Disturbance, Regeneration and Invasion: implications for recovery of degraded montane forests in Kenya

Forstyrrelse, regenerering og invasjon: konsekvenser for re-etablering av ødelagte fjellskogområder i Kenya

Philosophiae Doctor (PhD) Thesis

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Ås 2011

Thesis number 2011: 51

ISBN 978-82-575-1014-5

ISSN 1503-1667

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Acknowledgments

I have been fortunate to receive support from various people and organizations throughout my study period at Norwegian University of Life Sciences (UMB). For making my graduate lifestyle possible, I would first like to acknowledge the Norwegian State Educational Fund (Lånekassen), European Union (EU) and Government of Kenya (GOK). Each of these organizations provided funding for various aspects of my research and training.

Without my PhD supervisors this thesis would not be. I thank Ørjan Totland, who served as main supervisor till January 2011, for assisting me to secure a Quota scholarship, admission to UMB and for taking me as a PhD student. His in-depth knowledge in plant ecology and statistics lifted my cursory thoughts towards the development of articles with achievable and interesting goals. Kari Klanderud my initial co-supervisor and later the main supervisor for the remaining study period provided instructive guidance, open discussions and critique on the manuscripts. Special thanks to David Odee for encouraging me to pursue what seemed unattainable. These initial experiences with you, Ørjan and Kari motivated me to undertake the study.

I thank the FOREAIM project team for fascinating and stimulating support during the study period. Special thanks to Dr. Bernard Kigomo for giving me the opportunity to work in the project and his continued support during the study. A suite of project field staff, collaborating government departments and local volunteers conducted the work that yielded the data on which the thesis is based. For this am indebted to Boaz Ngonga, William Bii, the late Florence Muindi, Gervas Nyaguti, Samson Tobit (KEFRI), Moses Tzombe, Julius Kirui, Evans Ontiri, Joseph Maritim and Milka Sarinji (KFS). Special thanks to Mzee William Kibii for identifying many of the plant species saving me from spending too many hours wandering around the Kenya National Herbarium.

Emotional support is an essential part of anyone's graduate career and I am fortunate to have been bolstered by many good friends. Former PhD students at INA-among them Mary Namaganda, Per Larson, Diress Tsegaye, Panada Larpkern and postdocs, especially Amparo Lazaro and Ole-Gunnar Støen for helping me find my way at U-building , advice, discussions and helping with Norsk translation. In particular, I am grateful to Richard Bischof for shadowing me by taking out my last born girl together with his girls and for support. To my fellow PhD students, Paul, Samora, Belachew, Ram, Julia, Alex, Eivind and David for the enriching academic life we shared.

I appreciate the administrative and logistical support from UMB staff, Mette Solsvik, Tone Granerud, Ole Wigo Røstad, Anne Marthe Leinbø, Anne Ombustvedt, and Gunnar Jensen. I thank Siri Eriksen, Fred Midtgaard, Vilma Bischof, John Olala and Benjamin Otiende for welcoming and hosting my children and providing support and encouragement.

My Children have supported me in numerous ways, perhaps most importantly by not incessantly asking when I am going to finish. Faith Auma and Ismael Mullah had to bear with my long absence from home. Joy Elizabeth has served as shadow head of the family, helping little ones whenever I was stuck in the office or away on safaris. I thank Ian Bright and Hope Marion for their patience during a challenging but interesting life in Norway. Thank you all for your encouragement and confidence in me.

Memorial

In memory of Jaduong Ismael Mula Agot, Mama Agnes Odiero Mula and Pamella Otieno Amwatta – though all are now deceased their enthusiasm for my education provided vital inspiration.

Contents

Abstract

Tropical montane forest loss and degradation, as well as degradation of lands which formerly supported forests, are proceeding at unprecedented rates, eroding biological diversity. Inadequate understanding of disturbance-related succession of these forests severely limits attempts to anticipate the recovery of species diversity and composition following such disturbances. Abandoned fallows and degraded secondary forest were used to study the natural regeneration of community species richness and composition, to identify potential restoration tree species and to examine the community invasibility and the impact of the invasive tree *Fraxinus pennsylvanica* on plant species recovery in Mau forest, Kenya.

The secondary forest had higher species richness and abundance of all functional groups, except herbs and shrubs that were more abundant in the fallows. Similarly, species composition of trees differed between transition zones and secondary forest, indicating different abilities of individual species to establish and grow under habitat changes during recovery. There was a high presence of some generalist tree species in the abandoned fallows and in the secondary forest indicating that these could be potential restoration species. Two of these species, namely *Albizia gummifera* and *Neoboutonia macrocalyx*, showed positive relationships with the establishment and growth of other species, suggesting that these could promote species richness during forest recovery.

There were contrasting relationships between native community diversity and the density of the invasive *Fraxinus pennsylvanica* in abandoned fallows and secondary forest, suggesting that community diversity may facilitate *F. pennsylvanica* invasion in the abandoned fallows but inhibit the invading exotic in the secondary forest. In the study site, *Fraxinus* appears to impact the species diversity of understory plant communities in the secondary forest, suggesting threats to forest diversity. Thus,

specific tools for management and control of *Fraxinus* in Mau should include (1) complete elimination of livestock grazing in the forest to reduce disturbance, (2) cutting of adult *Fraxinus* trees in the secondary forest to avoid further recruitment, (3) planting trees in all abandoned fallows in the forest block, and (4) establish monitoring plans for alien species in Mau forest and other forests in the country.

List of papers

This PhD thesis consists of the following papers which are referred by their Roman numerical (I-IV).

Paper I

Collins J. A. Mullah, Ørjan Totland, and Kari Klanderud. Recovery of plant species richness and composition in an abandoned forest settlement area in Kenya. *Restoration Ecology: doi: 10.1111/j.1526-100X.2011.00810.x* (Reprinted with the kind permission of Wiley-Blackwell)

Paper II

Mullah C. J. A., Klanderud K., Totland Ø. and Kigomo B. Relationships between the density of two potential restoration tree species and plant species abundance and richness in a degraded afromontane forest of Kenya (*Submitted*)

Paper III

Mullah, C. J. A., Klanderud K., Totland Ø. and Odee D. Invasion by *Fraxinus pennsylvanica* trees after agricultural abandonment in a tropical forest is related to diversity and tree density (*Submitted*)

Paper IV

Mullah C. J. A. Relationship between an invasive tree, *Fraxinus pennsylvanica* and plant species diversity and abundance after agricultural abandonment in a tropical afromontane forest (*Submitted*)

1. Introduction

The latest map of the global species diversity of vascular plants emphasizes tropical montane areas as the world's most important biodiversity hotspots (Myers et al. 2000; Barthlott et al. 2005). Although these forests are not extensive, their biodiversity, endemism and conservation threats are unusually high (Richter 2008). Evergreen and semi-deciduous tropical montane forests harbor a larger species number per land area than lowland rainforests, and have paramount functions as water catchments and erosion barriers (Bussmann 2004; Richter 2008). Montane forests generally occur at altitudes between 1200 and 3000 m, and are sensitive ecosystems due to their steep relief, which makes them very prone to erosion under a high rainfall regime. They occur mainly in Latin America and Southeast Asia, with outposts in tropical Africa (Richter 2008), and provide vital ecosystem services for millions of people in the tropics.

Tropical montane forests have been subjected to heavy tree felling for decades due to increased population pressure and resource use (firewood, mineral resources, pasture, agriculture, settlements) and are increasingly being fragmented (FAO 1993; Bussmann 2004; Richter 2008), leading to significant changes in their species richness and composition (Bussmann 2002). The conversion of forests to degraded lands represents a potential loss of biodiversity, carbon stocks, watershed functions, soil structure and fertility, agricultural productivity, and increased fire (FAO 2005; Miller and Nair 2006; Nair 2007). Furthermore, in tropical regions, the majority of invasive events occur in disturbed habitats, with half of these occurring in previously forested habitats (Binggeli et al. 1998; Bosu et al. 2009).

In recent years, with the abandonment of forest areas previously used for agriculture, large areas of montane tropical forests have naturally regenerated (Brown and Lugo 1994; Aide et al. 1996, 2000; Finegan 1996; Pascarella et al. 2000; Aragón and Morales 2003). The regeneration of such abandoned fallows have created a patchwork of different succession stages with pioneer plant communities contributing to local richness (White and Jentsch 2001), and with this site-specific species mix determining the long-term prospects of recovery (Perz and Skole 2003). Knowledge from recovery of tropical lowland forests after disturbances has been used to design successful restoration strategies of these ecosystems (Denslow 1987; Walker et al. 1991, 1996). However, in striking contrast to lowland rainforests, there is deficit knowledge on succession processes after anthropogenic disturbances as well as regeneration potential of individual species for the tropical montane forest (Bussmann 2002; Richter 2008). Furthermore, the ecological and silvicultural requirements of potential restoration species are almost unknown for these ecosystems (Finegan 1996; Bussmann 2004; Wass 1995). If these requirements are not well understood, we risk using inappropriate species based on studies from lowland rainforest or seasonally dry tropical forests, where most of the studies on forest recovery are conducted.

In this thesis I evaluate the species diversity and composition of recovering degraded forest to determine the difference between abandoned fallows and secondary forest. Furthermore, I use the natural regeneration patterns of the degraded tropical montane forest as a tool to select potential restoration species. Finally, I examine the invasibility of abandoned fallows and secondary forest and assess if an alien invasive tree, *Fraxinus pennsylvanica,* affect community diversity and species composition. The scope of the four papers of this thesis attempts to illustrate key major issues of management concerns for tropical montane forests. The first paper focuses on species diversity and composition of abandoned fallows and secondary forests, and uses that knowledge to select potential restoration species for abandoned forest fallows (Paper I). The second paper examines how two potential restoration species may influence the species diversity and composition of abandoned fallows and secondary forests (Paper II). Third, I assess the relationship between community properties and species invasion during forest recovery (Paper III), and finally I examine if the invasive *Fraxinus* trees influence the community diversity and composition of different functional groups in a recovering degraded forest (Paper IV).

2. Methods

2.1 Study site

The study sites are located within the Mau forest complex (0°30' 60 South, 35°27'0 East), encompassing a range of ecological conditions and disturbances. Mau forest vegetation patterns have a broad altitudinal zonation from west to east, with lower montane forest below 2 300 m elevation giving way to thickets of bamboo (*Arundinaria alpina*) mixed with forest and grassland, and finally to montane sclerophyllous forest near the escarpment crest 3000 m elevation. The lower montane forest has been heavily and destructively logged, and large areas have been converted to plantation forest. The more open, destructively-logged forest holds good populations of many highland species, but densities of interior forest tree species are relatively low.

Mau forest ecosystem represents a vital resource for the people inhabiting the two study sites (Ngoda & Kariuki 2000). Yet different social and economic contexts define distinct problems for conservation, sustainable use and restoration of their ecosystems. Rural communities in the Kedowa site (0°14' 60 South 35°33'60 East, 2085 m a.s.l.) face high population growth, shrinking productive agricultural land, coupled with poverty and lack of alternative livelihoods, which have led to encroachment into forests and illegal forest extraction activities like charcoal production, selective harvesting, and livestock grazing. In contrast, the Itare site (0°22' 0 South 35°16'60 East, 2118 m a.s.l.) on the southwestern Mau is flanked by well-established smallholdings or large scale tea farmers and is regarded as being less utilized compared to Kedowa (Plate 1). In general the forest in these two sites share a number of threats for the conservation of viable populations of native tree species and their sustainable use, including deforestation, habitat degradation, overall loss of biodiversity and integrity of the forest landscape. Grazing remains a key degradation source shared by both sites. A legal framework is available to ensure regulation of grazing in the forest but this is weekly enforced. However, restoration is a critical input to sustainable management of the two sites, including the whole Mau complex forest resources, since the social and environmental impacts resulting from forest degradations have no boundary. In Kedowa the adjacent settlements are already experiencing scarcity of some forest products and services like water, grass, and honey production. In Itare, the tea farmers are not spared since rainfall patterns and amounts are rapidly changing; affecting tea production.

PLATE. 1. Small holder tea farms bordering forest at Itare (left) and adjacent farming community at Kedowa (right) in Mau forest. Photos: C. J. Amwatta Mullah

PLATE. 2. Livestock grazing (left) and used earth mound charcoal kiln (right) at Kedowa. Photos: C.J. Amwatta Mullah

2.2 Study species

I used abandoned fallows of various stages of succession to study natural regeneration of plant communities and to identify potential restoration tree species (paper I). Three tree species; *Albizia gummifera*, *Neoboutonia macrocalyx* and *Fraxinus pennsylvanica* were purposely studied for several reasons specific to each of them in papers II-IV. The first two are native species commonly found in the montane forest of East Africa, while the last is an alien invasive tree species. *Albizia gummifera* is nitrogen fixing and is known to facilitate establishment and growth of companion crops in agroforestry systems (Gathumbi et al. 2002). The influence of *N. macrocalyx* on establishment and growth of other tree species is first reported in this study (Paper II). *F. pennsylvanica* has been observed invading open areas in the forest at Mau and we examined the community invasibility (Paper III) and ask if the invader could be a threat to forest diversity in the tropics (Paper IV). *Fraxinus pennsylvanica* invasion has not previously been reported in Africa, only in the Northern hemisphere (Pyšek & Prach 2003).

2.3 Data collection and analyses

To obtain data of plant community richness, composition, species abundances and environmental conditions in the abandoned fallows and in the secondary forest, 40 plots were randomly positioned within the different zones in Kedowa and Itare forests in 2006 and 2007. I recorded tree seedlings, saplings and adults, shrubs, lianas, herbs and ferns in both abandoned fallows and in the secondary forest in two seasons (wet and dry).

To assess environmental differences across sites that might reflect various land use histories, I measured human disturbance variables, namely length of human/livestock trails and livestock dung in each plot. The species data and human disturbance variables were used in all the papers.

ANOVA was used with abandoned fallows and secondary forest as fixed factors and species richness and abundance of tree seedlings, saplings and adults, shrubs, herbs, ferns and lianas as response variables, followed by multiple pair-wise comparisons. P-values of all post-hoc pairwise comparisons were Bonferroni tested to compare the species richness and abundance between abandoned fallows and secondary forest in the two seasons (Paper I). The relationships between the degree of degradations, human paths, and grazing (environmental variables) and the species composition of functional groups were examined by the use of Canonical Correspondence Analysis (CCA) for abandoned fallows and the secondary forest. I conducted multivariate analyses for plots in the abandoned fallows and in the secondary forest separately to examine species composition of tree species in relation to the environmental variables, and used this information to select potential restoration tree species. The influence of potential restoration tree species on the species richness and abundance of other species was assessed using linear relationship between *Albizia* and *Neoboutonia* density and the abundance and richness of other functional groups in abandoned fallows and in the secondary forest (Paper II). Native community properties influencing recruitment of the invasive species *F. pennsylvanica* in the abandoned fallows and in the secondary forest were examined using generalized linear mixed models with Poisson distribution (Paper III). Non-significant main factors and interactions were deleted by stepwise removal. Impact of *Fraxinus* tree species on the native community properties in abandoned fallows and in the secondary forest and whether *Fraxinus* may be a threat to the secondary forest were tested using linear regression analyses (Paper IV).

The thesis is based on descriptive studies hence it has limitations in detecting cause-effect relationships. However, insights emerging from the thesis can improve our knowledge of the trends and patterns in species recovery and roles of community properties in facilitating or limiting invasions in Mau forest. Such information is quite useful for formulating explicit hypotheses on the trends in diversity recovery, selection of potential restoration species and understanding of possible consequences of invasion on community properties in degraded tropical montane forests.

3. Results and discussion

3.1 Recovery of species diversity and composition

The secondary forest had the highest richness and abundance of all functional groups except herbs and shrubs, which were higher in the abandoned fallows. However, tree species richness in the zones of advanced recovery (TZ II) showed a clear trend towards approaching that of the secondary forest (Paper I). This consisted of a structure and composition that resembles, but not necessarily identical to the neighboring secondary forest. This is consistent with previous studies in the tropical rainforest which showed that woody species richness of sites close to mature forest area can recover within 15-20 years after agricultural abandonment (Brown and Lugo 1994; Guarguata and Ostertag 2001). Seedling and sapling species composition were different between abandoned fallows and secondary forest in Mau forest (Paper I). For example, many individuals of canopy trees (e.g. *Diospyros abyssinica*, *Suregada procera*, *Tabernaemontana stapfiana*, *Xymalos monospora*, *Cassipoura malosana*, *Casearia battiscombei*) typical of secondary forest in the region recruited in the secondary forest; whereas several pioneer species (e.g. *Croton marcrostachyus*, *Pswata mahonii*, *Allophyllus abysinicus*, *Albizia gummifera*, *Makaranga kilimandscharica*, *Dombeya torrida*) recruited in the abandoned fallows. There was, however, a high presence of generalist tree species in all growth stages in both the abandoned fallows and in the secondary forest (Fig. 2). Overall, 19 years after abandonment, our results showed marked difference in species composition between abandoned fallows and the secondary forests. However, the successful establishment of many generalist tree species in the study site indicates a high level of resilience in the system. Given that natural forest succession processes cannot guarantee recovery of tree diversity on a time scale compatible with human needs (Brown and Lugo 1994), I recommend replanting a mix of native generalist tree and late–successional tree species as viable means of restoring richness and composition of the abandoned fallows in the study area. In addition, there is a need to establish a coordinated long-term network of monitoring sites in abandoned fallows and secondary forests to obtain critical insights for a more complete understanding of spatial and temporal turnover in tree species composition in Mau forest complex.

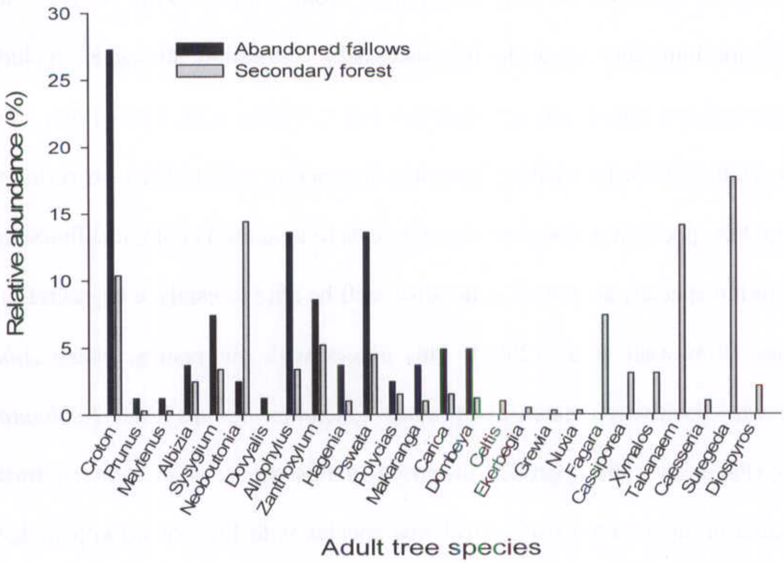

Fig. 2. Relative abundance of adult tree species in abandoned fallows and in the secondary forest, illustrating the difference in tree species composition between fallows and secondary forest in Mau forest, Kenya

3.2 Criteria for selecting potential restoration species

Techniques for successful restoration of degraded forest areas will require matching the tolerance of restoration species with environmental gradients at the microsite level (Parrotta et al. 1997; Ramirez-Marcial et al. 2001; Temperton et al. (2004). For instance, in this study, the microsite conditions such humidity, sunlight, nutrient availability, soil physical characteristics, vegetation cover, occurring in transition zones and in the secondary represent environmental filters, which may have defined the overall low similarity between tree species composition in abandoned fallows and in the secondary forest. However, some tree species were common in both abandoned fallows and secondary forest, offering a species pool from which we can select potential restoration tree species for the study area. This is in line with results from tropical lowland rainforests, which have shown that information from natural forest recovery after disturbances are important in designing successful restoration strategies, including selecting potential restoration species (Denslow 1987; Walker et al. 1991, 1996; Young et al. 2005; Halle 2007). In addition, potential interaction effects between restoration species and other species must be considered, to ensure long term ecological functioning of the restoration species, as, not all generalists will be able to catalyze regeneration of other species (Kanowski et al. (2003). This agrees with our results, where *Albizia gummifera* was positively related with more functional groups than *Neoboutonia macrocalyx* (Paper II). The approach proposed in this thesis, is in stark contrast to current restoration approaches using local tree species with little or no knowledge of their ecological requirements and their effects on other species. Our approach provides a practical criterion for selection of potential restoration species based on their regenerative capacity under different conditions during recovery processes. Others have, however, criticized the use of natural regeneration to select potential restoration species, as its outcomes can be highly unpredictable (MacMahon and Holl 2001), suggesting that experimental confirmations are needed to test their effects.

3.3 Community invasibility and Fraxinus invasion

We found a positive relationship between *Fraxinus* invasion and community diversity in the abandoned fallows which agrees with the 'rich get richer' hypothesis, that is supported by many observational studies (Stohlgren et al. 2003; Meiners et al. 2004; Gilbert and Lechowicz 2005; Fridley et al. 2007; Paper III). However, *Fraxinus* invasion related negatively with community diversity in the secondary forest which agrees with results from experimental and theoretical studies (Elton 1958, Hooper et al. 2005; Paper III). This suggests that invasion of a new site by a given alien plant species may be regulated by site characteristics such as light, shade, moisture and interactions with other species (Schupp et al. 1989; Davis and Pelsor 2001). This study therefore provides support to previous theoretical and empirical studies showing that specific site characteristics can affect the relationship between community diversity and exotic invasion and hence the success of invasion (Rejmanek and Richardson 1996; Stohlgren et al. 2001).

It is well recognized that intensive anthropogenic disturbances favor invasion. The on-going human related disturbances associated with selective and scattered logging of commercially valuable trees, charcoal production and grazing create community heterogeneity and environmental gradients inside the secondary forest. This may lead to gradual changes in the process of community assembly through time for example by modifying competitive interactions and successional pathways (Noble and Slatyer 1980). Our results indicate that the on-going disturbances may have provided establishment opportunities for *Fraxinus* in the secondary forest, where there was a negative relationship between community diversity and *Fraxinus* (paper III). In addition, tree seedling abundance related negatively with *Fraxinus* density in the secondary forest, suggesting competitive exclusion of native tree species (Paper IV). The results from studies described in Papers III & IV suggest that on-going anthropogenic disturbances in Mau will possibly increase invasion by *Fraxinus,* which may lead to gradual changes in succesional pathways by significantly favoring the invader at the expense of native tree species in Mau forest.

4. Conclusions

Based on our results, 19 years is not enough for abandoned fallows to recover to levels of species diversity and composition similar to secondary forest. Whereas the abundance of generalist species indicates recovery of tree diversity, insidious threat of *Fraxinus* invasion may slow the process. In our site, *Fraxinus* does impact upon the functional diversity of understory plant communities in the secondary forest, suggesting threats to forest diversity. Thus, specific tools for management and control of *Fraxinus* in Mau should include (1) complete elimination of livestock grazing in the forest to reduce disturbance, (2) Cutting of the adult *Fraxinus* trees in the secondary forest to avoid further recruitment, (3) Tree planting in abandoned fallows in the forest block, and (4) Establish monitoring plans for alien species in Mau forest and other forests in the country. Finally a broader use of generalist tree species that include nitrogen-fixing tree species in active restoration is recommended across all degraded forests.

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Paper I

Restoration Ecology
THE JOURNAL OF THE SOCIETY FOR ECOLOGICAL RESTORATION INTERNATIONAL

RESEARCH ARTICLE

Recovery of Plant Species Richness and Composition in an Abandoned Forest Settlement Area in Kenya

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Abstract

Cultivation of annual crops in the initial stage of reforestation has been commonly practiced in the tropics. In recent decades, however, cultivation of such areas has been discontinued, resulting in widespread abandoned settlements. In this article we used a former forest village settlement in Kenya, which had been cleared, cultivated and then abandoned, to study how natural vegetation recovers after such disturbances. Species richness, abundance, and composition of tree seedlings, saplings, adult trees, shrubs, and herbs were recorded in different zones, from a heavily degraded zone in the center of the settlement, through less disturbed transition zones (TZs), and in the surrounding secondary forest (SF). Species richness and abundance of tree seedlings, saplings, and adult trees increased gradually from the heavily degraded zone to the SF, whereas shrub and herb richness were the same for TZs and SF and abundance was lowest in the SF. Total species richness was highest in the SF. Some pioneer tree species were highly associated with the TZs, whereas sub-canopy tree species were associated with the SF. A group of tree species were not particularly associated with any of the four zones. Thus, these species might have good potential as restoration species. The results of our study contribute to the knowledge of natural regeneration in general, and of individual species characterizing the different stages of recovery of abandoned settlements in particular. Such information is urgently needed in designing ecologically sound management strategies for restoring abandoned forest settlements in tropical areas.

Key words: forest degradation, restoration species, species diversity, tree recruitment.

Introduction

Degradation of natural forests is widely acknowledged to be a serious problem that causes rural poverty, destruction of water catchments, loss of biodiversity, and increases in carbon emissions (Barnes 1990; FAO 2005). Degraded landscapes are expanding in the tropics as forests are converted to unsustainable pasture or cultivation and then abandoned (FAO 1978; Nair 1984; Bussmann 2004). In the 1940s, the forest village scheme (taungya system) was introduced to stop further spread of deforestation in tropical Asia and Africa. The scheme became widespread in various countries, such as Uganda, Gabon, India, Thailand, Cambodia, and Kenya, the study area of this article (Boonkird et al. 1984; Oduol 1986; Samapuddhi 2009). The system envisaged the sustainable use of forest land for food production by landless people who would otherwise be engaged in forest destruction to obtain food and cash. A forest village was established by giving each farmer a plot to construct a house, develop a home garden, and raise livestock. Cultivation proceeded until tree seedlings were big enough to shade and inhibit growth of annual crops, usually within 3–5 years. With increased population density and decreases in natural forest resources, forest village systems have proved expensive and are either facing slow growth or are being discontinued (Lamb & Tomlinson 1994).

The initial floristic composition (IFC) hypothesis (Egler 1954 see also van Breugel et al. 2007) is applicable to tropical post-agricultural succession where previous land use is of low intensity and seed sources are available in nearby natural forests, conditions typical of abandoned forest villages. The hypothesis proposes a sequential floristic or life form dominance of species. Early after abandonment, light-demanding species will dominate, but will eventually be replaced by shade-tolerant species due to differences in growth rate, longevity, and shade-tolerance among tree species that colonize an abandoned site. Several studies support the validity of the IFC hypothesis under different scenarios, such as those on fallows of contrasting duration since abandonment (Swaine & Hall 1983; Uhl et al. 1988; Chazdon 2003; Duncan & Chapman 2003), where some clear patterns have emerged. For instance, rates of recovery are accelerated if prior land use intensity was low, if the area of disturbance is small, and if there are remnant forest areas nearby (Swaine & Hall 1983;

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doi: 10.1111/j.1526-100X.2011.00810.x

Uhl et al. 1988; Guariguata & Ostertag 2001; Chinea 2002; Chazdon 2003; Duncan & Chapman 2003). For East African montane forests, however, only a few studies have been conducted on the impact of human use of vegetation resources (Bussmann 1996; Mathoko & Kariuki 2000; Bussmann 2002; Bussmann 2003; Bussmann 2004), regeneration after disturbance (Hitima et al. 2004; Farwig et al. 2006; Baldyga et al. 2007), and forest composition after abandonment (Kigomo et al. 1990; Duncan & Duncan 2000; Mwima & McNeilage 2003).

Various forms of taungya have been reported for Kenya (Oduol 1986), Tanzania (Chamshama et al. 1992), and Uganda (Chaudry & Silim 1980). For instance, in 1981–1983 an average of 413 households with a mean of 2,072 farmers was engaged in the shamba system (a form of taungya), which covered a total area of 5,831 hectares in 20 forest stations in Kenya (Oduol 1986), and 533 farmers were engaged in Northern Kilimanjaro in Tanzania (Chamshama et al. 1992). However, in later years of the twentieth century, the shamba system was discontinued in the region and forest settlements were vacated (Witcomb & Dorward 2009), chiefly due to increases in human population density and illegal activities (clearing, poaching, hunting). Abandoned forest settlements vary in size, which has resulted in discrete degraded areas that now dominate the Kenyan forest landscape. They form mosaics that comprise a range of habitat types, such as pastures, old plantations, and abandoned fallows left to succession with no management intervention. However, in Kenya, active restoration is being initiated by planting indigenous tree species to restore forests for soil protection, production, biodiversity conservation, and carbon sequestration (KEFRI, unpublished data). The restoration efforts are, however, hampered by inadequate understanding of silvicultural management and ecological requirements of many of the tropical tree species used (Wass 1995; Kinyamario et al. 2008). The results of our study will contribute to the knowledge of natural forest establishment after settlement abandonment, and will identify species that may be useful in active restoration of such sites and other disturbed areas in tropical forest ecosystems. Such information is urgently needed to design ecologically sound management strategies for restoration of abandoned settlements arising from failed forest village systems, which have become common since the late 1980s in tropical Asia and Africa, including Kenya (Samapuddhi 2009; Witcomb & Dorward 2009). Our study was carried out in Mau forest where about 15 hectares of forest was cleared and cultivated for 11 years and then abandoned 19 years ago. The shamba system is representative of land uses in the region, and Mau forest is a case study from which we might make references about the larger geographic area.

In this article we describe plant species richness, abundance, and composition in the previous settlement area and of the surrounding secondary forest (SF) to obtain an understanding of the natural recovery of degraded forest ecosystems in this area. In addition, we examined natural tree recruitment by recording tree seedling and sapling species composition in the different disturbance zones to better understand the colonization processes and to identify potential species for active restoration of abandoned areas. This article addresses the following questions: (1) How do species richness, abundance, and composition of different growth forms (herbs, ferns, lianas, shrubs, and tree seedlings, saplings, and adult trees) vary among degraded forest areas of different disturbance levels and in the SF? (2) How do ongoing disturbances such as grazing and human activities (selective logging, firewood collection) affect forest recovery? (3) Based on the species composition of different growth forms in the disturbed zones and in the SF, is colonization a function of surrounding vegetation or long distance dispersal? and (4) Which tree species may be suitable for active restoration of abandoned areas in the study site?

Methods

Study Area

Mau forest, which is divided into seven blocks, is the largest remaining near-continuous indigenous montane forest in East Africa. Since its designation as a Forest Reserve in 1964, Mau forest has lost almost 34,000 hectares of primary forest, or 9% of the original area. By 1999, the forest covered 360,000 hectares and comprised over 25% of Kenya's forest cover. The forest is one of the major water catchment areas in Kenya. Our study was conducted in a degraded site within the southwest forest block of Itare. The 83,395 hectares block is composed of natural forests, swamps, grasslands, fallows, and regenerating forests. The study area is at 2,120 m elevation, with an annual rainfall around 2,000 mm. Mean annual temperatures range from 12 to 16°C and potential evapo-transpiration varies between 1,400 and 1,800 mm (Jackson & McCarter 1994). The natural forest consists of Afromontane bamboo forest at higher elevations and secondary plant communities derived from logged rainforest at lower elevations. The forest has high biodiversity and hosts indigenous tree species, such as *Olea europaea* (Oleaceae), *Dombeya torrida* (Sterculiaceae), and various bamboo species. The forest is the home of the largest group of forest dwellers in Kenya, the Ogiek (Jackson & McCarter 1994).

Within the forest block, 15 hectares of previously cleared, cultivated, and then abandoned area surrounded by SF was chosen for this study. Detailed information on the history of land use was collected from Kenya Forest Service (KFS) records and by interviewing local people. The settlers removed all trees, logs and stumps, and hoed the soil by hand. They practiced a mixed crop system (corn, beans, and potatoes) during the 11 consecutive years that the settlement was active. Each year before planting, the area was burned and hoed to remove weedy grasses and herbs. Two plantings were made each year. Outside the village, the settlers partially removed trees to allow for grazing and some farming activities. The intensity of tree cutting in the surrounding area decreased with increasing distance from the village. The village was vacated and the land abandoned in 1987, except for periodic grazing by cattle, donkeys, and goats thereafter.

Nineteen years after abandonment, the site consists of three zones of recovery due to different degrees of degradation before abandonment, and continued grazing, selective logging, and firewood collection thereafter. Thus, the degradation is a combined effect of deforestation by clear cutting and selective logging, and overexploitation of the vegetation by grazing animals. In the area where the village was situated, there is a heavily degraded zone dominated by grasses and forbs, here termed the grass zone (GZ). Outside this zone, there is a less disturbed zone consisting of early colonizing shrubs and a few tree seedlings, termed transition zone I (TZI). Further out and closest to the SF, there is a zone of lesser degradation with shrubs, tree seedlings, tree saplings, and adult trees, termed transition zone II (TZII). Due to past selective logging, the SF is dominated by pioneer species (gap species) like *Tabernaemontana stapfiana* (Apocynaceae), *Celtis gomphophylla* (Ulmaceae), *Suregada procera* (Euphorbiaceae), *Xymalos monospora* (Monimiaceae), *Cassipourea malosana* (Rhizophoraceae), and *Fagaropsis angolensis* (Rutaceae). In addition, the presence of *Ehretia cymosa* (Boraginaceae), and *Achyranthes aspera* (Amaranthaceae) in the forest suggests that the Itare block is a SF (Mathoko & Kariuki 2000).

Data Collection

Data were collected in November 2006 in the middle of the dry season, and in March 2007 at the beginning of the rainy season. Each zone was divided into four sections along the cardinal directions. We randomly selected 40 plots within the different zones as follows: six plots in GZ, ten in TZI, ten in TZII and fourteen plots in SF. Each section of GZ, TZI, TZII, and SF had 1–2, 2–3, 2–3, and 3–4 plots, respectively. The plots in the SF were located at least 200 m away from the edge of the closest plot in TZII. We used plots of 5 × 30–m in GZ and TZI and 10 × 30–m in TZII and SF. We used larger plots in TZII and SF in order to capture the variation in species richness, abundance, and composition in these zones, where the species–area relationship differed from the other zones due to a greater number of larger trees. Each plot was divided into 6 subplots (for the 5 × 30–m plots) and 12 subplots (for the 10 × 30–m plots), and each subplot had a 1 × 1–m quadrat in its center. Adult trees and lianas (taller than 1.3 m and dbh >10 cm) were counted in all subplots. Tree saplings (young trees with dbh <10 cm and height >1.3 m) and shrubs were counted in every other subplot. Tree seedlings (<1.3-m height), ferns and herbs (percent cover) were recorded in every quadrat within each subplot. To enable comparison between the different plot sizes, corrections were done before data analyses. For the species abundance data, we divided abundance within the 10 × 30–m plots by 2. For the species richness data, we calculated the mean number of species within each of the two 5 × 30–m plots of a 10 × 30–m plot and used the mean of these plots in the analyses. We also collected information on environmental variables that could potentially explain the variation in species composition and richness among plots. As indicators of grazing pressure and human disturbance, we counted all animal droppings (cow and donkey) inside each of the plots and measured the length of human/animal paths crossing the plots, as described by Silori (2001) and Silori and Mishra (2001). A taxonomist assisted by local para-taxonomist and KFS staff identified the plant species. All unidentified species were deposited at the National Herbarium of Kenya for identification and voucher species were kept there. Nomenclature follows Agnew and Agnew (1994) and Beentje (1994).

Statistical Analyses

We used repeated-measures analyses of variance (ANOVAs) to examine how species richness and abundance of herbs, ferns, lianas, and tree seedlings (dependent variables) differed between GZ, TZI, TZII, and SF (zone, fixed factor) and between dry and wet seasons (season; repeated measures variable). Because we did not expect any of the following groups to be affected by season, we used one-way ANOVAs to examine how shrubs, tree saplings, adult trees, and the total species richness (dependent variables) differed between GZ, TZI, TZII, and SF (zone, fixed factor). We used Bonferroni post hoc tests to determine if dependent variables differed significantly between zones. To test for spatial autocorrelation, that is, whether the data points represented statistically independent sample units, we used two-way ANOVAs that included "section" and season as fixed factors, and species richness and mean abundance of species as response variables. Species–area relationships were examined by generating species accumulation curves for each growth form and within each zone with the program EstimateS (v.8.2.0), (Colwell 2009), and "true" species richness values were estimated using the Mao Tau estimator. These analyses showed that our plots did not capture the real species richness in the area, and the estimated "true" species richness was therefore used in the ANOVAs. R 2.10.0 (R Development Core Team 2009) was used for the species richness ANOVAs, and SYSTAT 10 for windows was used for the remaining analyses.

We used multivariate analyses to examine how species composition differed among zones (GZ, TZI, TZII, and SF, defined as dummy variables), and along gradients of animal grazing, and human disturbance. Detrended Correspondence Analysis (ter Braak & Prentice 1988; Eilertsen et al. 1990) was used to assess gradient length. Due to large variation in the species composition data (total variation >4.0 SD) for all growth forms, Canonical Correspondence Analyses (CCA, ter Braak 1986; ter Braak 1987; Leps & Smilauer 2005) were used to ordinate species composition of the different growth forms (separate analysis for each group) and environmental variables (zone, section, animal droppings, path length). We tested each environmental variable by forward selection, using 999 permutations with all variables included. For growth forms whose composition did not differ between seasons, namely saplings, adult trees, and shrubs, we present results only from the wet season. For those growth forms that differed in species composition between seasons, namely tree seedlings and herbs, we analyzed and present the data from wet and the dry seasons separately. For each analysis, we tested the significance of all canonical axes with 999 unrestricted permutations in a Monte Carlo test. We conducted all ordinations by using default settings in CANOCO 4.5 and used CanoDraw to produce ordination diagrams (ter Braak & Smilauer 2002).

Results

Species Richness and Abundance

Repeated-measures ANOVA showed that species richness of tree seedlings differed significantly between zones and between seasons (Table 1). In both seasons, richness was significantly highest in the SF, intermediate in the transition zones (TZs), and lowest in the GZ (Fig. 1a). ANOVAs showed that tree sapling and adult tree species richness were lowest in GZ and highest in the SF (Table 1; Fig. 1b & 1c). Species richness of herbs was significantly lower in GZ than in all the other zones, with significantly more species in the wet season in the zones (Table 1; Fig. 1d). Shrub species richness was higher in both TZs and in SF than in the GZ (Table 1; Fig. 1e). Liana species richness was higher in SF and TZII, compared to TZI and GZ in both seasons (Table 1). Species richness of ferns was higher in SF than in all other zones in the wet season (Table 1). TZI and TZII had higher total species richness than GZ, but lower than SF (Table 1; Fig. 1f).

Mean abundance of tree seedlings was higher in SF than in the other zones, but only in the wet season (Table 1; Fig. 1g). Abundance of tree saplings and adults was higher in SF than in both TZs, and higher in TZII compared to GZ (Table 1; Fig. 1h & 1i). Herb species cover was not significantly different in TZII compared to GZ or TZI in the dry season, but it was in the wet season (Table 1; Fig.1j). The abundance of shrubs was higher in the TZs than in both GZ and SF (Table 1; Fig. 1k). Liana species abundance was higher in SF and TZII compared to TZI and GZ in both seasons (Table1). The abundance of fern species was higher in SF than in all other zones in the wet season (Table 1). The ANOVA with section as a factor showed that there was no effect of section on species abundance or richness, suggesting that there was no spatial autocorrelation of species richness or abundance within the zones.

Species Composition

The position of plots among different "sections" did not affect species composition, suggesting lack of autocorrelation within the zones. The relationships between species composition and the different zones, human and animal disturbances are shown in CCA biplot ordination diagrams of species and environmental variables (Figs. 2 & 3). The whole CCA model was significant for the species composition of tree seedlings in the wet season, and for herbs and lianas (not shown) in both seasons (Figs. 2 & 3). The first canonical axis explained a large part of the variation in species composition of tree saplings, shrubs, herbs, and lianas. The CCA model was only close to significant for adult tree species composition

Table 1. Repeated-measurement ANOVAs of Mao Tau estimated species richness and mean abundance of tree seedlings, herbs, lianas, and ferns (dependent variables) in four different disturbance zones (zone; fixed factor) and in the wet and the dry season (repeated measure factor) and ANOVAs of Mao Tau estimated species richness and abundance of tree saplings, adult trees, shrubs, and all plants (dependent variable) in the four disturbance zones in Mau forest, Kenya.

	Zone		*Season*		*Zone × Season*	
	F	*p*	*F*	*p*	*F*	*p*
Repeat-ANOVAs						
Richness						
Tree seedlings	32.01	<0.001	514.74	<0.001	1.56	0.214
Herbs	17.40	0.362	49.89	<0.001	1.69	0.185
Ferns	56.12	<0.001	54.482	<0.001	3.26	0.092
Lianas	15.30	<0.001	488.53	<0.001	1.36	0.174
Abundance						
Tree seedlings	5.312	0.004	22.56	<0.001	6.57	<0.001
Herbs	38.07	<0.001	1.32	0.258	7.98	<0.001
Lianas	17.10	<0.001	7.09	0.011	1.87	0.153
Ferns	12.49	<0.001	18.21	<0.001	11.00	<0.001
ANOVAs						
Richness						
Saplings	307.54	<0.001				
Adult trees	492.54	<0.001				
Shrubs	249.14	<0.001				
All plants	331.55	<0.001				
Abundance						
Saplings	16.922	<0.001				
Adult trees	24.563	<0.001				
Shrubs	10.50	<0.001				

F and *p* values are shown.

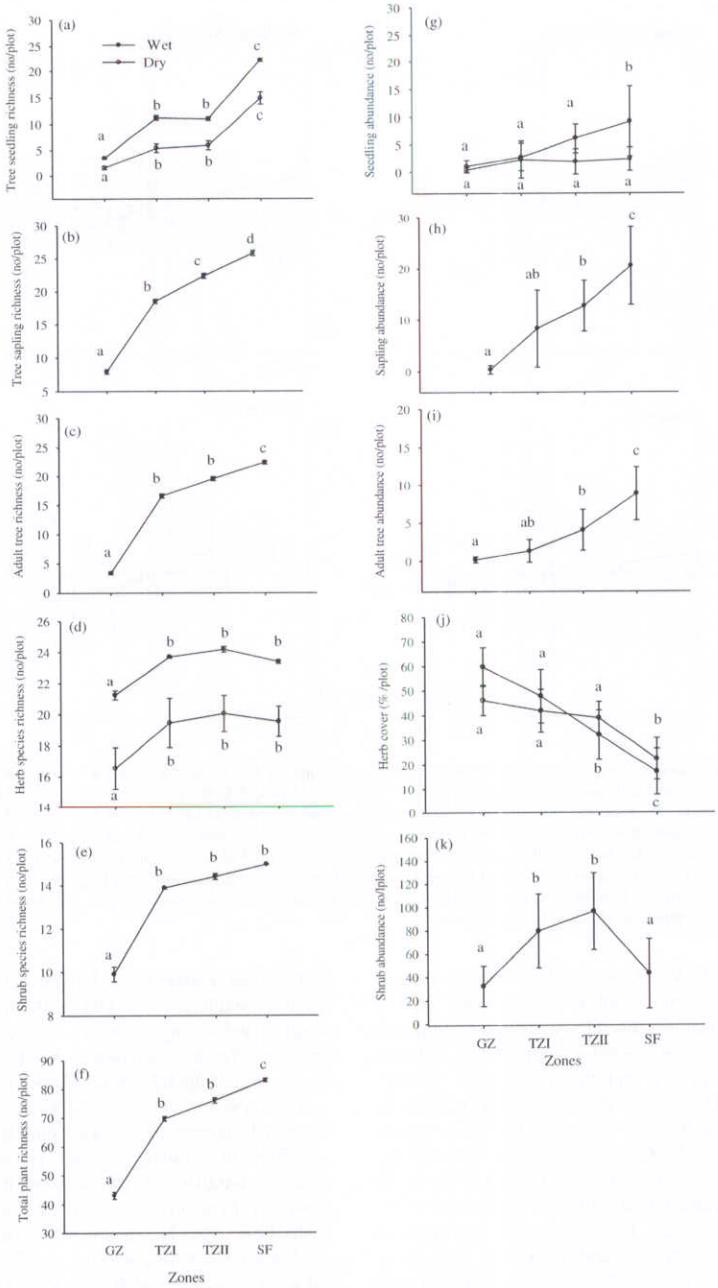

Figure 1. Mao Tau estimated species richness (mean ± SE) of (a) tree seedlings, (b) tree saplings, (c) adult trees, (d) herbs, and (e) shrubs, and (f) total species richness, and abundance (mean ± SE) of (g) tree seedlings, (h) tree saplings, (i) adult trees, (j) herbs, and (k) shrubs in different zones of disturbance; GZ, TZI, TZII, SF in Mau forest, Kenya. Both wet and dry season are shown for tree seedlings and herbs. Different letters indicate significant difference using Bonferroni pair wise mean comparison post hoc test. Only one set of letters is shown where there was no significant difference between the seasons.

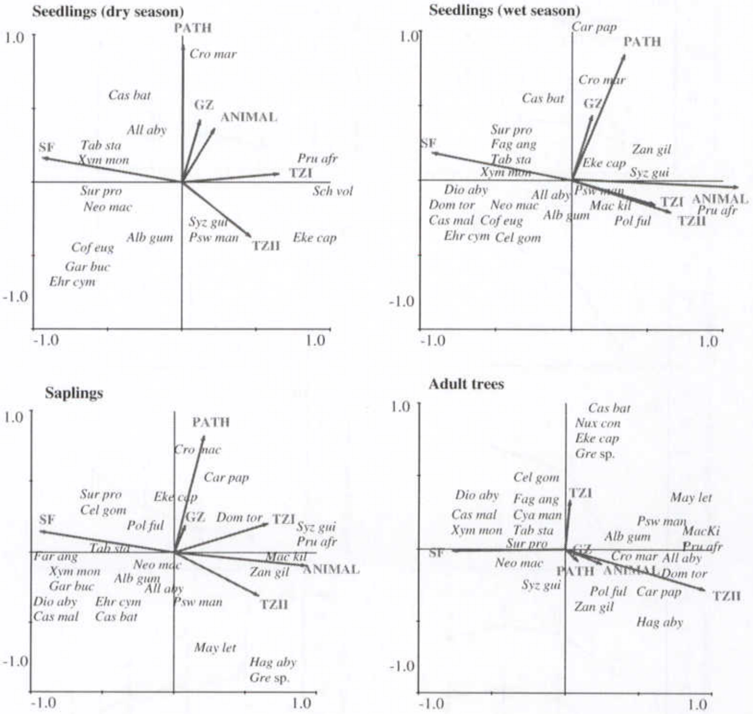

Figure 2. CCA ordination of seedlings, saplings, and adults of tree species, including six environmental variables in Mau forest, Kenya. Cro mac, *Croton macrostachyus*; Cas bat, *Casearia battiscombei*; Cas mal, *Cassipourea malosana*; All aby, *Allophylus abyssinicus*; Tab sta, *Tabernaemontana stapfiana*; Xym mon, *Xymalos monospora*; Sur pro, *Suregada procera*; Neo mac, *Neoboutonia macrocalyx*; Ehr cym, *Ehretia cymosa*; Gar buc, *Garcinia buchananii*; Cof eug, *Coffea eugenioides*; Alb gum, *Albizia gummifera*; Psy mah, *Psychotria mahonii*; Syz gui, *Syzygium guineense*; Eke cap, *Ekebergia capensis*; Pru afr, *Prunus africana*; Sch vol, *Schefflera volkensii*; Car pap, *Carica papaya*; Fag ang, *Fagaropsis angolensis*; Cel gom, *Celtis gomphophylla*; Dio aby, *Diospyros abyssinica*; Dom tor, *Dombeya torrida*; Zan gil, *Zanthoxylum gillettii*; Pol ful, *Polyscias fulva*; Mac kil, *Macaranga kilimandscharica*; May het, *Maytenus heterophylla*; Gre spp., *Grewia* species; Hag aby, *Hagenia abyssinica*; Nux con, *Nuxia congesta*; Cya man, *Cyathea manniana*. Only well-fitting species are shown in the figure.

($p = 0.058$, TI = 5.631, Var. Exp. = 1.081, Table 2; Fig. 2, TI [Total inertia] = the total variation of data; Var. Exp. = total variation explained of the TI by the environmental variables). The tree seedling species composition differed significantly between the SF and the other zones in both seasons ($p = 0.004$, TI = 3.969, Var. Exp. = 1.000, Table 2; Fig. 2). The species composition of tree saplings ($p = 0.002$, TI = 2.632, Var. Exp. = 0.685) and adult trees ($p = 0.002$, TI = 1.436, Var. Exp. = 0.718) differed significantly between the SF and the other zones, but did not differ between the TZs and the GZ (Table 2; Fig. 2). The herb species composition differed significantly between GZ and the SF and TZII, both in the wet ($p = 0.002$, TI = 2.007, Var. Exp. = 0.974) and the dry season ($p = 0.002$, TI = 2.768, Var. Exp. = 0.878, Table 2; Fig. 3). The species composition of shrubs ($p = 0.002$, TI = 2.163, Var. Exp. = 0.898) differed significantly between the TZII and the other zones and between the SF and the other zones (Table 2; Fig. 3). The CCA clearly showed that species composition differed between TZs and the SF for tree seedlings and saplings. However, only a few of the seedling and sapling species already occurred in the SF as adult trees, e.g. *Syzygium guineense* (Myrtaceae) and *Neouboutonia macrocalyx* (Euphorbiaceae) (Appendix).

Tree species composition of all life stages were well separated among the zones (Fig. 2). In the dry season, seedlings of *Prunus africana* (Rosaceae) and *Schefflera volkensii* (Araliaceae) were associated with TZI and *S. guineense*and *Psychotria mahonii* (Rubiaceae) were associated with TZII (Fig. 2). In the wet season, seedling species of *Macaranga kilimandscharica* (Euphorbiaceae), *Polyscias fulva* (Araliaceae), and *P. africana* occurred in both TZI and TZII. *Syzygium guineense* was associated with high grazing pressure in the wet season while *Croton macrostachyus* (Euphorbiaceae) was associated with animal and human paths in both seasons (Fig. 2). As opposed to the species mentioned above, some species, such as *Allophylus abyssinicus*

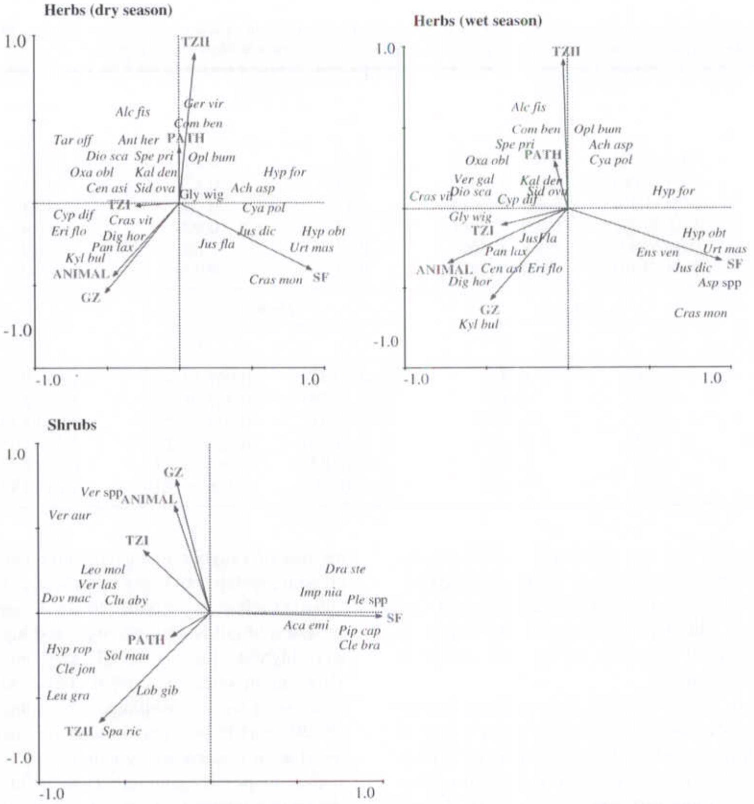

Figure 3. CCA ordination of herb and shrub species, including six environmental variables in Mau forest, Kenya. Vero spp., *Vernonia* species; Ver aur, *Vernonia auriculifera*; Leo mol, *Leonotis mollissima*; Hyp rop, *Hypericum roeperanum*; Sol man, *Solanecio mannii*; Cle joh, *Clerodendrum johnstonii*; Leu gra, *Leucas grandis*; Spa ric, *Sparmannia ricinocarpa*; Lob gig, *Lobelia giberroa*; Pip cap, *Piper capense*; Aca emi, *Acanthus eminens*; Cle bra, *Clematis brachiata*; Ple spp., *Plectranthus* species; Dov mac, *Dovyalis macrocalyx*; Dra ste, *Dracaena steudneri*; Imp nia, *Impatiens niamniamensis*; Ger vir, *Gerbera viridifolia*; Com ben, *Commelina benghalensis*; Alc fis, *Alchemilla fischeri*; Ant her, *Anthospermum herbaceum*; Opl bum, *Oplismenus burmannnii*; Kal den, *Kalanchoe densiflora*; Tar off, *Taraxacum officinale*; Sid ova, *Sida ovata*; Dio sca, *Diodia scandense*; Oxl obl, *Oxalis obliquifolia*; Cen asi, *Centella asiatica*; Cyp dif, *Cyperus difformis*; Gly wig, *Glycine weightii*; Cra mon, *Crassocephalum montuosum*; Eri flo, *Erigeron floribundus*; Pan lax, *Panicum laxum*; Dig hor, *Digitaria horizontalis*; Kyl bul, *Kyllinga bulbosa*; Jus fla, *Justicia flava*; Ach asp, *Achyranthes aspera*; Hyp for, *Hypoestes forskalei*; Cya pol, *Cyathula polycephala*; Jus dic, *Justicia diclipteroides*; Hyp obt, *Hypoxis obtusa*; Urt mas, *Urtica massaica*; Ens ven, *Ensete venricosum*

(Sapindaceae), *P. mahonii*, *Ekebergia capensis* (Meliaceae), *N. macrocalyx* (Euphorbiaceae), and *Albizia gummifera* (Fabaceae), had seedlings that were not associated with any zone.

Saplings of *Zanthoxylum gilletti* (Rutaceae) *and M. kilimandscharica* were closely associated with high grazing pressure (Fig. 2). A group of species, namely *P. mahonii*, *A. abyssinicus*, *A. gummifera*, *N. macrocalyx* and *P. fulva*, had saplings that were not associated with any zone or environmental variable. Adult trees of *Nuxia congesta* (Loganiaceae), *E. capensis*, and *Casaeria battiscombei* (Flacourtiaceae) were strongly associated with TZI (Fig. 2). TZII was characterized by adult tree species of *Dombeya torrida*, *C. macrostarchyus*, *S. guineense*, *P. fulva*, and *Hagenia abyssinica* (Rosaceae).

Discussion

Plant species richness, abundance, and composition differed substantially between zones in the Itare block of Mau Forest. The CCA ordinations showed that species composition of the different functional groups remained fairly well-separated among degradation zones, mainly because several species were strictly associated with the different zones. This supports previous findings that after establishment, species form distinct

Table 2. *F* and *p* values of environmental variables tested by forward selection in CCA in relation to the species composition of tree seedlings, tree saplings, adult trees, shrubs, herbs, and lianas in the wet and the dry (in parentheses) season in Mau forest, Kenya.

Environmental Variable	*Tree Seedlings*		*Saplings*		*Adult Trees*	
	F	*p*	*F*	*p*	*F*	*p*
Secondary forest	4.62 (2.62)	0.002 (0.002)	5.92	0.002	3.81	0.002
Transition zone II	2.35 (2.00)	0.022 (0.070)	1.54	0.128	1.71	0.086
Transition zone I	0.39 (1.33)	0.988 (0.208)	1.55	0.102	1.71	0.086
Grass zone	1.51 (0.23)	0.208 (0.706)	0.57	0.806	1.64	0.112
Path	0.84 (0.43)	0.506 (0.860)	0.87	0.868	0.54	0.790
Animal dung	0.39 (0.44)	0.988 (0.828)	0.33	0.970	0.12	0.954

	Shrubs		*Herbs*		*Lianas*	
	F	*p*	*F*	*p*	*F*	*p*
Secondary forest	14.81	0.002	20.44 (9.42)	0.002 (0.002)	18.81 (10.44)	0.002 (0.002)
Transition zone II	3.25	0.002	8.11 (3.59)	0.002 (0.002)	2.75 (9.78)	0.008 (0.002)
Transition zone I	2.13	0.174	3.12 (6.31)	0.544 (0.752)	0.67 (0.54)	0.768 (0.202)
Grass zone	1.77	0.146	2.19 (1.30)	0.024 (0.200)	0.42 (0.65)	0.982 (0.758)
Path	1.36	0.222	1.45 (0.87)	0.140 (0.506)	1.85 (1.23)	0.098 (0.124)
Animal dung	0.39	0.878	0.84 (0.76)	0.428 (0.590)	0.16 (0.44)	1.000 (0.904)

combinations, depending on the suitability of small-scale environmental conditions (Brown & Lugo 1994; Myster 2004). The gradual increase in species richness and abundance of tree seedlings, saplings and adult trees from the heavily degraded GZ to the SF is a good indication of the rate of forest regeneration after abandonment.

Muniz-Castro et al. (2006) found that sapling density decreased gradually with increasing distance from potential seed sources in the forest. We found a similar pattern in Mau forest, although a direct distinction between the effects of distance to the seed source and disturbances cannot be drawn, as the distance to the seed source correlated with the degree of disturbance, which likely explained most of the variation in species richness, abundance, and composition between the different zones (GZ, TZI, TZII, and SF). However, our results show that only a few of the seedlings and saplings species colonizing the TZs occurred in the SF as adult trees, suggesting that colonization of the site is a function of both neighbor vegetation and long distance dispersal. It is, however, worth noting that the fact that only a few of the tree seedling and sapling species found in TZs also occurred as adults in the SF may be a result of inadequate sampling.

The presence, abundance, and species composition of tree saplings are good indicators of recovery trends in degraded natural forest as they indicate how species composition and diversity may develop in the future (Duarte et al. 2006). Our results show that there were significant differences in sapling richness and abundance between the zone of lowest disturbance (TZII) and the SF. However, species richness and abundance of adult trees were high in both TZs and the SF, suggesting that previously disturbed areas transition toward a forest structure and composition that resembles, but is not necessarily identical to, SF. The TZs and SF had higher species richness of shrubs and herbs than GZ, but GZ and SF had lower abundance of shrubs than TZs, probably because of a higher light availability and more intense grazing pressure, which both benefit shrubs over trees (Piggot & Taylor 1994; Ostertag & Verville 2002). In general, 19 years after cessation of cultivation, the tree seedling and sapling richness were highest close to the SF edge and lower further away. This pattern agrees with other studies suggesting that species richness of woody seedlings and saplings can recover within 15–20 years in post-agricultural SFs that are close to mature forest areas (Guariguata & Dupuy 1997). In addition, previous studies of post-agricultural recovery in tropical forests have shown that recovery of species richness is far more rapid than recovery of species composition (Chazdon 2003), which is also suggested by our results. Overall, the observed forest regeneration trends in the Itare forest block shows that recovery to a closed forest canopy does not occur within 19 years. Species richness and abundance in the less disturbed zones were considerably lower than in the SF. Furthermore, species composition differed substantially between the SF, the transitional zones and the GZ.

Regeneration is a central process of forest ecosystem dynamics (Grubb 1977), and sustainable forest restoration is only possible if adequate information on regeneration of species is available. Unfortunately, this has been difficult to achieve because of propagation difficulties of many tropical hardwood tree species (Boots & Gullison 1995) and inadequate knowledge of their ecological requirements (Engel & Poggiani 1992). Consequently, it has been difficult to identify suitable tree species (early or late pioneers) for active restoration that could accelerate succession in degraded tropical forest systems (Wass 1995; MacDonald et al. 2003; Bussmann 2004). The presence of tree species in the different degradation zones of our study site could be one criterion used to identify species suitable for restoration. Our study identifies a group of tree species that appear to have relatively low affiliation with any zone (i.e. they occur close to the center in the ordination diagrams), suggesting that these species are habitat-generalists with few requirements for specific environmental conditions that change during succession. Such species may be particularly suitable for active restoration because they may germinate under most conditions and may persist for long periods during succession. The species that most clearly exhibited these characteristics in our study were *Psychotria mahonii*, *Allophylus abyssinicus*, *Albizia gummifera*, *Neouboutonia macrocalyx*, *Polyscias fulva*, *Dombeya torrida*, and *Ekebergia capensis*. These species may have potential for restoration of degraded tropical forests in areas where they occur naturally because they have the ability to establish as seedlings and survive as saplings in sites with different degrees of degradation. We propose that further studies should focus on the reproduction, dispersal, colonization, and abundance of various life-stages of these species under contrasting environmental conditions, and on how they influence recruitment and establishment of other species during succession.

The constraints on vegetation recovery from disturbances caused by the previous settlement are evident from the present plant species richness, abundance, and composition in Mau forest. All tree cover and most tree stumps were removed. Regeneration from the soil seed bank and/or through stump sprouting likely did not occur. This, together with the current grazing pressure and the distance from current seed source, may explain the low tree regeneration rate in the central GZ. Grazing has continued after abandonment of the settlement and is likely to impact soil and aboveground vegetation, which may significantly impede forest regeneration, particularly recovery of species composition. For example, Haggar et al. (1997) and Posada et al. (2000) reported that severe reduction in regeneration of trees and shrubs in pastures was due to intensive browsing by livestock. Intensive grazing, trampling, and uprooting by both large and small domestic herbivores in these grass/forb areas have perpetuated dominance by perennial grasses, such as *Digitaria horizontalis*, *Kyllinga bulbosa*, and *Panicum laxum*that are all abundant in the heavily degraded grasslands in Itare.

Recovery of degraded forest areas after agriculture is important for climate change mitigation, biodiversity conservation, rural development, and poverty reduction in Africa. Our study shows that 19 years are not sufficient for a degraded tropical forest site to recover to levels of species diversity and composition similar to a SF. However, the relatively high species richness and abundance of adult trees and saplings in the zone of lowest disturbance and closest proximity to the SF suggests that the site is in a transitional phase toward a structure that resembles a SF. The generality of our results may be limited as our study was conducted at a single abandoned settlement. Nevertheless, we believe our results are representative of recently abandoned settlements in East Africa, because management history and the forest landscapes are similar across the region (Chaudry & Silim 1980; Chamshama et al. 1992; Witcomb & Dorward 2009). Additional studies are needed both in comparable sites in the region and in other parts of the tropics to confirm whether our results are applicable elsewhere.

Implications for Practice

- Successful tropical montane forest restoration requires use of habitat generalist indigenous tree species.
- Because successional processes decline with increasing distance (20-170 m) from the forest edge, active restoration should be carried out about 100 m away from the SFs.
- Although regenerating forest on former settlement areas can rarely deliver all attributes of a primary forest, these forests are ecologically more valuable than single-species plantations. As such these forests require silvicultural management to promote the natural development of diverse SFs.

Acknowledgments

We are indebted to European Union for research funds to the FOREAIM (project no. INCO.CT-2005-510790) and the Royal Norwegian Government for scholarship for the first author. We are grateful to B. Ng'ong'a, W. Bii, and the late F. Muindi for field work, local para-taxonomists for species identification, the Itare Kenya Forest Service staff and Kenya Forestry Research Institute for logistical support. We thank R. Bussmann and D. Griffith for helpful comments, suggestions on statistical analysis and language revision that helped us improve the manuscript substantially.

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Appendix. Plants species sampled in grass zone (GZ), transition zones I and II (TZI and TZII) and secondary forest (SF) at Itare, Mau forest, Kenya.

Scientific Name	*Family*	*Life Form*	*Zone*
Cyperus alterniflorus Schwein.	Cyperaceae	Grass	GZ
Kyllinga bulbosa P. Beauv.	Cyperaceae	Grass	GZ
Digitaria horizontales Henrard	Poaceae	Grass	GZ
Panicum laxum Sw.	Poaceae	Grass	GZ
Scadoxus multiflorus (Martyn) Raf.	Amaryllidaceae	Herb	GZ
Erigeron floribudus (Kunth.) Sch. Bip.	Asteraceae	Herb	GZ
Plectranthus barbatus Andrews	Lamiaceae	Herb	GZ
Alchemilla fischeri Engl.	Rosaceae	Herb	GZ
Cissampelos pareira L.	Menispermaceae	Liana	GZ
Vernonia spp.	Asteraceae	Shrub	GZ
Cyperus difformis L.	Cyperaceae	Grass	TZI
Centella asiatica (L.) Urb.	Apiaceae	Herb	TZI
Crassocephalum vitellinum (Benth.) S. Moore	Asteraceae	Herb	TZI
Gerbera viridifolia (Dc.) Sch.Bip.	Asteraceae	Herb	TZI
Taraxacum officinale F.H. Wigg.	Asteraceae	Herb	TZI
Cynoglossum coeruleum A.DC.	Boraginaceae	Herb	TZI
Kalanchoe densiflora Rolfe	Crassulaceae	Herb	TZI
Sida ovata Forssk.	Malvaceae	Herb	TZI
Oxalis obliquifolia Steud.ex A.Rich.	Oxalidaceae	Herb	TZI
Glycine wightii (Taub.) Verdc.	Papilionaceae	Herb	TZI
Solanum indicum L.	Solanaceae	Herb	TZI
Solanum nigrum L.	Solanaceae	Herb	TZI
Diodia scandens Hutch. & Dalziel	Rubiaceae	Herb	TZI
Clutia abyssinica Jaub. & Spach.	Euphorbiaceae	Liana	TZI
Vernonia auriculifera Hiern	Asteraceae	Shrub	TZI
Vernonia lasiopus O. Hoffm.	Asteraceae	Shrub	TZI
Vernonia spp.	Asteraceae	Shrub	TZI
Solanecio mannii (Hook.f.) C. Jeffrey	Euphorbiaceae	Shrub	TZI
Indigofera volkensii Taub.	Fabaceae	Shrub	TZI
Leonotis mollissima Gurke.	Labiateae	Shrub	TZI
Grewia spp.	Malvaceae	Shrub	TZI
Dovyalis macrocalyx (Oliv.) Warb.	Silicaceae	Shrub	TZI
Nuxia congesta R.Br.ex Fresen	Stilbaceae	Shrub	TZI
Polyscias fulva (Hiern) Harms	Araliaceae	Tree	TZI
Schefflera volkensii (Engl.) Harms	Araliaceae	Tree	TZI
Maytenus heterophylla N. Robson	Celastraceae	Tree	TZI
Neoboutonia macrocalyx Pax	Euphorbiaceae	Tree	TZI
Albizia gummifera (J.F. Gmel.) C.A.sm.	Fabaceae	Tree	TZI
Ekebergia capensis Sparm.	Meliaceae	Tree	TZI
Oplismenus bumianii P. Beauv.	Poaceae	Grass	TZII
Achyranthes aspera L.	Amaranthaceae	Herb	TZII
Cyathula polycephala Baker	Amaranthaceae	Herb	TZII
Vernonia galamensis (Cass.) Less.	Asteraceae	Herb	TZII
Commellina benghalensis Forssk.	Commelinaceae	Herb	TZII
Kalanchoe densiflora Rolfe	Crassulaceae	Herb	TZII
Sida ovata Forssk.	Malvaceae	Herb	TZII
Oxalis obliquifolia Steud.ex A. Rich.	Oxalidaceae	Herb	TZII
Anthospermum herbaceum L.f.	Rubiaceae	Herb	TZII
Spermacoce princeae (K.Schum) Verdc.	Rubiaceae	Herb	TZII
Clutia abyssinica Jaub. & Spach.	Euphorbiaceae	Liana	TZII
Ipomoea hildebrandtii Vatke	Convolvulaceae	Liana	TZII
Scutia myrtina (Burm.f.) Kurz.	Rhamnaceae	Liana	TZII
Rubus steudneri (Olive.) R.A. Graham	Rosaceae	Liana	TZII
Physalis minima C.H. Wright	Solanaceae	Liana	TZII
Sparmannia ricinocarpa (Eckl. & Zeyh.) Kuntze	Tiliaceae	Liana	TZII
Cyphostemma orondo (Gil & M. Brandt) Desc.	Vitaceae	Liana	TZII
Acanthus eminens C.B. Clarke	Acanthaceae	Shrub	TZII
Launaea cornuta C. Jeffrey	Asteraceae	Shrub	TZII
Lobelia gibberoa Hemsl	Campanulaceae	Shrub	TZII
Hypericum roeperianum Schmp.ex A.Rich.	Hypericaceae	Shrub	TZII
Leucas grandis Vatke	Labiateae	Shrub	TZII

Appendix. Continued

Hibiscus ludwigii Eckle. & Zeyh.	Malvaceae	Shrub	TZII
Rumex usambarensis Dammer	Polygonaceae	Shrub	TZII
Solanum mauritianum Scop.	Solanaceae	Shrub	TZII
Solanum spp.	Solanaceae	Shrub	TZII
Solanum terminale Forssk.	Solanaceae	Shrub	TZII
Triumfetta rhomboidea Jacq.	Sterculiaceae	Shrub	TZII
Clerodendrum johnstonii Oliv	Verbenaceae	Shrub	TZII
Polyscias fulva (Hiern) Harms.	Araliaceae	Tree	TZII
Carica papaya L.	Caricaceae	Tree	TZII
Croton marcrostachyus Hochst.ex Delile	Euphorbiaceae	Tree	TZII
Macaranga kilimandscharica Pax	Euphorbiaceae	Tree	TZII
Neoboutonia macrocalyx Pax	Euphorbiaceae	Tree	TZII
Albizia gummifera (J.F. Gmel.) C.A.sm.	Fabaceae	Tree	TZII
Dombeya torrida Bamps.	Malvaceae	Tree	TZII
Ekebergia capensis Sparm.	Meliaceae	Tree	TZII
Hagenia abyssinica J.F. Gmel.	Rosaceae	Tree	TZII
Prunus africana (Hook.f.) Kalkman	Rosaceae	Tree	TZII
Psychotria mahonii C.H. Wright	Rubiaceae	Tree	TZII
Allophylus abyssinicus P. Beauv.	Sapindaceae	Tree	TZII
Ensete ventricosum (Welw.) Cheesman	Musaceae	Grass	SF
Justicia diclipteroides Lindau	Acanthaceae	Herb	SF
Justicia flava (Forssk.) Vahl.	Acanthaceae	Herb	SF
Crassocephalum montousum (S.Moore) Milne-Redh.	Asteraceae	Herb	SF
Impatiens niamniamensis Gilg.	Balsaminaceae	Herb	SF
Kalanchoe densiflora Rolfe	Crassulaceae	Herb	SF
Hypoxis obtusa Burch.	Hypoxidaceae	Herb	SF
Sida ovata Forssk.	Malvaceae	Herb	SF
Urtica massaica Mildbr.	Urticaceae	Herb	SF
Cyathea spp.	Amaranthaceae	Liana	SF
Landolphia buchananii (Hallier.f.) Sapf.	Apocynaceae	Liana	SF
Periploca linearifolia Quart.-Dill. & A. Rich.	Apocynaceae	Liana	SF
Zehneria scabra (L.f.) Sond.	Cucurbitaceae	Liana	SF
Gouania longispicata Engl.	Rhamnaceae	Liana	SF
Galium aparine L.	Rubiaceae	Liana	SF
Galium scioanum Chiov.	Rubiaceae	Liana	SF
Keetia guienzi (Sond.) Bridson	Rubiaceae	Liana	SF
Pauridiantha paucinervis (Hiern) Bremec	Rubiaceae	Liana	SF
Rubia cordifolia L.	Rubiaceae	Liana	SF
Toddalia asiatica (L.) Lam.	Rutaceae	Liana	SF
Smilax anceps Willd.	Smilacaceae	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
Unknown liana spp.	Unknown	Liana	SF
Cyphostemma orondo (Gil & M.Brandt) Desc.	Vitaceae	Liana	SF
Rhoicissus tridentata (L.f.) Wild & R.B.Drumm.	Vitaceae	Liana	SF
Dracaena steudneri Engl.	Asparagaceae	Shrub	SF
Asplenium spp.	Aspleniaceae	Shrub	SF
Pteris catoptera Kunze	Cyatheaceae	Shrub	SF
Erythrococca bongensis Pax	Euphorbiaceae	Shrub	SF
Plectranthus spp.	Labiateae	Shrub	SF
Clematis brachiata Thumb.	Ranunculaceae	Shrub	SF
Tabernaemontana stapfiana Britten	Apocynaceae	Tree	SF
Spilanthes mauritiana (A.Rich.ex Pers) DC.	Asteraceae	Tree	SF
Ehretia cymosa (R.Br.ex Fresen.) Brenan	Boraginaceae	Tree	SF
Celtis gomphophylla Baker	Cannabaceae	Tree	SF
Garcinia buchananii Baker	Clusiaceae	Tree	SF
Diospyros abyssinica (Hiern) F.White	Ebenaceae	Tree	SF
Neoboutonia macrocalyx Pax	Euphorbiaceae	Tree	SF
Suregada procera Croizat	Euphorbiaceae	Tree	SF
Albizia gummifera (J.F. Gmel.) C.A.sm.	Fabaceae	Tree	SF

Appendix. Continued

Trichilia emetica Vahl	Meliaceae	Tree	SF
Bersama abyssinica Verdc.	Melianthacaea	Tree	SF
Xymalos monospora (Harv.) Baill.ex Warb.	Monimiaceae	Tree	SF
Ficus capensis Hiern	Moraceae	Tree	SF
Syzygium guineense F. White	Myrtaceae	Tree	SF
Olea capensis L.	Oleaceae	Tree	SF
Olea europea ssp africana (Mill.) P.S. Green	Oleaceae	Tree	SF
Coffea eugenioides S. Moore	Rubiaceae	Tree	SF
Heinsenia diervilleoides K. Schum.	Rubiaceae	Tree	SF
Fagaropsis angolensis (Engl.) Dale	Rutaceae	Tree	SF
Teclea nobilis Delile	Rutaceae	Tree	SF
Casearia battiscombei R.E. Fr.	Salicaceae	Tree	SF
Allophylus abyssinicus P. Beauv.	Sapindaceae	Tree	SF
Unknown tree species	Unknown	Tree	SF

Paper II

Relationships Between the Density of two Potential Restoration tree species and Plant Species Abundance and Richness in a Degraded Afromontane Forest of Kenya

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Running title: Restoring montane forests

Abstract: In recent years, there have been considerable efforts to restore degraded montane forests of East Africa by active restoration using indigenous tree species. However, little is known about how species used for restoration influence other species. In this study, two potential restoration species, *Albizia gummifera* and *Neoboutonia macrocalyx* that commonly occur in forests throughout East Africa are investigated with regard to the relationship between their density and the abundance and richness of other plant species. The study was conducted in a degraded forest consisting of disturbed transition zones and secondary forest. Our results show positive relationships between the density of *A. gummifera* and the abundance of tree seedling and sapling richness in the transition zones and in the secondary forest. Shrub richness was negatively related to the density of *A. gummifera*. Abundance and richness of tree saplings and shrubs were positively related to *N. macrocalyx* density in both the transition zones and in the secondary forest. Herb species richness declined with *N. macrocalyx* density in the transition zones but increased with *N. macrocalyx* density in the secondary forest. The positive relationships between the two tree species and seedlings and saplings of other woody species suggest that both *A. gummifera* and *N. macrocalyx* can be suitable for active restoration of degraded montane forests within their natural range.

Key words: *Albizia gummifera,* facilitation, forest restoration, *Neoboutonia macrocalyx*, pioneer species, species interactions.

Introduction

The restoration of degraded tropical natural forests is receiving increasing attention (Parrotta, Turnbull & Jones, 1997; Kebrom & Tesfaye 2000; Guariguata & Ostertag 2001; Duncan & Chapman 2003; Teketay 2005; Ermias, Manfred & Tsegaye, 2009). Because of a dramatic reduction of forest cover (FAO, 2009), drought due to climate changes (Millar, Stephenson & Stephens, 2007), the scarcity of forest products (FAO, 2009), and increased pressure on remnant natural forests, large areas of natural forests remain in a highly degraded state. It is increasingly recognized that traditional restoration methods, in particular monoculture plantations of exotic species, may be inappropriate because it does not contribute to restore biodiversity (Evans & Turnbull, 2004) and ecosystem functions (Wormald, 1992). Thus, the transformation of abandoned forest fallows into a regenerating forest rather than monoculture plantation of exotic species is a better way to achieve the ecological values from forest ecosystem, such as high biodiversity, watershed functions, and soil stabilization (Shono, Cadaweng & Durst, 2007).

The most obvious change after disturbances in natural forests is the rapid emergence of pioneer plant species (Brokaw, 1987; Nykvist, 1996; Guariguata & Ostertag, 2001; Slik & Eichhorn, 2003). On severely disturbed forests, fast-growing pioneer tree species may both facilitate and inhibit recruitment of forest species during later successional phases (Kigomo, 1987; Teketay, 2005; Piotto, 2008). The properties of pioneer tree species that establish rapidly after forest disturbances vary between geographical regions within the tropics (Kigomo, Savil & Woodell, 1990; Grubb & Metcalfe, 1996; Chapman *et al.,* 1999). However, a guild of large-leaved, fast-growing pioneer species with umbrella-like crowns appears to exist in all regions (Richards, 1996). During succession, these species establish a canopy, where beneath shade-tolerant species can establish and grow. On the other hand, interactions between early succession species and other species can also be negative.

Facilitation, whereby the presence of one plant species enhances the survival and establishment of other plant species is most often documented in stressful environments, such as arid, saline, or cold ecosystems (e.g. Smit, Gusberti & Muller-Schaer, 2006). In such environments, the presence of a stress-tolerant facilitator can ameliorate the environmental conditions in its immediate vicinity through provision of, for example, shade or soil nutrients. Through such positive interactions, facilitators can strongly influence plant community composition and richness (e.g. Bertness & Callaway, 1994; Smit & Olff, 1998, Brooker *et al*., 2008). However, other previous studies indicate that on severely degraded land, fast growing pioneer tree species can prevent, or slow down, the colonization of other species (e.g. Bertness & Callaway, 1994; Chapman & Chapman, 1999) because of competition for resources (e.g. light, nutrients), and thus reduce the speed of forest succession (Berkowitz, Canham & Kelly, 1995) and potentially also change the direction of succession (Shono, Cadaweng & Durst,. 2007). Thus, knowledge about how pioneer species affect the establishment, abundance and species richness of later successional species is highly relevant for successful active restoration. Indeed, several authors have warned against the use of species whose effects on other species are unknown (Wormald, 1992; Montagnini, Ugalde & Navarro, 2003; Carnevale & Montagnini, 2002).

In Kenya, large areas of natural forests have been heavily disturbed through selective logging and clearing since colonial times (1930s) to 1986, after which logging was banned (MENR, 1994 unpublished data). The degraded areas form mosaics that comprise a range of habitat types, such as pastures, old plantations, and abandoned fallows left to succession. In the Mau natural forest, the area of this study, degraded areas are going through a recovery process whereby competition and facilitation possibly occur simultaneously during succession towards secondary forest. Exotic species have been planted to restore such degraded forest systems in the tropics, including Kenya, but this has mainly contributed to the creation of monocultures that decrease ecosystem function and biodiversity (Evans & Turnbull, 2004). In Kenya, active restoration of degraded forest areas has been initiated by planting a mixture of indigenous pioneer and non-pioneer tree species (GOK, 2005; KEFRI, 2008 unpublished data). However, most of these species' ecological and silvicultural requirements are not known. Overall there is lack of information to guide the selection of restoration species for degraded forests. Importantly, this information should not only include the ecological requirements of restoration species, but also how they potentially affect other species during succession; the focus of this study.

In a previous paper, Mullah *et al.* (in press) studied the abundance, richness and composition of regenerating forests along a disturbance gradient from abandoned fallows and into the secondary forest. The indigenous tree species *Albizia gummifera* (Fabaceae) and *Neoboutonia macrocalyx* (Euphorbiaceae) occurred in all life stages in both regenerating forest and in the secondary forest. This suggests that the two species may be good candidates for active restoration because they have the ability to establish as seedlings and survive as saplings in sites with different degrees of degradation. However, their potential influences on other species; i.e. whether they facilitate or hamper the abundance and richness of other species is not known, even though one of them (*A. gummifera*) is already promoted as a multipurpose species that can be used in active restoration (Bertness & Callaway, 1994; Bristow *et al.*, 2007).

In this study, we examined the relationship between the density of these two pioneer tree species and the species abundance and richness of the rest of the plant community, to examine their suitability for active restoration. In particular we ask, (1) Is there a relationship between the density of *A. gummifera* and *N. macrocalyx* and the abundance and richness of seedlings and saplings of other tree species, shrubs, lianas and herbs in disturbed transition zones and in the secondary forest? (2) How do the two species relate to each other in disturbed transition zones and in the secondary forest? and (3) What is the relationship between the two species and the composition of other tree seedling and sapling species in the transition zones and in the secondary forest?

Material and methods

STUDY AREA

Mau forest, which is divided into seven blocks, is the largest remaining near-continuous montane indigenous forest in East Africa. It is composed of natural primary forests, post- extraction secondary forests, swamps, grasslands, fallows and regenerating forests. The study area is at 2,120 m altitude with an annual rainfall around 2,000 mm. Mean annual temperature range from 12–16 ºC and potential evapo-transpiration varies between 1,400 and 1,800 mm (Jackson & McCarter, 1994). The natural forest consists of Afromontane bamboo at the higher altitudes and secondary plant communities derived from logged rainforest at lower altitudes. The forest has a high biodiversity and hosts indigenous tree species, such as *Olea africana* (Oleaceae) and *Dombeya goetzenii* (Sterculiaceae), and several bamboo species (MENR, 1994 unpublished data; Kinyanjui, 2009). Within Itare forest block, 15 ha of previously cleared, cultivated, and then abandoned area (19 years ago) surrounded by secondary forest, was chosen for this study. The study site consisted of zones of different degrees of disturbance, with the most degraded zone dominated by early colonizing shrubs and a few tree seedlings, here termed transition one (TZI), and a less degraded zone consisting of shrubs and seedlings, saplings and adult trees, termed transition two (TZII). The transition zones were surrounded by a secondary forest consisting of secondary plant communities derived from artisanal (pitsawing) logged rainforest. For more details about the study area, see Mullah *et al*. (in press).

STUDY SPECIES

In a previous study, Mullah *et al*. (in press) found seven indigenous tree species, *Psychotria mahonii* (Rubiaceae), *Allophylus abyssinicus* (Sapindaceae), *Albizia gummifera* (Fabiaceae), *Neouboutonia macrocalyx* (Euphorbiaceae), *Polyscias fulva* (Araliaceae), *Dombeya torrida* (Sterculiaceae), and *Ekebergia capensis* (Meliaceae) to be abundant and present in all life stages in both the disturbed transition zones and in the secondary forest in the study area. All these tree species could be good candidates as restoration species because of their ability to establish as seedlings in heavily disturbed sites and to survive as saplings and adults under different conditions in the area. In this study we focus on *A. gummifera* and *N. macrocalyx* because they had abundances (160 and 89 individuals/ha respectively, in transition zones, and 524 and 354 individuals/ha respectively, in the secondary forest) that allowed sound statistical assessments of their relationship with other species. Both of these species are regarded as pioneers of moist (Beentje 1994) and secondary forest (Bussmann 1999; Chapman et al. 1999).

Albizia gummifera is a medium to large deciduous tree, 15–30 m tall, native to African montane moist forests, and classified as a forest edge species (Beenjte 1994). The regeneration status of the species is poorly known, but seeds are dispersed by wind, which significantly increases its colonization success (Noad & Barnie, 1990). *A.*

gummifera is di-nitrogen fixing and increases soil nitrogen content and thus enhances nitrogen transfer to associated non-fixing species during natural succession (Requena et al. 2001; Odee *et al.,* 2002). Di-nitrogen fixing species may be key components of the natural succession in semi-arid ecosystems (Kadiata, Mulongoy & Isirimah, 1996). Furthermore, a growing number of studies report successful utilization of *A. gummifera* as a facilitator in agroforestry systems. For instance, farmers have intercropped the species as a shade tree among tea bushes in Malawi (Palmer & Pitman, 1972), and *A. gummifera* is used to improve soil fertility (especially N and P) resulting in increased productivity of associated crop plants (Teklay & Malmer, 2004).

Neoboutonia macrocalyx is an open-crown, 10–20 m high, fast-growing pioneer tree of disturbed forests or clearings in Africa (Katende, Birnie & Tengnas, 1995). It is an indigenous species which coppices well. The seeds are dispersed by animals (Chapman *et al*., 1999). As far as we know, there have not been any previous studies on *N. macrocalyx* and its relationship with other plants in any forest ecosystem.

DATA COLLECTION

We collected data in November 2006 in the middle of the dry season, and in March 2007 at the beginning of the rainy season. We randomly selected 34 plots as follows: twenty plots in the disturbed transition zones (TZ, areas in different stages of recovery from degradation) and fourteen plots in the secondary forest (SF). We counted individuals of *A. gummifera*, *N. macrocalyx*, and all other woody species, and estimated percentage cover of herbaceous species in all the plots. We used plots of 5 × 30 m in TZI and 10 × 30 m in TZII and SF. Each plot was divided into 6 subplots (for the 5 × 30 m plots) and 12 subplots (for the 10 × 30 m plots) and each subplot had a 1

× 1 m quadrat in its centre. Adult trees and lianas (taller than 1.3 m and dbh greater than 10 cm) were counted in all subplots. Tree saplings (young trees taller than 1.3 m and dbh less than 10 cm) and shrubs were counted in every other subplot. Tree seedlings (less than 1.3 m height) and herbs were recorded in a central quadrat within each subplot. We used larger plots in TZII and SF in order to capture the variation in tree species richness, abundance and composition in these zones. To enable comparison between the different plot sizes, corrections were done before data analyses. For the species abundance data, we divided abundance within 10 × 30 m plots by two. For the species richness data, we calculated the mean number of species within each of the two 5 × 30 m plots and used the mean of these in the analyses. A taxonomist assisted by local para-taxonomist and Kenya Forest Service staff identified the plant species. All unidentified species were deposited at the National Herbarium of Kenya for identification and voucher species were kept there. Nomenclature follows Agnew and Agnew (1994) and Beetje (1994).

STATISTICAL ANALYSES

We used simple linear regressions to examine the relationship between *A. gummifera* and *N. macrocalyx* density and the abundance and richness of other plant species. In the analysis we used the sum of adults and saplings (for sound statistical analyses) to represent the density of *A. gummifera* and *N. macrocalyx* as independent variables. To control for the difference in plots sizes used in our study, we computed 'true' richness by Mao Tao estimator using the software EstimatesS version 8.2.0 (Colwell, 2009) and used R 2.10.0 software (R-Development Core Team, 2009) to produce the species accumulation curves for each life form and zone. Mean abundance and 'true' species richness of seedlings and saplings of other tree species, shrubs, lianas and percentage cover of herbs were used as dependent variables in separate regression analyses. We also performed a correlation analysis to examine the extent to which the two species are associated. We conducted separate analyses for plots in the transition zones (transition zones I and II combined for sound statistical analyses) and in the secondary forest. The abundance and richness values were log-transformed prior to the analyses. SYSTAT 10 for windows was used for the regression analyses.

We used multivariate ordination analyses to examine how species composition of other trees was associated with the density of the two potential restoration tree species in the transition zones and in the secondary forest. The abundances of *A. gummifera* and *N. macrocalyx* were used as environmental variables in a canonical correspondence analysis (CCA), and their relationship with the species composition was tested by using 999 permutations. We did separate analyses for the transition zones and for the secondary forest, and for tree seedling and sapling species composition. We tested for the significance of all canonical axes together, with 999 unrestricted permutations in a Monte Carlo test. All the ordinations were done using default settings in CANOCO 4.5 and graphs produced in CanoDraw (ter Braak & Smilauer, 2002).

Results

RELATIONSHIPS BETWEEN OTHER SPECIES AND THE DENSITY OF *A. GUMMIFERA* AND *N. MACROCALYX*

Simple regressions showed that there was a positive relationship between species richness of seedlings and saplings of other tree species and the density of *A. gummifera* in the transition zones (Table I). Species richness and abundance of lianas were also positively related with *A. gummifera* density, whereas the abundance of seedlings and saplings of other tree species, shrubs, and herbs were not related to *A. gummifera* density in the transition zones (Table 1). In the secondary forest, tree sapling species richness and abundance were positively related with *A. gummifera* density (Table I), whereas shrub richness was negatively related to *A. gummifera* density (Table I). There were no significant relationships between species richness and abundance of tree seedlings, lianas, and shrub abundance, or herb cover with *A. gummifera* density in the secondary forest (Table I).

In the transition zones, there was a positive relationship between the abundance of tree saplings and *N. macrocalyx* density (Table I), whereas herb species richness was negatively related to *N. macrocalyx* (Table I). Mean species abundance and richness of tree seedlings, species richness of saplings, shrubs, and lianas were not related to *N. macrocalyx* density in the transition zones (Table I). In the secondary forest, the species abundance and richness of tree saplings and species richness of shrubs were positively related with *N. macrocalyx* density (Table I). In contrast, species richness of herb was negatively related with *N. macrocalyx* density in the secondary forest. Mean species abundance and richness of tree seedlings and lianas, and the abundance of shrubs and herb cover were not related with *N. macrocalyx* density in the secondary forest (Table I).

RELATIONSHIP BETWEEN *A. GUMMIFERA* AND *N. MACROCALYX*

There was a positive correlation between the abundance of *N. macrocalyx* seedlings and *A. gummifera* adults, whereas *N. macrocalyx* seedlings, saplings and adults were positively correlated with *A. gummifera* seedlings in the transition zones (Table II). There was no siginificant correlation between *N. macrocalyx* seedlings, saplings and adults and *A. gummifera* saplings in the transition zone (Table II). Mean abundance of *N. macrocalyx* saplings was negatively correlated with *A. gummifera* saplings density in the secondary forest (Table II).

RELATIONSHIP BETWEEN SPECIES COMPOSITION *AND THE ABUNDANCE OF A. GUMMIFERA* AND *N. MACROCALYX*

The CCA model was significant for tree saplings (F = 2.45, $p < 0.01$), but not for seedlings (F = 1.19, $p = 0.292$) in the transition zones (Figures 1a & 1b), and for seedlings (F = 3.50, $p < 0.01$) and saplings (F = 7.85, $p < 0.001$) in the secondary forest (Figures 1c & 1 d). In the transition zones, saplings of shade-intolerant pioneer species, for instance, *Hagenia abyssinica* (Rosaceae), *A. abyssinicus*, *Macaranga kilimandscharica* (Euphorbiaceae), and *Dovyalis macrocalyx* (Silicaceae) were positively associated with *A. gummifera,* whereas saplings of some forest interior (shade-tolerant) species like *Tabernaemontana stapfiana* (Apocynaceae) and *Polyscias fulva* (Araliaceae) were more related to *N. macrocalyx* (Figure 1b). In the secondary forest, seedlings and saplings of *Garcinia buchananii* (Clusiaceae), *Syzygium guineense* (Myrtaceae), *Casearia battiscombei* (Salicaceae), and *T. stapfiana*, most of which are forest interior species, were associated with *A. gummifera* (Figures. 1c & d). Seedlings of *Prunus africana* (Rosaceae), *P. fulva*, *Celtis gomphophylla* (Cannabaceae) *and A. abyssinicus,* which are shade-intolerant species, and saplings of *P. africana*, *D. torrida*, *Zanthoxylum gillettii* (Rutaceae), *Croton macrostachyus* (Euphorbiaceae), *P. fulva* and *Ehretia cymosa* (Boraginaceae) were associated with *N. macrocalyx* (Figures 1c & d). *Polyscias fulva* was associated with *N. macrocalyx* both in the transition zones and in the secondary forest, both as seedlings and saplings (Figures 1a - d).

Discussion

Our results on the potential role of *A. gummifera* and *N. macrocalyx* on the abundance of species and species richness, suggest that these two species may primarily aid the establishment and abundance of other species, and that they promote species richness during forest recovery. Tree seedlings and saplings in both the transition zones and in the secondary forest were positively related to *A. gummifera* density. Previous studies have found a strong influence of *A. gummifera* with associated plants due to its ability to fix nitrogen in different habitats and agricultural systems. For instance, strong influence of *A. gummifera* on associated plants in different agroforestry systems have been reported by Franco and DeFeria (1997) and Gathumbi *et al*. (2002) who found that *A. gummifera* may aid forest regeneration through its positive effect on soil nitrogen. Various species of *Eucalyptus* also grow better when mixed with woody legumes, such as *Albizia* and *Acacia* (Binkley et al. 1992; DeBell, Cole & Whitesell, 1997; Khanna, 1997; Bristow *et al*., 2007).

Furthermore, the symbiosis between *A. gummifera* and rhizobia has been shown to aid restoration of desertified ecosystems by providing 28–72% of the soil nitrogen through fixing of atmospheric nitrogen (Kadiata, Mulongoy & Isirimah, 1996). However, still considerably less is known about nitrogen fixation in tropical forest (Barron, Purve & Hedin, 2010). Furthermore results from lowland tropical forest, shows that leguminous trees are only able to fix nitrogen in areas with history of disturbance and in the forest gaps (Sylvavester-bradley *et al.*, 1980; Saur *et al.*, 1998; Koponen *et al.*, 2003), conditions similar to our study site. This suggests that it is possible that *A. gummifera* is able to fix nitrogen in the transition zones in our site. This offers strong support for the idea that nitrogen-fixing legumes like *A. gummifera* have the ability to assist other plants in a naturally regenerating degraded abandoned fallow in the tropics. Thus, our results, and those of others, strongly suggest that *A. gummifera* can be used successfully in active restoration. *Neoboutonia macrocalyx* had a positive relationship with tree saplings abundance in both the transition zones and in the secondary forest, suggesting that also this species may be used successfully in active restoration. *Neoboutonia macrocalyx* is not known to be nitrogen-fixing, and it is likely that it promotes the establishment of others by provision of shade. Overall, both species were related with less light-tolerant tree species in both zones, which agrees with Richards (1996), who reported that pioneer species provide a canopy beneath which shade-tolerant species establish. The two species *Polyscias fulva* and *Allophyllus abyssinicus* were associated with *A. gummifera* as saplings in the transition zone and with *N. macrocalyx Neoboutonia* as both seedlings and saplings in the secondary forest, suggesting that *N. macrocalyx* and *A. gummifera* assisted both the establishment and survival of these species.

Albizia gummifera and *Neoboutonia macrocalyx* differed in their relationships with the other plants in both the transition zones and in the secondary forest. In the transition zones, *A. gummifera* was positively related with a higher number of growth forms, such as tree seedlings, saplings and lianas, than *N. macrocalyx*, suggesting that during changing succession conditions, *A. gummifera* might be a better facilitator than *N. macrocalyx*. The reason could be that *A. gummifera*, through its positive effect on soil nitrogen, aids the establishment of other plants, as have been suggested in other studies (Kadiata, Mulongoy & Isirimah, 1996; Teklay & Malmer, 2004; Bristow *et al.*, 2007). Positive relationship between the density of *A. gummifera* and *N. macrocalyx* in the transition zones suggest that they may have complementary effects on each other and could be used together in restoration in the same 'systems' (i.e. planted in the same plot or block) including sites of varying degree of degradation. However, in the secondary forest, due to limited space in the gaps where they occur, the two species seem to compete.

Our non-experimental results suggest that *A. gummifera* and *N. macrocalyx* both assist and compete with other plant species. However, these patterns could also emerge through plant responses to other variables (e.g. grazing, wildings collection, soil nutrient availability, moisture) that affect both *A. gummifera* and *N. macrocalyx* density and the abundance of other species and the species richness. Simple correlative studies like ours often are the only way of practically assessing the suitability of species as restoration tools. It is beyond the scope of our study to draw additional conclusions about these other abiotic or ecological factors on the observed relationships. The emergency of these correlative relationships which support facilitation offers unique opportunity for further experimental studies to truly assess how these and other pioneer tree species interact with other plant species across ecosystems and disturbance types in the forest.

We argue that planting native pioneer tree species may complement and accelerate natural regeneration and support recovery of composition and biodiversity of degraded forests. Our results showed that *A. gummifera* and *N. macrocalyx* potentially have positive influence on tree recruitment, and suggest that both species have high potential as restoration species. These results contribute significantly to current knowledge on potential restoration species, information which is generally lacking in the tropics.

Acknowledgements

We are very grateful for information provided by farmers, data collection by Boaz Ngonga, William Bii and the late Florence Muindi, comments by David Odee and logistical assistance provided by Kenya Forestry Research Institute Londiani and Kenya Forest Service Itare stations. We thank the European Union for financial assistance through the project 'Bridging restoration and multi-functionality in degraded forest landscape of Eastern Africa and Indian Ocean Islands' (FOREAIM) and the Royal Norwegian Government for scholarship for the corresponding author.

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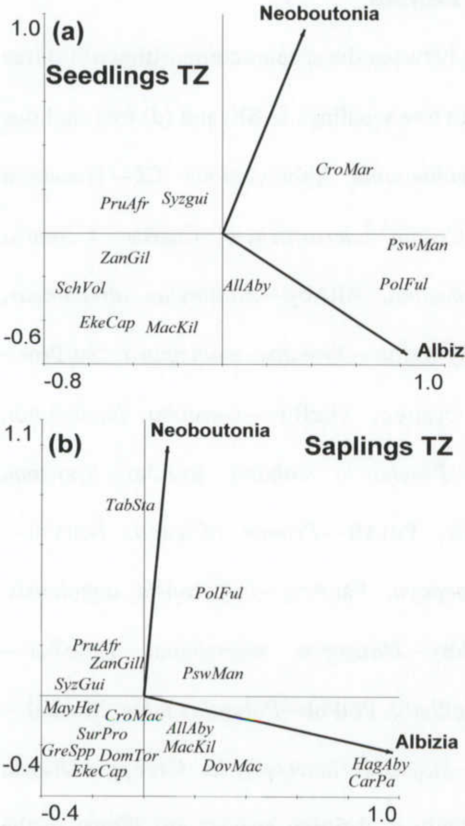
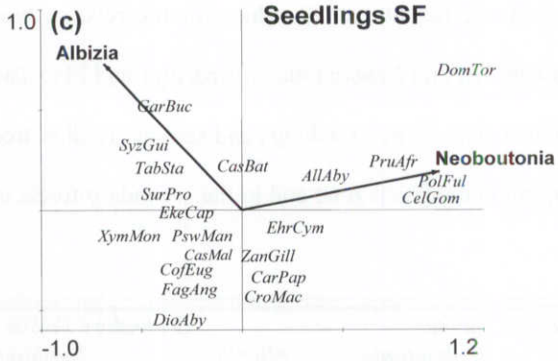
Figure Legends

FIGURE 1. CCA plots of the relationships between the species composition of (a) tree seedlings in TZ, (b) tree saplings in TZ, (c) tree seedlings in SF, and (d) tree saplings in SF, and the density of *Albizia* and *Neoboutonia*. Abbreviations: TZ—Transition zone, SF—Secondary forest, CroMac—*Croton macrostachyus,* CasBat—*Casearia battiscombei*, CasMal—*Cassipourea malosana*, AllAby—*Allophylus abyssinicus*, TabSta—*Tabernaemontana stapfiana*, XymMon—*Xymalos monospora*, SurPro—*Suregada procera*, EhrCym—*Ehretia cymosa*, GarBuc—*Garcinia buchananii*, CofEug—*Coffea eugenioides*, PsyMah—*Psychotria mahonii*, SyzGui—*Syzygium guineense*, EkeCap—*Ekebergia capensis*, PruAfr—*Prunus africana*, SchVol—*Schefflera volkensii*, CarPap—*Carica papaya*, FagAng—*Fagaropsis angolensis*, CelGom—*Celtis gomphophylla*, DioAby—*Diospyros abyssinica*, DomTor—*Dombeya torrida*, ZanGil—*Zanthoxylum gillettii*, PolFul—*Polyscias fulva*, MacKil—*Macaranga kilimandscharica*, MayHet—*Maytenus heterophylla*, GreSpp—*Grewia* species, HagAby—*Hagenia abyssinica*. Only well-fitting species are shown in the figure.


1.0
(a)
Seedlings TZ
Neoboutonia
CroMar
PruAfr
Syzgui
ZanGil
PswMan
SchVol
AllAby
PolFul
EkeCap
MacKil
-0.6
Albizia
-0.8
1.0
1.1
(b)
Neoboutonia
Saplings TZ
TabSta
PolFul
PruAfr
ZanGill
PswMan
SyzGui
MayHet
CroMac
AllAby
SurPro
MacKil
GreSpp
DomTor
Albizia
-0.4
EkeCap
DovMac
HagAby
CarPa
-0.4
1.0


(c)
Seedlings SF
1.0
-1.0
1.2
Albizia
Neoboutonia
DomTor
GarBuc
SyzGui
TabSta
CasBat
AllAby
PruAfr
PolFul
CelGom
SurPro
EkeCap
EhrCym
XymMon
PswMan
CasMal
ZanGill
CofEug
CarPap
FagAng
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DioAby

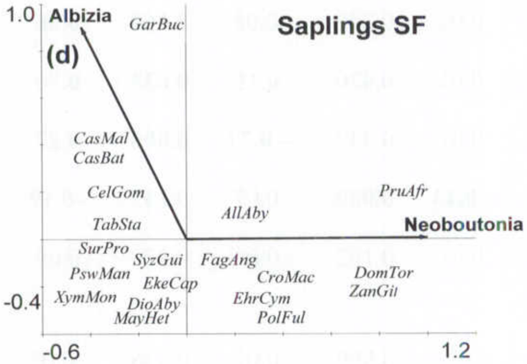
(d)
Saplings SF
1.0
-0.4
-0.6
1.2
Albizia
Neoboutonia
GarBuc
CasMal
CasBat
CelGom
PruAfr
TabSta
AllAby
SurPro
SyzGui
FagAng
PswMan
EkeCap
CroMac
DomTor
XymMon
DioAby
EhrCym
ZanGil
MayHet
PolFul

TABLE I. Simple linear regression coefficients and P-values for the relationships between the density of *Albizia gummifera* and *Neoboutonia macrocalyx* and Mao Tao estimated species richness and abundances of tree seedlings and sapling of other tree species, shrubs, herbs and lianas, in the transition zone and in the secondary forest in Mau forest, Kenya.

	Transition zone				*Secondary Forest*			
	Albizia		*Neoboutonia*		*Albizia*		*Neoboutonia*	
	Est.	*p*	*Est.*	*p*	*Est.*	*p*	*Est.*	*p*
Richness								
Seedling	**0.11**	**0.034**	0.02	0.249	0.08	0.160	0.06	0.361
Sapling	**0.17**	**0.008**	0.01	0.430	**0.16**	**0.033**	**0.30**	**0.002**
Shrub	0.03	0.073	0.01	0.332	**– 0.27**	**0.005**	**0.27**	**0.001**
Herb	0.08	0.122	**– 0.13**	**0.039**	0.07	0.133	**–0.19**	**0.022**
Liana	**0.13**	**0.014**	0.01	0.102	0.02	0.370	0.09	0.100
Abundance								
Seedling	0.03	0.082	5.07	0.069	0.01	0.456	0.03	0.069
Sapling	0.01	0.547	**0.37**	**0.043**	**0.23**	**0.009**	**0.14**	**0.004**
Shrub	0.05	0.264	8.19	0.150	0.01	0.264	0.02	0.083
Herb	0.28	0.050	3.86	0.127	0.02	0.087	0.01	0.852
Liana	**0.61**	**0.023**	9.11	0.859	0.02	0.533	0.02	0.074

Estimated coefficients (Est.) and significant values ($p < 0.05$) are in bold.

TABLE II. Results for correlation analysis between different growth forms of *Albizia gummifera* and *Neoboutonia macrocalyx* in the transition zones and in the secondary forest at Mau forest, Kenya.

	Albizia adults		*Albizia saplings*		*Albizia seedlings*	
	r	*p*	*r*	*p*	*r*	*p*
Transition zones						
Neoboutonia adult	**0.327**	**0.040**	–0.090	0.582	**0.471**	**0.002**
Neoboutonia saplings	0.238	0.139	–0.137	0.398	**0.374**	**0.017**
Neoboutonia seedlings	**0.309**	**0.052**	–0.055	0.738	**0.435**	**0.005**
Secondary forest						
Neoboutonia adult	–0.327	0.090	–0.103	0.603	–0.159	0.420
Neoboutonia saplings	–0.036	0.855	**–0.493**	**0.008**	–0.306	0.114
Neoboutonia seedlings	–0.168	0.392	–0.322	0.095	–0.077	0.698

Pearson's correlation coefficient *and P-values are shown for each predictor; significant values ($p < 0.05$) are in bold.*

Paper III

Invasion by *Fraxinus pennsylvanica* trees after agricultural abandonment in a tropical forest is related to diversity and tree density

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ABSTRACT

Whether exotic plant invasion may be aided by certain community properties is poorly understood for species-rich ecosystems such as tropical montane forests. In Kenya, *Fraxinus pennsylvanica* Marsh., an exotic tree species, has invaded degraded montane forests. We address the following questions: (1) Is invasion of *Fraxinus* related to community richness, diversity, evenness, or the abundance of saplings and adults of other tree species, shrubs, lianas, and herbs? (2) Do the relationships between *Fraxinus* invasion and community properties differ between abandoned fallows and the secondary forest? (3) Is invasion of *Fraxinus* related to propagule pressure (distance from the source)? We used generalized linear mixed models to examine the relative importance of the community properties to *Fraxinus* invasion in abandoned fallows and in the secondary forest. *Fraxinus* invasion was positively related to community diversity and the abundance of tree saplings, shrubs, ferns and herbs in the abandoned fallows. In contrast, *Fraxinus* invasion was negatively related to community diversity, and abundance of tree saplings, shrubs, lianas and ferns in the secondary forest. The number of *Fraxinus* recruits declined with declining propagule pressure in the fallows, but not in the secondary forest. Thus, our results show that site characteristics influence the relationship between community properties and the success of alien species invasion.

Key Words: Abandoned fallows; degraded forest; exotic tree invasions; East Africa; regeneration

THE NEGATIVE EFFECTS OF ALIEN SPECIES ON species diversity and functions of ecosystems are recognized (Chapin et al 2000, Loreau 2000) and have been the focus of many studies at many spatial scales on plants over the past decade (Elton 1958, Stohlgren *et al.* 1997, Lonsdale 1999, Levine & D'Antonio 1999, Hector *et al.* 2001). Of particular interest is the hypothesis that greater species richness increase resistance to species invasions, i.e. decrease invasibility (Elton 1958, Hooper *et al.* 2005). This hypothesis has been evaluated by a considerable number of observational, experimental, and theoretical studies, but with inconsistent results (see Levine & D'Antonio 1999; Hector *et al.* 2001, Shea & Chesson 2002, Hejda *et al.* 2009). The theory is based on the presumptive 'niche filling' properties of high native richness, whereby communities of greater species diversity exploit more completely the available resources and leave fewer open niches for colonization (Levine & D'antonio 1999). Observational and experimental studies both acknowledge that vulnerability to invasion depends not only on species richness but also on many other components, such as composition and species interactions (Hejda *et al.* 2009, Shea & Chesson 2002). Moreover, high indigenous species richness and evenness may also facilitate species invasion by means of habitat amelioration or protection from pests or predators (Bruno *et al.* 2003, Dunstan & Johnson 2006).

Human activities have resulted in degraded forests on local and global scales, leading to dramatic changes in tree species composition and richness, either due to loss of native species or to introduction of alien species (Richardson 1998, Ortega & Pearson 2005, Ditham *et al.* 2007). The major consequences of such changes in species richness and dominance include alteration of forest ecosystems properties and the environmental goods and services they provide (Davis *et al.* 2000, Webster *et al.* 2006). Alien plant species often establish successfully in communities that have been altered by human disturbances (Hobbs and Huenneke 1992), generally preferring mesic, disturbed habitats with high availability of resources, such as light and nutrients (Milbau & Nijs 2004). Numerous studies have concluded that light demand is among the most important species traits that best explain invasion of disturbed forests (Lodge 1993, Totland *et al*. 2005, Martin *et al*. 2007). However, recent studies have reported that also shade-tolerant alien species can invade both disturbed and undisturbed forest in both temperate and tropical ecosystems (Martin & Marks 2006, Martin *et al*. 2009).

Invasion of alien species and the invasibility of tropical ecosystems in general, and in Africa in particular, is under-studied (Nunez & Pauchard 2010). One effective way to understand the processes that determine the success of invasive plants is to study survivorship during the initial stages of establishment (i.e. seedlings and saplings) (Green *et al*. 2004). In Mau forest, the area of this study, *Fraxinus pennsylvanica* Marsh. (hereafter referred to as *Fraxinus*) was planted in the 1950s as a fire break around commercial forest plantations. Its seedlings and saplings are now growing in several habitats outside the areas of the original planting (Maundu & Tengnås 2005). Mau forest consists of a matrix of secondary forest and abandoned fallows, which makes it ideal to assess the role of disturbances on the invasion of an exotic species, and how the relationship between the establishment of *Fraxinus* and different community properties, such as resident species richness, diversity, evenness, and the abundance of different functional groups, may vary between areas of different disturbance regime.

In this study we aim to understand how community properties may influence *Fraxinus* colonization of abandoned fallows and secondary forests in the Mau Forest in Kenya. To our knowledge, this is the first study on *Fraxinus* invasion and assessment of patterns of plant invasion across different habitats in Kenya. Our main questions are: (1) Is invasion of *Fraxinus* related to community richness, diversity, evenness, the abundance of saplings and adults of other tree species, shrubs, lianas, and herbs, (2) Do the relationships between community properties and *Fraxinus* invasion differ between abandoned fallows and the secondary forest, (3) Is invasion of *Fraxinus* related to propagule pressure, measured as distance from the seed source?

METHODS

STUDY SPECIES AND SITE —Fraxinus pennsylvanica is a shade-tolerant tree species native to North America, which was introduced to Europe and South America in the early nineteenth century and subsequently planted for various purposes (Hegi 1908 as quoted by Kremer *et al.* 2006, Ghersa *et al.* 2002, Lesica 2009). Several life history traits, such as massive seed production of relatively small, wind-dispersed seeds, vegetative reproduction, fire-resistance, and fast growth, make it successful in fast invasion of new habitats (Lesica 2009, Groninger *et al.* 2004). Since at least the early 1960s, it has largely spread throughout the Great Plains in the United States, Canada, and Europe (Kremer *et al.* 2006, Lesica 2009).

The study was conducted in a degraded tropical montane forest in the Western Mau Forest (0°30'S. 35°27'E). The study area is at 2120 m altitude with an annual rainfall around 1500 mm. The mean annual temperature range from 12-16 °C and the potential evapo-transpiration is between 1400 and 1800 mm (Jackson & McCarter 1994). The 22 748 ha forest ranges from secondary forest in the interior to degraded areas bordering human settlements. A 10.6 ha of previously cleared, cultivated, and then abandoned area surrounded by secondary forest, and a planted belt of *Fraxinus* was chosen for this study. The abandoned fallows had *Cupressus lusitanica* plantation that was clear-felled in 1982, after which the area was cultivated under the shamba system (farmers tending tree seedlings on state-owned forest land in return for being permitted to intercrop annual food crops until canopy closure). The farmers removed logs, and stumps, and hoed soil by hand. The Shamba cultivation was banned in 2002 and the land abandoned except for periodic grazing by cattle, donkeys and goats thereafter. Five years after abandonment, the site consisted of zones of different degrees of degradation due to different intensities of disturbance before abandonment, and continued grazing, logging, charcoal burning, and firewood collection activities thereafter. The abandoned fallows comprised zones of initial state of recovery with colonizing herbs, shrubs, and a few tree seedlings and more advanced recovery stages with shrubs, tree seedlings, saplings and adult trees. The abandoned fallows are surrounded by a secondary forest and a fire belt of *Fraxinus* plantation. The secondary forest consists of Afromontane bamboo forest at the higher altitudes and secondary plant communities derived from logged rainforest at lower altitudes. The forest has a high biodiversity and hosts indigenous tree species, such as *Olea africana* and *Dombeya torrida* (Kinyanjui 2009).

DATA COLLECTION.—We collected data in October 2006 (dry season) and in April 2007 (rainy season). We randomly positioned 20 plots in the abandoned fallows and 14 in the surrounding secondary forest. The plots in the secondary forest were positioned at least 200 m away from the edge of the closest plot in the abandoned fallows. We used plots of 5 × 30 m in the most degraded fallows lacking adult trees, and 10 × 30 m in the less degraded fallows and in the secondary forest. We used larger plots in the latter in order to capture the variation in adult tree species richness and abundance. Each plot was divided into 6 sub-plots (for the 5 × 30 m plots) and 12 sub-plots (for the 10 × 30 m plots) and each sub-plot had a 1 × 1 m quadrat in its centre. Adult trees and lianas (taller than 1.3 m and dbh greater than 10 cm) were counted in all the sub-plots. Tree saplings (young trees of dbh less than 10 cm and height more than 1.3 m) and shrubs were counted in every other sub-plot. Tree seedlings (less than 1.3 m height), ferns and herbs were recorded in every 1 x 1 m quadrat within each sub-plot. *Fraxinus* seedlings and saplings data were collected following the same procedure. To enable comparison between different plot sizes, correction was done for the double plot sizes before data analysis by dividing abundance within the 10 × 30 m plots by two. For the species richness data, we calculated the mean number of species within each of the two 5 × 30 m plots and used the mean of these in the analyses. For each plot in the abandoned fallows and in the secondary forest we estimated the distance to the seed source as proxy for the propagule pressure. A taxonomist, assisted by a local para-taxonomist and Kenya Forest Service staff identified the plant species in the field. All unidentified species were deposited at the National Herbarium of Kenya for identification, and voucher species were kept there.

STATISTICAL ANALYSIS.—We used Generalized Linear Mixed Models (GLMM) with a loglink function and Poisson distribution family to examine the relative importance of factors that potentially could promote or inhibit the establishment and invasion of *Fraxinus*. *Fraxinus* invasion was explained by zone (abandoned fallow vs. secondary forest) and season (wet vs. dry) as categorical variables, and community richness, diversity, evenness, and the abundance of saplings and adults of other tree species, shrubs, lianas, ferns, and herbs, and distance to the source (propagule pressure) as continuous variables, and their interactions. The models are based on contrast matrices with abandoned fallows and dry season as reference categorical variables. *Fraxinus* seedling and sapling density were used as dependent variables in two separate analyses. The plots were used as a random term and nested in zone and season. The models were built using backward deletion of non-significant explanatory variables starting with the full model (F-test, P = 0.05). R 2.10.0 (R-Development Core Team 2009) was used in all the analyses. We calculated Shannon diversity (*H*') and evenness (Pielou 1975) indices per plot.

RESULTS

FRAXINUS PENNSYLVANICA ABUNDANCE AND COMMUNITY PROPERTIES.—The number of *Fraxinus* seedlings, saplings and adults were higher in the secondary forest than in the abandoned fallows (Fig. 1). The sapling stage was the most abundant in both habitats, especially in the secondary forest where saplings were two times more abundant than either seedlings or adults.

Generalized Linear Mixed Models (GLMM) results showed that there was a positive relationship between the density of *Fraxinus* seedlings and community evenness in the abandoned fallows (Fig. 2a) and a reverse relationship in the secondary forest (Fig. 2b). In contrast, *Fraxinus* sapling density was negatively related with evenness in abandoned fallows and positively in the secondary forest (Table 2). There was a positive relationship between *Fraxinus* sapling density and community diversity (Figure 2c) in the abandoned fallows, with a significant interaction showing that *Fraxinus* saplings decreased with diversity in the secondary forest (Table 2, Figure 2d). *Fraxinus* sapling density was also positively related with the abundance of saplings of other tree species and herbs in the abandoned fallows, but with significant interactions showing that *Fraxinus* saplings decreased with abundance of saplings of other tree species and lianas in the secondary forest (Table 2). *Fraxinus* sapling density was negatively related with the abundance of adults of other tree species, ferns, and propagule pressure (distance to the source) in the abandoned fallows (Table 2). However, significant interactions showed that *Fraxinus* sapling density related positively with abundance of adults of other tree species in the secondary forest (Table 2). *Fraxinus* seedling density was positively related to the abundance of shrubs, ferns, and herbs, but negatively related to abundance of lianas and adults of other trees in the abandoned fallows (Table 1). In contrast, significant interactions show that *Fraxinus* seedlings density decreased with abundance of shrubs and ferns in the secondary forest, but increased with abundance of lianas and adults of other tree species (Table 1). There was no significant relationship between *Fraxinus* seedling density and the abundance of saplings and community richness, diversity, season, or propagule pressure (distance to the source) in the abandoned fallows or in the secondary forest (Table 1).

DISCUSSION

Our results show that there was a positive relationship between native plant community diversity or evenness and *Fraxinus* invasion in the abandoned fallows, but a negative relationship in the secondary forest. The abandoned fallows are more open, drought stressed and under more intensive grazing pressure than the secondary forest. These environmental conditions may all have been ameliorated by a higher number of species that provide shade and protection from grazing, which agrees with theories of facilitation in stressful environments (Levine & D'antonio 1999, Hector *et al*. 2001, Bruno *et al*. 2003, Dunstan & Johnson 2006). Conversely, other studies have found higher native plant diversity to favor invasion due to habitat amelioration, for instance through nitrogen-fixation or disturbances (Levine & D'antonio 1999, Bruno et al. 2003, Dunstan & Johnson 2006). In the secondary forest on the other hand, the negative relationship between community diversity and *Fraxinus* density can be due to more intensive competition for light and space, limited propagule dispersal and less grazing pressure. This agrees with theory and previous studies suggesting that habitats with high species diversity have low invasibility (Pysek & Pysek 1995, Hooper *et al*. 2005, Mattingly *et al.* 2007, Martin *et al*. 2009) because communities are more resistant to invasion when local niches are filled by representatives from different functional groups (Zavaleta & Hulvey 2007). Moreover, a decrease in invasibility with increasing native plant diversity may also occur due to a greater probability of including species with traits similar to the invader, by more species utilizing a greater proportion of potentially available niches (Elton 1958, Gilbert & Lechowicz 2005), or a greater probability of including a strong competitive species (Fridley *et al.* 2007).

Previous studies on characteristics that could make a particular habitat more prone to invasion (Rejmanek & Richardson 1996, Gracia-Robledo & Murcia 2005) and the patterns and processes of the invasion by individual species to a specific habitat (Brown & Peet 2003, Milbau & Nijs 2004, Moira & Glenda 2005, Dunstan & Johnson 2006, Fridley *et al.* 2007) show that relationships between native diversity and species invasion can change due to differences in site characteristics. This fully agrees with our observations of community properties that are negatively related with *Fraxinus* invasion in the abandoned fallows and positively in the secondary forest and vice–versa.

The positive relationship between adults of other tree species and *Fraxinus* invasion in the secondary forest may occur through moderation of microclimate stress or suppression of competing herbs and shrubs (Pugnaire *et al.* 2004). This suggests that adult of other tree species in the secondary forest most likely contributed to rapid infilling of the gaps, suggesting a positive feedback with greater abundance of adult individuals increasing the likelihood of subsequent recruitment.

Anthropogenic disturbances which lead to gap creation in the forest are considered necessary for exotic invasion. Friday *et al.* (2008) reported a significantly greater recruitment of *Fraxinus uhdei* in gaps than at the edge of gaps or under intact *Acacia kao-Metrosideros polymorpha* forest canopy in Hawaii. Generally, species richness and abundance of invasive plants have been reported to increase with the fraction of tree basal area harvested or the size of canopy gaps (Totland *et al.* 2005, Belote *et al.* 2008). In our study site, gap creation in the secondary forest may favor not only *Fraxinus* but also lianas, herbs and shrubs proliferation as a result of increased light intensity. Thus, the negative relationship we observed between liana, fern and shrub density and *Fraxinus* invasion in the secondary forest may be due to competition for light and nutrients. This suggests that forest understory may be less invaded when it has high abundances of lianas, ferns, herbs and shrubs, as supported by Gilbert and Lechowicz (2005) and Friday *et al*. (2008). Our study shows community diversity, evenness and abundance of other species were related with *Fraxinus* abundance in the two habitats. However, as this is an observation study, we cannot conclude that these are causal relationships, as other variables may covariate with *Fraxinus* abundance in this system.

Our results show that the number of *Fraxinus* recruits in the abandoned fallows declined significantly with increasing distance to the seed source, thus, the evidence that propagule pressure was significant determinant of *Fraxinus* invasion. These results are entirely consistent with previous studies by Edward *et al.* (2008) who found propagule pressure to be the main driver of alien species invasion in Usambara Mountain forest in Tanzania. Similarly, Dawson *et al.* (2008) reported that propagule pressure, as measured by the number of plantations in Amani Botanic garden, was a significant correlate of invasion success in 26 introduced woody species in Amani Nature Reserve. Looking at real differences in invasibility requires assessing disturbance, invasion potential and propagule pressure (Lonsdale 1999, Chytry *et al*. 2008). Increasingly, propagule pressure is being identified as one of key drivers of invasion (Lockwood *et al.* 2005, Colautti *et al*. 2006) and without accounting for propagule pressure it is hardly possible to compare invasibility of different habitats (Lonsdale, 1999, Chytry *et al*., 2008, Edward *et al*., 2008). In the secondary forest, there was no relationship between *Fraxinus* recruitment and distance from the plantation, suggesting that *Fraxinus* invasion in the forest is better explained by the availability of suitable micro-habitats (gaps). Currently, the *Fraxinus* plantation is regarded as the main source of propagules, but according to our results, adult *Fraxinus* trees inside the secondary forest may become a new source of propagules in the near future. From a conservation perspective, we may be at a turning point, because when the *Fraxinus* adult population ('daughter stands') reaches reproductive age, new invasion foci will occur within the secondary forest.

Overall, our results show that *Fraxinus* is capable of invading both abandoned fallows and secondary forest. However, community diversity and evenness of each of these habitats appear to determine the invasion success by increasing invasibility of the abandoned fallows but decreasing invasibility of the secondary forest. These results from a tropical degraded forest area support previous theoretical and empirical studies from other systems that have emphasized the importance of specific habitat characteristics in determining the success of invasion by alien plant species.

ACKNOWLEDGMENTS

This study was supported by the European Union through the project 'Bridging restoration and multi-functionality in degraded forest landscape of Eastern Africa and Indian Ocean Islands' (FOREAIM). The first author is grateful to the Norwegian State Educational Loan Fund (Lånekassen) for providing financial assistance. We would like to thank farmers for information, Boaz Ngonga, William Bii and the late Florence Muindi, for their help in data collection, Solve Sæbø for assisting with GLMM analysis, Kenya Forestry Research Institute, Londiani, and Kenya Forest Service Itare stations for logistical support.

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FIGURE LEGENDS

FIGURE 1. Mean number of *Fraxinus pennsylvanica* seedlings, saplings and adults recorded in abandoned fallows and in the secondary forest at Kedowa in Mau forest, Kenya. The bars show mean ± SE.

FIGURE 2. Relationship between *Fraxinus pennsylvanica* seedling and sapling density and evenness (a, b) and community diversity (c, d) in the abandoned fallows and in the secondary forest at Kedowa in Mau forest, Kenya.

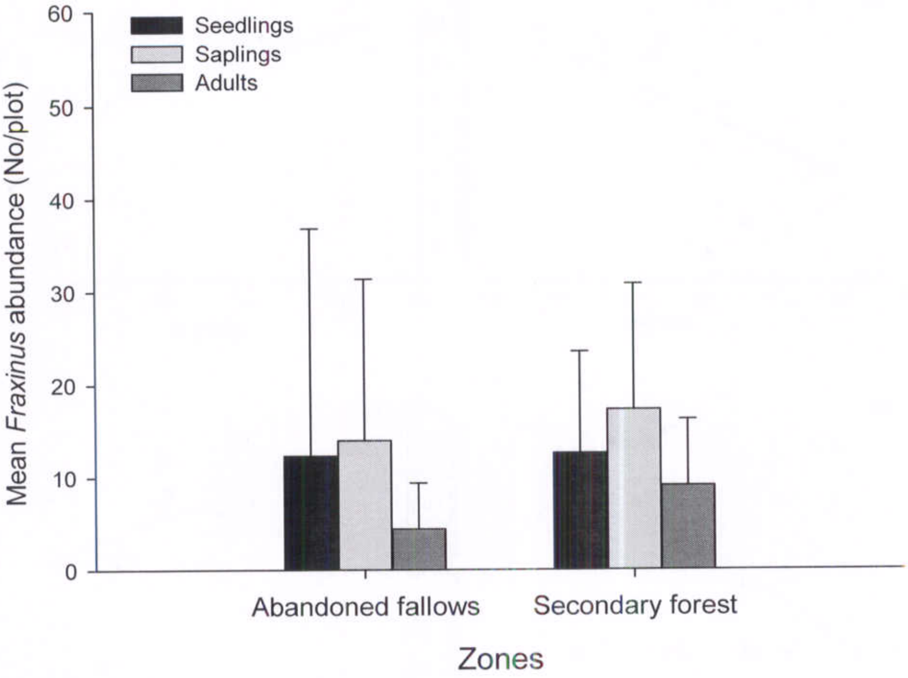
60
50
40
30
20
10
0
Mean Fraxinus abundance (No/plot)
Seedlings
Saplings
Adults
Abandoned fallows
Secondary forest
Zones

FIGURE I

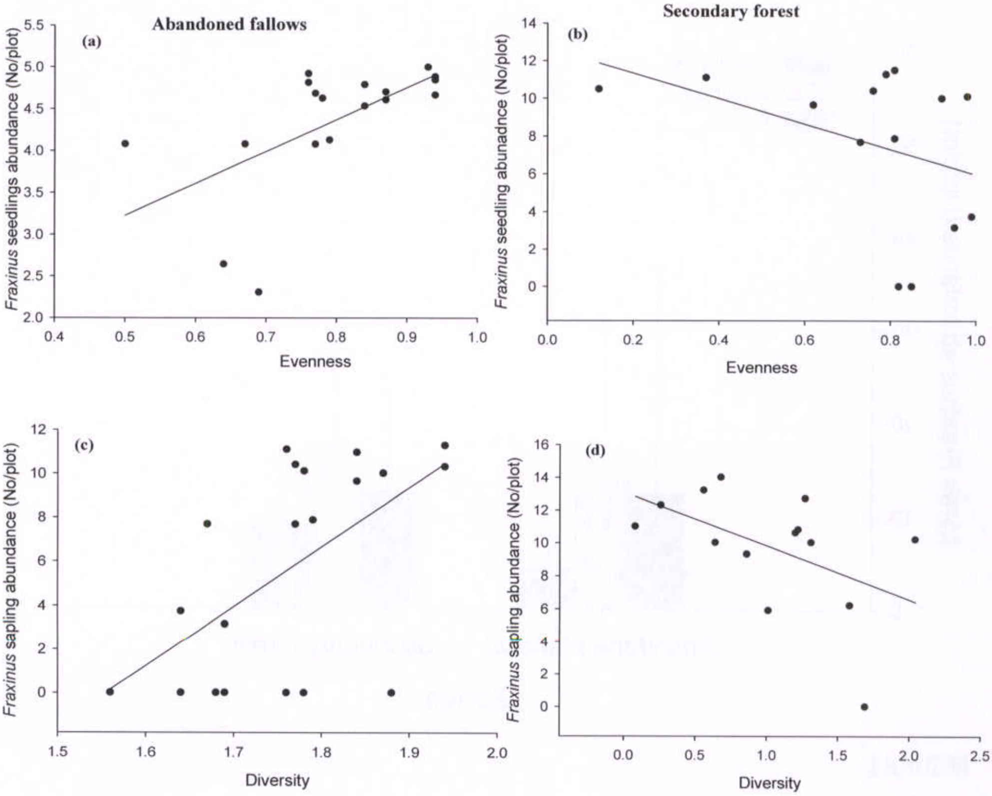
Abandoned fallows
Secondary forest
(a)
(b)
(c)
(d)
Fraxinus seedlings abundance (No/plot)
Fraxinus seedling abunadnce (No/plot)
Fraxinus sapling abundance (No/plot)
Fraxinus sapling abundance (No/plot)
Evenness
Evenness
Diversity
Diversity
2.0
2.5
3.0
3.5
4.0
4.5
5.0
5.5
0.4
0.5
0.6
0.7
0.8
0.9
1.0
0
2
4
6
8
10
12
14
0.0
0.2
0.4
0.6
0.8
1.0
0
2
4
6
8
10
12
1.5
1.6
1.7
1.8
1.9
2.0
0
2
4
6
8
10
12
14
16
0.0
0.5
1.0
1.5
2.0
2.5

FIGURE II

TABLE I. Results of generalized linear mixed model (GLMM) showing relationship between Fraxinus seedling density and zone (abandoned fallows vs secondary forest), season (dry vs wet) as categorical and community diversity, evenness, mean abundance of saplings and adult trees of other species, shrubs, lianas, ferns, herb, distance as continuous variables and their interactions. The reference categorical variables are abandoned fallows and dry season. Only significant variables are shown.

Variable	Estimate	Std.Error	z value	$P(>\|z\|)$
Intercept	-8.696	1.479	-5.877	< 0.001
Secondary forest	7.326	2.333	3.139	0.002
Evenness	8.668	1.428	6.069	< 0.001
Shrubs	0.038	0.007	5.530	< 0.001
Adults	-0.029	0.032	-0.899	0.369
Lianas	-0.117	0.016	-7.539	< 0.001
Ferns	0.304	0.042	7.260	< 0.001
Herb cover	0.017	0.006	2.9630	0.003
Secondary:lianas	0.098	0.021	4.792	< 0.001
Secondary:shrubs	-0.064	0.018	-3.596	< 0.001
Secondary:ferns	-0.381	0.051	-7.523	< 0.001
Secondary:adults	0.115	0.046	2.504	0.012
Secondary:Evenness	-6.984	2.018	-3.443	< 0.001

TABLE II. Results of generalized linear mixed model (GLMM) showing relationship between Fraxinus sapling density and zone (abandoned fallows vs secondary forest), season (dry vs wet) as categorical and community diversity, evenness mean abundance of saplings and adult trees of other species, shrubs, lianas, ferns, herb, distance as continuous variables and their interactions. The reference categorical variables are abandoned fallows and dry season. Only significant variables are shown.

Variable	Estimate	Std.Error	z value	$P(>\|z\|)$
Secondary forest	10.424	2.495	4.177	< 0.001
Diversity (*H*')	1.079	0.223	4.831	< 0.001
Evenness	-5.079	1.670	-3.042	0.002
Adults	-0.130	0.035	-3.742	< 0.001
saplings	0.012	0.002	5.277	< 0.001
Lianas	0.026	0.015	1.736	0.083
Ferns	-0.077	0.025	-3.058	0.002
Herb cover	0.023	0.005	4.867	< 0.001
Distance	-0.025	0.004	-5.834	< 0.001
Secondary:lianas	-0.048	0.006	-2.309	0.002
Secondary:saplings	-0.014	0.051	-7.523	0.021
Secondary:adults	0.102	0.039	0.010	0.009
Secondary:Diversity	-1.481	0.254	-5.820	< 0.001
Secondary:Evenness	5.577	2.008	2.777	0.005

Paper IV

Relationship between an invasive tree, *Fraxinus pennsylvanica* and plant species diversity and abundance after agricultural abandonment in a tropical afromontane forest

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Abstract Species invasion is an important driver of forest ecosystem degradation with large effects on biodiversity and ecological functions. Understanding impacts of species invasion on forest communities is becoming more important in the tropical world where there is increasing concern about exotic species invasion due to native species extinctions and failed attempts to restore degraded forest. Impacts of alien species depend on their biological attributes, the environmental characteristics of the invaded ecosystem and the biotic interactions with the receptive community. This study was conducted in a degraded tropical forest where invasion of *Fraxinus pennsylvanica* had been observed. I examined the relationships between *F. pennsylvanica* and the plant community richness, diversity, evenness, composition, and the richness and abundance of seedlings and saplings of other tree species, shrubs, lianas, and herbs in abandoned fallows and in the secondary forest. In the abandoned fallows, simple linear regressions showed a negative relationship between shrub and *F. pennsylvanica* density, whereas tree seedling richness of other tree species was positively related with the invading tree. In the secondary forest on the other hand, there was a negative relationship between the density of *F. pennsylvanica* and species richness of saplings of other tree species and the abundance of shrubs. There was also a negative relationship between community diversity and *F. pennsylvanica* in the secondary forest, which supports the widespread perception that alien invasive species may decrease native species diversity. There were positive relationships between *F. pennsylvanica* and the species composition of light demanding trees, shrubs, herbs, and lianas in the abandoned fallows but no such relationships in the secondary forest. Shade intolerant tree, herb, and liana species were negatively related with *F. pennsylvanica* suggesting competition for light. This study suggests that on-going forest degradation and subsequent plant invasion is likely to alter assemblage and diversity patterns that in the long-term may lead to changes in community structure, species composition and successional trajectory in Mau forest.

Keywords Disturbance, Exotic plant invasions, Forest Management, Indigenous tree species.

Introduction

In an increasingly globalized world, both frequency and extent of exotic plant invasions are growing rapidly, thus increasing the need to understand their ecological effects and monitor their spread (Vitousek et al. 1996; Meyerson and Mooney 2007). Alien species invasions, boosted by human activities and movement across the planet, represent one of the most important main threats to the world's biodiversity (Vitousek et al. 1996; Mooney and Hobbs 2000; Gurevitch and Paddilla 2004). Thus, there is a need for studies on the effects of invasive species on native plant community diversity across a range of infestation levels, especially where invasive species dominate and impact the abundance of other species in communities and ecosystems. Previous studies show that alien invasive species may inhibit the recruitment of resident native species by preventing seedlings establishment and growth (Gorchov and Trise 2003). Furthermore, invasive species may displace resident species through direct below and above ground competition for resources, such as space, water, nutrients, and light (Walck et al. 1999; Vila and Weiner 2004), and modify or 'engineer' ecosystem processes and the physical resources of the recipient community such as disturbance regimes and nutrient cycling (Mack and D'Antonio 1998; Yurkonis et al. 2005).

At the community level, the suppression of native plants is a result of the dominance invasive species may achieve in invaded habitats (Richardson 1998). Surprisingly, studies measuring the community level effects of plant invasions are rather scarce in the tropics in general (Hejda et al. 2009), and in Africa in particular (Nunez and Pauchard 2010). A few studies that have examined the relationship between invasive species and community properties have shown that impacts on species diversity and composition depend on the individual invader (Hulme and Bremner 2006; Hejda and Pyšek 2006). Similarly, native species also differ in their relationship with the invader; some are excluded from the communities more easily than others, and the impact on species richness is correlated with that of species composition (Standish et al. 2001). However, the establishment of an introduced alien invasive species does not necessarily constitute a problem *per se*, but negative impacts associated with high abundance of the introduced species may threaten native communities as a result of competitive displacement (Levine et al. 2003). Although many tree species have been extensively transferred across countries and continents, they have, until recently, not been perceived as a potential threat to the local communities in general. Studies on long-lived plant species, i.e. 'tree weeds', have reported that disturbed ecosystems are particularly vulnerable to invasion by alien species (Richardson et al. 1994; Richardson and Higgins 1998, Simberloff et al. 2002; Ghersa et al. 2002).

In this study, I assessed the relationships between the alien invasive tree species *Fraxinus pennysilvanica* Marsh. (Oleaceae) and plant community properties in abandoned fallows and in the secondary forest at Mau forest in Kenya. Other studies have suggested that *F. pennsylvanica* invasion has negative impacts on native plant performance (Kremer et al 2006; Lesica 2009), but none have tested its relationship with different tree growth stages. Germination and early growth stages of tree seedlings and saplings are critical and important stages of tree establishment, and it is therefore important to examine how they relate with *Fraxinus* density. The study aims to examine if an invasive species may affect community diversity, species abundances, and composition, and if the influence of an invasive species may depend on the degree of disturbance of the invaded area. Specifically I am asking 1) if there is a relationship between *F. pennsylvanica* density and species richness and abundance of tree seedlings and saplings of other tree species, shrubs, lianas, and herbs, and community richness, diversity, and evenness, 2) if there is a relationship between *F. pennsylvanica* density and the species composition of tree seedlings and saplings of other tree species (juveniles), herbs, shrubs and lianas, and 3) if any of these relationships differ between the abandoned fallows and the secondary forest.

Methods

Study species and site

Fraxinus pennsylvanica is a shade-tolerant tree species native to North America, which was introduced to Europe and South America in the 1920s and to Africa in the mid 50s and subsequently planted in the forest for various purposes (Hegi 1908, as quoted by Kremer *et al.* 2006; Ghersa et al. 2002; Lesica 2009). A negative effect of the species is its invasion into degraded forest or abandoned fallows (Lesica 2009), and *F. pennsylvanica* invasion has been perceived as a major ecological problem in the northern hemisphere (Török et al. 2003; Pyšek and Prach 2003; Kremer et.al. 2006) resulting in substantial changes in the invaded ecosystem, including major shifts in life-form dominance (Lesica 2009). No published record of the species invasion in Africa was encountered.

The study was conducted in a degraded tropical montane forest within the Western Mau Forest block (0°30’ 60’’ South 35°27’0’’ East). The 22748 ha forest comprise secondary forest and scattered patches of regenerating abandoned fallows and exotic commercial forest plantations. The study area is at 2120 m altitude with an annual rainfall around 1500 mm. Mean annual temperature ranges from 12-16ºC and a potential evapo-transpiration is between 1400 and 1800 mm (Jackson and McCarter 1994). Within the forest block, a 10.6 ha of previously cleared, cultivated, and then abandoned area surrounded by secondary forest and a fire-belt (a strip of plantation of fire resistant tree species used to prevent fire from commercial plantations) of *F. pennsylvanica* was chosen for this study. Detailed information on the history of land use was collected from Kenya Forest Service (KFS) records and by interviewing local people. Five years after abandonment, the site consisted of zones of different phases of recovery due to different degree of degradation before abandonment and continued grazing, selective logging, charcoal production and firewood collection activities thereafter. The abandoned fallows comprised of zones of initial stages of recovery with colonizing shrubs and a few tree seedlings and advanced recovery with shrubs, tree seedlings, tree saplings and adult trees. The secondary forest consists of Afromontane bamboo forest at the higher altitudes and secondary plant communities derived from logged rainforest at the lower altitudes. The forest has a high biodiversity and hosts indigenous tree species, such as *Olea africana* and *Dombeya torrida* (Kinyanjui 2009)

Data collection

Field work was done in October 2006 (dry season) and in April 2007 (rainy season). We randomly positioned 20 plots in the abandoned fallows and 14 in the secondary forest. The plots in the secondary forest were positioned at least 200 m away from the edge of the closest plot in the fallows. We used plots of 5 × 30 m in the most degraded fallows lacking adult trees, and 10 × 30 m in the less degraded fallows and in the secondary forest. We used larger plots in the latter in order to capture the variation in adult tree species richness and abundance. Each plot was divided into 6 sub-plots (for the 5 × 30 m plots) and 12 sub-plots (for the 10 × 30 m plots) and each sub-plot had a 1 × 1 m quadrat in its centre. Individual plants were enumerated and identified as far as possible to species or genus level. For adult trees and lianas with a height >1.3 m and dbh > 10 cm we counted the individuals of all species in all the sub-plots. Tree saplings and shrubs (dbh < 10 cm and height > 1.3 m) were counted in every other sub-plot. Tree seedlings (height < 1.3 m) and herbs were recorded in every 1 x 1 m quadrat within each sub-plot. *Fraxinus pennsylvanica* seedlings and saplings data were collected following the same procedure. To enable comparison between different plot sizes, correction was done for the double plot sizes before data analysis by dividing abundance within the 10 × 30 m plots by two. For the species richness data, we calculated the mean number of species within each of the two 5 × 30 m plots and used the mean of these in the analyses. A taxonomist, assisted by local para-taxonomist and KFS staff identified the plant species. All unidentified species were deposited at the National Herbarium of Kenya for identification and voucher species were kept there. Nomenclature follows Agnew and Agnew (1994) and Beetje (1994).

Statistical analysis

I used simple linear regressions to examine the relationships between *F. pennsylvanica* density and the community richness, diversity and evenness, and species richness and abundance of various functional groups. I calculated species diversity and evenness at the plot level. In the analysis I used the sum of adults and saplings (for sound statistical analyses) to represent the density of *F. pennsylvanica* as an independent variable. Mean abundance and species richness of seedlings and saplings of other tree species, shrubs, lianas and herbs, community richness, diversity, and evenness were used as dependent variables in separate analyses. I performed separate analyses for plots in the abandoned fallows and in the secondary forest. R 2.10.0 (R-Development Core Team 2009) was used in all the analyses.

I used multivariate analyses to assess how *F. pennsylvanica* density contributed in explaining the species composition of native trees, herbs, shrubs, and lianas in abandoned fallows and in the secondary forest. I combined the abundance of seedlings and saplings to represent the species composition of other trees. Detrended correspondence analyses (DCA) was used to examine the gradient length (> 4 SD) and canonical correspondence analysis (CCA) was used to assess the relationship between *F. pennsylvanica* density and species composition of all functional groups. I conducted separate analyses in abandoned fallows and in the secondary forest, and for each analysis, I tested the significance of all canonical axes with 999 unrestricted permutations in a Monte Carlo test. I conducted all ordinations by using default settings in CANOCO 4.5 and used CanoDraw to produce ordination diagrams (ter Braak and Smilauer 2002).

Results

Simple linear regressions showed that species richness of seedlings and abundance of saplings of other trees were positively related with *F. pennsylvanica* density in the abandoned fallows (Table 1). However, there was a negative relationship between shrub richness and the density of *Fraxinus pennsylvanica* in the abandoned fallows (Table 1). Mean abundance of tree seedlings and richness of tree saplings of other tree species, herbs, lianas, shrubs, community richness, diversity, and evenness were not related to *F. pennsylvanica* density in the abandoned fallows (Table 1).

In the secondary forest, there was a negative relationship between species richness of saplings of other trees, shrubs, community diversity and the density of *F. pennsylvanica* (Table 1). Abundance of shrubs was negatively related with *F. pennsylvanica* density in the secondary forest (Table 1). Species richness of seedlings of other trees, lianas, herbs, community richness, evenness, and mean abundance of seedlings of other tree species, lianas, and herbs were not related with *F. pennsylvanica* density in the secondary forest (Table1).

The CCA results showed a significant association between species composition of all functional groups and *F. pennsylvanica* density both in the abandoned fallows ($P < 0.006$; $F = 3.19$) and in the secondary forest ($P < 0.004$, $F = 2.17$). Some native tree species were positively associated with *F. pennsylvanica* in the abandoned fallows. These were mainly light demanding tree species namely, *Warbugia ugandensis* Sprague (Canellaceae), *Celtis africana* Burm. f. (Ulmaceae), *Prunus africana* Hook. f. Kalkman (Rosaceae), and *Grewia robusta* Burch. (Malvaceae) (Fig. 1a). Only one herb species, *Gerbera viridifolia* (Dc.) Sch.Bip. (Asteraceae), was positively related to *F. pennsylvanica,* and most shrubs and lianas were negatively related or showed week relationships with *F. pennsylvanica* in the abandoned fallows (Fig. 1a). In the secondary forest, *Olea capensis africana* Mill. (Oleaceae*), Juniperus procera* Endl. (Cupressaceaea), *Maytenus undata* Eckl. & Zeyh. (Celastraceae), *Euclea* *divinorum* Hiern (Ebanaceae), *Psydrax schimperiana* (A. Rich) Bridson (Rubiaceae) and *Albizia gummifera* J.F. Gmel. (Fabaceae) related positively with *F. pennsylvanica* density (Fig. 1b). These are mostly forest interior pioneers, or bush encroachers like *Euclea divinorum* Hiern (Ebanaceae). However, typical forest interior tree species like, *Diospyros abyssinica* (Hiern) F. White (Ebanaceae), *Cassipourea malosana* Bak. Alston (Rhizophoraceae), *Casearia battiscomei* R. E. Fr. (Salicaceae), *Croton macrostachyus* Del (Euphorbiaceae), *Podocarpus latifolius* (Thunb) Mirb. (P. milanjianus), *Casipourea malosana* (Bak.) Alston (Rhizophoraceae), *Macaranga kilimandscharica* Pax (Euphorbiaceae), *Polycias fulva* (Hiern) harms. (Araliaceae) were negatively related with *F. pennsylvanica* density in the secondary forest (Fig. 1b). To a lesser degree, several lianas, namely *Physalis minima* C.H. Wright (Solanaceae), *Zehneria scabra* (L.f.) Sond. *Clutia abyssinica* Jaub. & Spach. (Euphorbiaceae), and herbs *Achyranthes aspera* L. (Amaranthaceae), *Centella asiatica* (L.) Urb (Apiaceae), *Oplismenus bumianii* P. Beauv. (Poaceae), *Impatiens niamniamensis* Gilg. (Balsaminaceae) but only one shrub *Leonotis mollissima* Gurke. (Labiateae) were positively related with *F. pennsylvanica* density in the secondary forest. Conversely, most of the shrub, herb and liana species were not related with *F. pennsylvanica* density in the secondary forest. The shrubs *Dracaena steudneri* Engl. (Asparagaceae), *Acanthus eminens* C. B. Clarke (Acanthaceae), *Triumfetta macrophylla* K. Schum (Tiliaceae) and *Piper capense* L. f. (Piperaceae), the lianas *Urtica massaica* Mildbr. (Urticaceae), *Gouania longispicata* Engl. (Rhamnaceae), *Rhoicissus tridentata* (L. f.) Wild & R. B. Drumm. (Vitaceae), and the herb *Justicia flava* (Forssk.) Vahl (Acanthaceae) were negatively related with *F. pennsylvanica* density in the secondary forest.

Discussion

The results of this study show a positive relationship between species richness of seedlings and abundance of saplings of other tree species and *Fraxinus pennsylvanica* in the abandoned fallows. In contrast, there was a negative relationship between *F. pennsylvanica* and plant community diversity in the secondary forest, which support the widespread perception that alien species invasion is detrimental to species diversity (Groninger et al. 2004; Kremer et al. 2006). Kremer et al. (2006) found a similar trend of a decline in diversity with increasing *F. pennsylvanica* density, possibly representing a general relationship between an invader and native plant communities. Furthermore, Levine et al. (2003) and Yurkonis and Meiners (2004) found that negative impacts associated with high abundance of introduced species threatens native community biodiversity through reductions in colonization rates of native plants.

The individual species within the different functional groups did, however, respond differently to *F. pennsylvanica* invasion in both the fallows and in the secondary forest, leading to species composition that are not reflected by measures of diversity or richness. The results of this study show that the relationship between *F. pennsylvanica* and the juveniles of native tree species differs between abandoned fallows and secondary forest. This may reflect intraspecific variations in tree species susceptibility to *F. pennsylvanica* invasion, depending on tree species growth stage and the prevailing habitat condition. The positive correlation with some tree juvenile species shown in figure 1 indicate that increasing *F. pennsylvanica* invasion may favor recruitment of certain native tree species, such as *W. ugandensis, C. africana, P. africana and G. robusta,* at least in the abandoned fallows. The negative relationships between *F. pennsylvanica* densities and most of the interior tree species in the secondary forest, on the other hand, suggest that *F. pennsylvanica* may interfere with their recruitment here, suggesting competition for light. Evidence from studies in other tropical systems support the enduring influence of plant invasions and also show that alien invasive plants that establish during the initial phases of forest regeneration can limit native plant growth or slow the rate of change in species composition (Gorchove and Paddill 2003; Lichstein et al. 2004). This also seems to be supported by results of this study, hence, the abundance of interior tree species such as *P. fulva*, *P. latifolius*, *V. madagascariensis*, *C. malosana*, and *D. abyssinica* showing that seedlings of these key pioneer trees may favor less invaded areas. Thus, increasing *F. pennsylvanica* presence in the secondary forest will likely limit their recruitment. Similarly in heavily disturbed sites such as the abandoned fallows, invasive alien tree species may reduce the establishment of tree seedlings of most other tree species by competition as suggested by studies from other tropical forests (Brown and Peet 2003; Yurkonis et al. 2005).

The relationships between *F. pennsylvanica* invasion and tree species composition in abandoned fallows and in the secondary forest switch between suppressive or facilitative, likely due to the intensity of the disturbance. This perhaps shows that the invader is acting as a passenger of change in the abandoned fallows due to altered disturbance regimes creating an environment limiting establishment of most native species. This agrees with previous findings that rather than driving the transformation of native plant communities, invading alien species may be passengers of more fundamental environmental change that is limiting the native flora MacDougall and Turkington (2005) and Chytry et al. (2008).

Light-demanding graminoids, shrubs and lianas characterized the abandoned fallows and were generally negatively related to *F. pennsylvanica.* According to Brown et al. (2006) absence of dominant native trees facilitates alien plant establishment in recovering landscapes and alien invasive plants that are able to respond favorable to fluctuating post disturbance conditions, like *F. pennsylvanica,* will most likely outcompete the other species. In the secondary forest, heterogeneity results from various disturbance types acting at different scales, from mid-scale clearcuts (for charcoal kilns) and windthrows, to small-scale selective cuttings and soil erosion by domestic animals. These disturbances generate niches allowing for the coexistence of *F. pennsylvanica* and forest interior tree species like *Olea capensis*, *Juniperous procera,* the shrub *Clutia abyssinca,* and the herb *Oplismenus bumianii.* Nevertheless, the extent and degree to which alien invasive tree species influence species composition in tropical forests remains a point of considerable debate (Lugo 2004). One of the fundamental questions in this debate is whether alien invasive trees are transient or persistent members of the plant community. If an invader's dominance is ephemeral in a secondary forest, its establishment maybe considered as an initial step in a series of events leading to the recovery of native forests. In this case, the community assemblage will then converge on the pre-disturbance community at a rate that depends on the intensity, frequency, and time since the disturbance (Yurkonis and Meiners 2004). Alternatively, if the invaders do endure, fundamental, long lasting shifts in forest diversity patterns and community structure can result in a novel vegetation composition and assemblage (Lugo 2004).

Although the connection between competition and community structure is almost certain in plant ecology (Keddy 2001), the exact relationship between invasion success and competitive ability has rarely been confirmed experimentally (Davis 2003; Levine et al. 2003). Thus, the general role of alien species invasion as a driver of diversity decline has been challenged, since a correlation between exotic invasion and decline in diversity does not provide conclusive evidence of cause-effect relationships (Gurevitch and Padilla 2004; Didham et al. 2005). In line with the above, due to the correlative approach used in this study to investigate the relationships between *F. pennsylvanica* density and resident plant communities, the results presented do not indicate causation, and associations between *F. pennsylvanica* density and different native functional groups may have been coincidental or due to other covarying factors. However, correlation studies provide useful information which should be used to develop hypothesis for experimental testing as the next step. This study therefore adds valuable information of the effect of invasive species on tropical forests and provides relationships that validate and support existing empirical studies (Groninger et al. 2004; Kremer et al. 2006).

Conclusions

Fraxinus pennsylvanica invasion appears to impact community diversity, abundance and recruitment of seedlings of other tree species in Mau forest. Thus, conservation or management decisions should consider tree species potentially at risk from *F. pennsylvanica* invasion for effective conservation priorities and to facilitate effective policy and management strategies for areas of high conservation value in Kenya and elsewhere.

Acknowledgments

I thank Ørjan Totland and Kari Klanderud for proposing the study and for constructive comments. I would like to thank farmers for information, Boaz Ngonga, William Bii and the late Florence Muindi, their help in data collection. The European Union through the project 'Bridging restoration and multi-functionality in degraded forest landscape of Eastern Africa and Indian Ocean Islands' (FOREAIM) provided financial support. The Norwegian State Educational Loan Fund (Lånekassen) for scholarship and, Kenya Forestry Research Institute, Londiani, and Kenya Forest Service Itare stations for logistical support.

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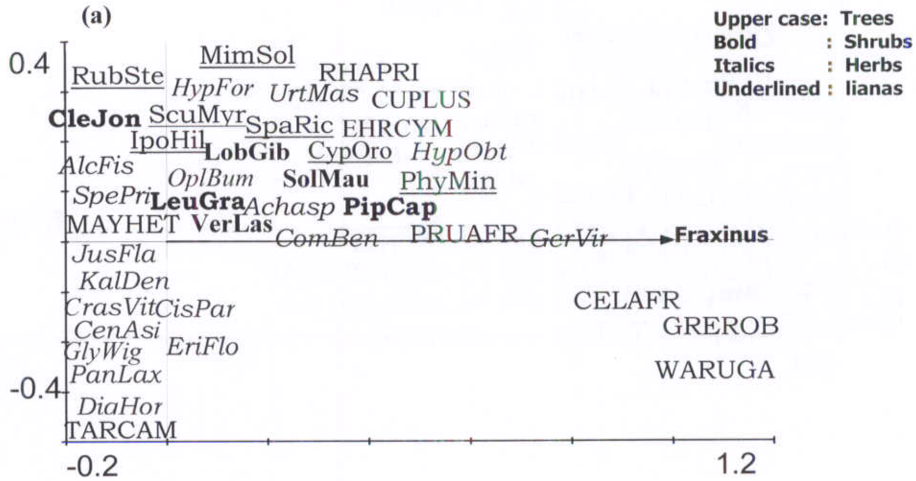
Legend

Fig. 1 CCA biplots of native species composition and *Fraxinus* (environmental variable) in (a) abandoned fallows and (b) in the secondary forest in Mau forest, Kenya. Only species with 10 and 5% fit are shown in figures 1a and b respectively. Full species names are shown in Appendix A.



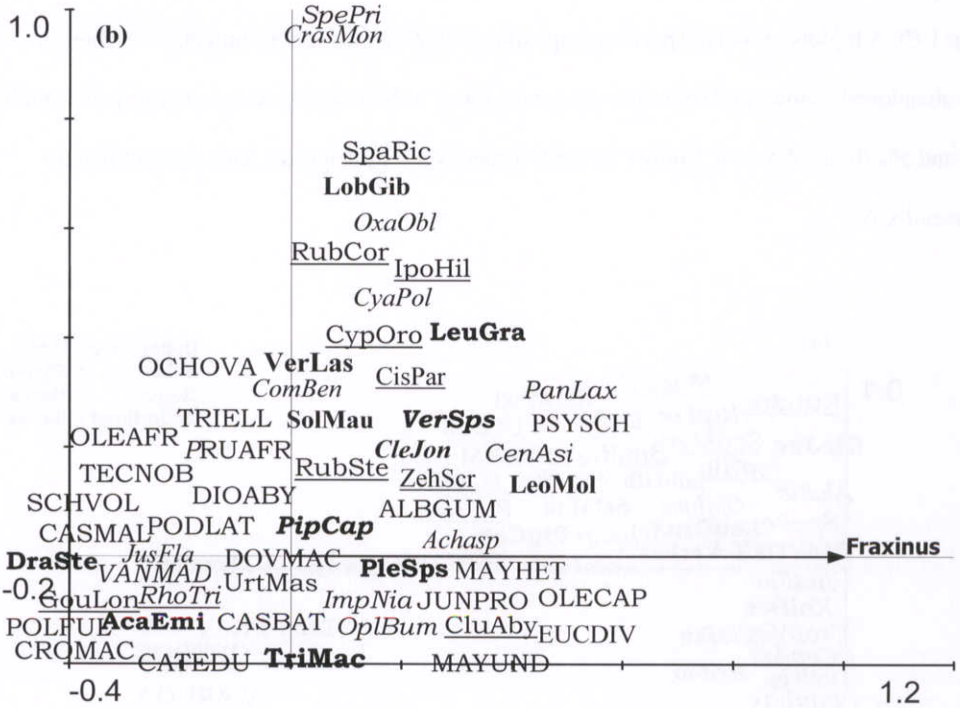

1.0
(b)
SpePri
CrasMon
SpaRic
LobGib
OxaObl
RubCor
IpoHil
CyaPol
CypOro
LeuGra
OCHOVA
VerLas
CisPar
ComBen
PanLax
TRIELL
SolMau
VerSps
PSYSCH
OLEAFR
PRUAFR
CleJon
CenAsi
TECNOB
RubSte
ZehScr
LeoMol
SCHVOL
DIOABY
ALBGUM
CASMAL
PODLAT
PipCap
Achasp
Fraxinus
DraSte
JusFla
DOVMAC
VANMAD
PleSps
MAYHET
-0.2
UrtMas
GouLon
RhoTri
ImpNia
JUNPRO
OLECAP
POLFUE
AcaEmi
CASBAT
OplBum
CluAby
EUCDIV
CROMAC
CATEDU
TriMac
MAYUND
-0.4
1.2

Table1 Simple linear coefficients and P-values (significant values $P < 0.05$ in bold) of the relationships between *Fraxinus pennsylvanica* density (predictor) and the community richness, diversity, evenness and species richness, and abundance of plant functional groups in abandoned fallows and secondary forest at Mau forest, Kenya

Response	Abandoned fallows		Secondary forest	
	Est.	P	Est.	P
Community properties				
Richness	0.01	0.501	**-0.08**	**0.022**
Diversity	0.61	0.068	**-0.35**	**0.004**
Evenness	-0.01	0.591	-0.21	0.232
Richness				
Tree seedlings	**0.24**	**0.001**	0.01	0.410
Tree saplings	0.61	0.068	**-0.27**	**0.023**
Shrubs	**-0.36**	**0.047**	**-0.25**	**0.021**
Lianas	-0.04	0.916	0.00	0.948
Herbs	0.00	0.498	-0.00	0.438
Abundance				
Tree seedlings	0.91	0.116	0.02	0.068
Tree saplings	**0.46**	**0.001**	0.12	0.232
Shrubs	- 0.02	0.371	**-0.32**	**0.002**
Lianas	0.00	0.920	-0.19	0.177
Herbs	0.83	0.213	0.17	0.159

Appendix A. Full species names of abbreviations used in Figs. 1a and b

Species		Family	Life form
DigHor	*Digitaria horizontales* Henrard	Poaceae	Herb
EriFlor	*Erigeron floribudus* (Kunth.) Sch.Bip.	Asteraceae	Herb
HypFor	*Hypoestes forskaolii* (Vahl.) Roem & Schult.	Acanthaceae	Herb
CenAsi	*Centella asiatica* (L.) Urb.	Apiaceae	Herb
KalDen	*Kalanchoe densiflora* Rolfe	Crassulaceae	Herb
OxaObli	*Oxalis obliquifolia* Steud.ex A.Rich.	Oxalidaceae	Herb
GlyWig	*Glycine wightii* (Taub.)Verdc.	Papilionaceae	Herb
OplBum	*Oplismenus bumianii* P.Beauv.	Poaceae	Herb
AchAsp	*Achyranthes aspera* L.	Amaranthaceae	Herb
ComBen	*Commellina benghalensis* Forssk.	Commelinaceae	Herb
JusFla	*Justicia flava* (Forssk.) Vahl.	Acanthaceae	Herb
HypObt	*Hypoxis obtusa* Burch.	Hypoxidaceae	Herb
SpePri	*Spermacoce princeae* (K.Schum) Verdc.	Rubiaceae	Herb
UrtMas	*Urtica massaica* Mildbr.	Urticaceae	Herb
ImpNam	*Impatiens namniamensis* Gilg.	Balsaminaceae	Herb
PanLax	*Panicum laxum* Sw.	Poaceae	Herb
CraMon	*Crassocephalum montousum* (S.Moore) Milne-Redh.	Asteraceae	Herb
CraVit	*Crassocephalum vittelinum* (Benth.) S.Moore	Asteraceae	Herb
CyaPol	*Cyathula polycephala* Baker	Amaranthaceae	Herb
GerVir	*Gerbera viridifolia* (Dc.) Sch. Bp.	Asteraceae	herb
GouLon	*Gouania longispicata* Engl.	Rhamnaceae	Liana
IpoHil	*Ipomoea hildebrandtii* Vatke	Convolvulaceae	Liana
MimSol	*Mimulopsis solmsii* Schweinf.	Acanthaceae	Liana
CisPar	*Cissampelos pareira* L.	Menispermaceae	Liana
CluAby	*Clutia abyssinica* Jaub. & Spach.	Euphorbiaceae	Liana
PyhMin	*Physalis minima*.C.H. Wright	Solanaceae	Liana
ZehSca	*Zehneria scabra* (L.f.) Sond.	Cucurbitaceae	Liana
ScuMyr	*Scutia myrtina* (Burm.f.)Kurz.	Rhamnaceae	Liana
RubSte	*Rubus steudneri* (Olive.) R.A. Graham	Rosaceae	Liana
SpaRic	*Sparmannia ricinocarpa* (Eckl.&Zeyh.)Kuntze	Tiliaceae	Liana
CypOro	*Cyphostemma orondo* (Gil & M.Brandt) Desc.	Vitaceae	Liana
RubCor	*Rubia cordifolia* L.	Rubiaceae	Liana
RhoTri	*Rhoicissus tridentata* (L.f.) Wild & R.B.Drumm.	Vitaceae	Liana
PipCap	*Piper capense* L.f.	Piperaceae	Shrub
CleJoh	*Clerodendrum johnstonii* Oliv.	Verbanaceae	Shrub
TriMac	*Triumfetta macrophylla* Vahl.	Tiliaceae	Shrub
AcaEmi	*Acanthus eminens* C.B.Clarke	Acanthaceae	Shrub
LobGib	*Lobelia gibberoa* Hemsl	Campanulaceae	Shrub

Appendix A. continued

Species		Family	Life form
LeuGra	*Leucas grandis* Vatke	Labiateae	Shrub
SolMau	*Solanum mauritianum* Scop.	Solanaceae	Shrub
LeoMol	*Leonotis mollissima* Gurke.	Labiateae	Shrub
DraSte	*Dracaena steudneri* Engl.	Asparagaceae	Shrub
PtrCat	*Pteris catoptera* Kunze	Cyatheaceae	Shrub
EryBon	*Erythrococca bongensis* Pax	Euphorbiaceae	Shrub
PleSpp	*Plectranthus* spp	Labiateae	Shrub
VerLas	*Vernonia lasiopus* O. Hoffm.	Asteraceae	Shrub
VerSpp	*Vernonia* spp	Asteraceae	Shrub
AlbGum	*Albizia gummifera* (J.F.Gmel.) C.A.sm.	Fabaceae	Tree
CupLus	*Cuppressus lusitanica* Miller	Cupressuceae	Tree
MayUnd	*Maytenus undata* (Thunb.) Balkelock	Celastraceae	Tree
JunPro	*Juniperus procera* Endl.	Cupressaceae	Tree
PruAfr	*Prunus africana* (Hook.f.) Kalkman	Rosaceae	Tree
PolFul	*Polyscias fulva* (Hiern) Harms	Araliaceae	Tree
CatEdu	*Catha edulis* (Vahl.) Endl.	Celastraceae	Tree
MayHet	*Maytenus heterophylla* N.Robson	Celastraceae	Tree
GreRob	*Grewia robusta Burch.*	Tiliaceae	Tree
OleCap	*Olea capensis* L.	Oleaceae	Tree
EhrCym	*Ehretia cymosa* (R.Br.ex Fresen.) Brenan	Boraginaceae	Tree
CelAfr	*Celtis Africana* Burn.f.	Ulmaceae	Tree
DioAby	*Diospyros abyssinica* (Hiern) F.White	Ebenaceae	Tree
OleAfr	*Olea europea ssp africana* (Mill.) P.S. Green	Oleaceae	Tree
TecNob	*Teclea nobilis* Delile	Rutaceae	Tree
CasBat	*Casearia battiscombei* R.E. Fr.	Salicaceae	Tree
VanMad	*Vangueria madagscariensis* J.F. Gmelin.	Rubiaceae	Tree
CroMac	*Croton marcrostachyus* Del.	Euphorbiaceae	Tree
FraPen	*Fraxinus pennsylvanica* Marsh.	Oleaceae	Tree
TriEll	*Tricholadus ellipticus* Eckl. & Zeyh.	Hamamelidaceae	Tree
OchOva	*Ochna ovata* F. Hoffm.	Ochnaceae	Tree
PodLat	*Podorcapus latifolius* (Thumb.) Mirb.	Podocarpaceae	Tree
EucDiv	*Euclea divinorum* Hiern.	Ebanaceae	Tree
CasMal	*Cassipourea malosana* Alston	Rhizophoraceae	Tree
TarCam	*Tarconanthus camphrotus* L.	Asteraceae	Tree
WarUga	*Warbugia ugandensis* Sprague	Canellaceae	Tree
PsySch	*Psydrax schimperiana* (A.Rich.) Bridson	Rubiaceae	Tree
DovyMac	*Dovyalis macrocalyx* (Oliv.)Warb.	Silicaceae	Tree
RhaPri	*Rhamnus prinoides* L'Herit	Rhamnaceae	Tree
SchVol	*Schefflera volkensii* (Engl.) Harms.	Araliaceae	Tree