	Bignoniaceae	2.2	14.6 (2.7)	19.4
Lepisanthes senegalensis (Poir.) Leenh.	Sapindaceae	5.6	16.8 (5.7)	32.5
Leptonychia mildbraedii Engl.	Malvaceae	16.2	15.6 (4.7)	32.0
Lindackeria spp.	Achariaceae	1.0	12.1 (2.1)	14.7
Lovoa spp.	Meliaceae	1.0	13.0 (1.4)	15.0
Lychnodiscus cerospermus Radlk.	Sapindaceae	0.6	21.2 (3.5)	23.4
Macaranga schweinfurthii Pax	Euphorbiaceae	0.8	14.5 (1.7)	16.4
Maesopsis eminii Engl.	Rhamnaceae	0.8	22.2 (8.4)	28.4
Margaritaria discoidea (Baill.) G. L. Webster	Phyllanthaceae	0.8	14.3 (2.0)	17.4
Markhamia lutea (Benth.) K. Schum.	Bignoniaceae	32.6	24.9 (15.3)	118.3
Millettia dura Dunn	Leguminosae	9.2	18.0 (8.4)	51.2
Mimusops bagshawei S. Moore	Sapotaceae	4.8	39.0 (34.4)	126.0
Monodora myristica (Gaertn.) Dunal	Annonaceae	0.2	56.4 (N/A)	56.4
Morus mesozygia Stapf	Moraceae	0.4	16.2 (2.0)	17.6
Myrianthus arboreus P. Beauv	Urticaceae	6.4	19.4 (7.9)	49.0
Neoboutonia macrocalyx Pax	Euphorbiaceae	3.0	34.4 (15.2)	63.5
Newtonia buchananii (Baker) G. C. C. Gilbert & Boutiqu	Leguminosae	2.0	20.1 (16.1)	54.5
Olea welwitschii Gilg & G. Schellenb.	Oleaceae	2.4	74.8 (42.5)	136.0

Species	Family	Stem density (stems/ha)	Mean DBH (±Std Dev) (cm)	Max DBH (cm)
Oncoba routledgei Sprague*	Salicaceae	-	-	-
Oxyanthus speciosus DC.	Rubiaceae	1.0	11.7 (1.7)	14.3
Oxyceros longiflorus (Lam.) T. Yamaz.	Rubiaceae	0.4	11.1 (0.3)	11.3
Ozoroa insignis Delile	Anacardiaceae	0.2	12.0 (N/A)	12.0
Pancovia turbinata Radlk.	Brachytheciaceae	6.6	15.6 (4.9)	29.8
Parinari excelsa Sabine	Chrysobalanaceae	3.6	52.1 (58.7)	196.9
Pleiocarpa pycnantha (K. Schum.) Stapf	Apocynaceae	1.6	13.5 (2.6)	19.2
Polyscias fulva (Hiern) Harms	Araliaceae	0.6	41.6 (14.2)	51.2
Pouteria altissima (A. Chev.) Baehni	Sapotaceae	2.6	64.4 (104.3)	350.0
Premna angolensis Gürke	Lamiaceae	4.6	51.7 (39.6)	167.0
Prunus africana (Hook. f.) Kalkman	Rosaceae	0.4	51.5 (14.8)	62.0
Pseudospondias microcarpa Engl.	Anacardiaceae	2.0	74.0 (75.1)	205.0
Rauvolfia vomitoria Afzel.	Apocynaceae	0.8	22.3 (10.0)	35.5
Rothmannia urcelliformis (Hiern) Bullock ex Robyns	Rubiaceae	3.0	12.5 (2.1)	16.4
Scolopia rhaniphylla Gilg	Salicaceae	0.8	12.3 (1.1)	13.5
Shirakiopsis elliptica (Hochst.) Esser	Euphorbiaceae	0.2	10.2 (N/A)	10.2
Spathodea campanulata P. Beauv.	Bignoniaceae	0.2	55.0 (N/A)	55.0
Strombosia scheffleri Engl.	Olacaceae	16.2	33.8 (25.5)	118.0
Strychnos mitis S. Moore	Loganiaceae	2.0	34.9 (19.3)	67.7
Symphonia globulifera L. f.	Clusiaceae	0.6	32.8 (15.5)	50.0
Tabernaemontana pachysiphon Stapf	Apocynaceae	1.2	14.1 (3.7)	21.0
Tabernaemontana spp.	Apocynaceae	1.0	11.7 (1.3)	13.7
Tarenna pavettoides (Harv.) Sim*	Rubiaceae	-	-	-
Trema orientalis (L.) Blume	Cannabaceae	0.2	11.7 (N/A)	11.7
Trichilia dregeana Sond.	Meliaceae	0.2	36.2 (N/A)	36.2
Trilepisium madagascariense DC.	Moraceae	55.2	15.9 (6.2)	91.1
Uvariopsis congensis Robyns & Ghesq.	Annonaceae	43.6	16.7 (5.1)	44.9
Vangueria apiculata K. Schum.	Rubiaceae	0.8	11.9 (3.0)	16.3
Vepris nobilis (Delile) Mziray	Rutaceae	20.2	15.1 (4.2)	28.6

Species	Family	Stem density (stems/ha)	Mean DBH (±Std Dev) (cm)	Max DBH (cm)
Zanthoxylum leprieurii Guill. & Perr.	Rutaceae	0.4	16.8 (0.7)	17.3

* NA indicates that standard deviation could not be calculated, *i.e.,* there was only one individual present

† Indicates not present in 2013 survey

Table 3-5. Results of the Principal Components Analysis of the Euclidean distance matrix

Cluster 1		Cluster 2		Cluster 3	
Transect	Distance	Transect	Distance	Transect	Distance
Plots most representative of their cluster					
Mik. 18	1.43	K15.26	2.03	K30.01	0.75
K14.15	1.72	K30.04	2.16	K30.06	1.73
K30.09	1.81	Mik. 21	2.27	K30.02	1.77
K30.10	2.16	K15.23	2.57	K14.16	2.09
K30.08	2.19	K30.05	2.71	K30.03	2.74
Plots least like other clusters					
K30.07	5.20	Mik. 20	5.55	K30.02	5.31
K30.10	4.91	K15.25	5.31	K30.03	5.04
K30.11	4.82	Mik. 19	5.23	K30.06	5.02
K30.09	4.01	K15.23	4.92	K30.01	4.06
K30.08	3.90	K15.22	4.69	K14.16	3.28

Table 3-6. Results of the indicator species analysis

		Positive predictive value			Fidelity		
Grouped by	Indicator	A	Lower CI	Upper CI	B	Lower CI	Upper CI
Ward clusters							
Cluster 1	*Strombosia scheffleri**	0.712	0.612	0.798	1.000	1.000	1.000
Cluster 2	*Euadenia eminems*	0.852	0.697	0.977	0.568	0.415	0.714
	Celtis africana + Neouboutonia macrocalyx*	0.711	0.523	0.866	0.409	0.261	0.558
	Cassipourea ruwensorensis	0.707	0.598	0.794	0.727	0.578	0.857
Cluster 3	*Uvariopsis congensis*	0.893	0.863	0.923	1.000	1.000	1.000
Logging compartment							
K30 (UL)	*Leptonychia mildbraedii*	0.700	0.561	0.809	0.636	0.488	0.775
	Ilex mitis	0.673	0.543	0.814	0.614	0.458	0.769
K14 (LL)	*Vepris (Teclea) nobilis*	0.645	0.562	0.733	1.000	1.000	1.000
Mikana (ML)	*Albizia grandibracteata + Neoboutonia macrocalyx*	0.885	0.736	0.979	0.625	0.375	0.833
	Blighia unijugata + Chaetachme aristata + Cassipourea ruwensorensis	0.757	0.568	0.904	0.500	0.238	0.765
K15 (HL)	*Cordia africana*	0.732	0.592	0.863	0.600	0.375	0.824
	Cassipourea ruwensorensis + Myrianthus arboreus	0.719	0.524	0.833	0.650	0.429	0.850

*Timber species harvested in compartments K14 *sensu lato* and/or K15

3.6.2 Figure captions

Figure 3-1.Map showing location of Kibale National Park, Uganda, and study area. a) Kibale National Park within Uganda, b) Kanyawara study area in northwestern Kibale (red rectangle), and c) 26 permanent study plots and forest types circa 1955 (based on descriptions in Osmaston 1959, and map from Uganda Forest Department 1960). Plots 01-12 are in compartment K30, Plots 13-21 are in compartment K14, and Plots 22-26 are in compartment K15. Plot 12 was removed from analysis as on close examination it became clear that logging in compartment K14 had crossed the road into compartment K30.

Figure 3-2.Dendrogram of tree assemblages based on Ward's hierarchical agglomerative clustering. The method provides a hierarchy depicting for the similarity of plots. Initially, each plot is treated as a singleton cluster and then successively merged into pairs of cluster such that each merger minimizes the increase in the total within-group error sum of squares, based on the Euclidean distance between centroids. The method tends to produce homogeneous clusters and a symmetric hierarchy.

Figure 3-3. Factor map of tree communities. The distribution of the points illustrates relatedness among the 25 permanent sampling plots defined by the three Ward's clusters. The distance between each plot and the center of its cluster (the square, called the barycenter) indicates their degree of representatiblity of that cluster. In Cluster 3, plot K30.01 is the most representative. Note that several plots in Cluster 2 have similar representatiblity (*i.e.,* they are similar distances to the center).

Figure 3-4. Principal Components Analysis of plots comparing grouping by Ward's clusters and logging history. Note degree of separation amongst groups ordinated with tree species composition (relative dominance ratio) of permanent sample plots. Tree communities were sampled in 25 permanent sampling plots (10 x 200 m). Plots are grouped by a) Ward's clusters: Cluster 1="*Trilepisium* cluster", Cluster 2="Heavily disturbed cluster", and Cluster 3= "*Uvariopsis* cluster", and b) logging history (compartments): UL=unlogged, LL=lightly logged, ML=moderately logged, HL=heavily logged. The clusters are well defined and separated from each other, whereas the logging compartments have a great deal of overlap. Note the variation within the unlogged compartment (demonstrated by the large polygon, which overlaps with all and most of the lightly and moderately logged polygons).

Figure 3-5. Proportion of *Trilepisium madagascariense* and *Uvariopsis congensis* in plots. Note near mutual exclusion in unlogged compartment K30: where either *T. madagascariense* (black bars) or *U. congensis* (grey bars) is dominant, the other is infrequent or absent altogether. Plots with high proportion of *T. madagascariense* tend to be in Cluster 1 (*i.e.,* plots 08-11, 14, 15, 18), plots with high proportion of *U. congensis* tend to be in Cluster 3 (*i.e.,* lots 01-03, 06, 16), and plots with few or none of either species are in Cluster 2 (*i.e.,* 04, 05, 19-26). Data shown are from 2013 survey (randomly chosen from four survey years).

Figure 3-1. Map of study area in Kibale National Park, Uganda

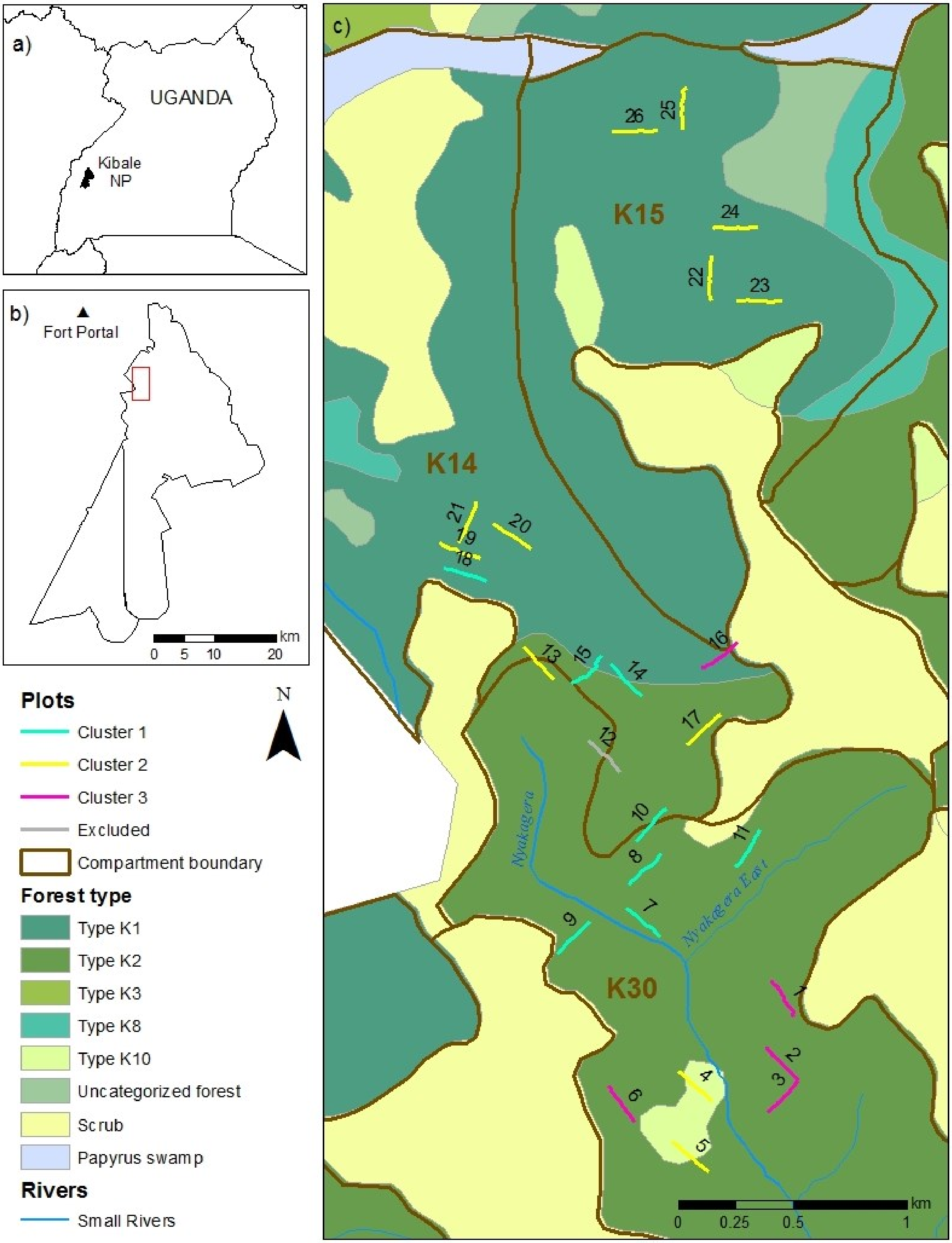


Figure 3-2. Dendrogram of tree assemblages based on Ward’s hierarchical agglomerative clustering

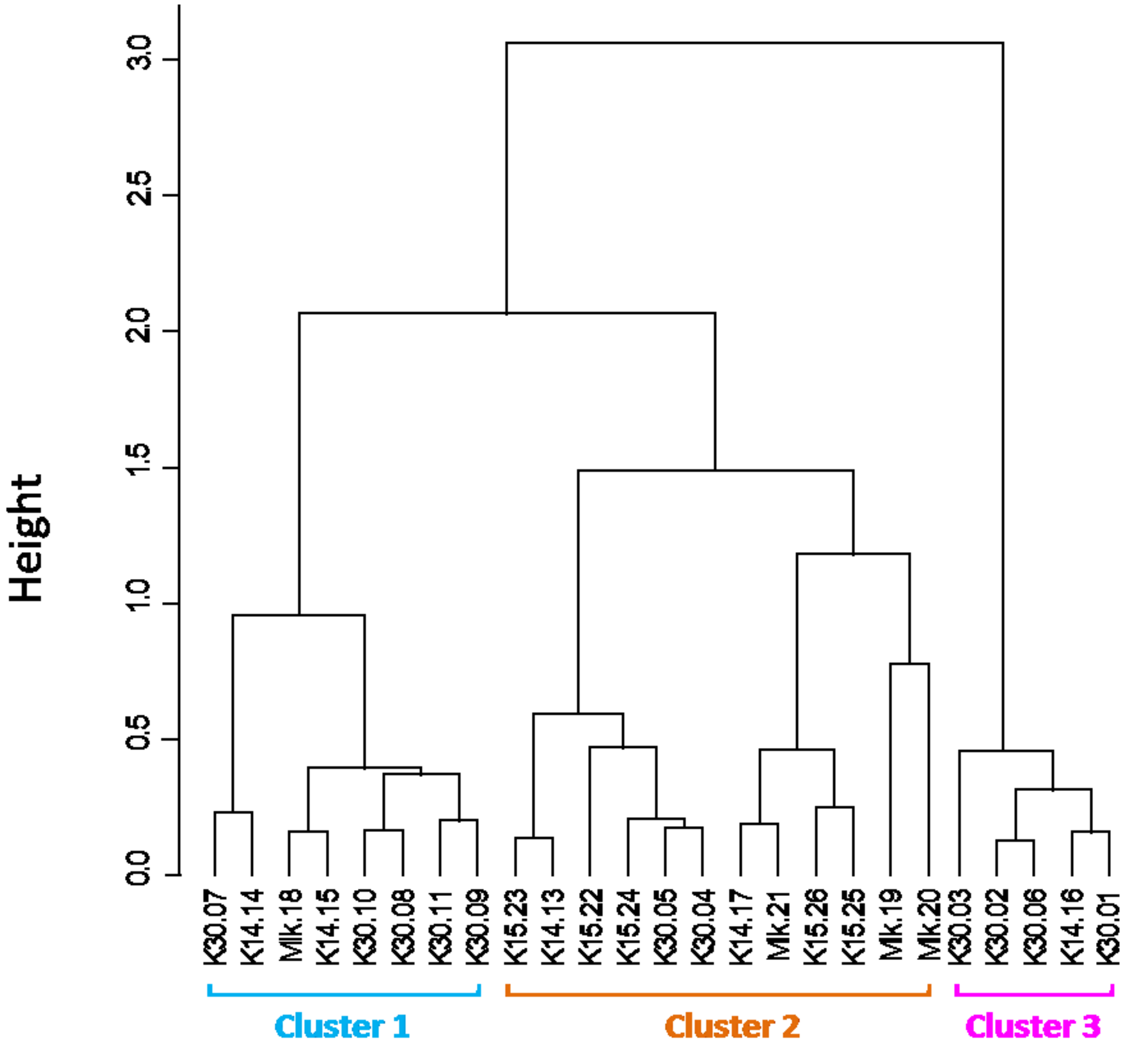


Figure 3-3. Factor map of tree communities

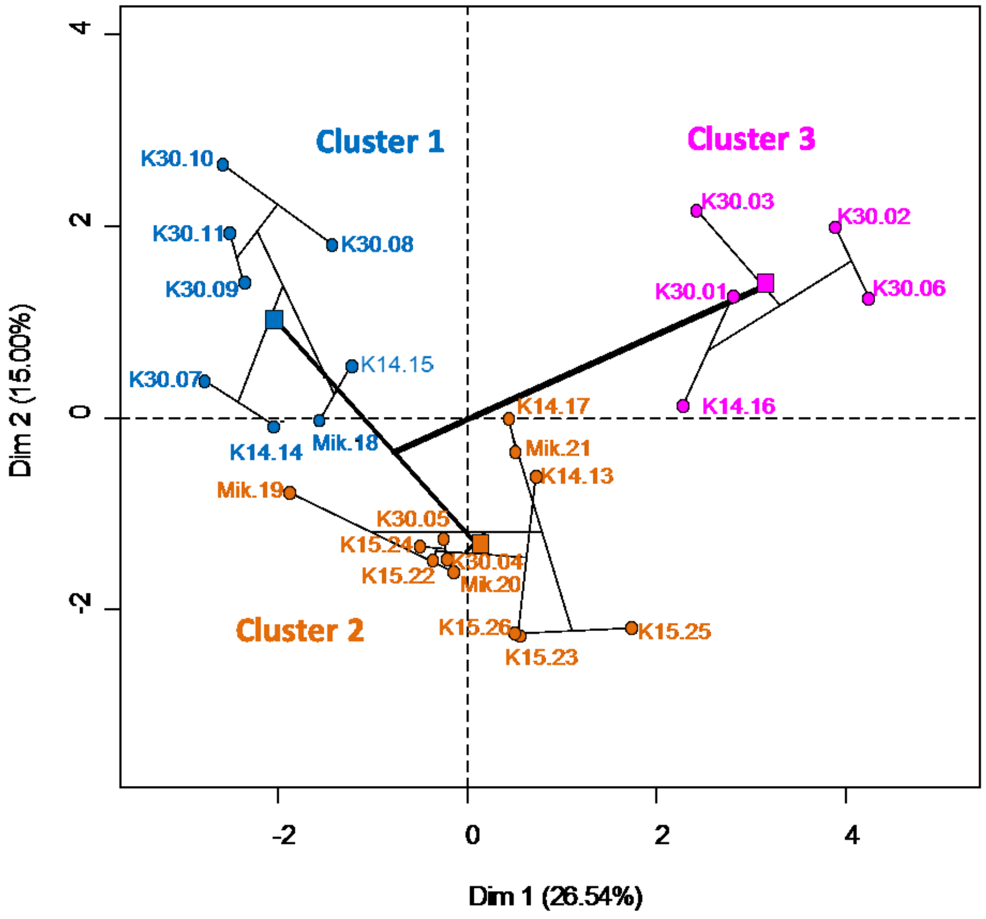


Figure 3-4. Principal Components Analysis of plots comparing grouping by Ward's clusters and logging history

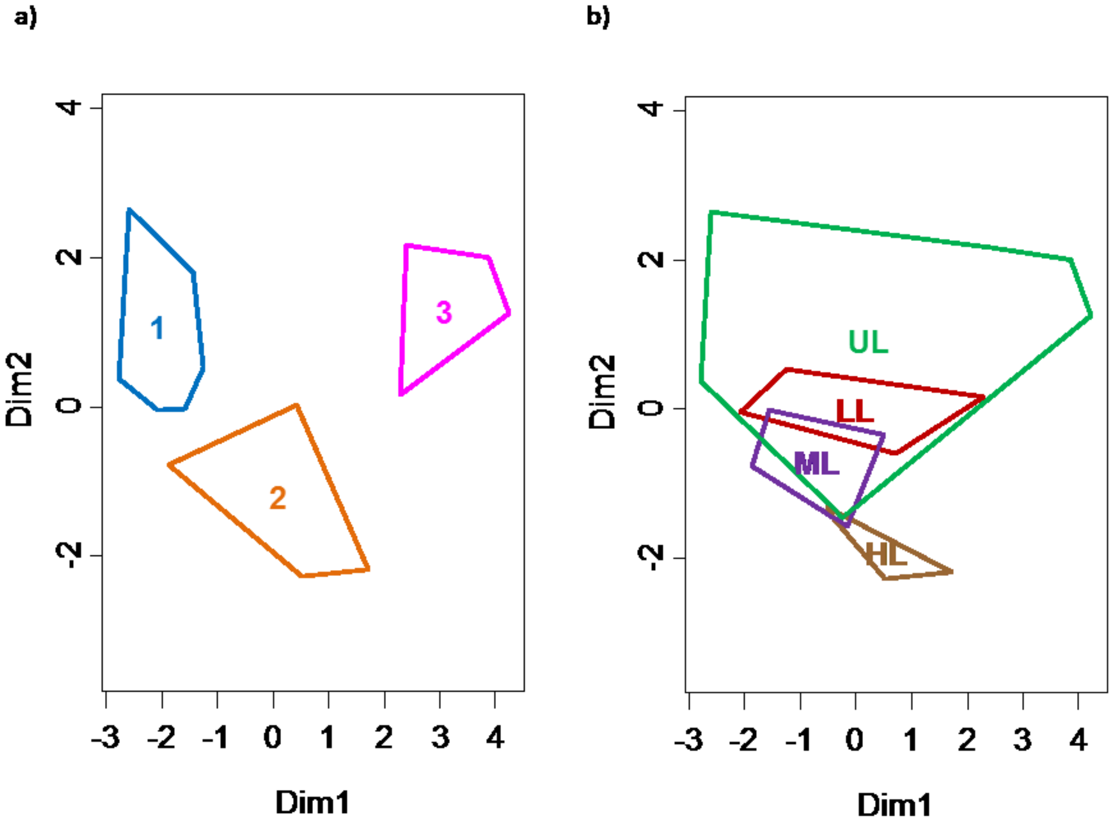
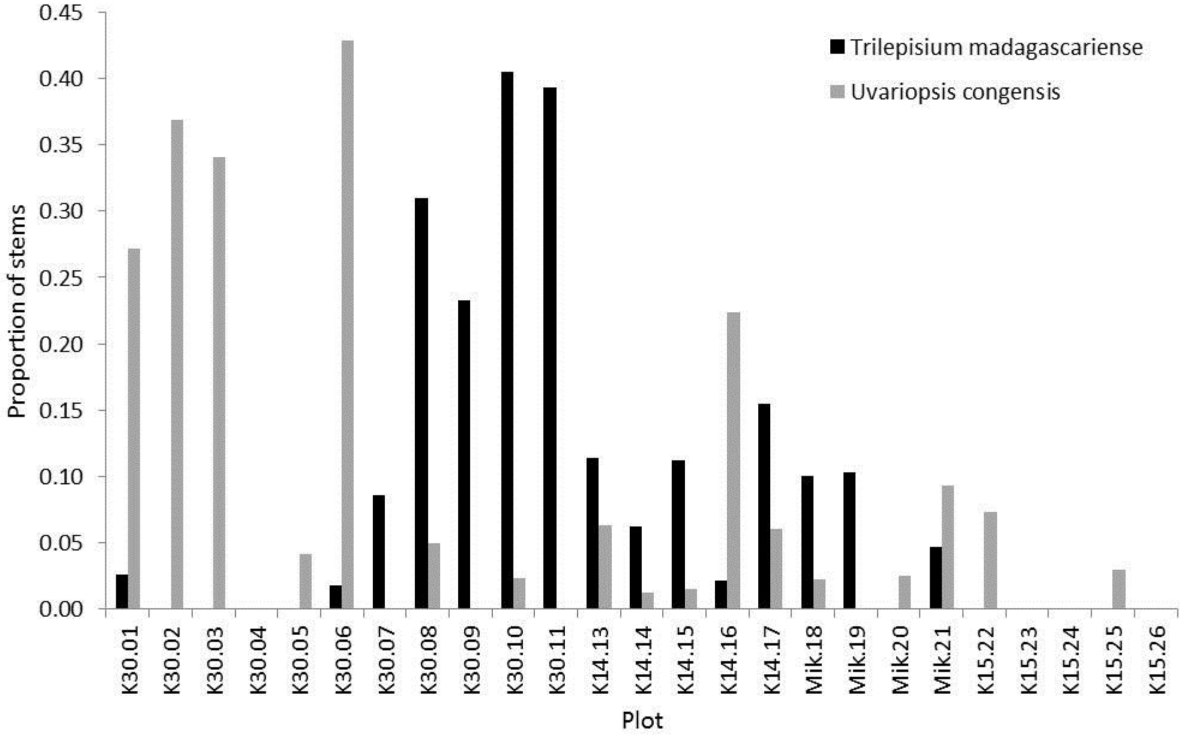


Figure 3-5. Proportion of *Trilepisium madagascariense* and *Uvariopsis congensis* in plots



LINKING STATEMENT 2

Using multivariate statistics and historical baseline information, in Chapter 3 I identified and interpreted considerable heterogeneity within logging compartments of the Kanyawara study area in northwestern Kibale. I found that tree assemblages varied more across space than across time, and that differences within the unlogged forest were greater than across the gradient of unlogged to heavily logged sites. The results of this chapter suggest caution should be taken for research aiming to test the effects of disturbance in complex, naturally heterogeneous environments such as tropical rainforest. Nonetheless, management plans and decisions typically are made on spatial scales associated with patterns of land-use well above the scale of most natural and anthropogenic disturbance events or even of habitat patches. For instance, managers might need different strategies to manage heavily logged and unlogged forest across an extensive and topographically diverse landscape. Similarly, interventions to restore forest on abandoned farmland or burned grassland are applied across larger spatial scales than individual farms or burnt patches. Many of these decisions are made a) using limited knowledge, time, and resources, and b) to maximize benefits for animals of conservation concern or particular ecosystem services.

In Kibale, animal biodiversity is regionally exceptional and at least two species are of global conservation concern: the chimpanzee *Pan troglodytes schweinfurthii* (IUCN: Endangered A4cd) and the Uganda red colobus monkey *Procolobus rufomitratus* ssp. *tephrosceles* (IUCN: Endangered B1ab(iii,v)). Management of animal populations poses two challenges. First, many large animals range widely within Kibale, depending on resources that vary within and among parts of the park. Second, to some degree management to the advantage of wildlife may conflict with management for the provision of ecosystem services valued by people. Wildlife management has long been practiced in Kibale but the only ecosystem service currently actively managed within the park boundary is carbon sequestration via the extensive planting project in abandoned farmland. Some local communities have agreements with park managers to access non-timber forest products such as firewood and honey but earlier agreements to access other forest products, including medicinal plants, craft materials, and wild coffee have been void in recent years as oversight and enforcement capacity was low and there was concern about the degree of related illegal resource extraction and poaching. Given the growing need to conserve animal populations while at the same time providing ecosystem services, it is becoming more necessary to understand how these resources vary across the range of land-use histories within Kibale.

In Chapter 4, I analyze data on tree communities that I collected during 2008-10 in 12 sites representing eight different land-use histories throughout Kibale. I used information that I collated from published and unpublished records on which tree species contributed to a) the diets of seven mammal species (elephants, chimpanzees, and five species monkeys), and b) cultural, provisioning, and regulating services in Kibale and Uganda. I used multivariate analyses to examine relationships among these variables in sites with different land-use histories, and compared synergies and trade-offs among them.

4 TRADEOFFS IN RESTORING BIODIVERSITY, ANIMAL FOODS, AND ECOSYSTEM SERVICES IN DEGRADED AFRICAN TROPICAL RAINFOREST

4.1 Abstract

Challenged to maintain multi-functional landscapes, natural resource managers must consider disparate and often competing demands to conserve biodiversity and provide ecosystem services. Synergies between these two spheres are possible, but so too are trade-offs, particularly in degraded landscapes. When researchers study relationships between biodiversity and ecosystem services, they usually consider species richness, not habitat suitability for particular species of conservation concern. This study empirically measures and compares the trade-offs among tree species diversity, animal habitat suitability, and provision of ecosystem services within the context of ecological restoration. I quantified how human disturbances and management interventions affected these three factors in undisturbed and degraded, regenerating forests in Kibale National Park, Uganda. In each site I quantified and compared tree diversity and estimates of food availability for seven mammal species (elephants, chimpanzees, and five monkeys) and indicators of provisioning, regulating, and cultural services. I found a high-low gradient of tree diversity related to the severity of disturbance and forest type. Greater tree diversity was related to greater availability of animal foods and most services. Primary foods for chimpanzees and folivorous and frugivorous monkeys bundle together, separate from primary foods for elephants and correlate positively with services related to wood. The availability of artisanal services was negatively related to tree diversity, animal foods, and wood-related services. Planting abandoned farmland with native trees did not result in greater tree diversity, animal foods, or ecosystem services compared to unplanted abandoned farmland, grassland protected from fire, or heavily disturbed forest. My results demonstrate that managing forest landscapes to maximize diversity can also maximize stocks of animal foods and ecosystem services. I discuss the biological and economic trade-offs managers need to consider when managing either intact or degraded tropical rainforest.

Keywords: biodiversity and ecosystem services; canonical discriminant analysis; forest regeneration; Kibale National Park, Uganda; restoration; trade-offs; tropical forest;

4.2 Introduction

Truly multi-functional landscapes simultaneously and sustainably conserve biodiversity and provide multiple *ecosystem services* (the benefits people obtain from ecosystems). Creating and maintaining this type of ‘win-win’ situation is challenging. In theory, and supported by experimental studies, synergies between the two are possible because higher levels of biodiversity can support higher ecosystem functions and services, especially over long time scales, large and heterogeneous areas, and under changing conditions (Duffy 2008, Rey Benayas et al. 2009, Isbell et al. 2011, Cardinale et al. 2012). However, research on the relationships between biodiversity and ecosystem function is more advanced than between biodiversity and ecosystem services (BES) (Cardinale et al. 2012). The balance of BES research focuses on provisioning and regulating services, particularly those easily linked to ecosystem function or material values, or that lend themselves well to writing policy (Bullock et al. 2011, Cardinale et al. 2012). The concept of ecosystem services is inherently attractive for natural resource management and is increasingly invoked in recent policy (Bullock et al. 2011). But the BES perspective necessarily sets up a hierarchy between services and biodiversity, and amongst services (Reyers et al. 2012). Services that are less connected to ecosystem function or area difficult to quantify or monetize, such as cultural values, are sometimes omitted because comparative methods are limited (Bullock et al. 2011, Daniel et al. 2012). In trying to balance the competing needs of multiple stakeholders, three key factors challenge managers to create and maintain resilient and productive multi-functional landscapes (Rey Benayas et al. 2009).

First, management decisions are inherently trade-offs among direct, indirect, and non-use values of ecosystems across space and time (Pearce 2001, Cardinale et al. 2012, Jacob et al. 2014b). Ultimately, some values eclipse others. For example, landscapes managed as protected areas generally aim to keep biodiversity in and people out (Bruner et al. 2001). Sometimes the majority of conservation effort is focused on key species (Walpole and Leader-Williams 2002, Sergio et al. 2006). Landscapes can also be managed to maximize one or a few services in isolation, usually for direct, short-term economic returns instead of more diffuse, long-term stability (Pearce 2001, Cardinale et al. 2012, Jacob et al. 2014b). Losing biodiversity is rarely – if ever – the motivating factor behind unsustainable land-uses; rather, it is an unintended consequence of multiple decisions made for other reasons (Rands et al. 2010). No matter where the management agenda falls on the gradient of exploiting to protecting resources, such decisions are made by people. The influence of political or economic values often trumps ecological or social values.

Second, heavy pressure on natural resources creates a positive feedback loop between ecosystem degradation and biodiversity loss. Threatened, biodiversity loss in turn becomes a major driver of ecosystem change (Hooper et al. 2012). Losing biodiversity threatens the continued provision of direct and indirect ecosystem goods and services (Gardner et al. 2009). It is associated with damages to human health, climate, watersheds, and the well-being of indigenous peoples (Pearce 2001, Foley et al. 2005, Cardinale et al. 2012, Hooper et al. 2012). Unfortunately, evidence of such damage may be delayed, with the length of time lags depending on the life history of species at risk (*e.g.,* long-lived, slow to die trees), the prevalence of long-term ecological data documenting gradual change, and the relationships between biodiversity components and ecosystem function (Tilman et al. 1994, Gardner et al. 2009, Cardinale et al. 2012).

Third, monitoring dissimilar components of biodiversity and ecosystem services is difficult. Connecting and quantifying how each species, functional group, or community contributes to a particular ecosystem service is hampered by identifying the species characteristics that supply the service, the difference in quality or efficiency of service delivery, the cumulative interactions between species in a community, and which sections of society benefit from the service now and in the future (Luck et al. 2009). The first hurdle could be addressed by developing methods to simultaneously compare biodiversity and services measured with different units. For instance, pollination services are variously measured in terms of the rate of pollinator visitation, the area of pollinator-dependent crops, the cost of renting domestic pollinators, or the weight of crop yield (Liss et al. 2013). It is harder still to consistently compare synergies and trade-offs among different services, landscapes, human values, and academic disciplines (Lautenbach et al. 2010, Liss et al. 2013). Clearly, managing landscapes for multiple facets of biodiversity and ecosystem services is difficult even under the best of circumstances.

Furthermore, managers must contend with damaged landscapes where ecological restoration is required to help recover and conserve lost and degraded biodiversity and services.

Successful restoration projects can have wide-ranging benefits, including helping to mitigate global climate change and alleviate poverty (Chazdon 2008, Hobbs et al. 2009, Rey Benayas et al. 2009). However, some services or components of biodiversity are more efficiently restored than others, and restored systems rarely reach the original levels of biodiversity and services (Gardner et al. 2007, Chazdon 2008, Rey Benayas et al. 2009, Gibson et al. 2011). The degree to which components of biodiversity and services can be recovered depends on the type, severity, and time since disturbance, health of the surrounding matrix, desired outcome of restoration, and time and financial and human resources available (Chazdon 2008). Monitoring the outcomes from different conservation approaches, including ecological restoration, market-based approaches to provide ecosystem services, and more traditional,approaches based on protected areas, have been identified as a major research needs (Goldman et al. 2008, Rey Benayas et al. 2009).

The need for maintaining and/or restoring multi-functional landscapes is greatest where hotspots of biodiversity overlap with high human population density and growth rates, poverty, and dependence on natural resources (Cincotta et al. 2000, Cordeiro et al. 2007, Luck 2007). In these places, livelihoods of the rural poor depend on the continued supply of ecosystem services provided by biodiversity (Persha et al. 2011), but biodiversity is threatened by small- and large-scale human activities (*e.g.,* subsistence and commercial land conversion, disturbance, and unsustainable resource extraction). Tropical forests provide one of the best examples of such juxtaposition between hotspots of biodiversity, ecosystem services, and human pressures on natural resources (Burgess et al. 2004, Cordeiro et al. 2007, United Nations 2013). They have outstanding levels of biodiversity, including high levels of species and family richness, species endemism**,** and as centers of evolutionary diversity (Millennium Assessment 2005b). Tropical forests also carry the largest proportion of the global terrestrial carbon sink (Saatchi et al. 2011), are key components of the global hydrological cycle (Wright 2010), provide essential pollination services for crops (Ricketts et al. 2004), and are associated with improved food security and childhood nutrition (Ickowitz et al. 2014). More than 800 million people live in or near tropical forests (Chomitz 2007) and directly depend on them for drinking water, fuelwood, and animal protein (Wright 2010). But tropical forests are imperiled by many human pressures, chief among them degradation to provide timber and fuel wood, and deforestation and conversion to provide agricultural land (Wright 2010, Kissinger et al. 2012). Such land uses and disturbances consistently reduce biodiversity (Gibson et al. 2011), with effects that reach inside protected areas as well as the surrounding matrix (Laurance et al. 2012). The problem is particularly pressing in sub-Saharan Africa: it is the poorest and least developed region in the world, and its rate of population growth exceeds the rate of poverty reduction (World Bank 2012). Furthermore, unlike the rest of the world, deforestation and degradation in Africa are predominantly driven by subsistence needs for farmland and fuelwood (Hosonuma et al. 2012, Kissinger et al. 2012); of all new land cleared for agriculture in Africa between 1980 and 2000, 95% came from forested or formerly forested land (Gibbs et al. 2010).

Broadly speaking, agricultural land-uses (including active and abandoned farmland) have greater detrimental effects on biodiversity than selective logging, agroforestry, ranching, and timber plantations (Gibson et al. 2011). Forests logged selectively, and only once, have slightly higher species richness than matched unlogged forest (Gibson et al. 2011), although composition of species and functional traits vary (Carreño-Rocabado et al. 2012). Africa is under-represented in terms of reforestation and carbon sequestration projects in the developing world, but it has one of the fastest growing markets for carbon storage (Greve et al. 2013). However, places with the most potential for carbon storage are not always the most beneficial in terms of the ancillary benefits, costs, and risks of reforestation projects. In a global analysis, areas prioritized for biodiversity conservation did not overlap with areas of high ecosystem service provision (Naidoo et al. 2008).

The Albertine Rift in western Uganda contains isolated, fragmented rainforests that are global hotspots biodiversity and endemism, surrounded by some of Africa’s densest and poorest rural populations (Balmford et al. 2001, Brooks et al. 2001, Plumptre et al. 2004, Cordeiro et al. 2007). Pressures on forest resources and forested land in this region are very high: between 2000 and 2009, Uganda lost more forest than any other of 12 East African countries (4,608 km2 in areal background forest loss, or 36.3% in relative background forest loss; Pfeifer et al. 2012). Land-use of forested and formerly forested land in western Uganda runs the gamut from full protection as national parks and partial protection as community forests, to subsistence and commercial agriculture, fallows, burning to improve grazing, commercial logging, exotic plantations for timber and fuelwood, and reforestation to sequester carbon. Access to land and natural resources have been significant factors in sparking and sustaining violent conflict in the region, operating from household to national levels (Huggins et al. 2005). Human pressure on natural resources in the Albertine Rift is expected to increase in the coming years because of the return of internally displaced people, immigration for the perceived benefits of tourism and oil extraction, increased market demand from urban areas, and the weak capacity and coherence of local civil society organizations, government, and infrastructure (Kaggwa et al. 2009a, MacKenzie and Hartter 2013, Van Alstine et al. In Press). If the synergies among conserving biodiversity and providing ecosystem services can be maximized, and the trade-offs among them minimized, there is hope for people and wildlife in the region to sustainably coexist.

In particular, for six reasons Kibale National Park offers an opportunity to study these types of critical synergies and trade-offs in ecosystem management. First, Kibale has a multi-functional mandate, existing to "*...protect the remarkable biodiversity and biophysical elements… and to preserve both tangible and intangible benefits from the protected environment including sustainable supplies of traditional forest products for local people, now and in the future"* (UWA 2003). Second, land cover in Kibale has been affected by a wide range of land-uses and disturbances, including elephant damage, natural and human-caused fire, selective logging, subsistence agriculture, and planting of native and non-native trees. This creates the opportunity to investigate how disturbance and forest restoration trade-offs between biodiversity and ecosystem services. Third, human pressure on natural resources within a five km radius of Kibale is intense and rapidly increased over the past 25 years (Jacob et al. 2014a). Patterns in land cover outside the park, where forest cover has decreased by half and agriculture has nearly doubled since 1984, are in stark contrast to those inside the park, where forest cover has marginally increased (Jacob et al. 2014a). Fourth, for over forty years Kibale researchers have studied how the legacies of human disturbance in the park have affected tree assemblages (Kasenene and Murphy 1991, Struhsaker 1997, Chapman et al. 2002c, Lwanga 2003, Omeja et al. 2009, Bonnell et al. 2011, Duclos et al. 2013) and animals (Kasenene 1984, Skorupa 1986, Weisenseel et al. 1993, McCoy 1995, Struhsaker et al. 1996, Struhsaker 1997, Dranzoa 1998, Gillespie et al. 2005, Massimino et al. 2008, Chapman et al. 2010b). These data and results provides a rich basis for comparative research. Fifth, researchers have begun to study local peoples' perceptions, attitudes and dependence on ecosystem services from Kibale and neighbouring fragmented natural areas (Hartter 2010, Naughton-Treves et al. 2011, MacKenzie 2012a). These services include the provision of non-timber forest products such as wild coffee and honey, medicinal plants, dead or fallen wood for fuel, thatching grass, and fishing. Sixth, researchers study the efficacy of actively restoring forest on degraded farmland for carbon sequestration (Klomp 2009, Omeja et al. 2011), and passively restoring forest on grasslands by preventing fire (Lwanga 2003). The park mandate, management history, and the legacy of past and ongoing research provide a good opportunity to explore how disturbance and restoration affect multiple aspects of both biodiversity and ecosystem services.

In this chapter I consider synergies and trade-offs between tree diversity, animal habitat, and ecosystem services in old-growth and regenerating tropical rainforest in Kibale National Park. I collected data on tree assemblages in 12 sites with different histories of land-use and disturbance and compared their tree species diversity. I used data on animal diet preferences specific to Kibale, and on human uses for different trees specific to Kibale and across Uganda, to quantify and compare the availability of food for seven mammals and nine ecosystem service indicators at each site. Specifically, I sought to answer the following questions:

1. How does tree species diversity vary in parts of Kibale with different land use histories?
2. How does the availability of primary and secondary foods for chimpanzees, elephants, folivorous monkeys and frugivorous monkeys vary in parts of Kibale with different land use histories?
3. How does the availability of nine ecosystem service indicators vary in parts of Kibale with different land use histories?
4. What are the synergies and trade-offs amongst these variables across differing land-use histories, degrees of disturbance, and ecosystem types?

4.3 Methods

4.3.1 Study area

Kibale National Park (795 km^2) is a mid-altitude, moist tropical rainforest in western Uganda (0˚11' - 0˚41' N and 30˚12' - 30˚32' E; Figure 4-1). The park ranks fifth in species richness and sixth in overall biodiversity importance among all Ugandan forests (Howard et al. 1997). Over 330 species of trees are found in Kibale (Plumptre et al. 2007) and it has the highest recorded density and biomass of primates in the world (Chapman and Lambert 2000, Chapman et al. 2005b). Human population density on the edge the park ranges from 71-611 people/km^2 (average 241 people/km2; MacKenzie and Hartter 2013). Agricultural and population pressures around the park are the second and third highest of all protected areas in Uganda (Hartley et al. 2010).

Kibale lies on a plateau at a maximum elevation of 1590 m in the north and minimum of 990 m in the southwest. The northern and central areas contain a series of undulating hills and valleys, with maximum elevation difference of 150-200 m (Chapman et al. 1997), while the southwestern area has an escarpment that drops off to become a flat plain. This high-low gradient in elevation corresponds to a north-south increase in temperature, decrease in rainfall (Howard 1991, Struhsaker 1997), and variation in forest type (Chapman et al. 1997). Mean daily minimum and maximum temperatures are 15.5 °C and 23.7 °C; mean annual rainfall in the region is 1750 mm, which is distributed mainly in two rainy seasons from March-May and September-November (Kingston 1967, Hartter et al. 2012).

Kibale's history has created a complex mosaic of mature forest and habitats regenerating after a variety of recent human disturbances. In the early 1900s, a combination of tribal conflict, disease, and livestock depredation caused people to abandon homesteads on grassy hilltops inside the Kibale forest (Lang Brown and Harrop 1962, Kingston 1967). In 1926, the British Protectorate Government designated the southwestern part of Kibale (340 km^2 of savannah-woodland) as a the Kibale Forest Corridor Game Reserve and managed it for controlled hunting and to promote the movement of large animals (Figure 4-1). In 1932, the northern, central, and southeastern parts of Kibale (455 km^2 of tropical high forest) were designated as a the Kibale Crown Forest Reserve and managed it for commercial timber extraction (Figure 4-1). In the 1950s, land cover in the game corridor was estimated as 61% grassland and 39% forest (Kingston 1967 in Ryan and Hartter 2012). In the 1960s, land cover in the forest reserve was estimated as 60% forest interspersed with 40% of various types of grassland, woodland-thicket, and recolonizing forest (Wing and Buss 1970). The most recent round of human disturbance started in the 1960s when much of northern Kibale was commercially logged and some grasslands were planted with fast-growing exotic trees (Kingston 1967, Struhsaker 1997). Shortly thereafter, during periods of civil unrest and resettlement from land shortages, thousands of people illegally encroached and settled throughout the game corridor and in small parts of the forest reserve (Van Orsdol 1986). These people were forcibly evicted in 1992, and in 1993 the forest reserve and game corridor were joined and upgraded to national park status. Forest succession over the last half-century shows a progressive loss of grassland and increase in native forest, primarily from preventing fire and intensive reforestation in the former game corridor (Jacob et al. 2014a). Today, land cover in the park is 74% unlogged and regenerating forest, 15% bare ground and short grasses, 6% tall grasses, 4% wetland, and 1% shrubs (Jacob et al. 2014a).

4.3.2 Study sites

I identified 12 sites spread throughout Kibale that represented unlogged or regenerating forests with eight distinct disturbance histories (Table 4-1, Figure 4-1). Study sites were chosen to reflect the range of habitats, land use histories, and management in Kibale, to take advantage of existing long-term data where possible, and for logistical reasons.

Unlogged forest: I selected three sites of unlogged forest spread throughout the park. Tree assemblages in these sites have been the focus of long-term research on forest change (Chapman et al. 1997). Compartment K30 contains mixed *Parinari* forest (type K2), Dura contains *Pterygota* and *Chrysophyllum-Celtis* forests, and Mainaro contains *Pterygota* and *Cynometra* forests (Kingston 1967, Howard 1991) (Table 4-1, Figure 4-1, Appendix 3). Prior to 1970, pit-sawyers removed 3-4 trees/km^2 from the K30 and Dura sites (Waser 1974, Skorupa 1988), and 1 tree/km^2 from the Mainaro site (Chapman et al. 2002b). These low levels of extraction are thought to have had little effect on forest composition and structure.

Logged forest: I chose four sites of selectively logged forest representing a range of harvest intensity (Table 4-1, Figure 4-1). These sites are the focus of long-term research on forest change; three sites are adjacent to each other in the Kanyawara area and contain *Parinari-Pouteria* (formerly *Aningeria)* forest (type K1) and/or mixed *Parinari* forest (type K2 unknown subtypes) (Appendix 2). This area was mechanically logged between 1968 and 1969: compartment K14 was lightly logged, compartment K15 was heavily logged, and compartment K13 was heavily logged followed by treatment with arboricide (see Table 4-1 and Appendix 4 for details). The fourth logged site, Sebatoli, lies the farthest north. It was logged sometime between 1950-1955 (Parag. 108 in Kingston 1967). Harvest records do not exist for Sebatoli, but previous work indicates the intensity was similar or slightly lower than in K15 (Chapman and

Lambert 2000). Non-directional felling and use of heavy machinery during harvest led to high incidental damage. The effects of logging on forest recovery in Kibale have been well summarized by Struhsaker (1997) and Chapman and Chapman (1997).

Grassland: Grasslands in Kibale tend to occur on hilltops and were created and maintained through fire and long-term cultivation by subsistence agriculturalists (Lang Brown and Harrop 1962, Kingston 1967). The grassland site used in this study, locally called Nyamasika, lies along the footpath between Kanyawara and the Ngogo field station (Table 4-1, Figure 4-1). Grassland plant assemblages in Kibale are described in Kingston (1967), Lang Brown and Harrop (1962) and Wing and Buss (1970).

Harvested conifer plantation: Exotic conifers were experimentally planted on grasslands in northern Kibale between 1953 and 1977 (Chapman and Chapman 1996, Struhsaker 1997, Omeja et al. 2009). Native forest naturally regenerated in the understory. Managers decided to harvest the exotic trees when Kibale became a national park in 1993. Harvested trees were not directionally felled and much of the native regenerating forest was damaged. The harvested conifer plantation in this study is locally called Nykatojo, which is believed to have been planted with *Pinus caribaea, P. patula,* and *Cupressus lusitanica* sometime between 1963 and 1965 (Table 4-1, Figure 4-1) (Chapman and Chapman 1996). Forest regeneration in this area is described in Chapman and Chapman (1996), Chapman et al. (2002c) and Kasenene (2007).

Abandoned farmland: Beginning with Idi Amin's *coup d'etat* in 1971, upwards of 55,000 people cleared, settled, and cultivated approximately 120 km^2 in the former game corridor (Van Orsdol 1986, Aluma et al. 1989, Eltringham and Malpas 1993, Ryan and Hartter 2012). Forest clearing and degradation fragmented the forest reserve into two discrete blocks and effectively extirpated large animals from the game corridor (Van Orsdol 1986, Aluma et al. 1989, Eltringham and Malpas 1993). Settlers were forcibly evicted in 1993 and today most of the abandoned farmland is tall grassland with recolonizing forest. Since 1995 local people have been paid to rear and plant native tree seedlings as part of a carbon sequestration project (Struhsaker 2003, Omeja et al. 2011, Ryan and Hartter 2012). Three study sites were located in the abandoned farmland: one each in the first and third phases of tree planting (Face the Future

2011) and one in an unplanted area called Isunga (Table 4-1, Figure 4-1). Forest regeneration in the planted area is described by Omeja et al. (2011).

4.3.3 Field sampling methods

In each site, I sampled woody plants in quadrats along trails approximately four km long (range 3.8-5.1 km). I used existing trails or cleared overgrown trail networks in the unlogged and logged areas, grassland and harvested conifer plantation. I cut new trails in the abandoned farmland. Between June 2008 and June 2010, I randomly placed thirty 10 m x 10 m sampling quadrats along each trail, randomly on the left or right side of the trail, and a random distance 0-50 m off the transect (n=360 0.1-ha quadrats; total sampling area=3.6 ha). If the location of a quadrat fell on a footpath, we sampled the next random location. In each quadrat, we measured elevation with a handheld GPS unit (below canopy accuracy always less than +/-5 m). I tallied individual saplings and trees with live woody stems ≥ 3.0 cm diameter-at-breast-height (DBH, measured at 1.2 m from the ground), identifying individuals to species level where possible. To ensure consistent accuracy, if the stem was on a hillside we measured DBH from the downhill side, and if the tree had large buttresses (*e.g.,* large *Olea welwitschii*) The DBH was measured above the top of the buttress using a meter stick and two observers to read the DBH. If a tree had multiple stems branching between ground and breast height, I measured and treated each stem individually. I excluded standing dead trees and included trees straddling the quadrat boundary only if ≥ 50% of the bole fell inside the quadrat.

4.3.4 Collation of literature on animal foods and ecosystem services

I conducted an extensive search of both published and grey literature to identify trees species a) eaten by monkeys, chimpanzees, or elephants in Kibale (Table 4-2), and b) used by people around Kibale and in Uganda for eight non-wood or non-timber forest products, *i.e.,* considered as indicators of provisioning services (Table 4-3). I used historical records to identify commercial timber trees, *i.e.,* those species commercially harvested from Kibale between 1950 and the early 1970s (Appendices 16 Part 1 and 17 in Kingston 1967). Information specific to communities adjacent to Kibale was available for trees used for house construction (Kakudidi 2007), traditional medicines (Namukobe et al. 2011), and cultural, social, or ceremonial purposes (Kakudidi 2004). Therefore, these four ecosystem service indicators will more heavily reflect use in Kibale than the other metrics, which rely on sources generalized across Uganda. Further details about animal foods and ecosystem services are described below.

4.3.5 Consolidation of the data matrix

I pruned the original field data of 360 quadrats to exclude 64 quadrats without trees (these were predominantly from the grassland and unplanted abandoned farmland sites). I also excluded six quadrats that in retrospect were not representative of the disturbance history characteristic at a site: four quadrats from the grassland and two quadrats from the unplanted abandoned farmland that fell within small patches of closed-canopy forest. I excluded the palm *Phoenix reclinata:* its stems are covered in a dense mat of broken and thorny dead fronds which makes measuring DBH and DGH difficult. I also excluded exotic tree species (*e.g., Eucalyptus* spp. in abandoned farmland). Finally, during field observations individual trees were occasionally recorded using only the genus but omitting the species name. Since most tree genera in Kibale are monospecific this generally was not a problem (*e.g., Parinari* could only be *Parinari excelsa* Sabine). However, a few genera have multiple species, in which case it was not possible *post hoc* to identify that record to species level. In these cases, I combined all observations at the genus level, *i.e., Acacia* (3 spp. recorded), *Albizia* (3 spp. recorded), *Cordia* (2 spp. recorded) *Croton* (2 spp. recorded) and *Ficus* (7 spp. recorded). The final dataset contained 290 quadrats of 98 tree taxa (Table 4-4).

4.3.6 Data analyses

4.3.6.1 Tree diversity

I calculated stem frequency, species richness, and Shannon entropy (Shannon-Wiener index, H’) using the R package BiodiversityR (Kindt and Coe 2005). Species richness remains the most common measure of success in restoring or conserving degraded ecosystems (Gotelli and Colwell 2011). However, it does not include other aspects of biodiversity such as species composition and abundance, which affect intra- and inter-specific interactions as well as ecosystem function (Zhang et al. 2012). Furthermore, it is difficult to accurately estimate species richness in complex and species-rich systems such as tropical rainforest (Gotelli and Colwell 2001). I used the *effective number of species* (also called the *equivalent number of species* or Hill number q=1) to compare species diversity among sites. Effective numbers represent the number of species that would be in a community if all were equally common (Jost 2006). I chose this transformation over classical diversity indices like Shannon's H' or Simpson's D, since the latter are actually entropies and not true measures of diversity (Jost 2006, Ellison 2010). I calculated the effective number of species based on Shannon entropy as HE=exp(H') (Jost 2006). I did not use rarefaction methods (Chao et al. 2014) because my sampling effort was equal: I sampled 30 randomly placed quadrats in each site; not all quadrats contained trees but that reflects land cover at those sites. I compared stem frequency, species richness, and effective number of species among sites using non-parametric Kruskal-Wallis tests.

4.3.6.2 Animal foods

The diversity, abundance, and quality of food influences the structure of animal communities, particularly primary consumers (Symington 1988, Oates et al. 1990, Ganzhorn 1992, Kay et al. 1997, Chapman and Chapman 1999, Stevenson 2001, but see Gogarten et al. 2012). However, neither leaf nor fruit food resources in tropical rainforests are evenly distributed in space or time (Terborgh 1986, Levey 1988, Chapman et al. 1997, Snaith and Chapman 2005, Potts et al. 2009). Furthermore, animals consume only a fraction of annual leaf and fruit production (Janson and Emmons 1990, but see Snaith and Chapman 2005 for ability of folivorous primates to deplete food patches) and may respond differently to food resources depending on diet specialization and size (Stevenson 2001). Therefore, estimates of food availability are best considered a useful but relative index of habitat suitability.

To compare habitat suitability among sites with different disturbance histories, I identified and quantified tree-based foods for seven mammal species in Kibale (Table 4-2). I chose these species for two reasons. First, they vary in body size, mobility, longevity, and diet specificity. Therefore, they experience the landscape at different spatial and temporal scales, use a wide range of habitats and resources, and differ in their sensitivity to forest disturbance. Second, extensive species-specific diet data was available from Kibale for each of these species. I identified native tree species eaten (*i.e.,* leaves, stems, fruit, or flowers) by: red colobus (Procolobus rufomitratus ssp. tephrosceles, Struhsaker 1975, Chapman and Chapman 2002, CAC unpubl. data, Struhsaker 2010), black-and-white colobus (Colobus guereza ssp. occidentalis, Oates 1977, Harris and Chapman 2007), grey-cheeked mangabeys (Lophocebus ugandae, Waser 1975, Olupot et al. 1994), blue monkeys (Cercopithecus mitis ssp. stuhlmanni, Rudran 1977, Butynski 1990), red-tailed monkeys (Cercopithecus ascanius ssp. schmidti, Stickler 2004 and unpubl. data, Rode et al. 2006 and unpubl. data), chimpanzees (Pan troglodytes ssp. schweinfurthii, Potts et al. 2011, Anonymous n.d., Wrangham n.d.), and elephants (Loxodonta africana, Wing and Buss 1970, Chiyo 2000) (Table 4-2). I grouped red colobus and black-and-white colobus as folivorous arboreal monkeys, and mangabeys, blue monkeys, red-tailed monkeys as frugivorous arboreal monkeys.

I categorized tree species into three food categories for each animal group: 1) primary food, 2) secondary food, and 3) non-food trees. Primary food trees were those whose leaves, stems, fruit, and/or flowers made up a large portion of the diet of one or more animal species in that group, defined as ≥4% of time spent feeding for folivorous and frugivorous monkeys, ≥ 1% of time spent feeding for chimpanzees, and ≥1% of stems eaten for elephants. I chose lower thresholds for primary chimpanzee and elephant foods because these animals have much wider diets than the monkeys. Secondary food trees were species eaten but less than the cut-off for primary food. Non-food trees were species never recorded as eaten by that animal in Kibale. I excluded trees < 10 cm DBH from calculations for folivorous and frugivorous monkeys since these they rarely feed in trees less than 10 cm DBH (<1.8% of feeding time, Chapman and Pavelka 2005). I used the well-documented power relationships between tree size and plant productivity (Leighton and Leighton 1982, Chapman et al. 1992, Chapman et al. 1994, Stevenson et al. 1998, Enquist et al. 1999, Sorensen and Fedigan 2000, Enquist and Bentley 2012), and the pattern between food availability and primate abundance (Skorupa 1986, Symington 1988, Oates et al. 1990, Ganzhorn 1992, Kay et al. 1997, Stevenson 2001, Hanya et al. 2011), as a relative index of animal habitat suitability (but see Wasserman and Chapman 2003, Hanya et al. 2006, Hanya et al. 2011, Gogarten et al. 2012 for importance of food quality and seasonality). I used DBH^2 to calculate an index of leaf and fruit biomass (Enquist and Niklas 2002, Snaith and Chapman 2008). I summed this index in each sampling quadrat (n=290) for primary and secondary foods for each of the four animal groups (total of eight animal-food categories; Table 4-4).

4.3.6.3 Ecosystem service indicators

I followed three steps to quantify indicators of ecosystem service provision: 1) identify and define each indicator, 2) identify the point of provision of each indicator, and 3) define measures to quantify each indicator.

I focused on three broad ecosystem services in Kibale: regulating, cultural, and provisioning services. First, I identified indicators of those services as carbon storage, spiritual and religious practices, and the production of food, fiber, natural medicines and ornamental resources (Table 4-3). I chose these indicators for three reasons. i) They are relevant to the needs and concerns of people for timber and non-timber forest products at local (Kakudidi 2007) and regional (Ndangalasi et al. 2007) scales. ii) They reflect historical and ongoing land management inside Kibale, including active forest restoration on abandoned farmland for carbon sequestration (Omeja et al. 2011) and passive forest restoration on grasslands (Lwanga 2003), and resources historically collected or desired by local people. iii) They are expected to vary with history of forest disturbance over the scale of my study.

Second, because the goal of this study was to examine the trade-offs amongst tree diversity, animal foods, and ecosystem services as the result of different land-uses and management practices, I defined services in terms of *stocks*, *i.e.,* the amount of a beneficial material in an given ecosystem, rather than *flows*, *i.e.,* the actual delivery of that benefit to people (Mace et al. 2012). This means that the estimate of the amount of each indicator in a particular site reflects the potential benefit(s) at a static point in time, not the realized benefit(s) currently used by people.

Third, I quantified the amount of each ecosystem service indicator, *i.e.,* the collective abundance of tree species used for human food and drink, livestock fodder, artisanal purposes, house construction, wood products, commercial timber, or traditional medicines (*provisioning service indicators*), for cultural, ceremonial, spiritual, or religious purposes (*cultural service indicator*), and for carbon storage (*regulating service indicator*) (Table 4-3). My emphasis on provisioning services reflects that people around Kibale identify material goods (*e.g.,* water, timber, non-timber forest products) as their main benefit from the park (Hartter 2007, MacKenzie 2012b); cultural, supporting, and regulating services are recognized to lesser degrees.

I conducted an extensive literature review to identify native tree species that people use for each indicator in Uganda (Table 4-4) (Hamilton 1981, Katende et al. 1995, Wong 2003, Kamatenesi-Mugisha and Oryem-Origa 2005, Krief et al. 2005, Baerts-Lehmann and Lehmann 2007, Orwa et al. 2009). I incorporated information specific to Kibale for commercial timber (Kingston 1967), house construction (Kakudidi 2007), traditional medicines (Namukobe et al. 2011), and cultural and social uses (Namukobe et al. 2011). I considered all species of trees as contributing to carbon storage. In this way, the trees used to provide each ecosystem service indicator are the service-providing units for that quadrat (sensu Luck et al. 2009). I selected one of two measures to quantify each ecosystem service indicator from individual trees in each of the 290 quadrats. For timber, I calculated wood volume of each tree using an equation for individual trees in African tropical rainforest:

$$Y=1.858-3.518*DBH + 10.283*DBH^2$$ (equation 1109 in Henry et al. 2013).

For all other ecosystem service indicators, I calculated aboveground biomass of each tree using a Uganda-specific generalized equation for individual trees in tropical moist deciduous forest:

$$Y=\exp(-0.89+2.053*\log10(DBH))$$ (equation 562 in Henry et al. 2011).

I made the simplifying assumption that an increase in biomass of the tree would proportionately increase abundance of whichever indicator was in question. I summed the volume or biomass estimate for each of the nine indicators for all quadrats in each of the 12 sites (Appendix 5).

4.3.6.4 Assessing synergies and trade-offs

The primary goal of this study was to compare tree diversity, animal foods, and ecosystem service indicators among 12 sites with different disturbance histories. All these measures are derived from data on tree species composition, abundance, and size in the quadrats sampled at each site. These quadrat data are heterogeneous at two spatial scales: both within and among sites. Since my focal interest is in differences among land-use histories, defined at the site-level, I wanted to focus on differences among sites. Following results from Chapter 3, I used Canonical Discriminants Analysis (CDA) in the R package candisc to quantitatively compare the multiple response variables tree diversity, animal foods, and ecosystem service indicators across sites (Friendly and Fox 2009).

CDA (also called canonical analysis of discriminants, canonical variates analysis, or discriminant function analysis) can be used to examine relationships between both nominal and continuous variables. Like many other multivariate methods, CDA tries to reduce statistical dimensionality by extracting the dominant gradients of variation from a set of multivariate observations. However, the most distinctive aspect of CDA is that it allows *a priori* designation of samples into groups (Gittins 1985, McGarigal et al. 2000, Legendre and Legendre 2012). In this case these groups are the 12 sites with different disturbance histories. CDA weights the contribution of variables by their effectiveness in minimizing the difference within each pre-defined group while maximizing differences among groups (Gittins 1985, McGarigal et al. 2000). Hence CDA lets me optimally compare sites differing in land-use history and provides insights into how tree diversity, animal foods, and ecosystem service components contribute to among-site differences.

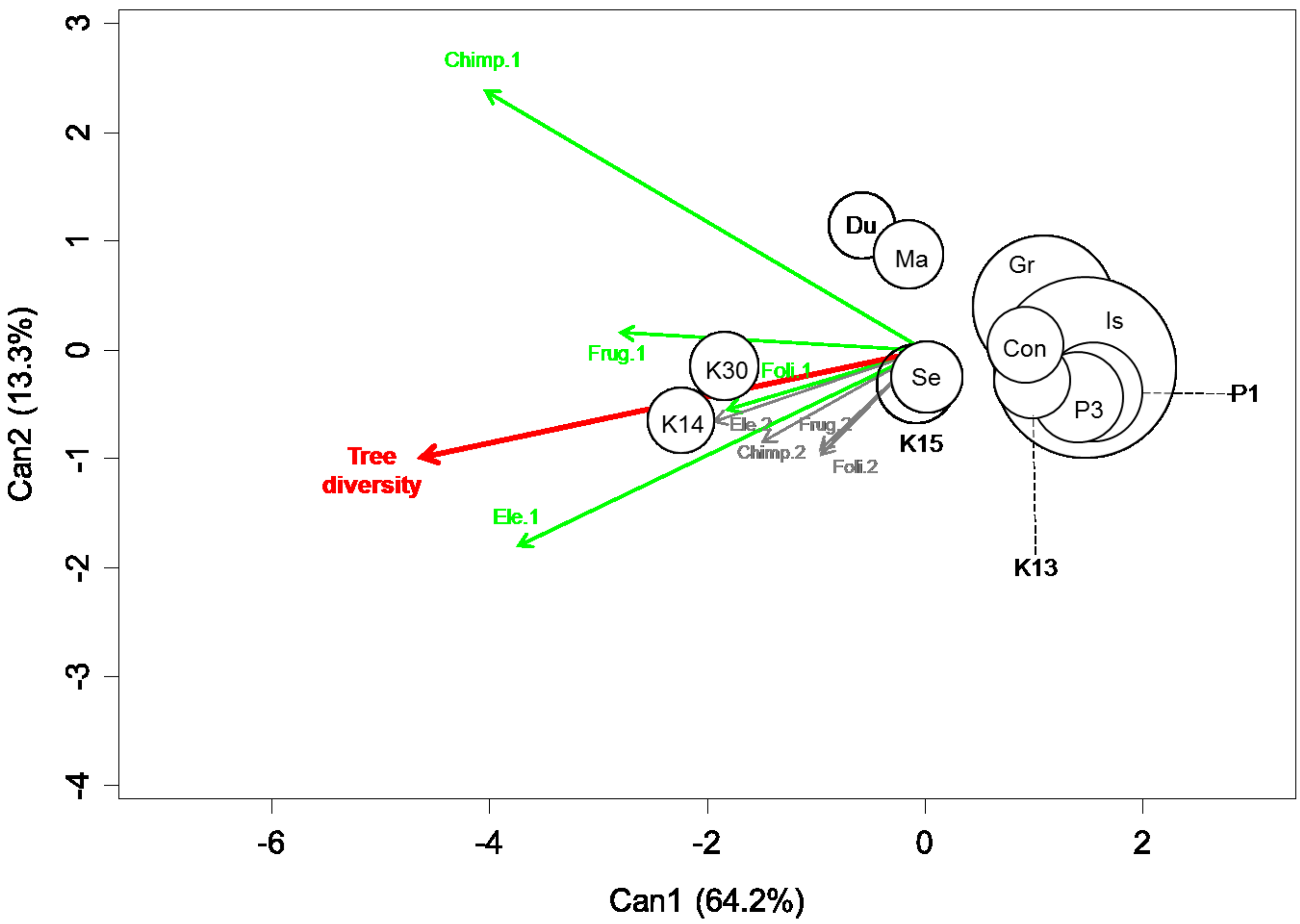
The CDA results are summarized graphically with each study quadrat located along the canonical axes. Each site (group of quadrats) is represented by the centroid of its constituent quadrats surrounded by a 99% confidence interval ellipse **(McGarigal et al. 2000)**. The elements of the canonical functions can be projected onto this graph as a biplot to illustrate how the variables contribute to separating sites based. The influence of each variable characterizing the quadrats (*i.e.,*. tree diversity and the availability of animal foods and ecosystem service components) is represented in the biplot by a directional vector. Longer vectors (arrows on the biplot) representing a particular variable of the quadrats (*e.g.,* tree diversity, primary chimpanzee food) indicate greater influence of that variable relative to others in distinguishing the overall differences amongst sites. Additionally, the direction of the vector illustrates the nature of the correlations among the quadrat characteristics. Vectors pointing in the same direction have similar influence. The more acute the angle separating any two vectors, the stronger is their joint effect. On the other hand, vectors pointing in opposite directions indicate strong trade-offs between those variables.

The overall matrix in the CDA consisted of 290 quadrats grouped into 12 sites and characterized by 18 response variables describing tree diversity, animal food availabilities, and ecosystem service indicators in each quadrat (Appendix 5). I initially conducted two separate analyses: 1) tree diversity and animal foods and 2) tree diversity and ecosystem services. Then I analysed the entire matrix to examine synergies and trade-offs among all response variables and identify bundles of animal foods and ecosystem services. In all the analyses I used biplots and associated statistical output to illustrate and evaluate the relationships among the response variables and the 12 study sites.

4.4 Results

4.4.1 Tree diversity

The number of stems, species richness, and the effective number of species were different among sites (Table 4-5; H=157, df=11, p<0.0001; H=173, df=11, p<0.0001; H=165, df=11, p<0.0001). The three CDAs showed that tree diversity was consistently the strongest vector in each of the biplots (**Error! Reference source not found.**,


Chimp.1
Frug.1
Foli.1
Ele.1
Tree diversity
Ele.2
Frug.2
Chimp.2
Foli.2
Du
Ma
Gr
Is
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Se
K30
K14
K15
P3
P1
K13
Can2 (13.3%)
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3
2
1
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-1
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-4
-2
0
2

Figure 4-3, and

Figure 4-4). Reading the perpendicular distance between the centroid of each site and the diversity vector results in a rank ordering of tree diversity at each site. The 12 sites fell into three general groups along the first axis. This reflected a gradient from high-to-low tree diversity (the effective number of species) and was related to the severity of disturbance and forest type. The highest diversity was in one group: the unlogged forest K30 and lightly logged forest K14. An intermediate level of diversity was in a second group: the unlogged forests Dura and Mainaro and the two heavily logged forests K15 and Sebatoli. These four sites separated into two groups on the second axis, which resulted in differences for some response variables but not for others. The lowest diversity was in a third group: the heavily logged and poisoned forest K13, the grassland, the harvested conifer plantation, and the unplanted and planted abandoned farmland sites Isunga, Phase 1 and Phase 3 (collectively the "heavily disturbed sites"). The grassland and unplanted abandoned farmland (Isunga) consistently had larger 99% confidence intervals than the other sites, indicating more variation in the tree assemblages at those two sites.

4.4.2 Animal foods

Together, the first and second canonical axes of the diversity-animal foods CDA captured 77.5% of the variation in amount of animal foods (*i.e.,* index of leaf and fruit availability DBH^2) among quadrats (Figure 4-2). Consistently, the most primary and secondary foods for all animal groups was in the unlogged forest K30 and the lightly logged forest, while the least was in the six heavily disturbed sites (Figure 4-2). Primary foods for folivorous and frugivorous monkeys bundled with primary foods for elephants. Secondary foods formed a tight bundle and had a weak positive relationship with tree diversity. Primary foods for chimpanzees and elephants increased with tree diversity, particularly for elephants. Both vectors had high ability to differentiate between sites (*i.e.,* long vectors) but were little related to each other (*i.e.,* the arrows are nearly orthogonal to each other in two-dimensional space). For chimpanzees, the amount of primary food in the two highest sites was equivalent to the unlogged forest Dura and only slightly more than the unlogged forest Mainaro. For elephants, the amount of primary elephant food in Dura and Mainaro was the same as the two heavily logged forests (K15 and Sebatoli) and only slightly more than the remaining six heavily disturbed sites (Figure 4-2). Primary foods for folivorous and frugivorous monkeys were closely related to diversity but had less power to discriminate among sites than for elephants and chimpanzees.

4.4.3 Ecosystem service indicators

Together, the first and second axes of the diversity-services CDA captured 73% of the variation in amount of ecosystem services (*i.e.,* biomass or volume) amongst quadrats. The twelve sites showed greater spread on both the first and second canonical axes from the diversity-and-services CDA (Figure 4-3) than from the diversity-and-animal foods CDA (Figure 4-2). This reflects the increased variety of uses of the tree assemblage for ecosystem service indicators: people use trees for more than just food.

Eight of the nine ecosystem service indicators showed a positive relationship with tree diversity (Figure 4-3). The strongest individual relationship between diversity and services was for carbon storage; the weakest relationship was for house construction materials. The most carbon storage is in the lightly logged and unlogged forest K30, followed by the unlogged forest Dura. There is slightly less carbon stored in the unlogged forest Mainaro and the two heavily logged forests (K15 and Sebatoli). Artisanal use was the only indicator to be weakly negatively related to tree diversity: it is at a slightly oblique angle to the diversity vector, at least on the first and second canonical axes. This means that there are more artisanal products in the heavily disturbed sites than in the lightly logged and unlogged forests – the opposite pattern for the other eight products as well as all primary and secondary foods. Planting trees on the abandoned farmland (Phase 1 and Phase 3) did not result in any more services, including carbon storage, than in the unplanted abandoned farmland or grassland protected from fire. There was marginally higher, timber volume in the lightly logged forest K14 than in the adjacent unlogged forest K30; there were the same amounts of commercial timber in the unlogged forests Dura as in the two heavily logged forests K15 and Sebatoli, and in the unlogged forest Mainaro as in the remaining six heavily disturbed sites (Figure 4-3).

There were many positive relationships among service indicators. They tended to form two bundles: wood products, carbon storage, and construction materials in one bundle (*wood indicators*), and cultural, medicinal, and agricultural plants in another (*non-wood indicators*). Timber did not have a strong joint effect with the bundle of wood indicators, although they are obviously related through species-specific properties (*e.g.,* wood density, grain). Similarly, human food and drink did not have a strong effect with the bundle of non-wood indicators. The amounts of both wood and non-wood indicators are greatest in the unlogged forest K30 and the lightly logged forest K14. Only one of the remaining unlogged forests, Dura, has more wood indicators than the two heavily logged forests and six heavily disturbed sites (Figure 4-4). In general the amount of non-wood indicators is not different between the unlogged forests Dura and Mainaro, the two heavily logged forests, and the six heavily disturbed sites (Figure 4-3).

4.4.4 Synergies and trade-offs

When diversity, animal foods, and ecosystem service indicators are considered together in a single CDA, it is clear that a high level of synergy exists among these three elements. This bears on management strategy. Together, the first and second canonical axes capture 65.4% of the total variation in diversity, animal foods, and ecosystem services amongst quadrats (Figure 4-4). The spread amongst sites was intermediate between the more tightly clustered arrangement of sites in the diversity-and-animal food CDA and the more spread out arrangement in the diversity-and-services CDA. Again, most separation happens along the first axis, but the second axis separates the unlogged forests Dura and Mainaro from the heavily logged forests Sebatoli and K15.

Higher tree diversity is related to higher availability of animal foods and services in all sites (Figure 4-4). When tree diversity, animal foods, and ecosystem service indicators were considered together, primary foods for chimpanzees and folivorous and frugivorous monkeys bundle together and separate from primary foods for elephants. The bundle of wood indicators and the bundle of non-wood indicators separate from each other and show more internal consistency: timber groups with the other wood indicators and human food and drink groups with the other non-wood indicators. The bundle of primary primate foods is more related to the bundle of wood indicators than to the bundle of non-wood indicators. Overall, the unlogged forest K30 and lightly logged forest K14 tended to have the most food and services while the six heavily disturbed sites tended to have the least (except for artisanal uses) (Figure 4-4). The most nuanced differences are between primary foods for elephants (and secondary foods for all animals) and the bundle of non-wood indicators among the three types of unlogged forests. Here, K30 has greater amounts of both while Dura and Mainaro are similar to the eight heavily disturbed sites (Figure 4-4). The lightly logged site K14 is consistently equivalent to the adjacent unlogged site K30. The situation is slightly different for primary foods of frugivorous and folivorous monkeys and the bundle of wood indicators. Here, K30 and K14 still have the most but Dura is intermediate between K30 and Mainaro; Mainaro is equivalent to the two heavily logged forests K15 and Sebatoli, which are greater than the remaining six heavily disturbed sites. There only differences among the six heavily disturbed sites occur between the heavily logged and poisoned forest K13 and the two planted abandoned farmland sites Phase 1 and Phase 3. Here, K13 has more primary chimpanzee food, perhaps marginally more primary frugivorous monkey food, and less artisanal-use trees than Phase 1 and Phase 3. However, these response variables did not differ among these sites when animal foods and indicators are considered separately (*i.e.,* Figures 2 and 3). Individual trade-offs occur among a number of animal foods and indicators, most notably between primary chimpanzee and frugivorous monkey foods and medicinal, fodder, and artisanal uses.

4.5 Discussion

Taken together, my results show a robust, positive relationship between tree diversity and the quantity of both animal foods and ecosystem services across land-use histories. This relationship was consistent for the primary and secondary foods of all mammal groups and for eight of the nine ecosystem service indicators. Given that most protected areas, including Kibale, have preservation of biodiversity as an essential part of their mandate, I use variation in tree diversity as the baseline to which variation in the provision of animal foods and ecosystem services can most usefully be related, first separately and then together. I discuss the relationships among tree diversity, animal food availability and ecosystem services across a range of land use histories in relation to their implications for management of biodiversity.

4.5.1 Tree diversity

The gradient in recovery of tree species diversity that I found from high in lightly logged and unlogged forest, intermediate in heavily logged forest, and low in the six heavily disturbed sites is consistent with previous research in Kibale (Chapman et al. 1997, Lwanga 2003, Bonnell et al. 2011, Omeja et al. 2011). Although slow, there is some recolonization by native trees in the highly disturbed, very large gaps in heavily logged forest and harvested conifer plantation (hundreds or thousands of m2: Kasenene 1987 and A. Jacob personal observation); there were juvenile trees of measurable size throughout each site (*i.e.,* ≥ 3 cm DBH; Table 4-5). This is in contrast to the more uneven recovery of tree diversity in abandoned, unplanted farmland (Isunga) and to grassland protected from fire (Grassland). Both of these latter disturbance histories generate only isolated patches of trees interspersed amongst short and tall grasses and shrubs (see Chapter 1 for discussion of legacy trees); many of the randomly sampled quadrats simply did not have any trees large enough to measure (Table 4-5).

In addition to differences in patterns of recovery in tree diversity, species composition and/or phenological patterns vary over both relatively small- and large- scales in Kibale where the most abundant or currently fruiting species in one area are not necessarily found in others (see Chapter 2 and Chapman et al. 1997). This occurs even in sites with similar land-use history such as unlogged forest. The effects that these differences in the composition and abundance of food trees, as well as the timing of fruit and leaf cycles, will have on animal feeding behaviour and ecology will depend on the degree of specificity of that animal's diet and whether less preferred food species are present (*e.g.,* fallback foods).

4.5.2 Animal foods

It is reasonable to assume that the diversity, abundance, and quality of food influences the structure of animal communities, particularly primary consumers such as primates (Symington 1988, Oates et al. 1990, Ganzhorn 1992, Kay et al. 1997, Stevenson 2001, Potts et al. 2009, Hanya et al. 2011, but see Gogarten et al. 2012). Two of the assumptions that this study rests on are that high quality habitat contains more food for particular animal species than low quality habitat, and that animal populations fare better in high quality habitat. For primates, these assumptions of bottom-up control are supported by empirical evidence from other tropical forests as well as a subset of these study sites in Kibale, although results varied depending on the animal species in question. In a meta-analysis across the Neotropics, primate species richness was positively correlated with plant species richness (Stevenson 2001). Furthermore, primate biomass was positively correlated with fruit abundance; incorporating the size of food trees positively correlated with biomass for frugivores but not folivores (Stevenson 2001). In Kibale, long-term studies showed that frugivorous and folivorous monkeys respond differently to habitat disturbance. In general, frugivores had lower group density in heavily logged forest (K15) than lightly logged (K14) or unlogged forest (K30) (Chapman et al. 2010b). This supports the idea that large-bodied frugivorous primates are most susceptible to habitat disturbance (Johns and Skorupa 1987). However, groups of black-and-white colobus, typically thought of as a generalist folivore, were more abundant in logged forest than adjacent unlogged forest, even though the former had fewer preferred foods trees (Skorupa 1988, Chapman et al. 2010b). In Kibale, density of red colobus (old-growth specialist folivores) occurred in sites with higher cumulative DBH of food trees and where red colobus had more diverse diets (Chapman and Chapman 1999). Finally, local differences in the dominance of certain tree species can also affect animal foraging. Folivorous red colobus and frugivorous grey-cheeked mangabeys spend a large proportion of their time feeding on leaves and fruit of *Cynometra alexandri* and less time resting in the unlogged Mainaro forest where *Cynometra* grows in mono-dominant stands (Chapman et al. 1997, Chapman and Chapman 1999).

Like the arboreal folivorous and frugivorous monkeys, and all other things being equal, chimpanzee populations fare better in higher quality habitat. Chimpanzees living in one unlogged forest in Kibale (Kanyawara) had lower population density and wider dietary diversity, presumed to reflect a paucity of high-quality food items, than chimpanzees living in a second unlogged forest that was less than 15 km away (Ngogo; Appendix 3) but had more high-quality food items (Potts et al. 2011). Kanyawara chimpanzees also had lower foraging efficiency and spent more time resting and less time doing more energetically expensive activities (like hunting and patrolling territory) compared to Ngogo chimpanzees (Potts et al. 2009, 2011). In this study, in addition to better discriminating amongst the sites, the analyses showed that primary chimpanzee foods noticeably diverged from primary foods for monkeys, especially if services are not considered (Figure 4-2). This is perhaps reflective of the more catholic and divergent diets of omnivorous chimpanzees compared to the monkeys. It is also because chimpanzees – and elephants – eat a wide variety and large amounts of non-tree plants, like shrubs, lianas, grasses, and forbs, which the arboreal monkeys do not. If other plants had been included in the data collection and analysis, the rank ordering of habitat suitability (*i.e.,* food availability) for chimpanzees and elephants would perhaps have shifted towards the more disturbed sites.

My index of food availability (DBH^2) should be viewed as an estimate of maximal food availability. Although I dealt with animal food preferences by classifying tree species as providers of primary or secondary foods, and by including data on diet preferences collected throughout Kibale, other environmental and species-specific characteristics play considerable roles in realized food availability. First, intra-specific diet can vary over spatial and temporal scales: spatial variation in the diet of red colobus in Kibale tended to outweigh temporal variation, and increase with increasing distance between monkey groups (Chapman et al. 2002b). This means that animals in one place might have different diets than animals of the same species nearby. Second, phenological patterns mean that leaf and fruit foods are not equally available over time. In a global meta-analysis, biomass of frugivorous primates increased with decreasing seasonality (Hanya et al. 2011). In Kibale, chimpanzee density appears to be related to the abundance of trees that synchronously produce fruit at times when other fruit resources are scarce (Potts et al. 2009). A study in Nyungwe National Park, Rwanda, a montane tropical rainforest approximately 400 km south of Kibale, demonstrates how primates respond to changes in food availability (Kaplin et al. 1998). Here, changes in phenology at the community-level did not decrease overall fruit availability but did result in seasonal scarcity of foods preferred by blue monkeys (Kaplin et al. 1998). The monkeys responded by diversifying their diet from more-preferred to less-preferred foods, including eating more leaves and seeds. Third, even if food is available in the environment it might not be accessible. For instance, non-territorial animals or groups have more flexibility in moving to and from high and low suitability habitat compared to territorial animals. The latter might not be able to supplant an existing territory holder. Therefore, arboreal monkeys may avoid a high quality food patch, or otherwise alter their behaviour, while it is occupied by chimpanzees in order to avoid predation (Stanford 2002). Fourth, food quality also plays a role in habitat suitability. High quality leaf food, as measured by a high ratio of protein to fibre in mature leaves, is positively correlated with colobine primate biomass at different spatial scales in Kibale (Chapman et al. 2002a), in forest fragments around Kibale (Chapman et al. 2004), and in Asia and Africa as a whole (Waterman et al. 1988, Oates et al. 1990, Davies 1994), as well as with biomass of folivorous lemurs in Madagascar (Ganzhorn 1992) and with density of primates in the Amazon (Peres 1997). Therefore, indices of maximal food availability like DBH^2 might not linearly translate to an animal's habitat use or population size. Nevertheless, although details will vary from location to location and time to time, indices based on tree size remain a practical way of quantifying potential food resources as well as strong predictors of primate species richness and biomass (Stevenson 2001, Hanya et al. 2011).

4.5.3 Ecosystem service indicators

Although tree diversity was better able to discriminate among sites than any individual ecosystem service indicator, it is noteworthy that the relationships between diversity and eight of the nine indicators of ecosystem services were broadly consistent across the differing disturbance histories (Figure 4-3). The greater spread among sites in the services-only analysis reflects the increased variety of uses of the tree assemblage since people use trees for more than just food. Certain trees are selected for particular purposes as a result of species-specific traits, although traits related to cultural uses may be less obvious or easily measured than traits related to, for instance, timber or artisanal uses.

My analysis showed two distinct bundles of ecosystem service indicators that both increased with tree diversity but to some degree traded off against each other (Figures 4-3 and 4-4). The first bundle included carbon storage, wood products, house construction, and commercial timber. Each of these four indicators depends on the properties of wood (*e.g.,* wood density). That there was higher biomass of indicators in the wood bundle in the lightly logged and unlogged forests, but not the heavily logged forests, reflects that trees with high wood density were removed during commercial logging (Figure 4-3). When ecosystem services were analysed without animal foods (Figure 4-3), the wood bundle was more spread out. The second bundle included trees used for livestock fodder and cultural and medicinal purposes, all non-wood forest products. It is harder to identify species-specific traits that would cluster these indicators together; for instance, what trait would make one tree species more suitable for religious purposes than another? The choice of particular medicinal and cultural plants differs amongst individual traditional medicine practitioners as well as amongst tribes in the region. This left two remaining services: human food and drink, and artisanal uses. Human food and drink were tightly correlated with tree diversity, likely reflecting the catholic definition of this indicator where multiple biological properties of the trees would come together to form that service, *e.g.,* fruit eaten or used to brew alcohol or trees targeted for bee forage to make honey. Artisanal uses for trees was unique among all services in that it was not related, or slightly negatively related, to tree diversity (Figure 4-3). This is one of the clearer representations of a trade-off among services, where forests in early stages of succession have the greatest biomass of ‘artisanal trees’, particularly in the grassland and harvested conifer plantation. This means that forest could not be managed for artisanal uses of trees as well as the other eight ecosystem services. However, since only 17 tree species are used for artisanal purposes, and all of them are used for at least one other non-wood forest product (*e.g.,* fodder, human food and drink, and traditional medicine, Table 4-

4), it would be possible to intensively manage small areas to maximize these uses (*i.e.,* a small plantation).

That the lightly logged site (K14) consistently has the highest diversity as well as levels of almost all ecosystem services is probably in part a reflection that the tree assemblage in this site (*i.e.,* trees sampled in the 30 quadrats) is a combination of two forest types: *Parinari-Pouteria* (type K1) and mixed *Parinari* (type K2 unknown subtypes) (Table 4-1). These two forest types differ in species composition, stem abundance, and basal area (see Chapter 2 and Appendix 3). On the other hand, quadrats in both Dura and Mainaro also fell in a mixture of forest types (Table 4-1) but this was not reflected in either greater amounts of ecosystem services or foods. Simply put, the number of trees and the effective number of species are one third lower in Dura, and one-half lower in Mainaro, than forest around Kanyawara (Table 4-5).

Compared to the large body of research on the relationships between Kibale primates and habitat, much less is known about how local people use trees. More residents near Kibale perceived more material benefits from wetlands than from forests, although this may reflect their use of community-owned forest fragments and exclusion from the national park (Hartter 2010). Results of this are most robust for those indicators for which I had access to Kibale-specific data: trees used for cultural and medicinal purposes, commercial timber, and house construction. Like animal foods, the relationships between sites and some service indicators would change if non-tree plants were included (shrubs, lianas, vines, forbs, sedges, rushes, grasses, and non-vascular plants). Indicators that depend on wood properties, like trees used for carbon storage, wood products, timber, and house construction, would likely not change even if non-woody plants were included in the sampling design. On the other hand, many non-tree plants have cultural, medicinal, fodder and artisanal uses.

When tree diversity, animal foods, and ecosystem services were analyzed together, there was not only increased correlation of individual vectors within each bundle of primate foods, wood-based services, and non-wood-based services, but also increased separation between the wood and non-wood bundles (Figure 4-4). Bundling was tighter between primary foods for chimpanzees and frugivorous monkeys than between chimpanzees and folivorous monkeys. Hence a forest managed to increase food for chimpanzees would have a stronger positive effect on the food supply for frugivorous monkeys than for folivorous monkeys, although the latter would still increase to some degree. This management scenario would also increase the stocks of the bundle of wood services, but also would have a strong trade-off with artisanal uses, and to a lesser degree with the bundle of non-wood services. At least half the artisanal tree species are eaten by elephants or chimpanzees but only one is a primary food (*Pseudospondias microcarpa* for chimpanzees), and only one is eaten by folivorous monkeys (*Albizia* spp., a primary food for both black-and-white and red colobus monkeys) (Table 4-4).

4.5.4 Trade-offs affecting management strategies in Kibale

The implications of the preceding results for management strategies in and around Kibale National Park are heartening. First, both the availability of animal food and the provision of ecosystem services generally increase with tree diversity. Therefore, it is theoretically possible to develop win-win management strategies with positive outcomes for all three considerations. Second, the correlations among tree diversity, the availability of food for wildlife, and the provision of ecosystem services for people do not have perfect positive correlations across the range of disturbance histories. This means that managers must accept some degree of trade-offs among the three considerations. No single strategy is likely to maximize potential returns on all three considerations, so there will be win-lose and win-neutral situations (Reyers et al. 2012). Third, sites with different disturbance histories also vary in levels of tree diversity, animal foods, and ecosystem services. Moreover, the relationships among the three considerations vary across disturbance histories. Hence an optimal management strategy for Kibale as a whole will necessarily involve a series of different but coordinated, flexible strategies respecting past and present patterns of disturbance. With these factors in mind, I review possible options to manage parts of the park with different disturbance histories: those that were originally forested versus those that were originally grassland.

4.5.4.1 Managing undisturbed and disturbed forests

Throughout this study, I based site selection on large-scale human disturbances to forest such as logging, not small-scale human, or large- or small-scale ‘natural’ disturbances such as pit-sawying, elephant damage, or disease. These latter disturbances certainly play important roles in the ecosystem, but do not lend themselves well to large-scale management. In terms of tree diversity, managing the unlogged forests and effectively restoring logged forests are high priorities. Two results that bear directly on management options are noteworthy. First, the three unlogged sites differ substantially with respect to diversity and availability of animal foods and ecosystem service indicators (Figure 4-4). No single site can represent the full range of value inherent in unlogged forests within the park; ongoing preservation of all three sites is essential. In the three unlogged forests, the greatest differences occur in primary food for elephants, secondary foods for all animals, and the bundle of non-wood indicators. In these respects, the lightly logged site K14 and the unlogged forest K30 hold more resources than the unlogged sites Dura or Mainaro, which are more like the two heavily logged sites K15 and Sebatoli. It is also possible that variation occurs on the third canonical axis not seen in a two-dimensional biplot, which could further separate the sites. If priority management was focused on chimpanzees, Dura and Mainaro would have equal value to K30 and K14. Indeed, chimpanzee viewing is the major reason tourists visit Kibale, which makes chimpanzee habitat a high management priority. Since 20% of visitor park fees are shared with local communities (UWA 2003), there may be a trade-off between accepting revenue generated from chimpanzee tourism in lieu of accessing stocks of services in the same location. Clearly there is heterogeneity in the amount of these components held in each of these forests (Chapter 3), as well as evidence that unlogged forests changing over relatively short time scales (Chapman et al. 2010a). Therefore, management must consider, anticipate, and even encourage dynamism in unlogged forests (Mori 2011).

Management of heavily logged forests is, in some ways, simpler than the decisions about how to manage unlogged forest. Although K13, K14, and K15 were logged at approximately the same time (Table 4-1), 35 years later the lightly logged site has recovered equivalent amounts diversity, animal foods, and ecosystem services to the adjacent unlogged site K30. Recovery is clearly related to the degree of disturbance (**Error! Reference source not found.**,

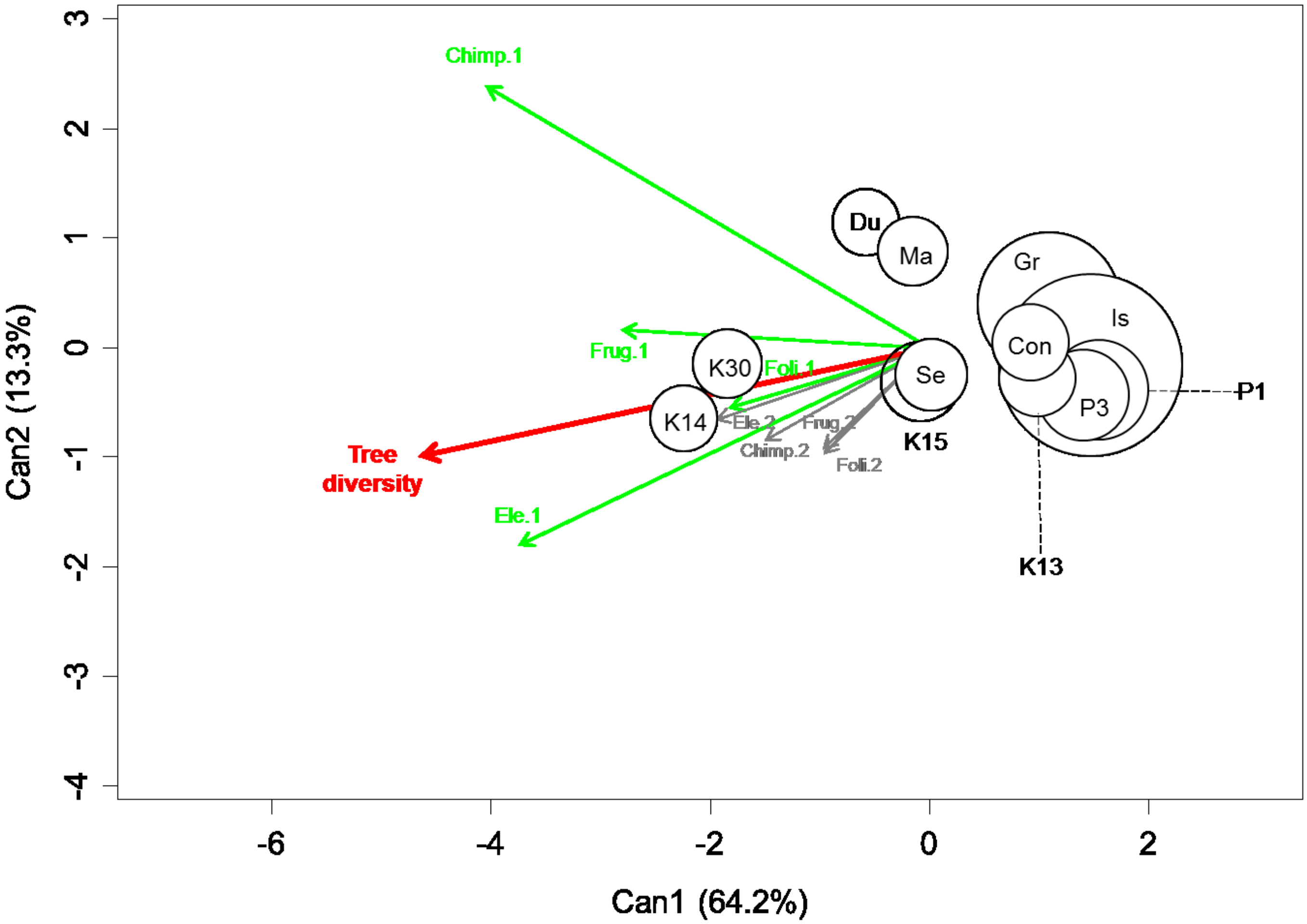
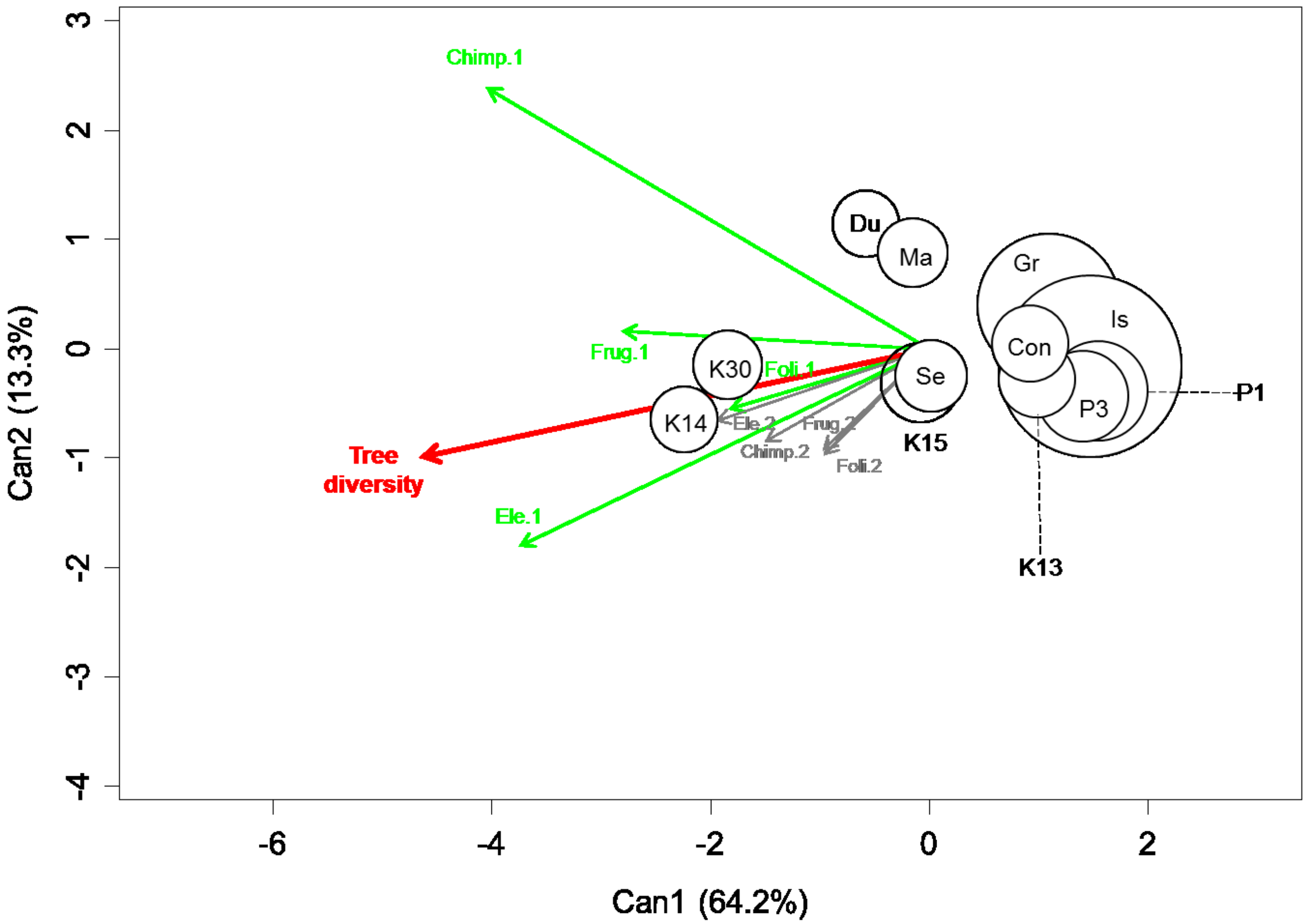

Chimp.1
Frug.1
Foli.1
Ele.1
Tree diversity
Ele.2
Frug.2
Chimp.2
Foli.2
Du
Ma
Gr
Is
Con
P3
P1
K30
K14
Se
K15
K13
Can2 (13.3%)
Can1 (64.2%)
3
2
1
0
-1
-2
-3
-4
-6
-4
-2
0
2

Figure 4-3,

Figure 4-4), as harvest in the heavily logged forests was at least 50% greater than in lightly logged K14, and K13 was subsequently treated with arboricide. Furthermore, in a study of forest regeneration in a range of logging intensities across East Africa, there was no difference in species richness or diversity of trees in heavily logged versus lightly logged sites, but there were consistently fewer late-successional trees – seedlings germinated but did not recruit into larger size classes (Kirika et al. 2010). This points to both the importance of forest ecologists considering different size classes as well as species identity, and subsequent role in the environment as animal food and/or ecosystem services, (Kirika et al. 2010). The trade-off between timber harvest and primate foods is particularly relevant as most timber trees in Africa are also food for primates (Skorupa 1988, Struhsaker 1997). This reflects the congruence between these two components (Figure 4-4). Therein lies the trade-off: harvested trees cannot also be animal food, nor can priority primate habitat be harvested. This trade-off might not be as stark in Asian tropical forests, where timber trees tend not to be eaten by primates (Johns and Skorupa 1987). In a tropical forest managed for timber harvest and animal habitat, there may be advantages to establishing a matrix of small harvested sites with larger blocks of more protected forest. However, this does not take into account the problems associated with timber harvest, such as fragmenting habitat with roads (called "the enemies of rainforest", Laurance et al. 2009) and increased bushmeat hunting (Poulsen et al. 2009). Multifunctional landscapes will have to contend with related threats that are perhaps not as pressing in single-function landscapes.

4.5.4.2 Managing former grasslands to restore forest

Five of the sites in this study were 'originally' grassland (*i.e.,* at the time of last major disturbance, Table 4-1): the two abandoned farmland sites planted with trees, the unplanted abandoned farmland site, the harvested conifer plantation, and the grassland protected from fire. My results did not find any differences in tree diversity, animal foods, or services among these five sites (**Error! Reference source not found.**,


Chimp.1
Frug.1
Foli.1
Tree
diversity
Ele.1
Ele.2
Frug.2
Chimp.2
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Is
Con
P3
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K30
K14
Se
K15
K13
3
2
1
0
-1
-2
-3
-4
-6
-4
-2
0
2
Can2 (13.3%)
Can1 (64.2%)

Figure 4-3,

Figure 4-4), at least not at this relatively early stage of restoration. This result is particularly interesting in light of considerable research and management resources directed to these projects, both within Kibale as well as similar projects throughout the tropics.

Aside from preventing fire, the tree planting project is the largest-scale restoration-oriented activity in Kibale (UWA 2003). It is an ambitious project employing several hundred local people who have planted over 1.4 million trees on 62 km^2 (Face the Future 2014). The predicted benefits include community development, climate change mitigation, biodiversity conservation, and soil erosion control (Face the Future 2011). By many accounts, forest regeneration in the planted area is promising and has ancillary benefits. My study builds on previous work on forest regeneration comparing one of my planted abandoned farmland sites (Phase 1) and the harvested conifer plantation with a grassland protected from fire in central Kibale (at Ngogo, see map in Appendix 3) (Omeja et al. 2011, 2012). Twelve years after planting, regenerating forest in Phase 1 had only 50% and 75% the aboveground woody biomass compared to same-aged forest regenerating in the Ngogo grassland and harvested plantation (Omeja et al. 2012). Tree species richness was also greater in forest regenerating in the Ngogo grassland (23 species in 0.5 ha) and harvested plantation (40 tree species in 2 ha) compared to Phase 1 (40 species in 4 ha). Biomass accumulation tapered off the longer grassland was protected from fire, which was attributed to initial recruitment and subsequent mortality of pioneer species replaced by later successional species (Omeja et al. 2012). Since some of the planted trees are later successional species (*e.g., Celtis durandii* and *Warburgia ugandensis*) this decline may not be as severe in the planted area as in the grassland. Evidence of animal- and bird-dispersed tree species naturally regenerating in the planted site (Omeja et al. 2012), and observations of animals typically thought of as old-growth specialists (such as red colobus, mangabeys and chimpanzees, Skorupa 1986, Struhsaker 1997; A. Jacob, personal observation) points to ancillary benefits of the planted site for biodiversity. Results of this study indicate that tree planting did not increase animal foods or ecosystem services compared to the grassland, harvested plantation, or unplanted abandoned agriculture (with the exception of a trend for more artisanal services, Figures 4-3 and 4-4). Given the significant financial and human resources required to rear, plant, and tend seedlings, the relative ecological versus socioeconomic benefits and costs of the tree planting program in Kibale should be evaluated. It costs $120,000 USD/$km^2$/yr to plant and maintain the reforested areas, but excluding fire alone costs $500

USD/km^2/yr (Omeja et al. 2012). It is clear that planted trees are recruiting and growing, and likely facilitating the regeneration of native forest, but my results raise the question of whether this is the best use of limited restoration resources.

An alternative to planting native tree seedlings is to plant exotic, fast-growing trees that can be harvested fairly soon for timber. However, the choice of which species to plant, and how to plant them, depends on the desired outcome of the re/afforestation project. The conifer plantation was established to quickly provide timber (Kingston 1967) – that it acted as an effective nurse crop for regenerating native forest was an unforeseen advantage. Approximately ten years after harvest, it seemed that the gain in native tree regeneration (species richness, density, and diversity) out-weighed the short-term losses of damage to native trees during harvest (Kasenene 2007), although such damage was considerable (Struhsaker 1997). Furthermore, damage can minimized and natural regeneration preserved if plantations are harvested manually instead of mechanically, *i.e.,* pit-sawing instead of saw-milling, and most of this regrowth is from coppicing (Kasenene 2007). It seems that enrichment planting does not facilitate native tree regeneration compared to natural regeneration in the plantation; in fact, Omeja et al. (2009) found that planted native seedlings were shorter, smaller, and less common than naturally regenerating seedlings of the same species.

Tree planting projects for the purpose of either short rotation timber harvests or carbon sequestration can have ancillary benefits for biodiversity through habitat restoration, and for local communities through employment growing and planting seedlings and ancillary ecosystem services like soil protection and flood regulation. Western and central Uganda have some of the highest ranked potentials for carbon storage across sub-Saharan Africa but become less attractive when socioeconomic factors are considered (Greve et al. 2013). Although the high human population density and agricultural intensity in these areas, leading to much deforestation and soil degradation, make them prime candidates for carbon stocking potential, these same factors make the human cost of reforestation too high to be feasible. The best locations for forest-based projects to store carbon will be in regions where levels of biodiversity and governance are high, the social costs of converting existing land-uses to forest are low, and local communities can obtain direct benefits from the reforestation project (*e.g.,* employment, harvest of non-timber forest products) and be involved in its planning and management (Greve et al. 2013).

4.5.4.3 Managing for multi-functionality

Managers have a serious conundrum with regard to decisions on opening the park to extraction of non-timber or non-wood forest products. Across African tropical rainforest parks, positive relationships with the local community was the best indicator of its success at conserving indigenous forest species (Struhsaker et al. 2005). And, understandably, people are more positively disposed to parks when they perceive its benefits outweighing the costs. A recent review of African community forests shows that decentralizing management over community forest resources to local communities is associated with increased biodiversity conservation (Persha et al. 2011). There is also evidence that ecosystem service projects can help conserve biodiversity (Goldman et al. 2008). Whether this is appropriate for protected areas like national parks is contentious. The high levels of tree diversity in the park are coincident with many ecosystem services that local people have exploited in the past, but is it feasible to manage levels of extraction sustainably and without adverse impact on wildlife?

People can lose access to park resources in two distinct ways: by being excluded from protected areas for conservation reasons, and by loss of the resource altogether through deforestation (Naughton-Treves et al. 2011). Although people living directly adjacent to the park bear the brunt of the costs through crop-raiding, a decade of interdisciplinary research on communities around Kibale showed that the park was not a ‘poverty trap’ (Naughton-Treves et al. 2011). Rather, drawing on non-timber forest products from the park was one of the mechanisms that very poor people, who usually live in the least desirable land adjacent to the park, used to increase their resilience to unforeseen circumstances, such as illness or death in the family, and avoid having to sell land in desperation (Naughton-Treves et al. 2011). However, managers in Kibale have had mixed success when allowing local communities to access resources. In some villages, access to park resources was associated with reduced illegal resource extraction, while in others the opposite pattern was true (MacKenzie et al. 2012).

In East Africa, there is reason to be cautious of “*pragmatic*” approaches to conserving forests like Kibale. A world-wide review of the extent and consequences of downgrading and degazetting protected areas over the last century showed that the proximate causes were access to and use of natural resources (Mascia et al. 2014). Of all countries considered, Uganda had suffered the most, with over 30 events of downgrading, downsizing, and degazetting affecting more than 55% of the national protected areas estate (Mascia et al. 2014). Creating a multiple-use zone in Kibale, *i.e.,* around a core protected area, would require downgrading protection status, but forest loss in buffer zones around East African protected areas is greater than in unprotected areas (Pfeifer et al. 2012). Nevertheless, across Africa, protected areas better conserved native rainforest biodiversity than alternative land uses (Struhsaker et al. 2005).

Whatever the ideal management might be for Kibale National Park, the foundation of sound decision-making is explicit information about the trade-offs that are made with different management scenarios. This allows multiple stakeholders to understand how various choices will affect outcomes for biodiversity as well as the resources that wildlife and people depend.

4.6 Tables and figures

4.6.1 Table captions

Table 4-1. Description of twelve study sites, representing eight disturbance histories, in Kibale National Park, Uganda. Mean elevation refers to the average of each sampling quadrat in that site, not the average elevation for the area as a whole. Disturbance refers to the last known major human disturbance. Land cover refers to the type in the majority of the area covered by quadrats in this study at the time of disturbance (Uganda Forest Department 1960, Kingston 1967, Van Orsdol 1986, Skorupa 1988, Eltringham and Malpas 1993, Struhsaker 1997, Chapman and Lambert 2000, Omeja et al. 2011). For this reason, land cover type estimates for well-defined areas may differ from estimates in other parts of the thesis such as the whole-compartment estimates for K14, K15 and K30 (*i.e.,* Table 3-2).

Table 4-2. Taxonomy, conservation status, and diet of animal species. Nomenclature and conservation status follow the IUCN Red List (2013). Note that only trees ≥10 cm diameter-at-breast-height were considered for the folivorous and frugivorous arboreal monkeys (sensu Chapman and Pavelka 2005).

Table 4-3. Definition of nine ecosystem service indicators. Indicators are measures of a static ecosystem attribute at a single point in time, representing ecosystem service stocks (the amount of a beneficial material in a given system) rather than flows (the actual delivery of that benefit to people) (sensu Mace et al. 2012). All relationships between indicators and services are positive. Various plant parts can be used to provide each indicator, *e.g.,* trunk, branches, roots, leaves, bark, fruit, seeds, flowers, sap, latex, etc. All sources are specific to human uses in Uganda; some sources also included information specific to Kibale National Park (indicated below).

Table 4-4. Tree species recorded. Plant taxonomy follows The Plant List (2013). Family codes are the first four letters of the family name; code extended to six letters to distinguish between Meliaceae and Melianthaceae. Animal species codes: RC=Red colobus, BWC=Black-and-white colobus (together "Folivores"), GCM=Grey-cheeked mangabey, RT=Red-tailed monkey, BM=Blue monkey (together "Frugivores"), CHI=Chimpanzee, ELE=Elephant. Animal food codes: 1=Primary food (≥4% of feeding time for five monkey species, ≥1% of feeding time for chimpanzees, ≥1% of stems eaten for elephants), 2=Secondary food (eaten but below threshold for primary food). Ecosystem service indicators: Art=Artisanal, Con=Construction (house), Cul=Cultural, Fod=Fodder (includes mulch), HFD=Human food and drink, Med=Medicine, Tim=Timber, Wood=Wood products, Carb=Carbon storage. Y indicates the tree species is eaten by that animal or used by people for that service indicator.

Table 4-5. Tree diversity characteristics for the twelve study sites. The number of sampling quadrats included in the canonical analyses, stem frequency, stem density, species richness (the number of species), and effective number of species (i.e., the number of species if all were equally common, sensu Jost 2006).

Table 4-1. Description of twelve study sites, representing eight disturbance histories, in Kibale National Park, Uganda.

Site name	Site code	Mean elevation (m asl)	Disturbance type	Years since disturbance	Disturbance description	Land cover type
K30	K30	1503	Unlogged	2-400+[1]	3-4 stems/km^2 removed by pit-sawyers over last 100 years	Mixed *Parinari* forest (type K2 unknown subtypes)
Dura	Du	1246	Unlogged	2-400+[1]	~0.1 stems/ha removed by pit-sawyers over last 100 years	Mixture of *Pterygota* (type K4)[2] and *Chrysophyllum-Celtis* forest (type K3)
Mainaro	Ma	1229	Unlogged	400+[1]	~0.1 stems/ha removed by pit-sawyers over last 100 years	Mixture of *Pterygota* (type K4)[2] and *Cynometra* (type K6) forest
Sebatoli[3]	Se	1458	Heavy logging	57	Logged in mid-1950s[4].Unknown intensity but thought to be similar to or slightly lower than K15[5]	Mixed Parinari forest (type K2 unknown subtypes)[6]
K13	K13	1480	Heavy logging + arboricide	44	Logged in 1969: removed 9.8 stems/ha[7] or 17 m3/ha[8]; ~50% original trees destroyed by logging or incidental damage; arboricide 2,4,5-T used to reduce 'undesirable' trees	*Parinari-Pouteria* (type K1)
K15	K15	1489	Heavy logging	44	Logged in 1968-69: removed 7.4 stems/ha[7] or 21 m^3/ha[8]; ~50% original trees destroyed by logging or incidental damage	*Parinari-Pouteria* forest (type K1)
K14	K14	1527	Light logging	44	Logged in 1969: removed 3.0 stems/ha[7] or 14 m3/ha[8], ~25% original trees destroyed by logging or incidental damage	Mixture of *Parinari-Pouteria* forest (type K1) and mixed *Parinari* forest (type K2 unknown subtypes)
Grassland (Nyamasika[9])	Gr	1529	Fire	20	Subsistence agriculture, grazing, and sporadic fire until early 1900s; sporadic fire until 1993 when fire was consistently prevented	Grassland and scrub[10]
Former	Con	1544	Exotic timber	15	Planted with *Pinus caribaea*, *P. patula*, and	Grassland and scrub[11]

Site name	Site code	Mean elevation (m asl)	Disturbance type	Years since disturbance	Disturbance description	Land cover type
conifers (Nyakatojo[9])			plantation, then harvested		*Cupressus lusitanica* 1963-1965[10], harvested 1993-1998, much incidental damage to regenerating native forest	
Isunga	Is	1361	Subsistence agriculture, fire	20	Grassland encroached and subsistence farmed (mainly bananas) from 1971-1993[12]; occasional fires until recent years	Grassland and scrub[13]
Phase 1	P1	1209	Subsistence agriculture, planting trees	18	Grassland encroached and subsistence farmed from 1971-1993; planted with native trees January-June 1995 (Phase1, compartment 102); poor recruitment	Grassland and scrub
Phase 3	P3	1223	Subsistence agriculture, planting trees	13	Grassland encroached and subsistence farmed from 1971-1993; planted with five spp. native trees July-December 1999 (Phase 3, compartment 206); better recruitment	Grassland and scrub[13]

[1] Based on Chapman et al. (2010a) and Struhsaker's (1975) observation that large parts of Kibale had not been disturbed for several hundred years. Kingston (Appendix 12 Section 6; 1967) thought that areas of Cynometra forest in southeastern Kibale represented nuclei of forest contraction several hundred years ago.

[2] Occasionally called "Poor forest type 1" (type K4) (Appendix 11 in Kingston 1967)

[3] Also spelled Sebutole or Sebitoli

[4] Historical records indicate that much of the 'northern block' of Kibale was logged by the mid-1960s (Uganda Forest Department 1960, Kingston 1967, Wing and Buss 1970)

[5] (Chapman and Lambert 2000)

[6] Likely *Parinari-Carapa-Strombosia* (type K2 subtype a) or *Parinari-Olea* (type K2 subtype b) (Kingston 1967)

[7] Kasenene (1987)

[8] Skorupa (1988)

[9] Local names, also spelled Nyamusika and Nyakajojo (Uganda Forest Department 1960)

[10] Chapman and Chapman (1996)

[11] Scrub forests defined by White (1983, p. 46) as physiognomic formation of local extent, intermediate in structure between forest and bushland and thicket, usually 10-15 m high. Trees (woody plants with well-defined and upright boles) are usually present but do not form a closed canopy. Smaller woody plants (bushes and shrubs) contribute at least as much as the trees to the appearance of vegetation and its phytomass. In Kibale, areas categorized as scrub would include a mosaic of scrub forest with tall and short grassland maintained by fire.

[12] Clearing forest in the Kibale Forest Reserve was started by Bakiga immigrants in 1971 (p. 63 in Hamilton 1984, Van Orsdol 1986). Settling in the grassy Kibale Game Corridor perhaps started some years earlier.

[13] Not covered by pre-logging forest map circa 1955 (Uganda Forest Department 1960), but likely grassland and scrub based on historical descriptions of the area (Van Orsdol 1986, Aluma et al. 1989, Eltringham and Malpas 1993).

Table 4-2. Taxonomy, conservation status, and diet of animal species

Common name	Species code	Scientific name	Conservation status	Diet	Diet references
Uganda red colobus	RC	*Procolobus rufomitratus* ssp. *tephrosceles* Peters, 1879	Endangered B1ab(iii,v)	Folivore	(Struhsaker 1975, Chapman and Chapman 2002, CAC unpubl. data, Struhsaker 2010)
Black-and-white colobus	BWC	*Colobus guereza* ssp. *occidentalis* Rüppell, 1835	Least Concern	Folivore	(Oates 1977, Harris and Chapman 2007)
Red-tailed monkey	RT	*Cercopithecus ascanius* ssp. *schmidti* Audebert, 1799	Least Concern	Frugivore	(Stickler 2004 and unpubl. data, Rode et al. 2006 and unpubl. data)
Grey-cheeked mangabey	GCM	*Lophocebus ugandae*	Unclear (endemic to Uganda)	Frugivore	(Waser 1975, Olupot et al. 1994)
Blue monkey	BM	*Cercopithecus mitis* ssp. *stuhlmanni* Wolf, 1822	Least Concern	Frugivore	(Rudran 1977, Butynski 1990)
Chimpanzee	CHI	*Pan troglodytes* ssp. *schweinfurthii* Blumenbach, 1799	Endangered A4cd	Omnivore	(Potts et al. 2011, Anonymous n.d., Wrangham n.d.)
African elephant	ELE	*Loxodonta africana* Blumenbach, 1797[1]	Vulnerable A2a	Bulk grazer and browser	(Wing and Buss 1970, Chiyo 2000)

[1] Recent genetic evidence suggests two separate species of African elephants: the savannah elephant *Loxodonta africana africana* Blumenbach, 1797 and the forest elephant *Loxodonta africana cyclotis* Matschie, 1900 (Rohland et al. 2010). Some have suggested that Kibale elephants are hybrids between savannah and forest elephants (Blanc 2007; Samuel Wasser, personal communication). The IUCN African Elephant Specialist Group suggests more research before reclassifying populations (IUCN 2013).

Table 4-3. Definition of nine ecosystem service indicators

Ecosystem service(s)[1]	Indicator name	Indicator definition
Cultural		
Spiritual and religious practices	Culture[2]	Biomass[3] (kg) of trees used for cultural, religious, spiritual, or social purposes, including ceremonies and witchcraft
Provisioning		
Production of natural medicines	Medicine[2]	Biomass (kg) of trees used for traditional medicines
Production of ornamental resources[4]	Artisanal	Biomass (kg) of trees used for cosmetics, jewelry, basketry, mats, dyes, ties, fibers, and crafts
Production of fiber	Construction[2]	Biomass (kg) of trees used for house construction, including posts and poles
Production of fiber	Timber[2]	Volume (m^3) of trees historically targeted for commercial harvest in Kibale[5]
Production of fiber	Wood products	Biomass (kg) of trees used for beehives, drums, canoes, liquid containers, tool handles, walking sticks, spears, or household utensils
Production of fiber	Fodder	Biomass (kg) of trees used for livestock fodder (includes mulch)
Production of food	Food and drink	Biomass (kg) of trees used for human food or drink, including ingredients to brew alcohol, oils and lipids, or trees targeted for bee forage (*i.e.,* to produce honey)
Regulating		
Climate regulation	Carbon	Biomass (kg) of trees as an index of carbon sequestration

Sources: (Kingston 1967, Hamilton 1981, Katende et al. 1995, Wong 2003, Kakudidi 2004, Kamatenesi-Mugisha and Oryem-Origa 2005, Krief et al. 2005, Cottray et al. 2006, Baerts-Lehmann and Lehmann 2007, Kakudidi 2007, Orwa et al. 2009, Namukobe et al. 2011).

[1] Ecosystem service definition and categories follow the Millennium Ecosystem Assessment (2005a) and Ecosystem Service Indicators Database (Layke 2009). Provisioning services are ecosystem products, *e.g.,* food, water, timber, and fiber. Regulating

services are ecosystem processes, *e.g.,* flood or climate regulation. Cultural services can be benefits for spiritual, recreational, and cultural reasons.

[2] Indicates that additional information was available specific to communities around Kibale National Park (Kingston 1967, Kakudidi 2004, 2007, Namukobe et al. 2011).

[3] Aboveground biomass (kg) calculated using Uganda-specific general equation for fresh aboveground biomass of individual tree in tropical moist deciduous forest (Equation 562: Y=Exp(–0.89+2.053*log10(DBH)) in Henry et al. 2011). Calculation is valid for trees 3-200 cm DBH includes trunk-underbark, gross branches (>7 cm diameter), thin branches (<7 cm diameter), leaves, bark, stump, and dead branches.

[4] Some items are fibers (*e.g.,* ties, rope) while others are ornamental (*i.e.,* cosmetics, soaps, jewelry).

[5] Timber trees are genera and species listed in Appendices 16-Part1 and 17 of Kingston (1967) as historically targeted for commercial harvest in Kibale: Timber groups 1-4 (Prime, good general purpose timbers, moderate general purpose or special purpose, and useable but poor timbers timbers) and group 5 (non-compulsory harvest species). General volume (m^3) equation for tropical rainforest trees (including bark and trunk) $Y=1.858-3.518*DBH+10.283*DBH^2$ (equation 1109 in Henry et al. 2013).

Table 4-4. Tree species recorded

		Animal species and foods														Ecosystem service indicators								
		RC		**BWC**		**GCM**		**BM**		**RT**		**CHI**		**ELE**		**Fod**	**Art**	**Con**	**Cul**	**HFD**	**Med**	**Tim^1**	**Wood**	**Carb^2**
Tree species	**Family**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**									
Acacia spp.	LEGU															Y	Y	Y			Y			Y
Alangium chinense	CORN														Y						Y			Y
Albizia spp.	LEGU	Y		Y			Y		Y		Y		Y		Y	Y	Y	Y		Y	Y	2	Y	Y
Antiaris toxicaria	MORA												Y		Y	Y	Y			Y	Y			Y†
Apodytes dimidiata	ICAC												Y		Y					Y	Y		Y	Y
Balanites wilsoniana	ZYGO		Y		Y		Y				Y		Y		Y	Y		Y					Y	Y
Baphiopsis parviflora	LEGU		Y				Y				Y							Y					Y	Y
Beilschmiedia ugandensis	LAUR												Y		Y					Y		5	Y	Y
Bersama abyssinica	MELIAN														Y					Y	Y		Y	Y
Blighia unijugata	SAPI				Y		Y		Y	Y			Y	Y				Y			Y	4		Y†,‡
Bridelia micrantha	PHYL		Y				Y		Y		Y		Y		Y	Y	Y	Y		Y	Y		Y	Y†,‡
Carapa procera	MELIAC												Y		Y					Y		2		Y
Casearia spp.	SALI														Y									Y
Cassipourea ruwensorensis	RHIZ										Y		Y											Y
Celtis africana	CANN	Y		Y			Y	Y			Y	Y			Y	Y		Y	Y		Y	4*	Y	Y
Celtis gomphophylla	CANN	Y		Y		Y		Y		Y			Y		Y	Y			Y		Y	4*		Y‡
Celtis mildbraedii	CANN												Y		Y			Y					Y	Y
Chaetachme aristata	ULMA		Y						Y		Y		Y		Y			Y			Y			Y
Chionanthus africanus	OLEA						Y		Y				Y		Y							5		Y
Chrysophyllum spp.	SAPO											Y						Y		Y		3	Y	Y
Citropsis articulata	RUTA														Y						Y		Y	Y
Clausena anisata	RUTA		Y						Y		Y				Y			Y			Y		Y	Y
Coffea spp.	RUBI												Y		Y			Y	Y	Y	Y		Y	Y
Cola gigantea	MALV		Y										Y		Y									Y
Cordia spp.	BIGN						Y				Y		Y			Y			Y	Y	Y	5	Y	Y
Craibia brownii	LEGU																	Y					Y	Y
Croton spp.	EUPH		Y			Y							Y		Y	Y		Y	Y	Y	Y	2	Y	Y
Cynometra alexandri	LEGU		Y		Y		Y				Y		Y					Y		Y	Y		Y	Y
Dasylepis eggelingii	ACHA												Y		Y									Y
Dictyandra arborescens	RUBI														Y									Y†
Diospyros abyssinica	EBEN		Y			Y		Y		Y			Y		Y			Y	Y	Y	Y	5	Y	Y†,‡
Dodonaea viscosa subsp. *angustifolia*	SAPI																				Y			Y
Dombeya kirkii	MALV		Y						Y		Y		Y		Y			Y			Y		Y	Y
Dovyalis spp.	SALI		Y								Y		Y		Y					Y	Y			Y
Drypetes gerrardii	PUTR												Y		Y								Y	Y

		Animal species and foods														Ecosystem service indicators								
		RC		BWC		GCM		BM		RT		CHI		ELE		Fod	Art	Con	Cul	HFD	Med	Tim^1	Wood	Carb^2
Tree species	Family	1	2	1	2	1	2	1	2	1	2	1	2	1	2									
Ehretia cymosa	BIGN		Y						Y		Y		Y		Y			Y			Y		Y	Y
Englerophytum oblanceolatum	SAPO												Y		Y									Y
Erythrina spp.	LEGU												Y			Y	Y		Y	Y	Y		Y	Y
Euadenia eminens	CAPP												Y		Y									Y
Fagaropsis angolensis	RUTA		Y				Y						Y		Y						Y	1*		Y†
Ficus spp.	MORA		Y		Y		Y		Y		Y		Y			Y	Y	Y	Y	Y	Y		Y	Y
Funtumia africana	APOC	Y			Y		Y				Y		Y		Y	Y				Y	Y	5	Y	Y†,‡
Harrisonia abyssinica	RUTA		Y				Y				Y		Y		Y			Y			Y			Y
Ilex mitis	AQUI																Y	Y		Y	Y		Y	Y
Kigelia africana	BIGN												Y		Y	Y	Y		Y	Y	Y		Y	Y
Lepisanthes senegalensis	SAPI												Y		Y			Y		Y			Y	Y†
Leptonychia mildbraedii	MALV														Y									Y
Lindackeria spp.	ACHA														Y									Y
Lovoa spp.	MELIAC														Y							1		Y
Lychnodiscus cerospermus	SAPI														Y									Y
Macaranga schweinfurthii	EUPH														Y			Y						Y
Maesa lanceolata	PRIM												Y		Y				Y		Y		Y	Y
Maesopsis eminii	RHAM															Y	Y	Y		Y	Y		Y	Y
Margaritaria discoidea	PHYL														Y	Y		Y			Y		Y	Y
Markhamia lutea	BIGN	Y		Y			Y	Y			Y		Y		Y	Y		Y		Y	Y	3	Y	Y†,‡
Millettia dura	LEGU		Y		Y		Y		Y				Y		Y	Y		Y					Y	Y
Mimusops bagshawei	SAPO		Y		Y		Y		Y		Y	Y		Y		Y				Y			Y	Y†
Monodora myristica	ANNO						Y		Y				Y		Y					Y	Y			Y
Morus mesozygia	MORA						Y					Y			Y								Y	Y
Myrianthus spp.	URTI												Y		Y	Y				Y	Y			Y
Neoboutonia spp.	EUPH												Y		Y			Y	Y		Y		Y	Y
Newtonia buchananii	LEGU		Y		Y		Y		Y				Y	Y		Y		Y	Y	Y	Y	2*	Y	Y†
Olea welwitschii	OLEA						Y		Y		Y		Y		Y	Y					Y	1*		Y
Oxyanthus speciosus	RUBI														Y			Y			Y		Y	Y
Oxyceros longiflorus	RUBI														Y									Y
Parinari excelsa	CHRY		Y						Y		Y		Y		Y			Y		Y	Y	3*	Y	Y†
Phoenix reclinata	AREC						Y				Y		Y		Y	Y	Y	Y	Y	Y	Y			Y
Pittosporum spp.	PITT												Y		Y						Y			Y
Pleiocarpa pycnantha	APOC												Y		Y									Y
Podocarpus spp.	PODO																Y			Y	Y			Y
Polyscias fulva	ARAL		Y		Y		Y		Y		Y				Y	Y		Y	Y		Y		Y	Y

		Animal species and foods														**Ecosystem service indicators**								
		RC		**BWC**		**GCM**		**BM**		**RT**		**CHI**		**ELE**		**Fod**	**Art**	**Con**	**Cul**	**HFD**	**Med**	**Tim**^{1}	**Wood**	**Carb**^{2}
Tree species	**Family**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**	**1**	**2**									
Pouteria altissima	SAPO		Y		Y		Y		Y		Y	Y			Y							2*		Y†
Premna angolensis	LAMI		Y		Y		Y	Y					Y		Y			Y					Y	Y
Prunus africana	ROSA	Y		Y					Y		Y		Y		Y	Y		Y	Y	Y	Y	2*		Y†,‡
Pseudospondias microcarpa	ANAC		Y				Y		Y		Y	Y			Y		Y			Y	Y		Y	Y
Pterygota mildbraedii	MALV		Y				Y		Y		Y	Y			Y							3		Y
Rauvolfia vomitoria	APOC												Y				Y			Y	Y			Y
Rothmannia urcelliformis	RUBI						Y				Y		Y		Y			Y						Y
Rubiaceae spp.	RUBI																							Y
Scolopia rhaniphylla	SALI														Y			Y		Y			Y	Y
Senna spectabilis	LEGU															Y				Y	Y		Y	Y
Shirakiopsis elliptica	EUPH		Y										Y		Y			Y			Y		Y	Y‡
Spathodea campanulata	BIGN				Y				Y				Y		Y	Y				Y	Y		Y	Y‡
Strombosia scheffleri	OLAC						Y		Y		Y		Y		Y							3	Y	Y†
Strychnos mitis	LOGA		Y				Y		Y		Y		Y		Y			Y			Y			Y
Symphonia globulifera	CLUS												Y		Y		Y	Y			Y		Y	Y
Syzygium cumini	MYRT												Y			Y	Y			Y	Y			Y
Tabernaemontana spp.	APOC														Y									Y
Tarenna pavettoides	RUBI														Y			Y			Y			Y
Treculia africana	MORA												Y		Y	Y	Y			Y	Y			Y†
Trema orientalis	CANN		Y										Y		Y	Y	Y	Y		Y	Y			Y
Trilepisium madagascariense	MORA		Y				Y		Y		Y		Y		Y			Y			Y		Y	Y
Turraeanthus africanus	MELIAC																							Y
Uvariopsis congensis	ANNO		Y		Y		Y	Y			Y	Y			Y								Y	Y†,‡
Vangueria apiculata	RUBI												Y			Y		Y		Y	Y		Y	Y
Vepris nobilis	RUTA		Y					Y			Y	Y		Y		Y		Y	Y	Y	Y		Y	Y
Warburgia ugandensis	CANE						Y				Y		Y			Y		Y		Y	Y			Y†,‡
Zanthoxylum leprieurii	RUTA										Y		Y		Y			Y			Y	1*	Y	Y
	Total	**6**	**30**	**5**	**13**	**3**	**32**	**7**	**24**	**3**	**34**	**9**	**61**	**4**	**74**	**32**	**17**	**47**	**16**	**41**	**61**	**23**	**52**	**98**

[1] Timber species targeted for commercial harvest in Kibale, with number indicating which of five groups that species was in: Group 1=prime timbers, Group 2=good general purpose timbers, Group 3=moderate general purpose or special purpose timbers, Group 4=useable but poor timbers, Group 5=non-compulsory harvest species (Appendix 16 Part 1 and Appendix 17 in Kingston 1967). An

asterisk indicates one of the nine tree species that made up more than 90% of total out-take for all logging compartments with harvest data available (Table 2.1 in Skorupa 1988).

[2] Some species were specifically planted by Face the Future Foundation in Kibale National Park to sequester carbon on abandoned farmland. The symblol † indicates planted in Phase 1 (1995) while ‡ indicates planted in Phase 3 (1999) (Appendix 2 in Klomp 2009, Face the Future 2011, Omeja et al. 2011). The majority of trees planted in Phase 3 were *Albizia* spp. *, Bridelia micrantha, Shirakiopsis elliptica, Celtis gomphophylla,* and *Warburgia ugandensis* (Omeja et al. 2011).

Table 4-5. Tree diversity characteristics for the twelve study sites

Site name	Site code	Land-use	No. quadrats	Stem frequency	Stem density (stems/ha)	Species richness	Effective number of species
K30	K30	Unlogged	29	554 (±9.4)	1847 (±31)	57 (±3.7)	25.6 (±3.5)
Dura	Du	Unlogged	30	387 (±5.2)	1290 (±17)	40 (±2.4)	16.4 (±2.1)
Mainaro	Ma	Unlogged	29	305 (±4.0)	1017 (±13)	32 (±1.7)	13.6 (±1.5)
K14	K14	Lightly logged	30	539 (±7.2)	1797 (±24)	59 (±3.6)	35.1 (±3.0)
K15	K15	Heavily logged	25	243 (±8.7)	810 (±29)	46 (±4.2)	32.8 (±3.4)
Sebatoli	Se	Heavily logged	28	188 (±4.4)	393 (±15)	47 (±2.5)	32.8 (±2.3)
K13	K13	Heavily logged + arboricide	26	88 (±2.4)	293 (±8)	25 (±1.4)	18.2 (±1.4)
Conifers	Con	Harvested conifer plantation	26	151 (±5.1)	503 (±17)	26 (±2.1)	14.8 (±1.7)
Grassland	Gr	Grassland protected from fire	14	91 (±5.2)	303 (±17)	15 (±1.6)	7.4 (±0.9)
Isunga	Is	Abandoned farmland, unplanted	11	32 (±1.6)	107 (±5)	9 (±0.7)	7.2 (±0.6)
Phase 1*	P1	Abandoned farmland, planted 1995	20	55 (±2.4)	183 (±8)	11 (±0.7)	6.7 (±0.6)
Phase 3*	P3	Abandoned farmland, planted 1999	22	79 (±2.4)	263 (±8)	14 (±1.1)	7.3 (±1.0)

*The tree planting project calls these areas Compartments 102 and 206, respectively (Face the Future 2011)

4.6.2 Figure captions

Figure 4-1. Map of study sites in Kibale National Park, Uganda. Dotted line indicates southernmost limit of commercial timber harvest starting in 1950 until early 1970s. Note division between Kibale Game Corridor and Kibale Forest Reserve, before they were joined to form Kibale National Park in 1993. Grey areas indicate abandoned farmland planted with native trees by Face the Future Foundation between 1994 and 2008.Disturbance history: Unlogged=K30, Dura, Mainaro; Lightly logged=K14; Heavily logged=K15, Sebatoli; Heavily logged and arboricide=K13; Planted abandoned farmland=Phase 1, Phase 3; Unplanted abandoned farmland=Isunga.

Figure 4-2. Canonical discriminant analysis biplots for tree diversity and primary and secondary foods. Primary animal foods are green arrows, secondary animal foods are grey arrows. Together, the first and second canonical axes account for 77.5% of variation. The mathematical center of the biplot, *i.e.*, where both x and y coordinates are zero, is the centroid for all 290 quadrats in multi-dimensional space projected in two dimensions. The length of each vector indicates the influence it has in detecting differences and discriminating among sites relative to the other vectors. Site codes are: Con=former conifer plantation, Du=Dura (unlogged), Gr=grassland protected from fire, Is=Isunga (unplanted abandoned farmland), K13=heavily logged and poisoned, K14=lightly logged, K15=heavily logged, K30=unlogged, Ma=Mainaro (unlogged), P1=Phase 1 (planted abandoned farmland), and P3=Phase 3 (planted abandoned farmland).

Figure 4-3. Canonical discriminant analysis biplots for tree diversity and nine ecosystem service indicators. Brown arrows represent bundle of wood-based service indicators, blue arrows represent bundle of non-wood based service indicators. Together, the first and second canonical axes account for 73.0% of variation. The mathematical center of the biplot, *i.e.*, where both x and y coordinates are zero, is the centroid for all 290 quadrats in multi-dimensional space projected in two dimensions. The length of each vector indicates the influence it has in detecting differences and discriminating among sites relative to the other vectors. Site codes are: Con=former conifer plantation, Du=Dura (unlogged), Gr=grassland protected from fire, Is=Isunga (unplanted abandoned farmland), K13=heavily logged and poisoned, K14=lightly logged, K15=heavily logged, K30=unlogged, Ma=Mainaro (unlogged), P1=Phase 1 (planted abandoned farmland), and P3=Phase 3 (planted abandoned farmland).

Figure 4-4. Canonical discriminant analysis biplots for tree diversity, primary and secondary animal foods and nine ecosystem service indicators. Primary animal foods are green arrows (secondary animal foods were included in the analysis but omitted from the biplot for clarity), brown arrows represent bundle of wood-based service indicators, blue arrows represent bundle of non-wood based service indicators. Together, the first and second canonical axes account for 65.4% of variation. The mathematical center of the biplot, *i.e.,* where both x and y coordinates are zero, is the centroid for all 290 quadrats in multi-dimensional space projected in two dimensions. The length of each vector indicates the influence it has in detecting differences and discriminating among sites relative to the other vectors. Site codes are: Con=former conifer plantation, Du=Dura (unlogged), Gr=grassland protected from fire, Is=Isunga (unplanted abandoned farmland), K13=heavily logged and poisoned, K14=lightly logged, K15=heavily logged, K30=unlogged, Ma=Mainaro (unlogged), P1=Phase 1 (planted abandoned farmland), and P3=Phase 3 (planted abandoned farmland).

Figure 4-1. Map of study sites in Kibale National Park, Uganda

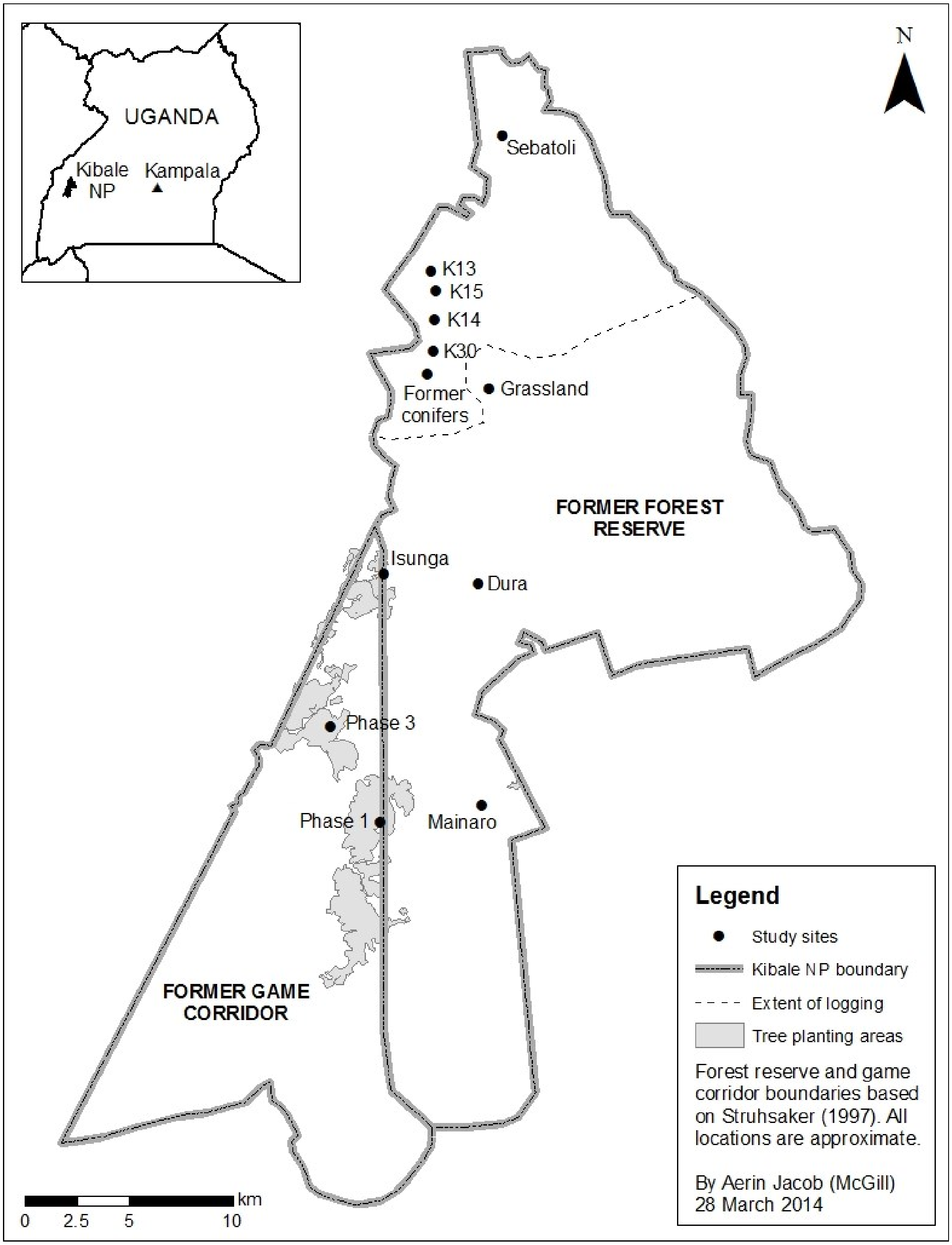


Figure 4-2. Canonical discriminants analysis biplot for tree diversity and primary and secondary animal foods

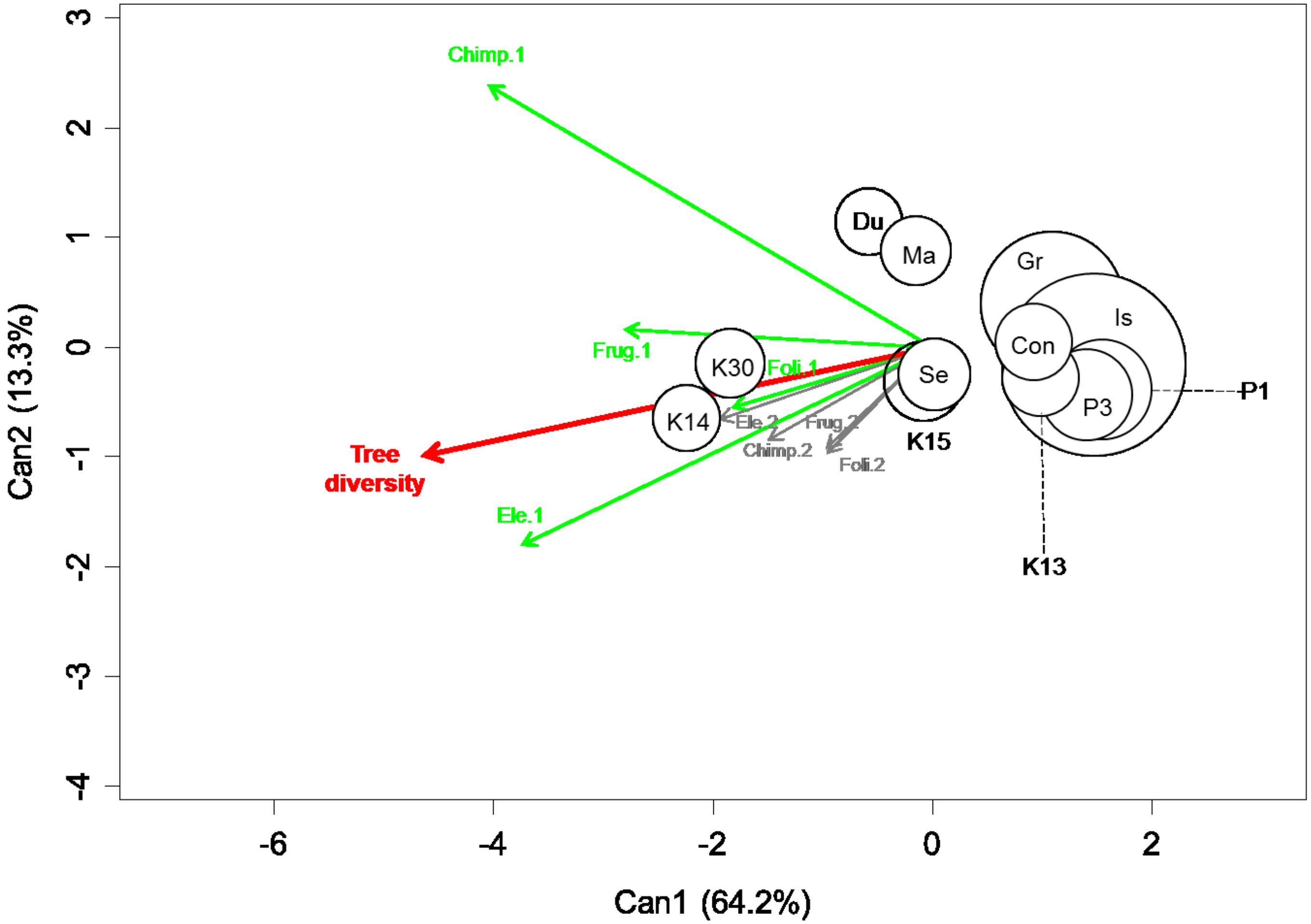


Figure 4-3. Canonical discriminant analysis biplot for tree diversity and nine ecosystem service indicators

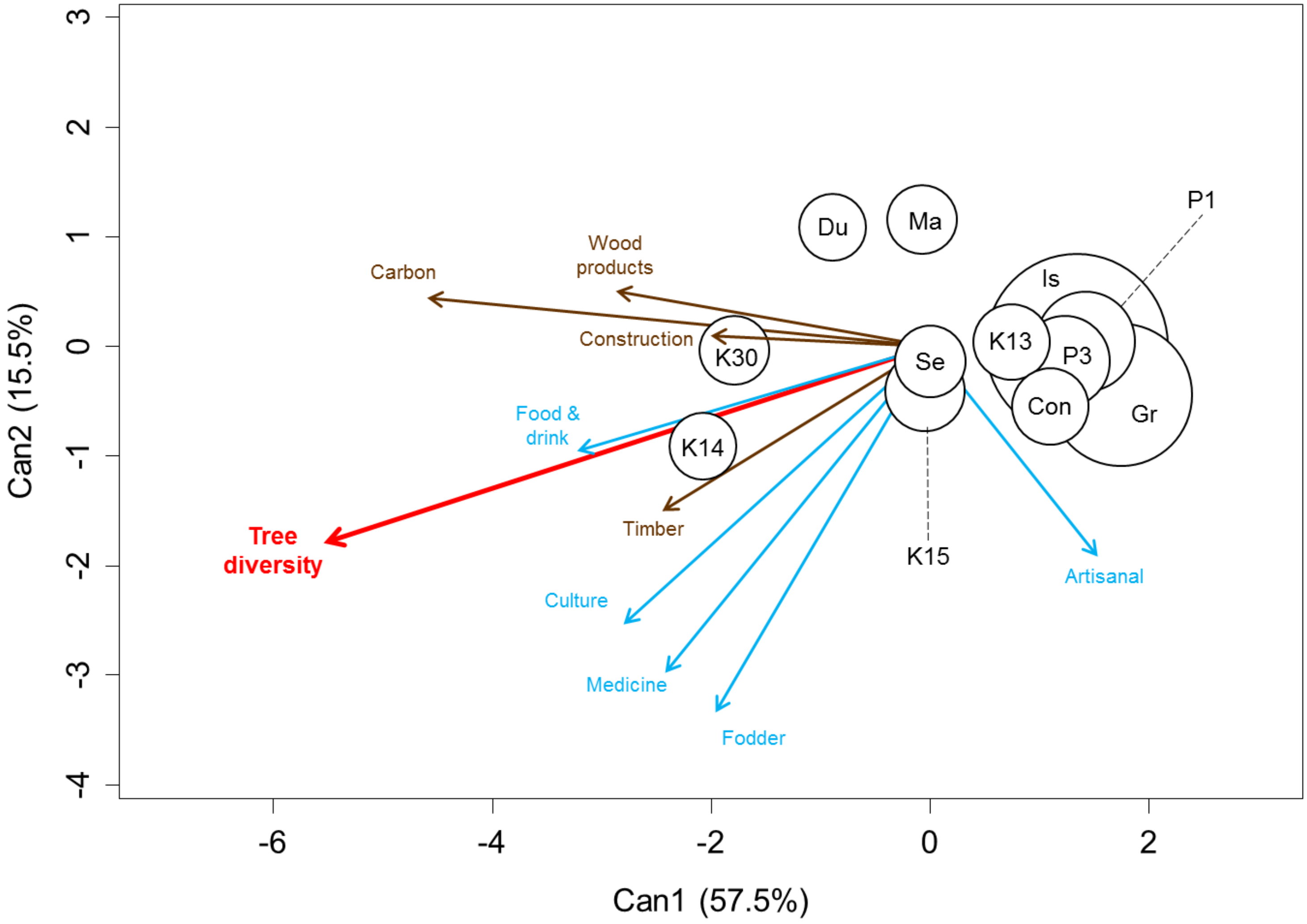
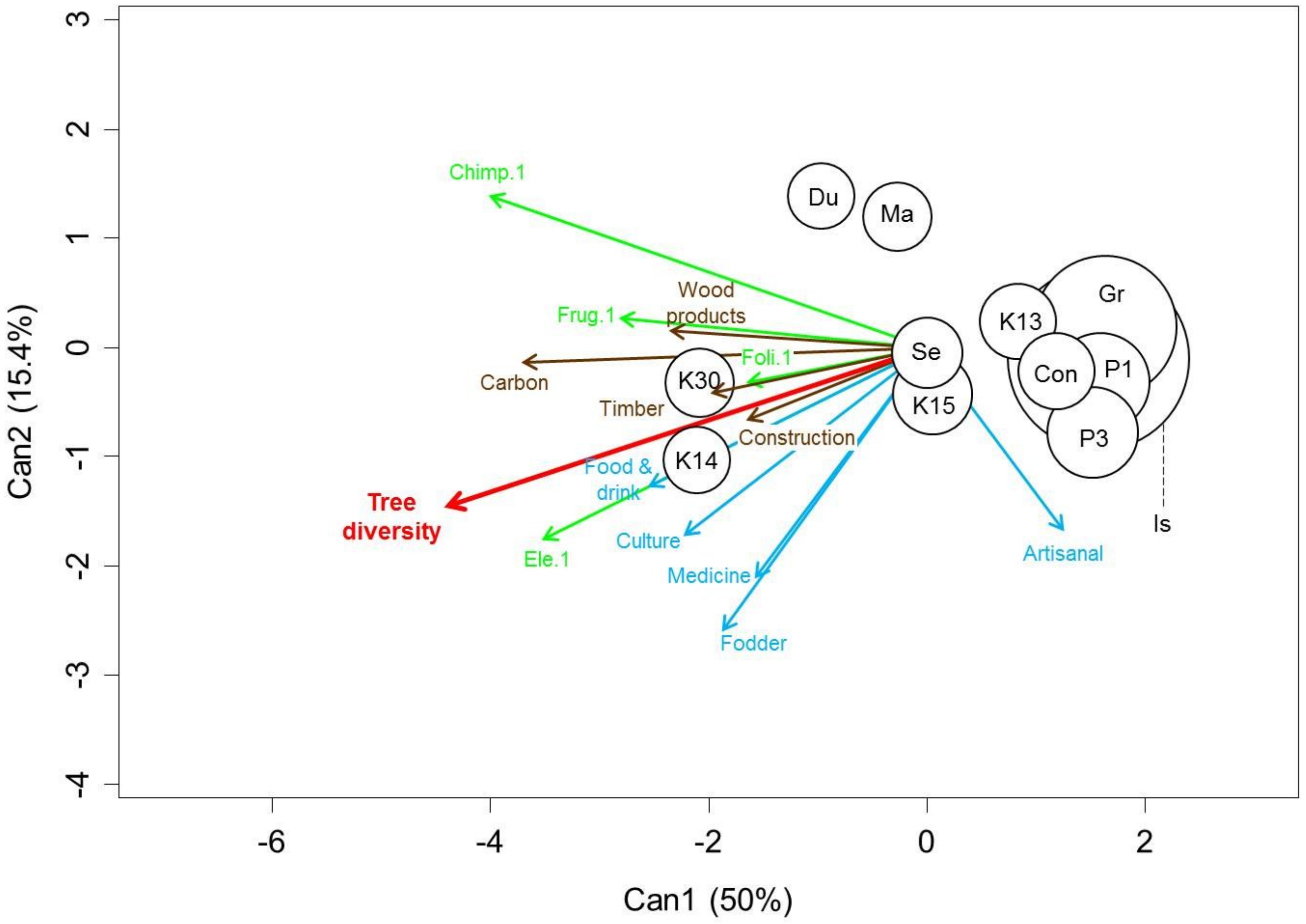


Figure 4-4. Canonical discriminant analysis biplot for tree diversity, primary and secondary (not shown) animal foods and ecosystem service indicators



5 GENERAL CONCLUSIONS

From the outset, one of the primary goals of my doctoral studies has been to conduct conservation-oriented research directly related to managing African tropical rainforests. Nearly three-quarters of conservation biologists believe that their published recommendations positively affect management (Flaspohler et al. 2000), but this is not always the case. When researchers perceive that their recommendations have been integrated into management, they credit 1) initiative from management agencies and 2) establishing effective and direct links with managers. In other words, successful conservation initiatives are often rooted in designing and communicating research with practitioners (Robinson 2006). When their recommendations were not integrated into management, most researchers blame neglect or lack of capacity from managers (Flaspohler et al. 2000). Bearing this in mind, throughout my fieldwork in Uganda I have endeavoured to discuss applied issues with the managers of protected areas and natural resources, long-term researchers, and people living around Kibale National Park; doing so was significantly aided by the presence of long-term research projects and relationships formed and maintained between these groups. This has helped me identify pressing research needs in and around Kibale National Park as well as gain a better appreciation for the inter-related challenges facing biodiversity conservation and human livelihoods in this region. These interactions influenced the design, conduct and interpretation of my research. Although rooted in a case-study of Kibale National Park, the results from each of my chapters have broader applicability within global views on priorities and concerns in biodiversity conservation and management

Recent surveys of experts in biodiversity conservation and ecology identified 100 research questions of global importance to their respective fields (Sutherland et al. 2009, Sutherland et al. 2013). Each of my thesis chapters addresses one or more questions posed in these visioning exercises, which were broadly focused on managing protected areas, on restoring ecosystems, on how environments vary over space and time, and on the interactions between biodiversity and ecosystem services. Across the tropics, there are increasing amounts of deforested, degraded, and abandoned land (Asner et al. 2009, DeFries and Rosenzweig 2010), and thus both increasing need and opportunity to conserve and restore biodiversity and ecosystem services (Chapter 4). Some of these areas might be slated for reforestation or afforestation to maximize carbon sequestration – these projects frequently have removing exotic species as part of their certification process (Chapter 2). Finally, evaluating how forests change over time requires identifying, and separating, spatial and temporal heterogeneity in tropical tree assemblages (Chapter 3). In this concluding section of my thesis I summarize the main results and interpretations from each thesis chapter, reflecting on my contributions to both local and more general discussions of key questions in strategies for biodiversity conservation and restoration ecology in African tropical rainforests.

5.1 Trait database for Ugandan trees

A prerequisite to my research was the compilation of reliable data on the characteristics of the trees occurring in Kibale. Trait databases allow plant ecologists to analyze interspecific differences in species' responses to environmental conditions including soil-vegetation dynamics, phenology, reproduction, interaction with animal dispersers, forest dynamics, and the provision of timber and non-timber forest products for local people. Such compilations of traits can be used to predict how plant populations and communities will respond to environmental change, aiding assessment of endangerment risk and prioritizing conservation and restoration programs. Examples of existing trait databases include The Plant Trait Database (TRY, worldwide scope, Kattge et al. 2011), MARIWEN (woody plant species of the Guiana Shield region of South America, Ollivier et al. 2007), the Seed Information Database (Royal Botanic Gardens Kew 2008), and LEDA Traitbase (flora of northwest Europe, Kleyer et al. 2008).

To assemble a trait database for the trees of Kibale, I conducted an extensive survey of both published and grey literature on 160 species of African trees and woody shrubs, from 124 genera and 52 families. To the best of my knowledge, this database, compiled from hundreds of often obscure publications, is the most complete and comprehensive summary of traits relevant to study the ecology and conservation of trees in Uganda. The compilation involved identifying consensus values for traits including growth form; height; guild; successional status; wood density; re-levant biomass and volume equations; mycorrhizal type; habitat affinities; distribution in Uganda; elevation range; degree of forest dependency; type, colour, number, size, and weight of seeds and fruits; dispersal mode; local names and meanings; use of different plant parts in the diets of diverse mammals and birds; and the variety of ways that each tree species is used by people. The information I collected will be made available and will be useful to others working in East and Central Africa.

5.2 Management practice and policy

Collecting management-oriented research is a priority for the Ugandan government, specifically research focused on biodiversity conservation and on how rural communities can access resources inside protected areas (Kaggwa et al. 2009b). Results from my research are related to a number of national and international policies and agreements for Uganda. Specifically, my findings help to address five identified gaps in knowledge, discussed below.

Reflecting the dependence of local livelihoods on natural resources, national policies regarding the management and conservation of forests and wildlife are linked with poverty eradication and sustainable development. The Poverty Eradication Action Plan (PEAP) is the overarching framework guiding poverty-alleviation and development in Uganda (Kaggwa et al. 2009b). The national aim for the wildlife sector reflects the influence of the PEAP on people-oriented approaches to conservation: "*To promote the long-term conservation of the country's wildlife and biodiversity in a cost-effective manner that maximizes the benefits to the people of Uganda*" (Kaggwa et al. 2009b). Achieving maximum benefit from natural resources management is echoed in the shift in Uganda's National Forest Policy over the last century from highly centralized and production-focused, through insecurity and instability, to locally-driven and people-oriented approaches (Turyahabwe and Banana 2008). Flaws in current forest management stem from a general lack of capacity to monitor forests and enforce existing rules and regulations (Turyahabwe and Banana 2008), as well as ineffective implementation of forest policies due to knowledge gaps about the 1) socioeconomic and cultural aspects of forest use, 2) type, scales, and extent of forest biodiversity, and 3) effects of species-poor forest restoration strategies on forest ecosystems (Lovera 2008).

Uganda pledged to achieve 24% forest cover by 2040 as part of its Rio+20 commitments (NEMA 2012). However, concern has been raised about banking on the "*trickle-down effects of afforestation*" to benefit forest biodiversity and ecosystems (Lovera 2008). Thus, although efforts are being made to increase forest cover the effects of these initiatives must be studied 4) across a wider range of species, and 5) to understand the trade-offs among different the methods (*e.g.,* planting tree-crops for agroforestry versus more diverse, but protected forests). Addressing these deficiencies are important elements for Uganda to reach its 2015 targets for the Convention on Biological Diversity (Lovera 2008) and 2040 commitments from Rio+20 (NEMA 2012).

The value of forests has traditionally been calculated in financial terms: for example, in Uganda the total economic value of forests was conservatively estimated to be USD 300 million, while the annual cost of biodiversity loss was USD 256 million (NEMA 2012). However, this information does not easily translate into on-the-ground management, especially in predominantly subsistence-based communities and economies. By applying the methodology I developed in Chapter 4, researchers and managers will be able to 1) assess the non-monetary costs and benefits of different land-uses and management interventions, including forest restoration via legacy trees (Chapter 2) and the inherent variation in forest ecosystems (Chapter 3), and 2) use this information to "*justify and influence decision makers*" to fund forest management to provide the desired benefits (NEMA 2012). Considering these policy related management issues in Uganda, I expand upon the contributions of my research specific to four issues of current management concern in Kibale: 1) the tree planting program, 2) the removal of exotic species, 3) grassland management, and 4) the recovery of logged areas.

5.2.1 Tree planting program

Ecological restoration that uses native species and enhances habitat connectivity, and the provision of ecosystem services is a priority for biodiversity conservation (CBD 2012). Although the tree planting program in Kibale is identified as both reforestation and afforestation, its stated goal is to replace elephant grass with the "*original vegetation*" with the anticipated benefits of increasing the area's water quality and biodiversity, specifically restoring habitat for primates (Face the Future 2014). Planting trees is said to be necessary because "*recurring fires and invasive grasses have made it impossible for the forest to recover naturally*" (Face the Future 2014). The project in Kibale is certified by both the Forest Stewardship Council (FSC, considered the gold standard for sustainable forest management certification) and the Verified Carbon Standard (VCS, the most widely used voluntary program in the global carbon market). To date, the project has planted an estimated 1.4 million trees over 62 km^2, sequestering an estimated 400,000 tonnes of CO_2 (Face the Future 2014). My results from Chapters 2 and 4 identify elements of the planting program that could be improved.

The goal of UWA's tree planting project is to use "*indigenous species to restore natural forest cover*" in the encroached area (UWA 2003). However, two aspects of the tree planting project qualify as creating a plantation, as defined by the Forest Stewardship Council: planting 1) few species of trees, and 2) at regular spacing and even ages (FSC 2012). Conversely, the planted forests contain some of the "*principal characteristics and key elements of natural forests*" (FSC 2012) including passively regenerating native species (Omeja et al. 2011) and some degree of use by animals typically thought of as old-growth specialists such as red colobus, mangabeys and chimpanzees (such as red colobus, mangabeys and chimpanzees, Skorupa 1986, Struhsaker 1997; A. Jacob, personal observation). These trends are promising, but my analyses in Chapter 4 did not detect differences in the tree species diversity or the availability of tree-based animal foods or ecosystem services among grassland protected from fire, and planted or unplanted abandoned farmland. Further analyses will indicate the degree to which associated ground vegetation (e.g., shrubs, herbs, grasses) provide these foods and services. Given the overall goal of restoring forest cover, I recommend augmenting the tree planting project to increase structural complexity, and diversity of species, habitat and function, perhaps with focus on trees important for animal diets or human use. Planting more diverse assemblages, at least in taxonomic if not phylogenetic and functional terms, may encourage greater ecosystem multi-functionality, as well as diversifying the ecosystem services and non-material values provided by forest (Reyers et al. 2012). Refining the tree planting program in these ways would be consistent with my results as well as with general recommendations to increase the efficacy of re/afforestation projects by focusing on specific ecological or phylogenetic traits (Struhsaker et al. 1996, Lamb et al. 2005, Kettle 2012b, Kettle 2012a, Tweheyo et al. 2013), spatial patterns (Cole et al. 2010), and social considerations (Lamb et al. 2005).

5.2.2 Exotic species

Kibale's Exotic Species Eradication policy states that "*no alien species will be permitted within the park*", gives priority to removing the more invasive species and notes the lack of monitoring for exotic species as a management challenge (UWA 2003). The tree planting project is tasked with removing exotics in their project area (UWA 2003). The FSC, which certifies Kibale's tree planting program, stipulates that active restoration should "*use native species and local genotypes… unless there is clear and convincing justification for using others*" (FSC 2012).

Furthermore, alien species should only be used "*when knowledge and/or experience shows that any invasive impacts can be controlled and effective mitigation measures are in place*" (FSC 2012). To my knowledge, before my research in Chapter 2, no one had considered or studied the potential positive effects of the exotic legacy trees on native forest regeneration in Kibale. Related questions from the aforementioned visioning exercises by Sutherland et al. (2009) are: 1) *What information is required to enable responsible authorities to decide when and how to manage non-native species*? and 2) *Under what circumstances do landscape structures such as corridors and stepping stones play important roles in the distribution and abundance of species*?

In Chapter 2 I provide strong empirical support for the hypothesis that legacy trees, particularly avocado and mango, accelerate the recovery of native forest on abandoned farmland. This phenomenon appeared to be particularly important for large-seeded late-successional tree species. Thus, I add to the small existing bodies of knowledge about 1) the role of exotic trees in restoring native forest on farmland in Africa (Berens et al. 2008) and 2) the role of isolated trees in native forest regeneration in Kibale grasslands (Majid et al. 2011). In addition, my results address the questions posed by Sutherland et al. (2009) by filling an existing gap in knowledge about possible benefits of legacy trees and identifying lines of research to weigh these benefits against possible costs. Furthermore, my results suggest legacy trees act as stepping stones for frugivorous wildlife coming from the forest into neighbouring grassland, and that this may be particularly important for the distribution and abundance of large-seeded, late successional tree species. This information can help to prioritize areas for tree planting, for example to connect existing patches of legacy trees to neighbouring forest. My results are both a counterpoint and complement to current restoration activity in Kibale, suggesting that some aspects of park policy may need to be reconsidered. My preliminary discussions on this subject with UWA have been positive and my input has been requested on their Invasive Species Management Strategy.

5.2.3 Grassland management

Interpreted one way, results from Chapter 4 indicate that the tree planting program did not result in significantly more tree diversity, animal foods, or ecosystem services than in unplanted grassland. A more optimistic interpretation might argue that preventing fire in grasslands is just as effective as tree planting, perhaps even more so when paired with legacy trees (Chapter 2). Either way, long-term data demonstrate significant forest regeneration (more stems and more species) when grasslands are consistently protected from fire (Lwanga 2003, Omeja et al. 2012). Such forest regeneration is a boon from the perspective of managing a degraded tropical rainforest. However, a gain in forest habitat comes at the price of losing grassland habitat, with negative consequences for grassland-dependent species; this paradox has been identified as a research need in Kibale (UWA 2003).

In Kibale, grasslands (*i.e., Pennisetum*-dominated areas) provide important habitat for large mammals, including buffalo, Uganda kob (*Kobus kob*), elephant, and baboon (*Papio anubis*) (Wanyama et al. 2010; Jacob and Chapman, unpublished data), as well as numerous other grassland-specialist or restricted-range bird and butterfly species (Howard et al. 1996). Many of these species are found elsewhere (a notable exception is the Button quail *Turnix sylvaticus*), and certainly the much larger Queen Elizabeth National Park just south of Kibale contains large amounts of grassy habitat. The degree to which species will be affected by loss of grassland habitat depends on species-specific ecology and life history traits (*e.g.,* degree of specialization, mobility); however, the responses of some species have ramifications beyond biodiversity inventories. For instance, at some points in time the diet of elephants in Kibale has been over 90% grass (Buss 1961). Restricting the availability of forage could result in increased crop raiding on farms bordering the park, as has been shown for elephants in Zimbabwe (Osborn 2004) and primates in Kibale (Naughton-Treves et al. 1998). It is for managers to decide whether the local loss of grassland and potential risk of stressing grassland-sensitive species is outweighed by the benefit of increased forest cover and habitat quality for forest-sensitive species. The methods and results from Chapter 4 provide a framework for comparing these values measured in different ways and will aid in this discussion.

5.2.4 The recovery of logged areas

It is widely recognized that complex ecosystems like tropical rainforests can show considerable variation over small areas, and that such underlying environmental heterogeneity can make it difficult to detect the effects of disturbance (Potts 2011, Laufer et al. 2013). Since some tropical trees can live for hundreds or thousands of years (Condit 1995, Rees et al. 2001), without baseline information on how environments varied before disturbance, forest ecologists are challenged to monitor long term change in tree assemblages.

Monitoring if, when, and how forest in Kibale recovers after logging has been a key concern for researchers and managers for nearly 60 years (see references in Chapter 3.2, Osmaston 1959, and Struhsaker 1997). Forest regenerates relatively well in a 'lightly logged' area but poorly in adjacent 'heavily logged' areas (Chapman and Chapman 1997, Struhsaker 1997, Bonnell et al. 2011). Reasons for the latter stem from harvest creating very large gaps in the forest (upwards of 7000 m2, Kasenene 1987) resulting in increased seed predation, growth of herbaceous vegetation, and elephant activity (Struhsaker 1997). Altogether, forest regeneration in heavily logged areas is greatly diminished: structural recovery (*e.g.,* basal area) is anticipated to take well over a century (Bonnell et al. 2011), use by most animals other than elephants is lower than in adjacent unlogged forest (Struhsaker 1997), and there is ample reason to believe that the recovery of plant species composition will take much longer (Chazdon et al. 2009).

My research helps address these issues, in addition to a related question from Sutherland et al.'s (2013) visioning exercise: *How do spatial and temporal environmental heterogeneity influence diversity at different scales?* In Chapter 3 I used longitudinal records of tree assemblages in logged and unlogged forest to demonstrate 1) greater variation across space (*i.e.*, within one survey year) than across time (*i.e.,* between survey years), and 2) that this heterogeneity was greater in the tree assemblage within a 10 ha area of unlogged forest than across the range of logging intensity. These results, backed up by additional historical observations, call into question the dogma of equivalent baseline conditions among the three logging compartments traditionally used to study forest recovery in Kibale (K14, K15, and K30; Appendix 3). In Chapter 4 I used a multivariate method that de-emphasizes within-group heterogeneity in order to assess overall differences among groups of samples. I found that lightly logged forest had equivalent, or in some cases slightly more tree diversity, animal foods, and ecosystem services than adjacent unlogged forest. While this should not be taken as a prescription for low-intensity logging throughout Kibale National Park, the result does suggest that silvicultural practices consistent with natural patterns of disturbance are possible in East African rainforests. Low intensity, selective harvests can provide levels of high quality animal habitat and non-timber forest products comparable to levels in nearby unlogged forest.

5.3 Reconciling biodiversity and ecosystem services

The issues addressed in Chapter 4 are larger in scope than those in Chapters 2 and 3. In Chapter 4 I developed and applied a method addressing a management issue of increasing importance: evaluating trade-offs among biodiversity conservation and human livelihoods. This is a topical issue of broad interest: *Under what circumstances can afforestation and reforestation benefit biodiversity conservation?* (Sutherland et al. 2009, Sutherland et al. 2013)

In Uganda, several key ecosystem services are critically stressed, including providing food, fiber, and fuel, and regulating and purifying water (Kaggwa et al. 2009b). The sources of this stress are human-caused deforestation, conversion of wetlands and other natural land covers, and poaching. In light of predicted changes in regional population distribution, developing methods to evaluate these kind of trade-offs is important for protected areas in the Albertine Rift. The 2006 discovery of substantial oil deposits in the Albertine Rift is likely to increase pressure on forest resources and land as a result of human migration to the area during resource exploration, development, and extraction (Kaggwa et al. 2009a). Furthermore, reduced conflict in northern Uganda and the African Great Lakes region will mean the return of millions of internally displaced people (Bjorkhaug et al. 2007, Huggins 2009). Access to land for cultivation is critical for vulnerable populations including newcomers and returnees; indeed, land disputes in these regions may play a substantial role in fomenting or sustaining conflict (Huggins 2009).

Results from Chapter 4 address the effects of land-use history on tree species diversity, on the availability of foods for monkeys, chimpanzees, and elephants, and on provisioning, regulating, and cultural ecosystem services. I identified consistent, positive relationships between tree diversity, animal foods, and all but one ecosystem service indicator (artisanal services). Services supplied by rainforest trees fell into two groups, one bundle of services linked directly to timber availability and the other to non-timber uses of trees. This is consistent with FAO categorization of non-timber and non-wood forest products (FAO 1999). The timber-based bundle of ecosystem services showed a positive relationship with the availability of primary foods for primates, consistent with knowledge that most African timber trees are also food trees for primates (Johns and Skorupa 1987). These results are important in light of debate regarding the role of devolving management control over protected tropical forests from centralized authorities focused on protection to local communities for multiple use (Struhsaker et al. 2005, Persha et al. 2011, Pfeifer et al. 2012, Mascia et al. 2014). Armed with methods to quantitatively compare the trade-offs among specific interest groups (*e.g.,* harvesting construction materials that are also primary chimpanzee foods), stakeholders can make more-informed decisions about where to direct management efforts.

Informed, evidence-based management requires flexible analytical techniques considering components of ecosystems measured and valued in different ways. This is not just comparing apples and oranges, but even more widely different variables like timber, medicine, culture, and wildlife. The method I developed in Chapter 4 provides 1) a relatively simple framework for quantifying these variables and 2) identifying synergies and trade-offs among them. In situations like Kibale, provision of ecosystem services positively correlates with greater tree diversity and animal food – precisely the pre-requisite for sustainability in multifunctional landscapes. Some trade-offs are inevitable but there is plenty of room to develop win-win management strategies. In summary, this thesis significantly advances our knowledge of aspects of restoration ecology in degraded African tropical rainforest. Although the results are specific to selected sites within Kibale, the methods and findings will have applicability to other forests in the Albertine Rift and Eastern Afromontane forests. The degree to which resource management in Kibale will be participatory and decentralized with the local community ultimately will be decided by the Ugandan Wildlife Authority. I hope my findings will prove useful in their deliberations.

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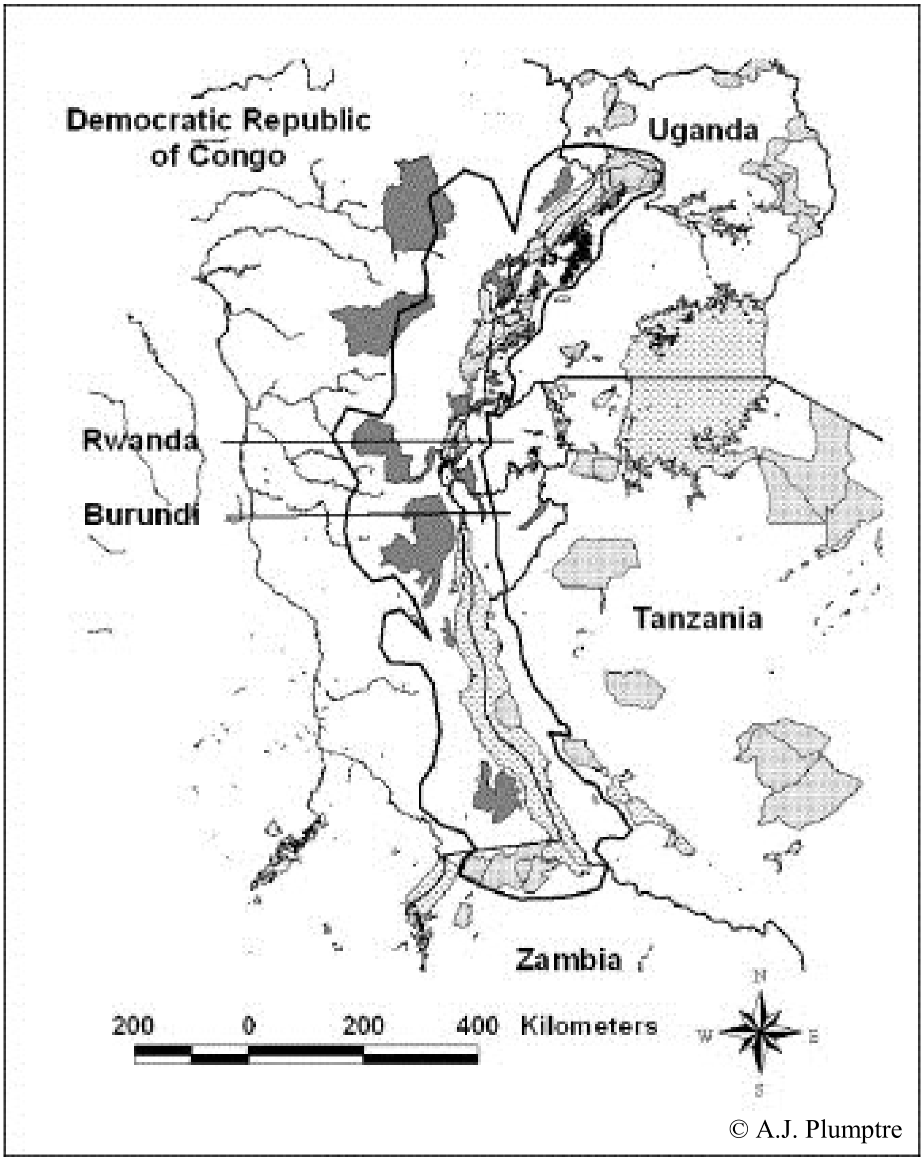
7 APPENDICES

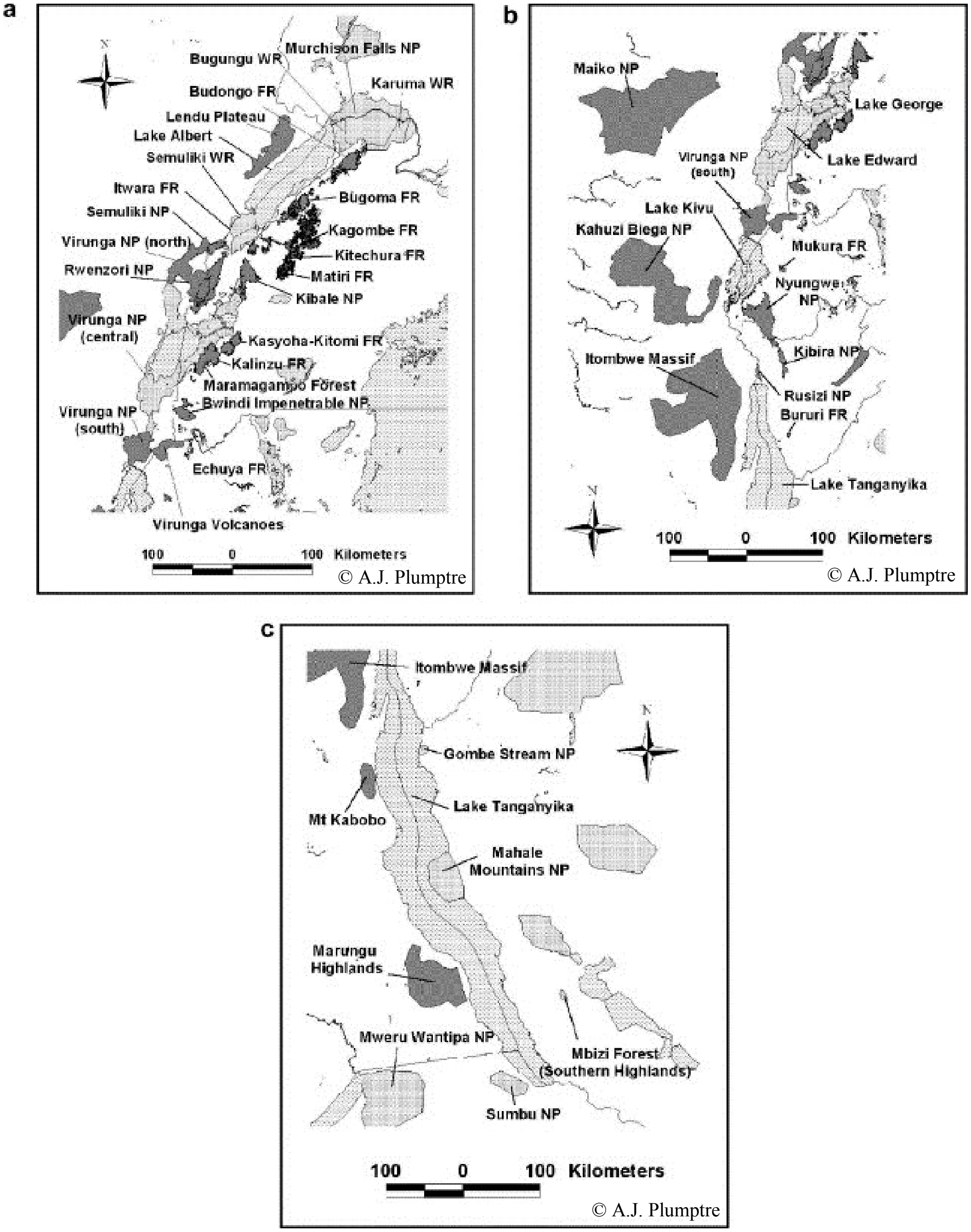
7.1 Appendix 1

Figure 7-1. Map of the Albertine Rift, central Africa from (from Plumptre et al. 2007).



The dark line is the approximate boundary of the Albertine Rift. Forested protected areas (or surveyed areas) are in dark grey and savanna/miombo woodland protected areas are in light grey. Figure from Plumptre et al. (2007).

Figure 7-2. Locations of 38 protected areas in the a) northern, b) central, and c) southern Albertine Rift (from Plumptre et al. 2007).



Darker shaded areas are forested and lighter shaded areas are grassland or woodland. Suffix codes are as follows: NP=national park, FR=forest reserve, WR=wildlife reserve; no code indicates an ungazetted area. Kibale National Park is in the center of the northern map. Figure from Plumptre et al. (2007).

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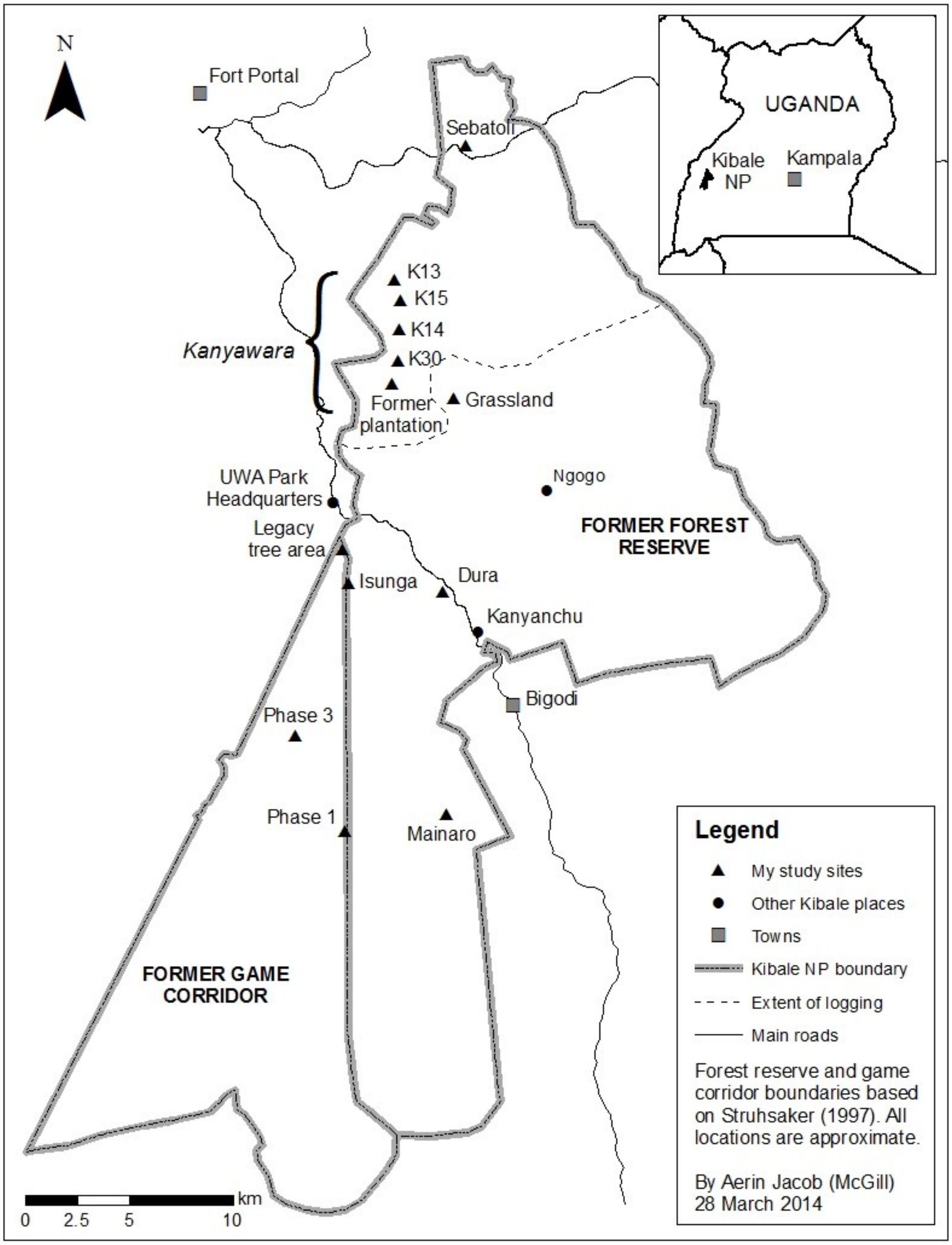
7.2 Appendix 2

Figure 7-3. Map of landscape around Kibale National Park, Uganda



Note that the Kibale Central Forest Reserve was split into three sections divided by the main Fort Portal-Kampala and Fort Portal-Kamwenge roads: the North Block, Central Block, and South Block. Logging only occurred in the North and northern Central Blocks.

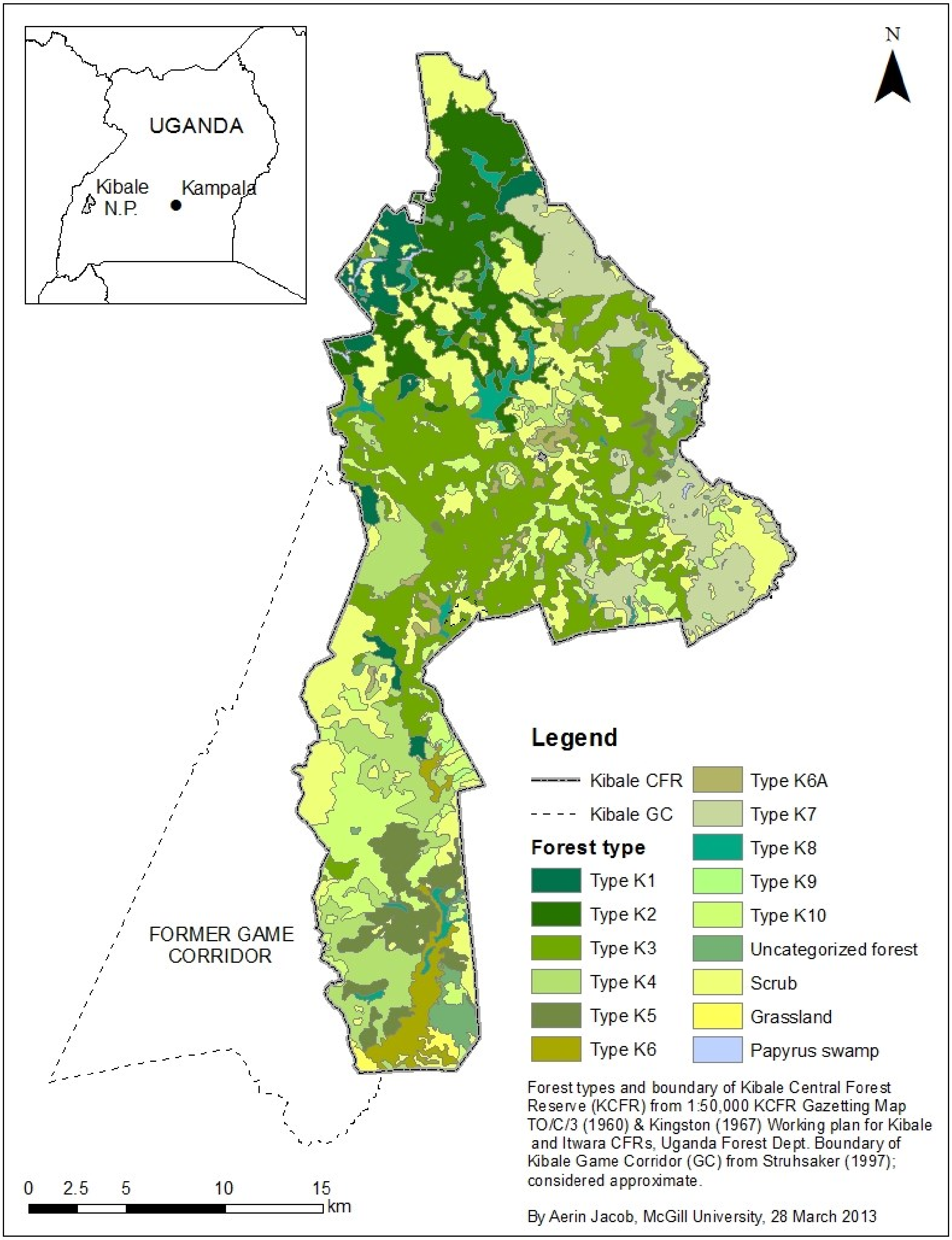
7.3 Appendix 3

During 1954-56, the Uganda Forest Department used a combination of aerial photography and extensive ground work to survey map forest types throughout the Kibale Forest Reserve (Figure 7-4) (Osmaston 1959). Fieldwork included a 1% enumeration covering two-thirds of the forest (*i.e.,* 2.6 km^2 over 260 km^2) and requiring over 130 km of transect lines (Webster and Osmaston 2013). The goal was to evaluate the reserve's forestry potential and draw up management plans for a polycyclic timber harvest. Thirteen forest types were identified and mapped (Osmaston 1959, Uganda Forest Department 1960) (Figure 7-4, Table 7-1).

I digitized forest types from the Kibale CFR gazetting map in ArcMap version 10.1 (ESRI 2012) (Figure 7-4). First, I geo-referenced the map using 287 control points (road intersections, river branching, large water bodies, and park boundary) with the transformation type set to spline. Second, I digitized all land cover types (Table 7-1), large water bodies, peaks, rivers (large, small and seasonal), and roads (major, motorable, minor, and tracks). I used three topology rules to validate these layers: land cover polygons must not 1) overlap or 2) have gaps, and 3) all forest boundaries must not overlap. Third, I dissolved boundaries between land cover polygons, and calculated edge length (perimeter), total area, and percentage of the forest reserve for each land cover class. Sometimes it was unclear which land cover class should be assigned to a particular polygon, *i.e.,* the scanned Kibale CFR gazetting map was smudged or there were no apparent boundaries between clearly identified land cover classes. In this case, I referred to other 1:50,000 Uganda Department of Lands and Surveys topographic maps of the area that, which were less detailed in terms of natural forest cover (*i.e.,* not differentiating between different forest types) but did distinguish between forest and scrub land cover. These maps included Fort Portal Sheet 56/4, Kahunge Sheet 66/2, Kamwenge Sheet 66/4, and Kyenjojo Sheet 57/3 (Uganda Department of Lands and Surveys 1965). I used the final digitized layer in GIS to calculate the area of each forest type throughout the Kibale Central Forest Reserve (Table 7-1).

Spatially explicit data on forest types will be published separately from the thesis and will be available upon request from the author.

Figure 7-4. Map of forest types in Kibale Central Forest Reserve, circa 1955.



Forest types and boundary of Kibale Central Forest Reserve (KCFR) from 1:50,000 KCFR Gazetting Map TO/C/3 (1960) & Kingston (1967) Working plan for Kibale and Itwara CFRs, Uganda Forest Dept. Boundary of Kibale Game Corridor (GC) from Struhsaker (1997); considered approximate.

By Aerin Jacob, McGill University, 28 March 2013

Table 7-1. Area of forest types in Kibale Central Forest Reserve, circa 1955.

Forest type	Forest type name	% of reserve	Area (ha)	Area (km^2)
Type K1	*Parinari-Pouteria (Aningeria)*	3.22	1,837.46	18.37
Type K2	mixed Parinari subtypes	10.51	6,007.92	60.08
Type K3	*Chrysophyllum-Celtis*	24.14	13,796.21	137.96
Type K4	*Pterygota*	9.38	5,362.59	53.63
Type K5	Poor Mixed	4.37	2,496.00	24.96
Type K6	Cynometra	2.35	1,340.38	13.40
Type 6A	Piptadeniastrum	1.06	606.12	6.06
Type K7	Mixed 2	10.17	5,811.28	58.11
Type K8	Swamp	2.08	1,187.62	11.88
Type K9	Young forest	0.16	92.83	0.93
Type K10	Colonizing woodland/ forest	9.87	5,641.56	56.42
Untyped forest	-	1.89	1,079.80	10.80
Grassland	-	0.46	264.46	2.64
Papyrus swamp	-	0.21	120.19	1.20
Scrub	-	20.12	11,496.05	114.96
	TOTAL	**100.00**	**57,140.47**	**571.40**[1]

[1] Note that the total calculated here is larger than the 560 km^2 size reported elsewhere.

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7.4 Appendix 4

The management plans for Kibale Forest Reserve (Osmaston 1959, Kingston 1967) list and describe tree species targeted during commercial timber harvest.

Desirable trees were those species capable of promoting the objectives of management, *i.e.,* one which either supplies the required products or the required conditions. Nurse or ground-cover species are therefore included, as they have value for silviculture even if not for market. Trees were classified according to three Desirability Classes of Grades A, B, C (and weeds) according to six factors (not including relative abundance of the species) (Table 7-2 and Table 7-3):

1) Timber quality and form and freedom from defect;
2) Types of timer likely to be in demand 60 years hence;
3) Speed of growth;
4) Ease and abundance of regeneration;
5) A long list of desirables confused men on tending work; and,
6) Restriction of the number of species in the crop simplifies both silviculture and utilization

Table 7-2. Classes of timber species harvested from Kibale National Park, Uganda

Grade A	Species yielding good quality timber and which will be sufficiently abundant to make a valuable contribution to the future crop: *Carapa, Entandrophragma, Fagaropsis, Lovoa, Newtonia, Olea, Piptadeniastrum, Trhicilia splendida,* and *Zanthoxylum (Fagara)*
Grade B	Species which may be very abundant in the regeneration but yield only a moderate quality timber, or minor forest produce: *Albizia, Cordia, Croton megalocarpus, Parinari, Pouteria (Aningeria), Prunus (Pygeum), Pterygota,* and *Strombosia*
Grade C	All other species of good stem form, commonly attaining 1.52 m (5 ft.) girth above buttress and yielding timber not known to be worthless.
Weeds	Species which rarely or never attain a satisfactory timber size (5' girth above buttress), form or quality and which have no other species products or which are considered silviculturally harmful: *Balanites wilsoniana, Celtis durandii, Ficus* spp., *Psuedospondias microcarpa,* and all shrubs except *Coffea canephora*; also defective

	individuals of desirable species, which owing to form damage or disease are capable of yielding satisfactory produce at the next harvest.

Table 7-3. Groups of timber species harvested from Kibale National Park, Uganda

Group 1: Prime timbers	*Entandrophragma, Fagaropsis, Lovoa, Olea,* and *Zanthoxylum (Fagara)*
Group 2: Good general purpose timber	*Albizia, Carapa, Croton megalocarpus, Newtonia*, Piptadeniastrum*, Pouteria (Aningeria) Prunus (Pygeum),* and *Trichilia splendida*
Group 3: Moderate general purpose or special purpose timbers	*Chrysophyllym, Markhamia, Parnari, Pterygota,* and *Strombosia*
Group 4: Useable but poor timbers	*Blighia, Cassine (Eleaodendron),* and *Celtis*
Group 5:†	*Beilschmiedia, Chionanthus (Linociera), Cordia, Croton macrostachys, Diospyros (Maba), Funtumia,* and *Premna*

* *Piptadeniastrum* was not distinguished from *Newtonia* for the first part of the 1954-56 enumeration, so in forest types K1 and K2 much *Piptadeniastrum* might really be *Newtonia*

† Unnamed – presumably optional harvest trees

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7.5 Appendix 5

Response variables include the effective number of species (a measure of species diversity, see Jost 2006, Jost 2007, and Ellison 2010 for discussion), eight categories of animal foods, and nine categories of ecosystem services. This table is the input matrix for the canonical discriminant analysis. Land-use history, stem number, and species richness are shown for comparative purposes; these values would not be in the input matrix. The values for animal foods and ecosystem services are shown separately because of space constraints. QuadratID code: Du=Dura, Gr=Grassland, Is=Isunga, Ma=Mainaro, P1=Phase 1, P3=Phase 3, Se=Sebatoli. Land use categories are as follows: AgPl=planted abandoned farmland, AgUn=unplanted abandoned farmland, Gr=grassland, HL=heavily logged, HL+P=heavily logged and poisoned, LL=lightly logged, Con=former plantation, UL=unlogged.

Animal food categories are as follows: Chimp=chimpanzee, Ele=elephant, Frugiv=frugivorous arboreal monkey (*i.e.,* blue monkey, red-tailed monkey, and grey-cheeked mangabey), Foliv=folivorous arboreal monkey (*i.e.,* red colobus or black-and-white colobus). In animal foods, 'primary' refers to ≥ 1% of time spent feeding on that tree species for chimpanzees, ≥4% of time for folivorous and frugivorous monkeys, and ≥1% of stems eaten for elephants. 'Secondary' refers to a tree species eaten but below threshold for primary food. Units for all foods are DBH^2 (an index of leaf and fruit abundance) (Table 7-4).

Ecosystem service categories are as follows: Artisanal=trees used for basketry, mats, dyes, ties, fibers, and crafts; Carbon=total aboveground biomass as an index of carbon sequestration; Construction=trees used for house construction, including posts and poles; Culture=trees used for cultural or social purposes, including ceremonies and witchcraft or magic; Fodder=trees used for livestock fodder or mulch; Food and drink = trees used to prepare human food or drink, including ingredients to brew alcohol, oils and lipids, or trees used for bee forage; Medicine=trees used for traditional medicine; Timber=trees historically targeted for commercial harvest in Kibale National Park; and Wood products=trees used for beehives, drums, canoes, liquid containers, tool handles, walking sticks, or household utensils. Units for ecosystem services are as follows: Timber is quantified in m^3 (*i.e.,* volume), all other service indicators are quantified in kg (*i.e.,* aboveground biomass as an index of that service) (Table 7-5).

Table 7-4. Canonical table for animal foods

					Animal foods (DBH^2)							
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Chimp primary	Chimp secondary	Ele primary	Ele secondary	Frugiv primary	Frugiv secondary	Foliv primary	Foliv secondary
Du. 01	UL	14	8	7. 2	76. 63	1,132. 86	16. 00	642. 35	420. 25	424. 36	420. 25	0. 00
Du. 02	UL	17	8	6. 5	1,105. 03	938. 70	0. 00	1,131. 18	906. 50	0. 00	0. 00	906. 50
Du. 03	UL	19	6	3. 1	1,340. 40	951. 79	0. 00	2,405. 72	1,049. 94	0. 00	0. 00	1,049. 94
Du. 04	UL	3	2	1. 9	0. 00	1,018. 02	0. 00	1,018. 02	958. 73	0. 00	958. 73	0. 00
Du. 05	UL	18	5	3. 2	4,989. 10	1,697. 03	0. 00	2,522. 12	1,287. 45	0. 00	590. 49	696. 96
Du. 06	UL	11	7	5. 9	141. 33	367. 05	0. 00	495. 95	144. 00	0. 00	0. 00	144. 00
Du. 07	UL	12	6	4. 4	0. 00	7,058. 13	0. 00	7,164. 28	4,967. 65	729. 00	4,967. 65	0. 00
Du. 08	UL	10	5	3. 9	2,138. 42	509. 00	0. 00	588. 21	0. 00	0. 00	0. 00	0. 00
Du. 09	UL	9	6	4. 9	34. 69	2,097. 00	0. 00	2,163. 28	0. 00	0. 00	0. 00	0. 00
Du. 10	UL	3	2	1. 9	0. 00	39. 69	0. 00	39. 69	0. 00	0. 00	0. 00	0. 00
Du. 11	UL	15	6	4. 4	3,225. 72	1,716. 45	0. 00	1,771. 21	0. 00	412. 09	0. 00	412. 09
Du. 12	UL	10	6	5. 0	0. 00	80. 97	0. 00	139. 75	0. 00	0. 00	0. 00	0. 00
Du. 13	UL	17	7	6. 0	149. 78	13,177. 35	0. 00	13,422.30	1,904. 68	10,648. 29	2,552. 97	10,000. 00
Du. 14	UL	20	11	8. 3	686. 58	589. 08	57. 76	1,211. 05	687. 08	0. 00	491. 08	196. 00
Du. 15	UL	20	10	7. 5	312. 39	2,781. 42	42. 50	3,034. 15	2,304. 00	0. 00	2,304. 00	0. 00
Du. 16	UL	20	13	11. 7	2,537. 88	2,118. 59	115. 75	2,720. 67	1,972. 66	0. 00	1,972. 66	0. 00
Du. 17	UL	11	7	5. 3	236. 65	154. 78	0. 00	382. 43	136. 89	106. 09	0. 00	136. 89
Du. 18	UL	14	6	4. 8	1,164. 91	144. 35	0. 00	502. 31	264. 50	0. 00	0. 00	264. 50
Du. 19	UL	23	7	6. 2	0. 00	463. 17	0. 00	518. 15	0. 00	132. 25	0. 00	132. 25
Du. 20	UL	15	7	5. 4	31. 14	625. 22	0. 00	668. 14	0. 00	144. 00	144. 00	0. 00
Du. 21	UL	16	7	3. 8	647. 73	8,590. 55	64. 00	9,174. 28	4,946. 94	0. 00	4,730. 85	3,961. 53
Du. 22	UL	11	7	6. 3	4,956. 25	809. 32	0. 00	5,765. 57	358. 25	5,151. 98	553. 98	4,956. 25
Du. 23	UL	16	6	5. 4	970. 31	17,941. 15	0. 00	18,910.79	761. 76	17,689. 00	0. 00	18,450. 76
Du. 24	UL	9	4	3. 6	0. 00	409. 34	0. 00	471. 04	0. 00	349. 69	349. 69	0. 00
Du. 25	UL	12	5	4. 6	90. 23	2,628. 61	0. 00	2,810. 94	0. 00	0. 00	0. 00	0. 00
Du. 26	UL	6	3	2. 4	0. 00	1,300. 66	0. 00	1,300. 66	112. 36	1,179. 30	112. 36	1,179. 30
Du. 27	UL	4	3	2. 8	82. 49	1,260. 25	0. 00	1,260. 25	0. 00	0. 00	0. 00	0. 00
Du. 28	UL	12	6	4. 9	567. 34	2,815. 14	0. 00	3,411. 73	916. 24	1,056. 25	441. 00	475. 24
Du. 29	UL	8	4	3. 5	65. 31	11,901. 59	0. 00	11,954.65	0. 00	8,154. 09	0. 00	0. 00
Du. 30	UL	12	8	6. 7	264. 18	1,320. 69	0. 00	1,918. 62	1,262. 09	127. 69	1,156. 00	233. 78

					Animal foods (DBH^2)							
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Chimp primary	Chimp secondary	Ele primary	Ele secondary	Frugiv primary	Frugiv secondary	Foliv primary	Foliv secondary
Gr. 04	Gr	7	1	1. 0	0. 00	5,610. 85	0. 00	5,610. 85	0. 00	5,610. 85	5,610. 85	0. 00
Gr. 05	Gr	3	2	1. 9	0. 00	3,143. 82	0. 00	3,143. 82	0. 00	3,143. 82	1,337. 57	1,806. 25
Gr. 06	Gr	15	6	3. 2	49. 00	1,010. 59	0. 00	997. 18	335. 69	324. 00	659. 69	0. 00
Gr. 07	Gr	2	2	2. 0	0. 00	17. 64	0. 00	17. 64	0. 00	0. 00	0. 00	0. 00
Gr. 08	Gr	16	6	4. 1	450. 79	828. 80	0. 00	1,007. 34	353. 80	0. 00	353. 80	0. 00
Gr. 10	Gr	10	2	1. 6	0. 00	987. 59	0. 00	987. 59	0. 00	676. 56	0. 00	676. 56
Gr. 11	Gr	7	2	1. 8	0. 00	124. 95	0. 00	124. 95	0. 00	0. 00	0. 00	0. 00
Gr. 12	Gr	3	1	1. 0	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
Gr. 14	Gr	2	2	2. 0	28. 09	114. 49	28. 09	114. 49	0. 00	114. 49	114. 49	0. 00
Gr. 16	Gr	1	1	1. 0	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
Gr. 19	Gr	13	2	1. 3	70. 56	1,123. 78	0. 00	1,194. 34	0. 00	595. 74	0. 00	595. 74
Gr. 21	Gr	3	1	1. 0	0. 00	1,691. 81	0. 00	1,691. 81	0. 00	1,691. 81	1,691. 81	0. 00
Gr. 22	Gr	7	2	1. 8	0. 00	453. 14	0. 00	453. 14	0. 00	250. 45	250. 45	0. 00
Gr. 30	Gr	2	2	2. 0	0. 00	650. 00	0. 00	650. 00	0. 00	625. 00	625. 00	0. 00
Is. 02	AgUn	2	2	2. 0	0. 00	100. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
Is. 08	AgUn	1	1	1. 0	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
Is. 09	AgUn	5	3	2. 9	0. 00	1,212. 07	0. 00	1,212. 07	0. 00	823. 69	0. 00	823. 69
Is. 11	AgUn	5	2	2. 0	0. 00	1,314. 55	0. 00	1,314. 55	0. 00	492. 49	0. 00	1,314. 55
Is. 15	AgUn	3	1	1. 0	0. 00	1,111. 28	0. 00	1,111. 28	0. 00	1,065. 04	0. 00	1,065. 04
Is. 16	AgUn	2	2	2. 0	0. 00	1,627. 06	0. 00	1,627. 06	1,190. 25	436. 81	436. 81	1,190. 25
Is. 19	AgUn	5	2	2. 0	0. 00	1,384. 91	0. 00	1,384. 91	0. 00	636. 26	636. 26	660. 29
Is. 21	AgUn	4	2	1. 8	0. 00	1,106. 73	0. 00	1,106. 73	0. 00	757. 04	0. 00	757. 04
Is. 23	AgUn	3	1	1. 0	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
Is. 25	AgUn	1	1	1. 0	0. 00	331. 24	0. 00	331. 24	0. 00	331. 24	0. 00	331. 24
Is. 28	AgUn	1	1	1. 0	0. 00	400. 00	0. 00	400. 00	0. 00	400. 00	400. 00	0. 00
K13. 03	HL+P	10	3	1. 9	0. 00	600. 25	0. 00	4,497. 32	0. 00	0. 00	0. 00	600. 25
K13. 04	HL+P	4	4	4. 0	0. 00	3,328. 19	1,764. 00	1,564. 19	1,346. 89	1,887. 21	0. 00	3,234. 10
K13. 05	HL+P	2	2	2. 0	0. 00	543. 25	0. 00	543. 25	361. 00	182. 25	361. 00	182. 25
K13. 06	HL+P	1	1	1. 0	0. 00	615. 04	0. 00	615. 04	0. 00	0. 00	0. 00	0. 00
K13. 07	HL+P	2	2	2. 0	0. 00	2,374. 25	0. 00	2,374. 25	1,444. 00	930. 25	1,444. 00	930. 25
K13. 08	HL+P	2	1	1. 0	0. 00	2,459. 41	0. 00	2,459. 41	2,459. 41	0. 00	0. 00	2,459. 41
K13. 09	HL+P	2	1	1. 0	0. 00	248. 77	0. 00	248. 77	0. 00	0. 00	0. 00	0. 00

					Animal foods (DBH^2)							
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Chimp primary	Chimp secondary	Ele primary	Ele secondary	Frugiv primary	Frugiv secondary	Foliv primary	Foliv secondary
K13. 10	HL+P	1	1	1. 0	0. 00	302. 76	0. 00	302. 76	0. 00	302. 76	0. 00	302. 76
K13. 11	HL+P	2	2	2. 0	0. 00	2,752. 21	0. 00	2,752. 21	2,641. 96	0. 00	2,641. 96	0. 00
K13. 13	HL+P	5	4	3. 8	0. 00	6,613. 61	0. 00	7,606. 41	6,613. 61	0. 00	6,613. 61	0. 00
K13. 14	HL+P	5	3	2. 6	0. 00	851. 65	0. 00	851. 65	153. 76	289. 00	153. 76	289. 00
K13. 15	HL+P	1	1	1. 0	0. 00	134. 56	0. 00	134. 56	134. 56	0. 00	0. 00	134. 56
K13. 16	HL+P	6	6	6. 0	0. 00	6,096. 58	0. 00	6,196. 58	1,730. 44	4,164. 50	132. 25	1,730. 44
K13. 17	HL+P	5	4	3. 8	0. 00	2,387. 50	0. 00	1,631. 25	0. 00	966. 50	0. 00	210. 25
K13. 18	HL+P	9	4	2. 7	0. 00	2,436. 42	445. 21	1,991. 21	1,024. 00	1,412. 42	0. 00	1,469. 21
K13. 20	HL+P	3	3	3. 0	0. 00	2,900. 50	0. 00	2,394. 25	2,394. 25	506. 25	324. 00	2,070. 25
K13. 21	HL+P	1	1	1. 0	0. 00	219. 04	0. 00	219. 04	0. 00	219. 04	0. 00	0. 00
K13. 22	HL+P	1	1	1. 0	0. 00	488. 41	0. 00	488. 41	0. 00	488. 41	0. 00	0. 00
K13. 23	HL+P	5	3	2. 9	361. 00	1,003. 73	0. 00	1,364. 73	478. 89	885. 84	478. 89	361. 00
K13. 24	HL+P	3	1	1. 0	0. 00	676. 41	0. 00	676. 41	607. 52	0. 00	607. 52	0. 00
K13. 25	HL+P	4	3	2. 8	112. 36	2,420. 64	0. 00	2,743. 25	0. 00	112. 36	0. 00	112. 36
K13. 26	HL+P	2	1	1. 0	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
K13. 27	HL+P	5	5	5. 0	0. 00	6,021. 89	0. 00	6,142. 89	1,728. 64	2,401. 00	432. 64	1,296. 00
K13. 28	HL+P	1	1	1. 0	0. 00	1,398. 76	0. 00	1,398. 76	1,398. 76	0. 00	1,398. 76	0. 00
K13. 29	HL+P	3	3	3. 0	0. 00	992. 13	0. 00	992. 13	0. 00	992. 13	231. 04	121. 00
K13. 30	HL+P	3	3	3. 0	125. 44	1,628. 18	125. 44	1,628. 18	125. 44	1,628. 18	1,466. 89	125. 44
K14. 01	LL	16	9	8. 2	282. 24	3,171. 24	282. 24	3,323. 65	0. 00	2,915. 37	2,633. 13	282. 24
K14. 02	LL	27	18	14. 8	479. 41	2,032. 78	385. 26	2,118. 98	973. 25	867. 61	605. 16	1,235. 70
K14. 03	LL	28	12	9. 0	984. 85	1,550. 19	838. 21	1,895. 46	1,889. 73	0. 00	338. 56	1,551. 17
K14. 04	LL	24	14	11. 2	1,839. 51	228. 34	690. 89	1,700. 11	1,699. 65	0. 00	0. 00	1,699. 65
K14. 05	LL	18	11	9. 7	305. 02	1,252. 55	77. 41	1,531. 41	856. 25	240. 25	756. 25	100. 00
K14. 06	LL	22	10	8. 5	154. 60	1,950. 43	166. 85	1,546. 45	1,407. 42	256. 00	1,407. 42	256. 00
K14. 07	LL	16	10	8. 9	282. 18	8,807. 08	30. 25	9,059. 01	1,000. 20	7,106. 49	139. 24	860. 96
K14. 08	LL	28	14	10. 2	1,361. 84	4,334. 42	614. 69	5,213. 38	5,416. 77	0. 00	2,443. 41	2,973. 36
K14. 09	LL	16	12	10. 6	210. 73	465. 57	76. 96	589. 12	123. 21	163. 84	123. 21	0. 00
K14. 10	LL	6	3	2. 7	0. 00	1,209. 22	0. 00	1,209. 22	0. 00	0. 00	0. 00	0. 00
K14. 11	LL	20	10	8. 0	1,561. 29	2,212. 45	70. 56	3,703. 18	2,260. 37	963. 72	1,378. 28	1,845. 81
K14. 12	LL	6	4	3. 5	37. 21	187. 34	37. 21	127. 25	0. 00	0. 00	0. 00	0. 00
K14. 13	LL	27	13	11. 2	1,010. 35	17,206. 40	43. 04	18,157.71	2,510. 76	14,969. 95	2,088. 03	1,003. 38

					Animal foods (DBH^2)							
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Chimp primary	Chimp secondary	Ele primary	Ele secondary	Frugiv primary	Frugiv secondary	Foliv primary	Foliv secondary
K14. 14	LL	10	6	5. 5	37. 21	47. 59	19. 89	585. 34	0. 00	0. 00	0. 00	0. 00
K14. 15	LL	9	6	5. 3	153. 41	2,847. 44	0. 00	3,000. 85	2,582. 50	182. 25	132. 25	2,450. 25
K14. 16	LL	7	7	7. 0	186. 49	3,689. 42	12. 25	3,879. 66	3,812. 68	0. 00	2,983. 24	829. 44
K14. 17	LL	14	9	7. 9	79. 42	2,089. 24	78. 80	2,060. 96	1,615. 73	0. 00	1,466. 89	148. 84
K14. 18	LL	18	12	9. 2	12. 25	6,271. 33	28. 25	6,255. 33	2,267. 89	3,600. 51	3,109. 64	2,026. 70
K14. 19	LL	5	5	5. 0	0. 00	279. 22	98. 01	172. 21	0. 00	129. 96	0. 00	129. 96
K14. 20	LL	11	9	8. 5	60. 84	2,882. 77	437. 98	2,426. 52	262. 80	2,209. 78	158. 76	438. 93
K14. 21	LL	17	12	10. 1	498. 10	1,463. 11	426. 10	6,640. 76	1,676. 81	5,041. 00	104. 04	6,613. 77
K14. 22	LL	16	7	5. 6	391. 46	1,227. 97	0. 00	1,664. 80	1,305. 37	0. 00	0. 00	1,305. 37
K14. 23	LL	16	11	10. 0	143. 04	1,279. 15	156. 00	1,629. 05	204. 04	1,049. 76	1,153. 80	100. 00
K14. 24	LL	19	12	10. 3	108. 16	3,098. 88	139. 52	3,179. 75	1,667. 16	144. 00	1,559. 00	252. 16
K14. 25	LL	20	15	13. 4	79. 37	821. 03	62. 84	952. 30	400. 00	279. 77	400. 00	171. 61
K14. 26	LL	21	11	8. 5	231. 04	17,983. 59	231. 04	3,981. 03	3,275. 54	14,643. 56	1,748. 50	16,170. 60
K14. 27	LL	24	13	11. 1	414. 36	2,297. 38	404. 36	2,518. 09	967. 50	1,295. 08	2,016. 14	246. 44
K14. 28	LL	28	14	11. 1	96. 56	7,358. 94	116. 81	7,637. 47	5,266. 42	1,814. 65	6,692. 98	388. 09
K14. 29	LL	29	14	12. 0	1,062. 90	2,307. 75	364. 13	3,422. 82	1,499. 09	1,566. 10	1,794. 11	1,271. 08
K14. 30	LL	21	16	15. 1	274. 98	3,128. 05	138. 10	1,307. 90	0. 00	2,762. 10	691. 85	0. 00
K15. 01	HL	12	5	3. 9	0. 00	1,045. 32	0. 00	1,045. 32	536. 25	210. 25	746. 50	0. 00
K15. 02	HL	5	3	2. 9	0. 00	764. 03	0. 00	764. 03	0. 00	610. 09	610. 09	0. 00
K15. 03	HL	2	1	1. 0	0. 00	151. 56	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
K15. 04	HL	2	2	2. 0	497. 29	416. 16	0. 00	913. 45	913. 45	0. 00	497. 29	416. 16
K15. 05	HL	1	1	1. 0	0. 00	484. 00	0. 00	484. 00	0. 00	0. 00	0. 00	0. 00
K15. 06	HL	12	8	7. 2	0. 00	3,088. 54	528. 61	2,486. 16	479. 61	2,352. 25	0. 00	2,831. 86
K15. 08	HL	1	1	1. 0	0. 00	231. 04	0. 00	231. 04	0. 00	231. 04	231. 04	0. 00
K15. 10	HL	4	4	4. 0	0. 00	3,515. 45	0. 00	5,311. 95	0. 00	2,621. 44	0. 00	2,621. 44
K15. 11	HL	16	8	5. 6	1,281. 64	2,738. 65	312. 09	3,741. 84	1,566. 69	1,946. 60	1,281. 64	285. 05
K15. 12	HL	28	15	12. 3	529. 39	18,851. 87	370. 93	19,140.50	18,650.33	287. 14	13,102. 18	5,725. 04
K15. 14	HL	10	6	5. 5	0. 00	5,029. 23	0. 00	5,058. 88	0. 00	4,684. 49	0. 00	2,190. 24
K15. 15	HL	7	6	5. 7	0. 00	1,187. 62	0. 00	1,187. 62	756. 25	359. 84	0. 00	920. 09
K15. 16	HL	4	2	1. 8	0. 00	246. 78	0. 00	197. 78	0. 00	0. 00	0. 00	0. 00
K15. 17	HL	5	3	2. 6	0. 00	506. 89	36. 00	470. 89	0. 00	0. 00	0. 00	0. 00
K15. 18	HL	12	7	6. 0	228. 01	1,422. 54	0. 00	1,396. 53	0. 00	412. 25	0. 00	661. 78

					Animal foods (DBH^2)							
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Chimp primary	Chimp secondary	Ele primary	Ele secondary	Frugiv primary	Frugiv secondary	Foliv primary	Foliv secondary
K15. 19	HL	7	6	5. 7	0. 00	1,651. 73	0. 00	1,696. 62	552. 05	0. 00	552. 05	0. 00
K15. 20	HL	2	1	1. 0	0. 00	300. 37	0. 00	300. 37	0. 00	0. 00	0. 00	0. 00
K15. 21	HL	17	8	5. 8	0. 00	20,852. 67	0. 00	20,852.67	18,298.89	2,190. 90	17,108. 64	1,311. 25
K15. 22	HL	31	8	4. 0	42. 25	1,362. 57	167. 69	2,284. 61	1,085. 25	125. 44	1,085. 25	125. 44
K15. 23	HL	4	4	4. 0	0. 00	1,945. 89	0. 00	1,918. 85	841. 00	0. 00	0. 00	841. 00
K15. 24	HL	2	2	2. 0	0. 00	208. 09	0. 00	208. 09	0. 00	156. 25	0. 00	156. 25
K15. 25	HL	15	10	9. 1	196. 77	1,179. 78	34. 81	1,384. 82	950. 44	141. 61	262. 61	829. 44
K15. 28	HL	1	1	1. 0	0. 00	20. 25	0. 00	20. 25	0. 00	0. 00	0. 00	0. 00
K15. 29	HL	23	14	11. 9	155. 25	3,347. 40	194. 69	3,477. 75	2,904. 01	112. 36	0. 00	3,016. 37
K15. 30	HL	20	13	11. 2	1,207. 38	6,791. 42	0. 00	7,970. 23	938. 45	6,493. 16	938. 45	252. 16
K30. 01	UL	12	6	5. 1	1,200. 39	33. 41	1,200. 39	81. 50	1,128. 74	0. 00	0. 00	1,128. 74
K30. 02	UL	17	10	8. 6	168. 99	1,369. 24	0. 00	1,427. 54	0. 00	1,052. 82	349. 69	0. 00
K30. 03	UL	20	10	7. 5	802. 19	5,019. 03	92. 50	5,725. 63	453. 69	4,903. 56	0. 00	4,809. 69
K30. 04	UL	8	7	6. 7	158. 76	390. 27	158. 76	454. 52	158. 76	283. 54	132. 25	310. 05
K30. 06	UL	3	2	1. 9	0. 00	195. 40	0. 00	195. 40	0. 00	174. 24	0. 00	174. 24
K30. 07	UL	5	3	2. 6	0. 00	629. 20	0. 00	629. 20	0. 00	558. 28	0. 00	558. 28
K30. 08	UL	28	19	16. 8	116. 50	15,821. 66	56. 25	16,138. 49	4,096. 00	11,261. 00	5,357. 00	0. 00
K30. 09	UL	24	19	17. 2	280. 65	2,147. 91	170. 63	2,543. 42	1,412. 19	424. 36	978. 06	858. 49
K30. 10	UL	27	12	10. 4	2,027. 48	3,981. 09	1,824. 74	4,071. 25	3,604. 91	1,584. 04	0. 00	5,188. 95
K30. 11	UL	13	11	10. 1	84. 80	6,031. 14	121. 29	5,951. 56	100. 00	5,535. 36	5,635. 36	0. 00
K30. 12	UL	18	10	8. 3	162. 81	7,778. 23	182. 17	8,019. 16	0. 00	7,623. 54	313. 29	0. 00
K30. 13	UL	16	8	6. 3	881. 83	619. 61	148. 84	1,352. 60	810. 68	305. 29	104. 04	1,011. 93
K30. 14	UL	10	7	6. 6	132. 25	1,044. 17	168. 25	1,008. 17	967. 46	0. 00	835. 21	132. 25
K30. 15	UL	17	8	7. 1	145. 02	2,550. 40	168. 06	2,572. 86	1,849. 00	501. 21	2,350. 21	0. 00
K30. 16	UL	16	11	9. 5	113. 00	1,295. 45	113. 00	1,562. 80	605. 16	670. 93	997. 20	0. 00
K30. 17	UL	48	8	5. 1	835. 58	4,012. 14	0. 00	4,938. 96	685. 79	2,180. 35	0. 00	2,866. 14
K30. 18	UL	21	13	11. 8	1,065. 34	14,835. 38	78. 01	16,060. 52	756. 25	14,833. 84	196. 00	15,081. 09
K30. 19	UL	26	9	5. 0	623. 14	64. 21	550. 89	154. 21	452. 25	0. 00	0. 00	452. 25
K30. 20	UL	23	9	5. 1	441. 00	4,937. 21	10. 89	5,416. 00	4,941. 49	240. 25	0. 00	5,181. 74
K30. 21	UL	17	9	7. 5	3,195. 40	110. 50	3,220. 65	531. 17	0. 00	3,180. 96	0. 00	3,180. 96

					Animal foods (DBH^2)							
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Chimp primary	Chimp secondary	Ele primary	Ele secondary	Frugiv primary	Frugiv secondary	Foliv primary	Foliv secondary
K30. 22	UL	23	12	7. 5	0. 00	4,513. 61	0. 00	4,404. 35	2,438. 21	2,004. 24	3,359. 49	457. 96
K30. 23	UL	10	7	6. 6	68. 89	1,000. 42	125. 00	1,083. 55	408. 04	534. 89	408. 04	200. 00
K30. 24	UL	16	6	4. 2	935. 11	316. 84	198. 81	1,067. 58	1,098. 51	0. 00	0. 00	1,098. 51
K30. 25	UL	17	9	7. 7	650. 68	16,807. 79	354. 56	928. 51	815. 76	16,447. 29	201. 64	17,061. 41
K30. 26	UL	24	12	10. 0	238. 50	3,132. 77	206. 25	3,477. 18	232. 25	2,972. 03	626. 51	1,171. 52
K30. 27	UL	20	9	7. 5	334. 77	353. 69	334. 77	15,853. 94	0. 00	15,500. 25	0. 00	15,500. 25
K30. 28	UL	26	10	4. 5	252. 81	1,616. 68	252. 81	1,201. 36	1,238. 50	0. 00	1,056. 25	182. 25
K30. 29	UL	38	12	7. 5	74. 45	2,139. 75	20. 25	2,169. 79	523. 85	1,095. 46	944. 10	0. 00
K30. 30	UL	11	5	3. 2	219. 04	2,313. 86	219. 04	2,394. 86	219. 04	568. 44	0. 00	787. 48
Ma. 01	UL	10	5	3. 4	50. 41	578. 82	50. 41	635. 07	377. 28	841. 00	377. 28	841. 00
Ma. 02	UL	10	4	2. 6	361. 00	388. 04	0. 00	749. 04	479. 81	102. 01	479. 81	102. 01
Ma. 03	UL	11	6	5. 3	0. 00	2,164. 57	0. 00	313. 91	0. 00	1,981. 74	0. 00	1,877. 70
Ma. 04	UL	7	3	2. 2	0. 00	40. 96	0. 00	40. 96	0. 00	0. 00	0. 00	0. 00
Ma. 05	UL	7	3	2. 2	23. 04	0. 00	23. 04	27. 04	0. 00	0. 00	0. 00	0. 00
Ma. 06	UL	21	7	5. 0	291. 19	1,541. 17	22. 09	1,810. 27	1,132. 72	0. 00	737. 51	395. 21
Ma. 07	UL	7	3	2. 2	0. 00	1,027. 00	0. 00	574. 26	493. 01	420. 25	493. 01	420. 25
Ma. 08	UL	9	4	3. 4	146. 25	636. 25	0. 00	782. 50	600. 25	0. 00	0. 00	600. 25
Ma. 09	UL	7	4	3. 2	428. 49	9,229. 05	0. 00	9,229. 05	322. 49	0. 00	322. 49	0. 00
Ma. 10	UL	15	2	1. 3	0. 00	12,996. 00	0. 00	0. 00	0. 00	12,996. 00	0. 00	12,996. 00
Ma. 11	UL	13	4	3. 1	23. 04	16,384. 00	23. 04	140. 62	0. 00	16,384. 00	0. 00	16,384. 00
Ma. 12	UL	21	10	8. 8	625. 47	3,059. 22	28. 09	3,623. 79	2,069. 91	0. 00	1,209. 41	860. 50
Ma. 13	UL	14	2	1. 7	0. 00	15,067. 56	0. 00	0. 00	0. 00	15,067. 56	0. 00	15,067. 56
Ma. 14	UL	7	4	3. 6	487. 65	821. 01	457. 96	850. 70	991. 57	0. 00	0. 00	991. 57
Ma. 15	UL	3	3	3. 0	0. 00	1,066. 01	0. 00	153. 97	0. 00	912. 04	0. 00	912. 04
Ma. 16	UL	8	5	4. 0	811. 02	610. 25	0. 00	1,021. 27	960. 43	400. 00	210. 25	1,150. 18
Ma. 17	UL	10	5	3. 9	51. 84	643. 70	51. 84	1,216. 19	0. 00	146. 41	0. 00	146. 41
Ma. 18	UL	5	5	5. 0	122. 18	397. 81	68. 89	127. 10	0. 00	324. 00	0. 00	324. 00
Ma. 20	UL	9	5	3. 7	1,795. 41	20. 25	0. 00	651. 42	605. 16	0. 00	0. 00	605. 16
Ma. 21	UL	9	5	4. 2	0. 00	510. 40	0. 00	612. 41	100. 00	216. 09	316. 09	0. 00
Ma. 22	UL	13	2	1. 3	0. 00	1,157. 73	0. 00	1,157. 73	0. 00	108. 16	108. 16	0. 00
Ma. 23	UL	9	5	4. 3	0. 00	164. 84	0. 00	202. 05	0. 00	123. 21	0. 00	0. 00

					Animal foods (DBH^2)							
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Chimp primary	Chimp secondary	Ele primary	Ele secondary	Frugiv primary	Frugiv secondary	Foliv primary	Foliv secondary
Ma. 24	UL	10	4	2. 6	368. 26	800. 89	0. 00	826. 90	0. 00	0. 00	0. 00	0. 00
Ma. 25	UL	11	3	2. 4	5,812. 38	0. 00	0. 00	114. 49	114. 49	0. 00	0. 00	114. 49
Ma. 26	UL	11	6	4. 7	841. 69	30. 25	265. 69	1,005. 10	576. 00	265. 69	0. 00	841. 69
Ma. 27	UL	13	6	4. 6	339. 12	650. 25	25. 00	952. 34	225. 00	0. 00	0. 00	225. 00
Ma. 28	UL	11	4	3. 5	370. 98	0. 00	0. 00	424. 27	320. 41	0. 00	0. 00	320. 41
Ma. 29	UL	13	6	4. 6	9,435. 06	151. 29	6,323. 30	1,023. 27	954. 38	6,439. 78	0. 00	7,394. 16
Ma. 30	UL	11	6	4. 7	15,993. 71	98. 00	0. 00	15,936. 62	821. 61	14,981. 76	0. 00	15,803. 37
P1. 03	AgPl	1	1	1. 0	0. 00	256. 00	0. 00	256. 00	0. 00	256. 00	256. 00	0. 00
P1. 04	AgPl	3	1	1. 0	0. 00	298. 28	0. 00	298. 28	0. 00	169. 00	169. 00	0. 00
P1. 06	AgPl	1	1	1. 0	0. 00	985. 96	0. 00	985. 96	0. 00	985. 96	0. 00	985. 96
P1. 07	AgPl	4	1	1. 0	0. 00	232. 05	0. 00	232. 05	0. 00	0. 00	0. 00	0. 00
P1. 08	AgPl	1	1	1. 0	0. 00	156. 25	0. 00	156. 25	0. 00	156. 25	0. 00	156. 25
P1. 09	AgPl	1	1	1. 0	0. 00	930. 25	0. 00	930. 25	0. 00	0. 00	0. 00	930. 25
P1. 10	AgPl	1	1	1. 0	0. 00	179. 56	0. 00	179. 56	0. 00	179. 56	179. 56	0. 00
P1. 13	AgPl	7	4	3. 6	0. 00	6,565. 80	338. 56	5,752. 74	2,181. 81	0. 00	0. 00	6,001. 05
P1. 14	AgPl	3	1	1. 0	0. 00	2,709. 00	0. 00	2,709. 00	0. 00	0. 00	0. 00	2,709. 00
P1. 15	AgPl	4	1	1. 0	0. 00	1,969. 26	0. 00	1,969. 26	1,969. 26	0. 00	0. 00	1,969. 26
P1. 17	AgPl	3	2	1. 9	0. 00	1,327. 36	0. 00	1,327. 36	0. 00	1,296. 00	0. 00	1,296. 00
P1. 18	AgPl	7	1	1. 0	0. 00	13,867. 42	0. 00	13,867. 42	0. 00	13,867. 42	0. 00	13,867. 42
P1. 19	AgPl	2	2	2. 0	0. 00	520. 84	0. 00	520. 84	0. 00	295. 84	0. 00	520. 84
P1. 20	AgPl	1	1	1. 0	0. 00	353. 44	0. 00	353. 44	0. 00	353. 44	0. 00	353. 44
P1. 22	AgPl	1	1	1. 0	0. 00	0. 00	0. 00	625. 00	0. 00	0. 00	0. 00	0. 00
P1. 23	AgPl	2	1	1. 0	0. 00	695. 89	0. 00	695. 89	695. 89	0. 00	0. 00	695. 89
P1. 24	AgPl	1	1	1. 0	0. 00	342. 25	0. 00	342. 25	0. 00	342. 25	0. 00	342. 25
P1. 26	AgPl	1	1	1. 0	0. 00	81. 00	0. 00	81. 00	0. 00	0. 00	0. 00	0. 00
P1. 27	AgPl	9	2	2. 0	0. 00	3,779. 06	0. 00	854. 84	0. 00	794. 00	0. 00	794. 00
P1. 30	AgPl	2	1	1. 0	0. 00	522. 29	0. 00	522. 29	0. 00	522. 29	0. 00	522. 29
P3. 01	AgPl	4	4	4. 0	0. 00	1,935. 83	0. 00	1,338. 34	0. 00	1,719. 74	0. 00	1,710. 83
P3. 02	AgPl	1	1	1. 0	0. 00	174. 24	0. 00	174. 24	0. 00	174. 24	0. 00	174. 24
P3. 03	AgPl	1	1	1. 0	0. 00	457. 96	0. 00	457. 96	0. 00	0. 00	0. 00	457. 96

					Animal foods (DBH^2)							
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Chimp primary	Chimp secondary	Ele primary	Ele secondary	Frugiv primary	Frugiv secondary	Foliv primary	Foliv secondary
P3. 05	AgPl	3	2	1. 9	0. 00	1,364. 84	0. 00	1,364. 84	0. 00	0. 00	0. 00	1,364. 84
P3. 06	AgPl	6	3	2. 7	0. 00	2,078. 26	0. 00	1,017. 29	0. 00	821. 29	821. 29	196. 00
P3. 07	AgPl	5	1	1. 0	0. 00	2,616. 38	0. 00	2,616. 38	0. 00	0. 00	0. 00	2,616. 38
P3. 08	AgPl	3	2	1. 9	0. 00	1,115. 93	0. 00	525. 44	0. 00	0. 00	0. 00	525. 44
P3. 09	AgPl	3	2	1. 9	0. 00	839. 25	0. 00	839. 25	0. 00	121. 00	0. 00	839. 25
P3. 10	AgPl	5	3	2. 6	0. 00	3,058. 03	0. 00	3,058. 03	320. 41	166. 41	166. 41	2,891. 62
P3. 12	AgPl	2	1	1. 0	0. 00	539. 45	0. 00	539. 45	0. 00	0. 00	0. 00	539. 45
P3. 13	AgPl	2	2	2. 0	0. 00	2,505. 54	0. 00	2,505. 54	2,381.44	0. 00	0. 00	2,505. 54
P3. 16	AgPl	2	2	2. 0	0. 00	742. 69	0. 00	742. 69	0. 00	289. 00	0. 00	742. 69
P3. 17	AgPl	3	2	1. 9	0. 00	579. 89	0. 00	237. 64	0. 00	342. 25	0. 00	201. 64
P3. 18	AgPl	1	1	1. 0	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
P3. 19	AgPl	7	3	2. 6	0. 00	2,268. 49	0. 00	1,184. 25	0. 00	100. 00	0. 00	1,184. 25
P3. 20	AgPl	3	1	1. 0	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
P3. 21	AgPl	1	1	1. 0	0. 00	182. 25	0. 00	182. 25	0. 00	182. 25	182. 25	0. 00
P3. 23	AgPl	2	2	2. 0	0. 00	871. 25	0. 00	342. 25	0. 00	0. 00	0. 00	342. 25
P3. 24	AgPl	8	3	2. 1	0. 00	2,586. 30	0. 00	2,478. 14	0. 00	2,080. 05	0. 00	2,586. 30
P3. 25	AgPl	10	5	4. 4	0. 00	1,591. 29	0. 00	1,301. 29	0. 00	421. 04	0. 00	1,301. 29
P3. 29	AgPl	3	1	1. 0	0. 00	133. 25	0. 00	133. 25	0. 00	0. 00	0. 00	0. 00
P3. 30	AgPl	4	3	2. 8	0. 00	1,156. 00	0. 00	1,156. 00	0. 00	1,156. 00	1,156. 00	0. 00
Pin. 01	Pin	4	2	1. 8	0. 00	371. 86	0. 00	371. 86	0. 00	309. 06	0. 00	309. 06
Pin. 02	Pin	2	1	1. 0	0. 00	154. 25	0. 00	154. 25	0. 00	0. 00	0. 00	0. 00
Pin. 03	Pin	5	3	2. 9	0. 00	1,471. 85	0. 00	1,471. 85	207. 36	1,089. 00	1,296. 36	0. 00
Pin. 04	Pin	3	2	1. 9	0. 00	422. 05	0. 00	422. 05	0. 00	373. 05	174. 24	198. 81
Pin. 05	Pin	5	1	1. 0	0. 00	515. 34	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
Pin. 06	Pin	2	1	1. 0	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
Pin. 07	Pin	1	1	1. 0	0. 00	50. 41	0. 00	50. 41	0. 00	0. 00	0. 00	0. 00
Pin. 09	Pin	4	4	4. 0	0. 00	1,241. 80	0. 00	1,241. 80	0. 00	1,068. 74	210. 25	858. 49
Pin. 10	Pin	3	1	1. 0	0. 00	538. 28	0. 00	538. 28	486. 44	0. 00	0. 00	486. 44
Pin. 11	Pin	2	2	2. 0	0. 00	768. 16	0. 00	92. 16	0. 00	676. 00	0. 00	0. 00
Pin. 12	Pin	4	3	2. 8	0. 00	196. 94	0. 00	196. 94	0. 00	0. 00	0. 00	0. 00
Pin. 13	Pin	1	1	1. 0	0. 00	32. 49	0. 00	32. 49	0. 00	0. 00	0. 00	0. 00
Pin. 14	Pin	3	2	1. 9	0. 00	112. 94	0. 00	112. 94	0. 00	0. 00	0. 00	0. 00

					Animal foods (DBH^2)							
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Chimp primary	Chimp secondary	Ele primary	Ele secondary	Frugiv primary	Frugiv secondary	Foliv primary	Foliv secondary
Pin. 15	Pin	9	5	4. 6	0. 00	645. 96	0. 00	645. 96	0. 00	0. 00	0. 00	357. 21
Pin. 16	Pin	8	3	2. 6	82. 65	888. 67	0. 00	971. 32	100. 00	716. 42	816. 42	0. 00
Pin. 17	Pin	5	1	1. 0	0. 00	1,521. 73	0. 00	1,521. 73	0. 00	1,471. 71	1,471. 71	0. 00
Pin. 19	Pin	5	2	2. 0	0. 00	1,217. 66	0. 00	1,217. 66	112. 36	954. 81	1,067. 17	0. 00
Pin. 20	Pin	4	2	1. 8	0. 00	108. 27	0. 00	108. 27	0. 00	0. 00	0. 00	0. 00
Pin. 23	Pin	4	3	2. 8	0. 00	238. 83	0. 00	238. 83	0. 00	118. 81	118. 81	0. 00
Pin. 24	Pin	5	3	2. 6	0. 00	4,639. 87	0. 00	647. 21	0. 00	556. 96	556. 96	0. 00
Pin. 25	Pin	10	3	2. 5	0. 00	1,396. 89	0. 00	1,396. 89	1,065. 06	0. 00	1,065. 06	0. 00
Pin. 26	Pin	23	10	8. 6	2,694. 27	5,356. 82	0. 00	8,474. 94	5,525. 14	2,190. 80	4,459. 86	1,266. 92
Pin. 27	Pin	7	3	2. 2	0. 00	1,132. 46	0. 00	1,132. 46	0. 00	1,036. 77	0. 00	1,036. 77
Pin. 28	Pin	19	8	5. 4	108. 16	1,102. 05	49. 00	1,152. 73	108. 16	642. 41	534. 25	216. 32
Pin. 29	Pin	5	3	2. 9	0. 00	171. 50	0. 00	238. 50	0. 00	0. 00	0. 00	0. 00
Pin. 30	Pin	8	4	3. 4	0. 00	1,562. 54	0. 00	333. 26	0. 00	1,425. 65	179. 56	1,246. 09
Se. 01	HL	8	8	8. 0	469. 09	692. 68	28. 09	692. 68	246. 44	400. 00	646. 44	0. 00
Se. 02	HL	6	3	2. 4	0. 00	6,889. 00	6,889.00	1,183. 78	0. 00	6,889. 00	0. 00	6,889. 00
Se. 03	HL	2	2	2. 0	0. 00	13,970. 09	13,806.25	163. 84	0. 00	13,806. 25	0. 00	13,806. 25
Se. 04	HL	15	9	8. 0	0. 00	3,267. 55	78. 21	3,283. 52	0. 00	2,862. 25	2,862. 25	0. 00
Se. 05	HL	3	3	3. 0	0. 00	230. 50	0. 00	320. 50	0. 00	0. 00	0. 00	0. 00
Se. 06	HL	16	8	6. 4	30. 50	5,411. 58	16. 81	5,869. 39	0. 00	5,069. 44	973. 44	0. 00
Se. 07	HL	12	6	4. 8	0. 00	4,222. 09	0. 00	1,953. 10	311. 89	3,826. 12	957. 05	3,180. 96
Se. 08	HL	12	9	8. 5	0. 00	4,455. 44	10. 24	4,536. 24	2,777. 29	1,521. 00	1,521. 00	2,777. 29
Se. 09	HL	16	5	4. 6	263. 65	6,309. 15	0. 00	6,887. 84	0. 00	5,844. 25	5,844. 25	0. 00
Se. 10	HL	12	10	9. 1	185. 81	2,701. 13	1,269. 97	1,547. 53	0. 00	2,302. 92	1,049. 76	1,253. 16
Se. 11	HL	9	6	5. 3	2,088. 49	3,195. 05	2,088. 49	3,395. 72	0. 00	5,147. 41	207. 36	2,088. 49
Se. 12	HL	4	4	4. 0	0. 00	353. 80	0. 00	470. 54	353. 80	0. 00	353. 80	0. 00
Se. 14	HL	6	3	2. 4	0. 00	1,811. 47	0. 00	1,583. 46	0. 00	1,770. 51	146. 41	0. 00
Se. 15	HL	4	4	4. 0	0. 00	3,290. 22	0. 00	3,302. 47	2,520. 04	470. 89	0. 00	2,990. 93
Se. 16	HL	7	4	3. 2	18. 49	10. 24	0. 00	219. 99	0. 00	0. 00	0. 00	0. 00
Se. 17	HL	3	3	3. 0	90. 25	25. 61	0. 00	25. 61	0. 00	0. 00	0. 00	0. 00
Se. 18	HL	10	6	5. 5	961. 00	1,495. 79	0. 00	2,224. 79	148. 84	670. 81	148. 84	0. 00
Se. 19	HL	1	1	1. 0	0. 00	272. 25	0. 00	272. 25	272. 25	0. 00	0. 00	272. 25
Se. 20	HL	3	3	3. 0	0. 00	0. 00	0. 00	2,639. 57	0. 00	2,560. 36	0. 00	2,560. 36

					Animal foods (DBH^2)							
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Chimp primary	Chimp secondary	Ele primary	Ele secondary	Frugiv primary	Frugiv secondary	Foliv primary	Foliv secondary
Se. 21	HL	2	2	2. 0	0. 00	134. 26	0. 00	134. 26	0. 00	0. 00	0. 00	0. 00
Se. 22	HL	7	6	5. 7	0. 00	3,620. 22	0. 00	3,587. 73	110. 25	3,422. 50	452. 50	0. 00
Se. 23	HL	7	6	5. 7	334. 89	1,377. 50	0. 00	1,565. 22	1,310. 44	0. 00	0. 00	1,310. 44
Se. 24	HL	4	3	2. 8	0. 00	339. 49	0. 00	395. 19	0. 00	272. 25	0. 00	0. 00
Se. 25	HL	6	6	6. 0	0. 00	2,318. 44	0. 00	2,318. 44	1,944. 81	265. 69	0. 00	2,210. 50
Se. 26	HL	3	1	1. 0	0. 00	453. 68	0. 00	453. 68	324. 00	0. 00	324. 00	0. 00
Se. 27	HL	3	2	1. 9	0. 00	188. 68	0. 00	243. 44	0. 00	0. 00	0. 00	0. 00
Se. 28	HL	4	2	1. 8	36. 00	741. 50	0. 00	741. 50	716. 50	0. 00	0. 00	716. 50
Se. 30	HL	3	3	3. 0	132. 25	2,563. 24	132. 25	2,563. 24	132. 25	538. 24	538. 24	132. 25

Table 7-5. Canonical table for ecosystem service indicators

All services are quantified in terms of aboveground biomass (kg), except timber which is measured in volume (m^3).

					Ecosystem services								
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Fodder	Artisanal	Carbon	Construction	Culture	Food & Drink	Medicine	Timber	Wood Products
Du. 01	UL	14	8	7. 2	11. 93	0. 00	48. 83	10. 99	7. 48	9. 85	11. 93	0. 20	11. 36
Du. 02	UL	17	8	6. 5	11. 88	0. 00	46. 38	18. 26	1. 54	21. 90	13. 41	0. 00	41. 09
Du. 03	UL	19	6	3. 1	0. 00	0. 00	57. 96	7. 81	0. 00	7. 81	0. 00	0. 00	45. 25
Du. 04	UL	3	2	1. 9	11. 60	0. 00	14. 14	0. 00	11. 60	0. 00	11. 60	0. 51	0. 00
Du. 05	UL	18	5	3. 2	7. 06	0. 00	67. 84	22. 77	7. 06	22. 77	7. 06	3. 34	43. 14
Du. 06	UL	11	7	5. 9	4. 15	2. 09	23. 74	8. 06	6. 56	11. 50	10. 00	0. 05	17. 09
Du. 07	UL	12	6	4. 4	22. 99	0. 00	56. 71	33. 95	0. 00	31. 56	22. 99	4. 32	33. 95
Du. 08	UL	10	5	3. 9	0. 00	0. 00	42. 28	31. 21	0. 00	18. 07	0. 00	1. 19	34. 10
Du. 09	UL	9	6	4. 9	0. 00	0. 00	33. 29	22. 57	0. 00	12. 34	0. 00	0. 00	23. 92
Du. 10	UL	3	2	1. 9	0. 00	0. 00	8. 63	6. 51	0. 00	0. 00	0. 00	0. 00	6. 51
Du. 11	UL	15	6	4. 4	0. 00	0. 00	69. 37	38. 03	0. 00	20. 50	6. 02	2. 15	34. 46
Du. 12	UL	10	6	5. 0	0. 00	0. 00	20. 17	11. 56	0. 00	0. 00	1. 19	0. 00	10. 37
Du. 13	UL	17	7	6. 0	30. 67	2. 68	84. 73	33. 03	17. 28	21. 50	55. 60	1. 38	18. 82
Du. 14	UL	20	11	8. 3	11. 95	0. 00	51. 41	18. 92	6. 60	17. 32	11. 95	0. 27	31. 64
Du. 15	UL	20	10	7. 5	16. 09	0. 00	49. 92	4. 86	14. 21	6. 73	16. 03	1. 60	21. 02
Du. 16	UL	20	13	11. 7	25. 28	0. 00	71. 99	25. 68	22. 66	22. 64	25. 28	2. 86	31. 58
Du. 17	UL	11	7	5. 3	1. 09	0. 00	22. 22	6. 79	1. 09	1. 72	1. 09	0. 04	14. 30
Du. 18	UL	14	6	4. 8	0. 00	0. 00	37. 88	21. 20	0. 00	18. 15	1. 72	0. 31	31. 06
Du. 19	UL	23	7	6. 2	7. 91	0. 00	47. 40	19. 29	0. 00	7. 91	7. 91	0. 00	27. 20
Du. 20	UL	15	7	5. 4	15. 62	0. 00	31. 96	9. 47	0. 00	18. 38	16. 91	0. 05	18. 38
Du. 21	UL	16	7	3. 8	26. 14	0. 00	70. 23	9. 14	19. 62	9. 14	26. 14	3. 62	32. 39
Du. 22	UL	11	7	6. 3	17. 52	17. 98	47. 32	3. 08	7. 54	27. 96	37. 16	0. 22	33. 25
Du. 23	UL	16	6	5. 4	34. 91	0. 00	68. 14	39. 44	0. 00	4. 52	0. 00	0. 00	54. 24
Du. 24	UL	9	4	3. 6	7. 35	0. 00	21. 96	8. 96	0. 00	7. 35	7. 35	0. 16	16. 31
Du. 25	UL	12	5	4. 6	0. 00	0. 00	36. 44	0. 00	0. 00	0. 00	0. 00	0. 00	6. 56
Du. 26	UL	6	3	2. 4	3. 37	0. 00	24. 01	20. 64	3. 37	0. 00	21. 27	0. 04	2. 74
Du. 27	UL	4	3	2. 8	0. 00	0. 00	16. 94	7. 04	0. 00	4. 13	0. 00	0. 00	7. 04
Du. 28	UL	12	6	4. 9	6. 20	0. 00	48. 52	15. 35	0. 00	6. 20	17. 56	0. 82	29. 90

					Ecosystem services								
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Fodder	Artisanal	Carbon	Construction	Culture	Food & Drink	Medicine	Timber	Wood Products
Du. 29	UL	8	4	3. 5	0. 00	0. 00	52. 49	1. 25	0. 00	24. 02	22. 76	0. 00	5. 68
Du. 30	UL	12	8	6. 7	9. 53	0. 00	38. 56	6. 19	9. 53	2. 62	13. 09	0. 68	9. 02
Gr. 04	Gr	7	1	1. 0	53. 63	53. 63	0. 00	53. 63	0. 00	0. 00	53. 63	3. 25	53. 63
Gr. 05	Gr	3	2	1. 9	25. 57	13. 94	11. 62	13. 94	0. 00	11. 62	25. 57	0. 74	25. 57
Gr. 06	Gr	15	6	3. 2	37. 97	11. 18	35. 27	18. 81	26. 91	5. 30	40. 68	0. 27	13. 03
Gr. 07	Gr	2	2	2. 0	3. 29	3. 29	3. 29	1. 82	1. 48	1. 48	3. 29	0. 00	1. 48
Gr. 08	Gr	16	6	4. 1	41. 18	5. 00	42. 87	31. 41	20. 68	7. 68	25. 06	0. 14	39. 09
Gr. 10	Gr	10	2	1. 6	29. 95	4. 35	25. 60	29. 95	0. 00	0. 00	4. 35	0. 00	29. 95
Gr. 11	Gr	7	2	1. 8	7. 12	7. 12	10. 22	10. 22	0. 00	7. 12	10. 22	0. 00	10. 22
Gr. 12	Gr	3	1	1. 0	6. 13	6. 13	6. 13	6. 13	0. 00	0. 00	6. 13	0. 00	0. 00
Gr. 14	Gr	2	2	2. 0	5. 22	0. 00	5. 22	1. 82	1. 82	5. 22	5. 22	0. 04	5. 22
Gr. 16	Gr	1	1	1. 0	5. 78	5. 78	5. 78	5. 78	0. 00	0. 00	5. 78	0. 00	0. 00
Gr. 19	Gr	13	2	1. 3	39. 03	0. 00	39. 03	39. 03	2. 74	0. 00	2. 74	0. 00	39. 03
Gr. 21	Gr	3	1	1. 0	19. 48	19. 48	0. 00	19. 48	0. 00	0. 00	19. 48	0. 90	19. 48
Gr. 22	Gr	7	2	1. 8	17. 63	7. 05	10. 58	17. 63	0. 00	0. 00	7. 05	0. 09	17. 63
Gr. 30	Gr	2	2	2. 0	8. 97	7. 24	1. 72	7. 24	1. 72	0. 00	8. 97	0. 32	7. 24
Is. 02	AgUn	2	2	2. 0	6. 17	2. 97	6. 17	6. 17	0. 00	3. 20	6. 17	0. 00	3. 20
Is. 08	AgUn	1	1	1. 0	4. 59	4. 59	4. 59	4. 59	0. 00	0. 00	4. 59	0. 00	0. 00
Is. 09	AgUn	5	3	2. 9	10. 75	10. 75	20. 38	13. 52	6. 85	10. 75	20. 38	0. 00	20. 38
Is. 11	AgUn	5	2	2. 0	9. 54	9. 54	24. 56	24. 56	0. 00	9. 54	24. 56	0. 00	24. 56
Is. 15	AgUn	3	1	1. 0	14. 30	0. 00	14. 30	14. 30	0. 00	0. 00	0. 00	0. 00	14. 30
Is. 16	AgUn	2	2	2. 0	6. 17	0. 00	15. 83	9. 65	0. 00	6. 17	6. 17	0. 21	15. 83
Is. 19	AgUn	5	2	2. 0	13. 67	0. 00	24. 55	10. 89	0. 00	13. 67	24. 55	0. 28	24. 55
Is. 21	AgUn	4	2	1. 8	14. 24	14. 24	19. 84	14. 24	5. 59	14. 24	19. 84	0. 00	19. 84
Is. 23	AgUn	3	1	1. 0	18. 95	18. 95	18. 95	18. 95	0. 00	0. 00	18. 95	0. 00	0. 00
Is. 25	AgUn	1	1	1. 0	5. 46	5. 46	5. 46	5. 46	0. 00	5. 46	5. 46	0. 00	5. 46
Is. 28	AgUn	1	1	1. 0	5. 94	5. 94	0. 00	5. 94	0. 00	0. 00	5. 94	0. 19	5. 94
K13. 03	HL+P	10	3	1. 9	0. 00	0. 00	60. 46	53. 79	0. 00	0. 00	7. 11	0. 00	7. 11
K13. 04	HL+P	4	4	4. 0	18. 13	0. 00	28. 33	25. 21	21. 70	24. 81	24. 81	1. 98	28. 33
K13. 05	HL+P	2	2	2. 0	9. 85	0. 00	9. 85	4. 18	5. 67	0. 00	5. 67	0. 16	4. 18
K13. 06	HL+P	1	1	1. 0	0. 00	0. 00	7. 19	7. 19	7. 19	0. 00	7. 19	0. 00	7. 19
K13. 07	HL+P	2	2	2. 0	19. 17	0. 00	19. 17	8. 65	10. 52	0. 00	10. 52	0. 90	8. 65

					Ecosystem services								
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Fodder	Artisanal	Carbon	Construction	Culture	Food & Drink	Medicine	Timber	Wood Products
K13. 08	HL+P	2	1	1. 0	19. 24	0. 00	19. 24	19. 24	19. 24	19. 24	19. 24	1. 50	19. 24
K13. 09	HL+P	2	1	1. 0	0. 00	0. 00	7. 05	7. 05	7. 05	0. 00	7. 05	0. 00	7. 05
K13. 10	HL+P	1	1	1. 0	5. 24	0. 00	5. 24	5. 24	0. 00	0. 00	0. 00	0. 00	5. 24
K13. 11	HL+P	2	2	2. 0	17. 11	3. 34	17. 11	0. 00	17. 11	3. 34	17. 11	1. 89	3. 34
K13. 13	HL+P	5	4	3. 8	36. 52	0. 00	48. 37	19. 78	16. 74	19. 78	36. 52	4. 76	19. 78
K13. 14	HL+P	5	3	2. 6	14. 86	0. 00	19. 99	9. 01	0. 00	14. 86	19. 99	0. 06	9. 01
K13. 15	HL+P	1	1	1. 0	0. 00	0. 00	3. 65	3. 65	3. 65	3. 65	3. 65	0. 05	3. 65
K13. 16	HL+P	6	6	6. 0	18. 72	3. 62	39. 51	18. 93	10. 72	15. 09	18. 72	4. 17	35. 56
K13. 17	HL+P	5	4	3. 8	21. 56	0. 00	30. 88	4. 86	7. 88	26. 42	26. 01	0. 49	12. 75
K13. 18	HL+P	9	4	2. 7	6. 23	0. 00	51. 28	15. 25	15. 25	15. 25	15. 25	1. 35	24. 05
K13. 20	HL+P	3	3	3. 0	24. 35	0. 00	24. 35	12. 35	24. 35	18. 95	24. 35	1. 79	18. 95
K13. 21	HL+P	1	1	1. 0	0. 00	0. 00	4. 54	0. 00	0. 00	0. 00	0. 00	0. 09	4. 54
K13. 22	HL+P	1	1	1. 0	0. 00	0. 00	6. 49	0. 00	0. 00	0. 00	0. 00	0. 24	6. 49
K13. 23	HL+P	5	3	2. 9	9. 25	0. 00	24. 58	0. 00	9. 25	0. 00	9. 25	0. 59	9. 66
K13. 24	HL+P	3	1	1. 0	13. 19	0. 00	13. 19	0. 00	13. 19	0. 00	13. 19	0. 26	0. 00
K13. 25	HL+P	4	3	2. 8	0. 00	0. 00	23. 16	13. 24	13. 24	0. 00	13. 24	0. 04	13. 24
K13. 26	HL+P	2	1	1. 0	0. 00	0. 00	14. 81	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
K13. 27	HL+P	5	5	5. 0	16. 17	0. 00	44. 72	21. 89	28. 04	10. 03	28. 04	2. 67	35. 09
K13. 28	HL+P	1	1	1. 0	10. 37	0. 00	10. 37	0. 00	10. 37	0. 00	10. 37	0. 86	0. 00
K13. 29	HL+P	3	3	3. 0	4. 65	0. 00	15. 45	3. 48	0. 00	4. 65	8. 13	0. 43	15. 45
K13. 30	HL+P	3	3	3. 0	14. 13	0. 00	18. 09	3. 54	3. 54	14. 13	14. 13	0. 98	18. 09
K14. 01	LL	16	9	8. 2	41. 26	0. 00	56. 77	9. 59	4. 35	38. 32	47. 19	1. 54	33. 00
K14. 02	LL	27	18	14. 8	31. 18	5. 16	68. 96	48. 27	27. 01	54. 69	52. 27	0. 82	52. 01
K14. 03	LL	28	12	9. 0	29. 83	7. 96	68. 32	29. 83	31. 74	35. 66	39. 70	0. 66	38. 80
K14. 04	LL	24	14	11. 2	16. 81	1. 19	62. 33	26. 83	15. 62	23. 10	23. 47	0. 04	40. 18
K14. 05	LL	18	11	9. 7	11. 96	0. 00	49. 75	10. 76	10. 83	12. 96	12. 70	0. 50	26. 75
K14. 06	LL	22	10	8. 5	43. 56	11. 24	56. 55	26. 63	40. 54	30. 05	44. 86	0. 68	28. 45
K14. 07	LL	16	10	8. 9	29. 11	0. 00	65. 50	17. 01	15. 21	18. 26	37. 87	6. 79	31. 20
K14. 08	LL	28	14	10. 2	37. 21	1. 57	96. 42	42. 94	45. 16	42. 81	56. 65	2. 47	66. 41
K14. 09	LL	16	12	10. 6	17. 24	1. 19	31. 59	15. 05	8. 88	16. 24	17. 24	0. 04	22. 47
K14. 10	LL	6	3	2. 7	15. 63	12. 46	20. 93	5. 29	20. 93	17. 75	20. 93	0. 00	17. 75
K14. 11	LL	20	10	8. 0	40. 33	0. 00	69. 98	51. 96	39. 30	19. 41	54. 27	1. 34	52. 56

					Ecosystem services								
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Fodder	Artisanal	Carbon	Construction	Culture	Food & Drink	Medicine	Timber	Wood Products
K14. 12	LL	6	4	3. 5	9. 05	2. 42	11. 85	9. 43	4. 48	9. 05	11. 85	0. 00	9. 05
K14. 13	LL	27	13	11. 2	79. 27	0. 00	121.49	43. 04	38. 63	27. 69	100. 63	14. 51	64. 21
K14. 14	LL	10	6	5. 5	0. 00	2. 62	19. 96	4. 91	0. 00	2. 62	4. 91	0. 23	4. 68
K14. 15	LL	9	6	5. 3	10. 35	0. 00	33. 31	29. 13	18. 54	16. 23	26. 92	1. 84	27. 84
K14. 16	LL	7	7	7. 0	19. 51	0. 00	32. 58	15. 51	27. 72	11. 41	29. 66	2. 56	17. 02
K14. 17	LL	14	9	7. 9	25. 16	2. 73	39. 35	27. 65	5. 14	20. 97	24. 87	0. 97	28. 84
K14. 18	LL	18	12	9. 2	37. 11	7. 16	76. 89	27. 37	10. 77	20. 56	36. 52	2. 41	55. 14
K14. 19	LL	5	5	5. 0	10. 04	3. 57	13. 61	11. 43	3. 17	10. 01	10. 01	0. 00	11. 43
K14. 20	LL	11	9	8. 5	16. 69	4. 86	44. 17	24. 08	13. 48	26. 10	26. 93	1. 48	21. 24
K14. 21	LL	17	12	10. 1	37. 85	0. 00	62. 05	45. 65	40. 21	30. 47	47. 21	0. 80	49. 10
K14. 22	LL	16	7	5. 6	0. 00	0. 00	47. 40	25. 08	16. 15	22. 20	16. 15	0. 46	34. 95
K14. 23	LL	16	11	10. 0	22. 98	11. 60	37. 17	18. 99	7. 87	12. 84	22. 48	0. 77	19. 49
K14. 24	LL	19	12	10. 3	31. 18	2. 03	65. 98	40. 52	12. 30	31. 67	36. 42	0. 76	33. 31
K14. 25	LL	20	15	13. 4	21. 47	7. 58	43. 43	25. 57	10. 55	29. 23	27. 79	0. 22	24. 31
K14. 26	LL	21	11	8. 5	55. 63	30. 33	101.94	81. 21	49. 19	60. 12	86. 69	1. 69	58. 77
K14. 27	LL	24	13	11. 1	47. 83	2. 09	72. 26	18. 49	22. 53	35. 88	42. 11	1. 10	33. 79
K14. 28	LL	28	14	11. 1	58. 82	0. 00	115.38	15. 72	43. 00	28. 25	58.70	4.28	34.10
K14. 29	LL	29	14	12. 0	23. 79	0. 00	82. 90	22. 36	1. 25	27. 87	33. 85	1. 12	41. 31
K14. 30	LL	21	16	15. 1	33. 12	2. 61	60. 85	12. 72	17. 77	34. 27	34. 54	1. 71	44. 12
K15. 01	HL	12	5	3. 9	27. 90	9. 47	22. 82	12. 45	21. 41	3. 14	32. 29	0. 29	12. 45
K15. 02	HL	5	3	2. 9	15. 25	10. 39	8. 09	12. 03	3. 23	3. 23	10. 39	0. 31	15. 25
K15. 03	HL	2	1	1. 0	5. 65	5. 65	5. 65	0. 00	5. 65	5. 65	5. 65	0. 00	5. 65
K15. 04	HL	2	2	2. 0	6. 54	0. 00	12. 58	12. 58	12. 58	6. 04	12. 58	0. 44	12. 58
K15. 05	HL	1	1	1. 0	0. 00	0. 00	6. 46	6. 46	6. 46	0. 00	6. 46	0. 00	6. 46
K15. 06	HL	12	8	7. 2	11. 03	0. 00	42. 38	34. 54	0. 00	1. 88	28. 61	0. 23	24. 72
K15. 08	HL	1	1	1. 0	4. 65	4. 65	0. 00	4. 65	0. 00	0. 00	4. 65	0. 09	4. 65
K15. 10	HL	4	4	4. 0	0. 00	0. 00	37. 26	13. 72	0. 00	8. 50	22. 22	0. 06	22. 22
K15. 11	HL	16	8	5. 6	31. 04	6. 08	54. 65	48. 77	13. 06	18. 06	51. 86	2. 11	46. 46
K15. 12	HL	28	15	12. 3	50. 58	3. 84	121.89	76. 62	62. 31	26. 90	84. 59	13. 54	70. 46
K15. 14	HL	10	6	5. 5	21. 31	8. 65	47. 57	41. 36	9. 48	9. 48	36. 12	1. 48	48. 79
K15. 15	HL	7	6	5. 7	5. 93	3. 60	20. 93	15. 47	7. 88	9. 55	12. 90	0. 48	15. 47
K15. 16	HL	4	2	1. 8	7. 66	7. 66	9. 99	0. 00	7. 66	7. 66	7. 66	0. 00	7. 66

					Ecosystem services								
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Fodder	Artisanal	Carbon	Construction	Culture	Food & Drink	Medicine	Timber	Wood Products
K15.17	HL	5	3	2.6	8.41	13.84	15.86	9.48	8.41	15.86	15.86	0.00	15.86
K15.18	HL	12	7	6.0	16.63	1.91	39.84	17.93	1.91	17.35	22.13	0.20	19.84
K15.19	HL	7	6	5.7	21.82	0.00	27.26	11.63	3.14	20.40	23.54	0.24	11.63
K15.20	HL	2	1	1.0	7.67	7.67	7.67	0.00	7.67	7.67	7.67	0.00	7.67
K15.21	HL	17	8	5.8	35.15	0.00	90.86	24.07	43.74	13.48	53.81	20.63	23.16
K15.22	HL	31	8	4.0	22.28	0.00	75.08	29.47	8.69	25.25	26.79	0.55	26.79
K15.23	HL	4	4	4.0	3.60	1.82	21.00	19.18	19.21	11.87	21.00	0.46	21.00
K15.24	HL	2	2	2.0	3.90	0.00	6.29	6.29	0.00	0.00	0.00	0.00	3.90
K15.25	HL	15	10	9.1	24.15	10.07	46.66	30.85	15.85	28.43	37.29	0.55	39.10
K15.28	HL	1	1	1.0	0.00	0.00	1.57	1.57	1.57	1.57	1.57	0.00	1.57
K15.29	HL	23	14	11.9	12.22	2.48	61.30	43.51	36.47	40.13	45.08	1.99	43.33
K15.30	HL	20	13	11.2	40.34	0.00	69.97	27.46	16.39	6.26	50.70	5.93	34.65
K30.01	UL	12	6	5.1	17.66	0.00	33.96	20.52	17.66	21.77	20.52	0.00	20.52
K30.02	UL	17	10	8.6	16.86	11.27	48.55	13.98	7.71	21.31	17.95	0.47	35.29
K30.03	UL	20	10	7.5	11.36	0.00	72.99	13.93	4.54	9.40	28.58	3.88	15.68
K30.04	UL	8	7	6.7	10.70	1.51	21.36	10.92	3.93	10.70	18.39	0.10	14.54
K30.06	UL	3	2	1.9	5.70	0.00	8.03	5.70	0.00	0.00	0.00	0.00	5.70
K30.07	UL	5	3	2.6	10.10	4.91	15.02	5.19	4.91	4.91	9.83	0.11	10.10
K30.08	UL	28	19	16.8	67.05	3.58	100.40	20.05	19.54	27.66	72.47	13.63	37.89
K30.09	UL	24	19	17.2	29.80	1.25	69.72	29.15	22.37	36.64	43.18	0.92	39.59
K30.10	UL	27	12	10.4	29.92	4.65	83.36	62.98	45.07	75.25	51.03	2.37	79.85
K30.11	UL	13	11	10.1	33.48	5.07	49.54	18.59	6.97	31.83	40.25	4.73	38.37
K30.12	UL	18	10	8.3	18.89	0.00	61.17	12.01	9.77	18.89	22.48	6.75	41.92
K30.13	UL	16	8	6.3	7.08	0.00	44.70	25.29	9.11	8.41	22.72	0.04	26.73
K30.14	UL	10	7	6.6	19.07	9.63	33.62	18.35	5.65	23.53	23.53	0.46	19.64
K30.15	UL	17	8	7.1	35.19	0.00	45.48	15.68	23.16	26.46	36.42	1.43	27.68
K30.16	UL	16	11	9.5	17.97	1.25	48.61	11.08	12.09	12.09	24.10	0.61	22.02
K30.17	UL	48	8	5.1	4.06	4.06	124.88	85.94	1.79	15.65	53.72	0.00	34.18
K30.18	UL	21	13	11.8	16.48	0.00	83.83	31.62	8.86	39.23	44.02	15.17	57.60
K30.19	UL	26	9	5.0	17.19	3.45	59.92	25.74	15.81	21.09	22.98	0.00	25.74
K30.20	UL	23	9	5.1	0.00	0.00	74.29	35.76	33.31	37.82	39.23	3.20	44.02
K30.21	UL	17	9	7.5	19.08	3.35	47.95	4.12	4.12	20.43	5.47	0.00	20.43

					Ecosystem services								
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Fodder	Artisanal	Carbon	Construction	Culture	Food & Drink	Medicine	Timber	Wood Products
K30.22	UL	23	12	7.5	34.40	1.54	94.60	9.44	25.66	31.85	43.65	2.60	31.41
K30.23	UL	10	7	6.6	13.62	0.00	34.13	7.63	13.62	4.92	16.82	0.41	15.06
K30.24	UL	16	6	4.2	4.35	0.00	47.94	11.78	9.21	9.21	9.21	0.11	25.99
K30.25	UL	17	9	7.7	44.09	30.91	72.41	50.48	40.80	39.72	54.85	0.08	47.06
K30.26	UL	24	12	10.0	32.99	4.61	81.35	22.44	5.80	18.97	47.01	1.16	17.99
K30.27	UL	20	9	7.5	57.95	9.32	80.71	50.86	42.50	27.65	57.14	0.00	48.63
K30.28	UL	26	10	4.5	25.78	1.66	90.07	18.81	16.07	16.63	27.81	0.61	14.96
K30.29	UL	38	12	7.5	25.86	6.83	100.55	33.13	9.81	20.34	25.39	0.42	14.60
K30.30	UL	11	5	3.2	14.56	10.03	42.20	29.26	4.54	20.18	33.67	0.00	10.16
Ma.01	UL	10	5	3.4	20.56	0.00	32.75	10.62	20.56	2.36	20.56	0.13	10.62
Ma.02	UL	10	4	2.6	22.39	0.00	27.35	10.62	22.39	0.00	22.39	0.21	10.62
Ma.03	UL	11	6	5.3	0.00	0.00	40.34	27.77	0.00	21.26	21.26	0.04	27.77
Ma.04	UL	7	3	2.2	0.00	0.00	16.55	14.40	0.00	0.00	0.00	0.00	14.40
Ma.05	UL	7	3	2.2	1.66	0.00	18.70	16.92	1.66	1.66	1.66	0.00	16.92
Ma.06	UL	21	7	5.0	42.43	0.00	59.78	27.40	41.05	3.01	42.43	0.27	24.04
Ma.07	UL	7	3	2.2	24.07	6.07	24.07	8.01	22.14	8.01	24.07	0.19	8.01
Ma.08	UL	9	4	3.4	0.00	0.00	24.89	18.20	7.11	7.11	7.11	0.31	22.86
Ma.09	UL	7	4	3.2	12.65	0.00	47.01	34.36	12.65	6.12	12.65	0.31	34.36
Ma.10	UL	15	2	1.3	0.00	0.00	57.15	57.15	0.00	28.02	28.02	0.00	57.15
Ma.11	UL	13	4	3.1	1.66	0.00	56.11	47.26	1.66	32.73	32.73	0.00	47.26
Ma.12	UL	21	10	8.8	29.20	0.00	75.96	55.59	29.20	11.60	29.20	0.51	58.42
Ma.13	UL	14	2	1.7	0.00	0.00	80.00	80.00	0.00	51.42	51.42	0.00	80.00
Ma.14	UL	7	4	3.6	13.05	0.00	24.07	21.33	13.05	21.33	13.05	0.26	24.07
Ma.15	UL	3	3	3.0	0.00	0.00	14.25	14.25	0.00	11.60	8.57	0.00	14.25
Ma.16	UL	8	5	4.0	7.02	0.00	33.15	11.81	7.02	5.94	12.96	0.08	28.70
Ma.17	UL	10	5	3.9	2.39	0.00	40.20	30.32	2.39	8.93	6.18	0.00	26.53
Ma.18	UL	5	5	5.0	8.11	5.40	14.62	10.32	8.11	8.11	10.32	0.00	10.53
Ma.20	UL	9	5	3.7	0.00	0.00	28.97	18.50	0.00	9.65	0.00	0.71	25.64
Ma.21	UL	9	5	4.2	14.92	4.51	18.09	8.97	10.41	2.73	14.92	0.12	8.97
Ma.22	UL	13	2	1.3	23.15	0.00	30.78	7.63	0.00	30.78	23.15	0.04	30.78
Ma.23	UL	9	5	4.3	0.00	0.00	18.60	10.52	0.00	1.44	0.00	0.04	10.52
Ma.24	UL	10	4	2.6	0.00	0.00	32.06	30.31	0.00	5.54	0.00	0.15	32.06

					Ecosystem services								
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Fodder	Artisanal	Carbon	Construction	Culture	Food & Drink	Medicine	Timber	Wood Products
Ma.25	UL	11	3	2.4	0.00	0.00	58.00	54.60	0.00	31.63	0.00	4.25	58.00
Ma.26	UL	11	6	4.7	4.95	0.00	34.82	10.73	0.00	4.95	0.00	0.00	22.66
Ma.27	UL	13	6	4.6	1.72	0.00	33.96	24.17	1.72	4.23	1.72	0.00	30.67
Ma.28	UL	11	4	3.5	0.00	0.00	24.46	10.89	0.00	0.00	0.00	0.00	19.54
Ma.29	UL	13	6	4.6	22.27	0.00	67.05	25.27	2.00	38.52	5.85	1.42	67.05
Ma.30	UL	11	6	4.7	0.00	29.85	62.19	13.33	2.33	37.79	34.51	0.04	62.19
P1.03	AgPl	1	1	1.0	4.86	4.86	0.00	4.86	0.00	0.00	4.86	0.11	4.86
P1.04	AgPl	3	1	1.0	9.28	9.28	0.00	9.28	0.00	0.00	9.28	0.06	9.28
P1.06	AgPl	1	1	1.0	8.87	8.87	8.87	8.87	0.00	8.87	8.87	0.00	8.87
P1.07	AgPl	4	1	1.0	9.65	9.65	9.65	9.65	0.00	9.65	9.65	0.00	9.65
P1.08	AgPl	1	1	1.0	3.90	3.90	3.90	3.90	0.00	3.90	3.90	0.00	3.90
P1.09	AgPl	1	1	1.0	0.00	0.00	8.65	8.65	0.00	0.00	8.65	0.00	8.65
P1.10	AgPl	1	1	1.0	4.15	0.00	4.15	0.00	0.00	4.15	4.15	0.07	4.15
P1.13	AgPl	7	4	3.6	9.16	9.16	50.27	41.11	28.53	28.53	50.27	1.24	44.76
P1.14	AgPl	3	1	1.0	0.00	0.00	23.59	23.59	0.00	0.00	23.59	0.00	23.59
P1.15	AgPl	4	1	1.0	0.00	0.00	25.07	25.07	0.00	0.00	0.00	0.00	25.07
P1.17	AgPl	3	2	1.9	0.00	0.00	11.93	11.93	0.00	0.00	11.93	0.00	0.00
P1.18	AgPl	7	1	1.0	79.33	79.33	79.33	79.33	0.00	79.33	79.33	0.00	79.33
P1.19	AgPl	2	2	2.0	5.19	5.19	9.78	9.78	0.00	5.19	9.78	0.00	9.78
P1.20	AgPl	1	1	1.0	5.62	5.62	5.62	5.62	0.00	5.62	5.62	0.00	5.62
P1.22	AgPl	1	1	1.0	0.00	0.00	7.24	0.00	0.00	0.00	0.00	0.00	0.00
P1.23	AgPl	2	1	1.0	0.00	0.00	11.15	11.15	11.15	11.15	11.15	0.31	11.15
P1.24	AgPl	1	1	1.0	5.54	0.00	5.54	0.00	0.00	5.54	5.54	0.00	5.54
P1.26	AgPl	1	1	1.0	2.91	2.91	2.91	2.91	0.00	2.91	2.91	0.00	2.91
P1.27	AgPl	9	2	2.0	49.25	49.25	49.25	19.83	29.42	49.25	49.25	0.00	49.25
P1.30	AgPl	2	1	1.0	9.63	9.63	9.63	9.63	0.00	9.63	9.63	0.00	9.63
P3.01	AgPl	4	4	4.0	19.75	15.15	24.26	24.26	5.75	19.75	24.26	0.00	19.66
P3.02	AgPl	1	1	1.0	4.10	4.10	4.10	4.10	0.00	4.10	4.10	0.00	4.10
P3.03	AgPl	1	1	1.0	0.00	0.00	6.30	6.30	0.00	0.00	6.30	0.00	6.30
P3.05	AgPl	3	2	1.9	21.38	21.38	36.44	36.44	0.00	0.00	36.44	0.00	15.05
P3.06	AgPl	6	3	2.7	11.94	16.53	32.79	4.32	0.00	28.47	32.79	0.39	16.26
P3.07	AgPl	5	1	1.0	0.00	0.00	32.82	32.82	0.00	0.00	32.82	0.00	32.82

					Ecosystem services								
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Fodder	Artisanal	Carbon	Construction	Culture	Food & Drink	Medicine	Timber	Wood Products
P3. 08	AgPl	3	2	1. 9	7. 06	7. 06	16. 54	9. 48	7. 06	7. 06	16. 54	0. 00	16. 54
P3. 09	AgPl	3	2	1. 9	3. 48	3. 48	13. 96	13. 96	0. 00	3. 48	13. 96	0. 00	13. 96
P3. 10	AgPl	5	3	2. 6	9. 39	0. 00	32. 15	28. 14	5. 38	9. 39	32. 15	0. 20	32. 15
P3. 12	AgPl	2	1	1. 0	0. 00	0. 00	9. 92	9. 92	0. 00	0. 00	9. 92	0. 00	9. 92
P3. 13	AgPl	2	2	2. 0	0. 00	0. 00	16. 67	16. 67	13. 15	13. 15	16. 67	1. 66	16. 67
P3. 16	AgPl	2	2	2. 0	5. 14	5. 14	11. 41	11. 41	0. 00	5. 14	11. 41	0. 00	11. 41
P3. 17	AgPl	3	2	1. 9	5. 54	0. 00	11. 94	11. 94	0. 00	5. 54	11. 94	0. 00	6. 40
P3. 18	AgPl	1	1	1. 0	13. 20	13. 20	13. 20	13. 20	0. 00	0. 00	13. 20	0. 00	0. 00
P3. 19	AgPl	7	3	2. 6	3. 20	16. 40	35. 65	22. 45	0. 00	16. 40	35. 65	0. 00	22. 45
P3. 20	AgPl	3	1	1. 0	8. 31	8. 31	8. 31	8. 31	0. 00	0. 00	8. 31	0. 00	0. 00
P3. 21	AgPl	1	1	1. 0	4. 18	4. 18	0. 00	4. 18	0. 00	0. 00	4. 18	0. 07	4. 18
P3. 23	AgPl	2	2	2. 0	0. 00	6. 72	12. 26	5. 54	0. 00	6. 72	12. 26	0. 00	5. 54
P3. 24	AgPl	8	3	2. 1	34. 62	34. 62	41. 21	41. 21	3. 31	34. 62	41. 21	0. 00	41. 21
P3. 25	AgPl	10	5	4. 4	11. 06	33. 54	55. 45	29. 49	0. 00	37. 02	55. 45	0. 00	26. 01
P3. 29	AgPl	3	1	1. 0	0. 00	0. 00	6. 52	0. 00	0. 00	6. 52	6. 52	0. 00	0. 00
P3. 30	AgPl	4	3	2. 8	21. 45	20. 91	23. 30	9. 53	0. 00	23. 30	32. 83	0. 68	21. 45
Pin. 01	Pin	4	2	1. 8	9. 66	0. 00	11. 50	9. 66	0. 00	0. 00	0. 00	0. 00	9. 66
Pin. 02	Pin	2	1	1. 0	5. 68	0. 00	5. 68	0. 00	5. 68	0. 00	5. 68	0. 00	0. 00
Pin. 03	Pin	5	3	2. 9	19. 03	11. 52	9. 60	13. 60	9. 60	2. 09	21. 12	0. 72	13. 60
Pin. 04	Pin	3	2	1. 9	10. 77	6. 43	4. 35	10. 77	0. 00	0. 00	6. 43	0. 07	10. 77
Pin. 05	Pin	5	1	1. 0	15. 65	15. 65	15. 65	0. 00	15. 65	15. 65	15. 65	0. 00	15. 65
Pin. 06	Pin	2	1	1. 0	0. 00	0. 00	5. 14	0. 00	0. 00	0. 00	0. 00	0. 00	0. 00
Pin. 07	Pin	1	1	1. 0	2. 36	2. 36	2. 36	2. 36	0. 00	2. 36	2. 36	0. 00	0. 00
Pin. 09	Pin	4	4	4. 0	15. 86	0. 00	18. 80	2. 94	6. 00	15. 74	18. 80	0. 08	15. 74
Pin. 10	Pin	3	1	1. 0	0. 00	0. 00	11. 60	11. 60	0. 00	0. 00	0. 00	0. 00	11. 60
Pin. 11	Pin	2	2	2. 0	10. 59	3. 09	7. 50	3. 09	7. 50	7. 50	10. 59	0. 35	10. 59
Pin. 12	Pin	4	3	2. 8	9. 18	5. 09	4. 08	5. 09	1. 76	2. 33	9. 18	0. 00	7. 42
Pin. 13	Pin	1	1	1. 0	1. 94	0. 00	1. 94	0. 00	0. 00	0. 00	1. 94	0. 00	0. 00
Pin. 14	Pin	3	2	1. 9	3. 72	0. 00	6. 07	2. 36	6. 07	2. 36	6. 07	0. 00	2. 36
Pin. 15	Pin	9	5	4. 6	21. 04	8. 56	18. 12	12. 77	6. 76	15. 58	21. 04	0. 00	8. 64
Pin. 16	Pin	8	3	2. 6	23. 49	14. 05	9. 44	20. 29	9. 44	0. 00	23. 49	0. 36	20. 29
Pin. 17	Pin	5	1	1. 0	20. 57	20. 57	0. 00	20. 57	0. 00	0. 00	20. 57	0. 81	20. 57

					Ecosystem services								
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Fodder	Artisanal	Carbon	Construction	Culture	Food & Drink	Medicine	Timber	Wood Products
Pin. 19	Pin	5	2	2. 0	19. 13	10. 87	8. 26	10. 87	8. 26	0. 00	19. 13	0. 58	10. 87
Pin. 20	Pin	4	2	1. 8	7. 11	2. 03	5. 08	2. 03	0. 00	5. 08	7. 11	0. 00	7. 11
Pin. 23	Pin	4	3	2. 8	6. 16	0. 00	9. 64	3. 48	1. 82	7. 98	9. 64	0. 04	9. 64
Pin. 24	Pin	5	3	2. 6	37. 63	37. 63	30. 75	6. 88	30. 75	30. 75	37. 63	0. 28	37. 63
Pin. 25	Pin	10	3	2. 5	26. 39	0. 00	28. 24	1. 85	21. 28	8. 81	28. 24	0. 58	8. 81
Pin. 26	Pin	23	10	8. 6	58. 82	0. 00	95. 35	46. 44	52. 72	19. 48	69. 39	4. 77	55. 04
Pin. 27	Pin	7	3	2. 2	22. 95	1. 72	22. 58	3. 07	1. 35	22. 58	24. 30	0. 00	24. 30
Pin. 28	Pin	19	8	5. 4	35. 77	24. 13	20. 04	37. 79	1. 25	4. 89	35. 37	0. 23	40. 59
Pin. 29	Pin	5	3	2. 9	7. 26	4. 78	12. 35	7. 26	0. 00	7. 26	12. 35	0. 00	7. 26
Pin. 30	Pin	8	4	3. 4	22. 82	9. 85	24. 27	9. 85	13. 64	19. 04	24. 27	0. 07	19. 04
Se. 01	HL	8	8	8. 0	15. 93	1. 16	35. 91	11. 56	6. 46	18. 65	15. 93	0. 48	18. 65
Se. 02	HL	6	3	2. 4	21. 11	0. 00	38. 09	21. 11	21. 11	21. 11	30. 19	6. 15	21. 11
Se. 03	HL	2	2	2. 0	32. 77	3. 99	32. 77	28. 78	32. 77	32. 77	32. 77	14. 45	32. 77
Se. 04	HL	15	9	8. 0	16. 30	2. 03	40. 30	8. 15	3. 35	20. 15	25. 35	2. 09	20. 15
Se. 05	HL	3	3	3. 0	4. 46	4. 46	9. 37	0. 00	4. 46	4. 46	4. 46	0. 00	4. 46
Se. 06	HL	16	8	6. 4	10. 27	0. 00	53. 73	9. 85	1. 44	11. 59	17. 35	3. 80	35. 69
Se. 07	HL	12	6	4. 8	33. 40	14. 96	56. 11	28. 02	14. 96	35. 37	33. 40	0. 45	35. 37
Se. 08	HL	12	9	8. 5	33. 01	3. 76	41. 18	29. 60	24. 85	33. 01	35. 68	2. 97	18. 49
Se. 09	HL	16	5	4. 6	58. 86	10. 41	83. 95	7. 22	0. 00	66. 07	58. 86	3. 95	55. 66
Se. 10	HL	12	10	9. 1	20. 45	0. 00	48. 40	15. 36	11. 32	24. 49	20. 45	1. 43	24. 49
Se. 11	HL	9	6	5. 3	16. 83	0. 00	45. 87	0. 00	0. 00	16. 83	4. 43	2. 16	31. 08
Se. 12	HL	4	4	4. 0	11. 25	0. 00	13. 13	7. 10	4. 15	4. 10	11. 25	0. 14	7. 10
Se. 14	HL	6	3	2. 4	3. 79	0. 00	28. 90	0. 00	0. 00	3. 79	3. 79	0. 75	24. 28
Se. 15	HL	4	4	4. 0	13. 48	0. 00	26. 34	25. 08	18. 70	13. 48	25. 08	1. 78	18. 70
Se. 16	HL	7	4	3. 2	0. 00	0. 00	12. 75	0. 00	0. 00	0. 00	0. 00	0. 00	1. 51
Se. 17	HL	3	3	3. 0	0. 00	0. 00	5. 60	3. 06	0. 00	4. 18	1. 13	0. 00	3. 06
Se. 18	HL	10	6	5. 5	3. 82	0. 00	46. 59	14. 11	3. 82	20. 18	11. 58	1. 14	18. 28
Se. 19	HL	1	1	1. 0	0. 00	0. 00	5. 00	5. 00	0. 00	0. 00	0. 00	0. 00	5. 00
Se. 20	HL	3	3	3. 0	19. 36	5. 78	22. 24	19. 36	13. 58	0. 00	19. 36	0. 00	13. 58
Se. 21	HL	2	2	2. 0	0. 00	0. 00	5. 04	1. 69	0. 00	3. 34	0. 00	0. 04	0. 00
Se. 22	HL	7	6	5. 7	10. 13	0. 00	29. 92	15. 91	4. 60	5. 54	26. 82	2. 47	20. 28
Se. 23	HL	7	6	5. 7	10. 07	0. 00	26. 10	17. 65	10. 07	15. 56	10. 07	0. 95	17. 92

					Ecosystem services								
Quadrat ID	Land-use history	Stem #	# spp.	Eff. # spp.	Fodder	Artisanal	Carbon	Construction	Culture	Food & Drink	Medicine	Timber	Wood Products
Se. 24	HL	4	3	2. 8	0. 00	0. 00	11. 25	2. 68	0. 00	0. 00	0. 00	0. 12	5. 00
Se. 25	HL	6	6	6. 0	19. 14	2. 18	23. 97	18. 59	14. 19	16. 04	16. 04	1. 30	20. 49
Se. 26	HL	3	1	1. 0	10. 51	0. 00	10. 51	10. 51	0. 00	10. 51	10. 51	0. 14	10. 51
Se. 27	HL	3	2	1. 9	6. 23	6. 23	8. 67	0. 00	6. 23	6. 23	6. 23	0. 00	6. 23
Se. 28	HL	4	2	1. 8	0. 00	0. 00	14. 80	14. 80	0. 00	2. 03	0. 00	0. 00	14. 80
Se. 30	HL	3	3	3. 0	10. 40	6. 78	15. 86	22. 63	15. 86	3. 62	22. 63	0. 27	22. 63

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