

Community invasibility and invasion by non-native Fraxinus pennsylvanica trees in a degraded tropical forest

Collins Jared Amwatta Mullah, Kari Klanderud, Ørjan Totland & David Odee

Biological Invasions

ISSN 1387-3547

Biol Invasions
DOI 10.1007/s10530-014-0701-6



Your article is protected by copyright and all rights are held exclusively by Springer International Publishing Switzerland. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at link.springer.com".

Community invasibility and invasion by non-native *Fraxinus pennsylvanica* trees in a degraded tropical forest

Collins Jared Amwatta Mullah ·
Kari Klanderud · Ørjan Totland · David Odee

Received: 6 February 2013 / Accepted: 7 April 2014
© Springer International Publishing Switzerland 2014

Abstract Whether invasion of introduced plant species may be aided by certain community properties is poorly understood for species-rich ecosystems, such as tropical montane forests. In Kenya, the non-native tree *Fraxinus pennsylvanica* has invaded degraded montane forests. We used generalized linear mixed models to examine the relative importance of different community properties to *Fraxinus* invasion after agricultural abandonment and in the secondary forest. *Fraxinus* invasion was positively related to plant community species diversity and the abundance of tree saplings, shrubs, ferns, and herbs in the abandoned fallows, but negatively related to the same community properties in the secondary forest. The number of *Fraxinus* recruits declined with declining propagule pressure in the fallows, but not in the secondary forest. Although adult and saplings of *Fraxinus* were positively related to community diversity in the fallows, *Fraxinus* appeared to decrease diversity in the secondary forest. These results show that the success of non-native species invasion and the effects of an invader on the resident community may depend both

on properties and degree of disturbance of the community. Plant community diversity and evenness appeared to determine the invasion success by increasing invasibility of the abandoned fallows, but decreasing invasibility of the secondary forest. Our results from a tropical degraded forest emphasize the importance of including habitat characteristics when predicting both the potential of non-native plant invasion and effects of invasives on the particular community.

Keywords Community species diversity · Disturbance · Degraded forest · Tree invasions · Regeneration

Introduction

There is a need for studies on the effects of non-native species on native plant community diversity across a range of ecosystems and invasion levels. Tropical forests are of particularly value globally due to their carbon uptake and biodiversity, and at the same time, they are also prone to degradation. 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 non-native species (Richardson 1998; Ortega and Pearson 2005; Ditham et al. 2007). Introduced species often establish successfully in communities that have already been altered by human disturbances (Hobbs and Huenneke

C. J. A. Mullah · K. Klanderud (✉) · Ø. Totland
Department of Ecology and Natural Resource
Management, Norwegian University of Life Sciences,
P.O. Box 5003, 1432 Ås, Norway
e-mail: kari.klanderud@nmbu.no

C. J. A. Mullah · D. Odee
Kenya Forestry Research Institute (KEFRI),
P.O. Box 20412-00200, Nairobi, Kenya

1992; Gilbert and Lechowicz 2005), generally preferring moist habitats with high availability of light and nutrients (Milbau and Nijs 2004). Surprisingly, studies assessing invasibility (i.e. the susceptibility of a community to invasion of new species; Burke and Grime 1996 and effects of plant invasions on plant community diversity are scarce in the tropics in general (Hejda et al. 2009), and in Africa in particular (Nunez and Pauchard 2010).

Higher species richness may increase resistance to species invasions, i.e. decrease invasibility (e.g. 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 (e.g. Levine and D'Antonio 1999; Hector et al. 2001; Shea and Chesson 2002; Hejda et al. 2009). The theory is based on the presumptive 'niche filling' whereby communities of greater species diversity exploit more completely the available resources and leave fewer open niches for colonization (Levine and 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 species composition and interactions (Hejda et al. 2009; Shea and 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 and Johnson 2006).

At community level, the suppression of native plants is a result of the dominance introduced species may achieve in invaded habitats (Richardson 1998). Non-native species may displace resident species through competition for resources, such as space, water, nutrients, and light (Walck et al. 1999; Vila and Weiner 2004), and modify or 'engineer' processes and physical resources of the recipient community, such as disturbance regimes and nutrient cycling (Mack and D'Antonio 1998; Yurkonis et al. 2005). Previous studies also show that non-native invasive species may inhibit the recruitment of resident native species by preventing seedling establishment and growth (Gorchov and Trisel 2003). 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, as some are excluded from the communities more easily than others (Standish et al. 2001). The establishment of an introduced invasive species does not necessarily constitute a problem per se, but high abundance of the introduced species may threaten native communities as a result of competitive displacement (Levine et al. 2003).

One way to understand the processes that determine the success of invasive plants is to study survival during the initial stages of establishment (i.e. seedlings and saplings) (Green et al. 2004). In Mau forest, *Fraxinus pennsylvanica* Marsh. (hereafter referred to as *Fraxinus*) was planted in 1948 as a fire break around commercial forest plantations. *Fraxinus* seedlings, saplings and adults are now growing in several habitats outside the areas of the original planting (Maundu and Tengnas 2005). Mau forest consists of a matrix of abandoned fallows and secondary forest, which makes it ideal to assess the role of disturbances for the invasion of a non-native species, and how the relationship between *Fraxinus* establishment and different community properties may vary between areas of different degrees of disturbance. Other studies have suggested that *Fraxinus* invasion has negative impacts on native plant performance (Kremer et al. 2006; Lesica 2009). The seedling and sapling stages of a tree's life cycle are critical stages of tree establishment, and it is therefore important to examine how the performance of these may be related with *Fraxinus* density. Specifically, we ask (1) if invasion of *Fraxinus* depend on habitat disturbance and community attributes, such as species richness and abundance of other species, (2) if invasion of *Fraxinus* is related to propagule pressure, measured as distance from the seed source, and (3) if *Fraxinus* decrease diversity and abundance of other species.

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 to East Africa in the late 1940s (Hegi 1908 as quoted by Kremer et al. 2006; Ghersa et al. 2002; Maundu and Tengnas 2005; Lesica 2009). Several life history traits, such as massive seed production of

relatively small, wind-dispersed seeds, vegetative reproduction, fire-resistance, and fast growth, provide fast invasion of new habitats (Lesica 2009; Groninger et al. 2004). Since the early 1960s, it has 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 2,120 m altitude where annual rainfall is around 1,500 mm. The mean annual temperature range from 12 to 16 °C and the potential evapo-transpiration is between 1,400 and 1,800 mm (Jackson and Mccarter 1994). The 22,748 ha forest ranges from secondary forest in the interior to degraded areas bordering human settlements. A previously cleared, cultivated, and then abandoned area (ca 11 ha) surrounded by secondary forest (ca 3,680 ha) and a planted belt of *Fraxinus* (ca 13 ha) 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. 5 years after abandonment, the fallows consisted of two 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 most disturbed zone was in an early state of recovery with colonizing herbs, shrubs, and a few tree seedlings, whereas the less disturbed zone had shrubs, tree seedlings, saplings and adult trees. The secondary forest surrounding the fallows 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 with more than 280 vascular plant species consisting of ca 64 trees, 38 shrubs, 46 climbers and 132 herbaceous species (Kinyanjui 2009).

Data collection

We collected data in October 2006 (dry season) and in April 2007 (rainy season). We randomly positioned ten

plots in each of the two disturbance zones of the abandoned fallows and fourteen 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 six sub-plots (for the 5 × 30 m plots) and twelve 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) were counted as number of individuals 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) and ferns were counted as number of individuals, and herbs were recorded as percentage cover in every 1 × 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 to examine the relative importance of factors that potentially could promote or inhibit the establishment and invasion of *Fraxinus*. Initial analyses showed no effects of the two different fallow zones, and data from these were therefore pooled. *Fraxinus* invasion was explained by habitat (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 habitat 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 used simple linear regressions to examine the relationships between *Fraxinus* density and community richness, diversity and evenness, and species richness and abundance of various functional groups. In the analysis we used the sum of adults and saplings (for sound statistical analyses) to represent the density of *Fraxinus* 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. We 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. We calculated Shannon diversity (H') and evenness (Pielou 1975) indices per plot.

Results

Fraxinus pennsylvanica invasion and community type and properties

Generalized linear mixed models showed that there was a positive relationship between *Fraxinus* recruitment (seedling density) and community evenness in the abandoned fallows and a reverse relationship in the secondary forest (Table 1; Fig. 1b). There was also a positive relationship between *Fraxinus* sapling density and community diversity (Fig. 1c) in the abandoned fallows, with a significant interaction showing that *Fraxinus* saplings decreased with diversity in the secondary forest (Table 2; Fig. 1d). In contrast, *Fraxinus* sapling density was negatively related with evenness in abandoned fallows and positively in the secondary forest (Table 2). *Fraxinus* sapling density

Table 1 Results of generalized linear mixed model (GLMM) showing relationship between *Fraxinus* seedling density and community type (abandoned fallows vs. secondary forest) as a categorical variable, and community evenness, abundance of adult trees of other species, shrubs, lianas, ferns, and herbs as continuous variables, and their interactions

Variable	Estimate	SE	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

The reference categorical variable is abandoned fallows. Only significant variables are shown

was 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 the 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).

Fig. 1 Relationship between *Fraxinus pennsylvanica* seedling and sapling density and evenness (a, b) and community diversity (c, d) in abandoned fallows and in secondary forest in Mau forest, Kenya

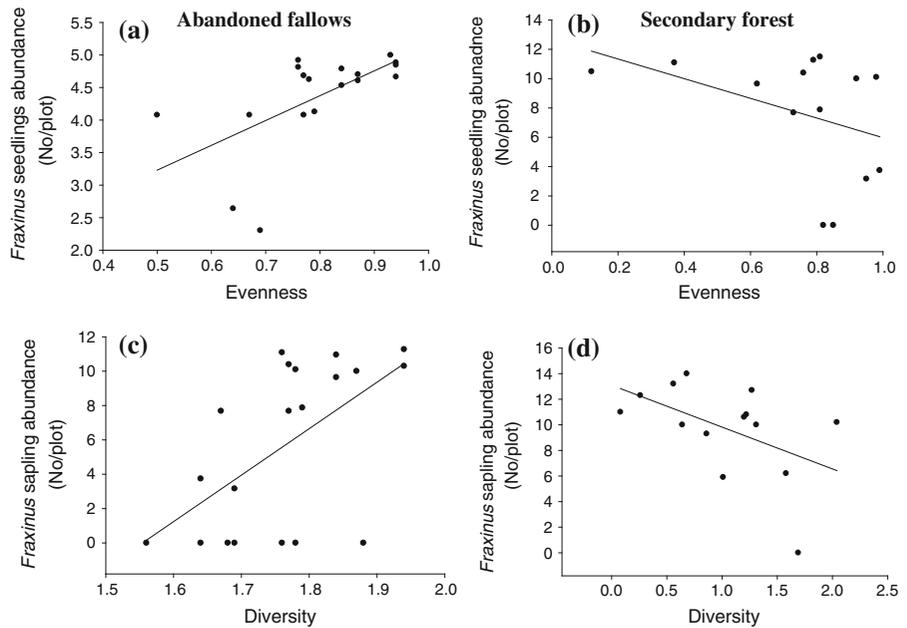


Table 2 Results of generalized linear mixed model (GLMM) showing relationship between *Fraxinus* sapling density and community type (abandoned fallows vs. secondary forest) as a categorical variable, and community diversity, evenness, abundance of saplings and adult trees of other species, lianas, ferns, herbs, and distance to the seed source as continuous variables, and their interactions

Variable	Estimate	SE	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:adult	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

The reference categorical variable is abandoned fallows Only significant variables are shown

Simple linear regressions showed that species richness of seedlings and abundance of saplings of other trees were positively related with *Fraxinus*

Table 3 Simple linear coefficients and P values (significant values $P < 0.05$ in bold) of the relationships between *Fraxinus pennsylvanica* (adults and saplings) density (predictor) and community richness, diversity, evenness and species richness and abundance of tree seedlings and saplings of other tree species, shrubs, lianas and herbs in abandoned fallows and secondary forest in Mau forest, Kenya

Responses	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

adults and saplings in the abandoned fallows (Table 3). However, there was a negative relationship between shrub richness and the density of *Fraxinus* in

the abandoned fallows (Table 3). 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 *Fraxinus* density in the abandoned fallows (Table 3). In the secondary forest, there was a negative relationship between species richness of saplings of other trees, shrubs, community diversity and the density of *Fraxinus* (Table 3). Abundance of shrubs was negatively related with *Fraxinus* density in the secondary forest (Table 3). 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 *Fraxinus* density in the secondary forest (Table 3).

Discussion

There was a positive relationship between native plant community diversity and evenness and *Fraxinus* invasion in the abandoned fallows, but negative relationships 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 and D'Antonio 1999; Hector et al. 2001; Bruno et al. 2003; Dunstan and 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 and D'Antonio 1999; Bruno et al. 2003; Dunstan and Johnson 2006). In the secondary forest on the other hand, the negative relationship between community evenness and diversity and *Fraxinus* seedling and sapling recruitment may be due to more intensive competition for light and space, limited propagule dispersal and less grazing pressure. This agrees with the diversity–stability theory and previous studies suggesting that habitats with high species diversity have low invasibility (Pyšek and Pyšek 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 and 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 and 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 and Richardson 1996; Gracia-Robledo and Murcia 2005), and the patterns and processes of the invasion by individual species to a specific habitat (Brown and Peet 2003; Milbau and Nijs 2004; Moira and Glenda 2005; Dunstan and 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.

Anthropogenic disturbances which lead to gap creation in the forest are considered necessary for non-native invasion. Friday et al. (2008) reported a 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 is likely 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). Moreover, the positive relationship between adults of other tree species and *Fraxinus* invasion observed in the secondary forest may be due to suppression of competing herbs and shrubs (Pugnaire et al. 2004), suggesting that a greater abundance of adult trees indirectly facilitated *Fraxinus* recruitment.

The number of *Fraxinus* recruits in the abandoned fallows clearly declined with increasing distance to the seed source, suggesting that propagule pressure is a

significant determinant of *Fraxinus* invasion. These results are 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 Botanical gardens, was a significant correlate of invasion success of 26 introduced woody species. Estimating invasibility requires assessing disturbance, invasion potential and propagule pressure (Lonsdale 1999; Chytry et al. 2008), with propagule pressure increasingly being identified as one of the key drivers of invasion (Colautti et al. 2006; Lonsdale 1999; Chytry et al. 2008; Edward et al. 2008). In the secondary forest on the other hand, 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.

Our results also show a positive relationship between adults and saplings of *Fraxinus* and species richness of seedlings and abundance of saplings of other tree species in the abandoned fallows, but a negative relationship between *Fraxinus* and plant community diversity in the secondary forest. This supports the widespread perception that non-native species invasion is detrimental to species diversity in the long term (Groninger et al. 2004; Kremer et al. 2006). Although *Fraxinus* trees might facilitate other species in the early successional stages in the fallows, it might outcompete them and thereby decrease diversity in later successional stages. Kremer et al. (2006) found a similar trend of a decline in diversity with increasing *Fraxinus* density. These results appear to represent a general relationship between an invader and native plant communities, where high abundances of introduced species threatens native community biodiversity through reductions in colonization rates of native plants (Levine et al. 2003; Yurkonis and Meiners 2004).

One of the fundamental questions is whether introduced invasive trees are transient or persistent members of the plant community. If an invader's dominance is ephemeral, its establishment may be considered as an initial step in a series of events leading to the recovery of native forests, as seen in the fallows in this study, where *Fraxinus* appeared to facilitate other species. In this case, the community might converge to 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 endure, as suggested by the high abundance of *Fraxinus* in the secondary forest in the study area, fundamental, long lasting shifts in forest diversity patterns and community structure can result in a novel vegetation composition and assemblage (Lugo 2004).

The relationship between invasion success and competitive ability has rarely been confirmed experimentally (Davis 2003; Levine et al. 2003). Thus, the general role of species invasion as a driver of diversity decline has been challenged, since a correlation between non-native invasion and decline in diversity does not provide conclusive evidence of cause-effect relationships (Gurevitch and Padilla 2004; Didham et al. 2005). Due to the observational approach of this study, observed relationships between community properties and *Fraxinus* 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 about forest community invasibility and on 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).

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 non-native plant species. *Fraxinus* invasion appears to impact community diversity, species richness of seedlings and abundance of tree sapling 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 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.

References

- Belote RT, Jones RH, Hood SM, Wender BW (2008) Diversity–invasibility across an experimental disturbance gradient in Appalachian forests. *Ecology* 89:183–192
- Brown RL, Peet RK (2003) Diversity and invasibility of southern Appalachian plant communities. *Ecology* 84:32–39
- Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends Ecol Evol* 18:119–125
- Burke MJ, Grime WJP (1996) An experimental study of plant community invasibility. *Ecology* 77:776–790
- Chytry M, Jarosik V, Pyšek P, Hajek O, Knollova I, Danihelka J (2008) Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89:1541–1553
- Colautti RI, Grigorovich IA, Macisaac HJ (2006) Propagule pressure: a null model for biological invasions. *Bio Invasions* 8:1023–1037
- Davis MA (2003) Biotic globalization: does competition from introduced species threaten biodiversity. *Bioscience* 53:481–489
- Dawson W, Mndolwa AS, Burslem DFRP, Hulme PE (2008) Assessing the risks of plant invasions arising from collections in tropical botanical gardens. *Biodivers Conserv* 17:1979–1995
- Didham RK, Tylianakis JM, Hutchison MA, Ewers RM, Gemmel NJ (2005) Are invasive species the drivers of ecological change? *Trends Eco Evol* 20:470–474
- Ditham RK, Tylianakis JM, Gemmel NJ, Rand TA, Ewers RM (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends Ecol Evol* 22:489–496
- Dunstan PK, Johnson CR (2006) Linking richness, community variability and invasion resistance with patch size. *Ecology* 87:2842–2850
- Edward E, Munishi PKT, Hulme PE (2008) Relative roles of disturbance and propagule pressure on the invasion of humid tropical forestry by *Cordia alliodora* (Boraginaceae) in Tanzania. *Biotropica* 41:171–178
- Elton CS (1958) The ecology of invasion by animal and plants. Wiley, London
- Friday JB, Scowcroft PG, Ares A (2008) Responses of native and invasive plant species to selective logging in an *Acacia koa*-*Metrosideros polymorpha* forest in Hawaii. *Appl Veg Sci* 11:471–482
- Fridley JD, Vandermost DB, Kuppinger DM, Manthey M, Peet RK (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology* 88:3–17
- Ghersa CM, De La Fuente E, Suarez S, Leon RJC (2002) Woody species invasion in the Rolling Pampa grasslands, Argentina. *Agric Ecosyst Environ* 88:271–278
- Gilbert B, Lechowicz MJ (2005) Invasibility and abiotic gradients: the positive correlation between native and exotics plant diversity. *Ecology* 86:1848–1855
- Gorchov DL, Trisel DE (2003) Competitive effects of the invasive shrub, *Lonicera mackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree seedlings. *Plant Ecol* 166:13–24
- Gracia-robledo CA, Murcia C (2005) Comparative habitat susceptibility to invasion by Chinese ash (*Fraxinus chinense*: Oleaceae) in a tropical Andean landscape. *Biol Invasions* 7:405–415
- Green PT, Lake PS, O'Dowd DJ (2004) Resistance of island rainforest to invasion by alien plants: influence of micro-habitat and herbivory on seedling performance. *Biol Invasions* 6:1–9
- Groninger JW, Baer SG, Bassana DA, Allen DH (2004) Planted green ash (*Fraxinus pennsylvanica* Marsh.) and herbaceous vegetation response to initial composition control during the first 3 years of afforestation. *For Ecol Manag* 189:161–170
- Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *TREE* 19:470–474
- Hector A, Dobson K, Minns A, Bazeley-White E, Lawton JH (2001) Community diversity and invasion resistance: an experimental test in a grassland ecosystem and a review of comparable studies. *Ecol Res* 16:819–831
- Hejda M, Pyšek P (2006) What is the impact of *Impatiens glandulifera* on species diversity of invaded riparian vegetation? *Biol Conserv* 132:143–152
- Hejda M, Pyšek P, Jarosik V (2009) Impact of invasive plants on the species richness, diversity and composition of invaded communities. *J Ecol* 97:393–403
- Hobbs RJ, Huenneke LF (1992) Disturbance, diversity and invasion: implication for conservation. *Conserv Biol* 6:324–337
- Hooper DU, Chapin FS III, Ewel JJ, Hector A, Inchausti P, Lavorel S, Lawt JH, Lodge M, Loreau DM, Naeem S, Schmid B, Setälä H, Symstad AJ, Vandermeer J, Wardle DA (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol Monogr* 75:3–35
- Hulme PE, Bremner ET (2006) Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. *J Appl Ecol* 43:43–50
- Jackson AJH, Mccarter PS (1994) A profile of Mau forest complex. KEFCON, Nairobi

- Kinyanjui JM (2009) The effect of human encroachment on forest cover, structure and composition in western blocks of Mau forest, Kenya. Ph.D. Dissertation, Egerton University, Njoro, Kenya
- Kremer D, Cavlovic J, Bozic M (2006) Growth characteristics of introduced green ash (*Fraxinus pennsylvanica* marshall) and narrow-leaved ash (*F-Angustifolia* L.) in lowland forest region in Croatia. *New Forests* 31:211–224
- Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos* 87:15–26
- Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavorel S (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proc Royal Soc Biol Sci* 270:775–781
- Lesica P (2009) Can regeneration of green ash (*Fraxinus pennsylvanica*) be restored in declining woodlands in Eastern Montana? *Rangel Ecol & Manag* 62:564–571
- Lonsdale WM (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536
- Lugo AE (2004) The outcome of alien tree invasions in Puerto Rico. *Front Ecol Environ* 2:265–273
- Mack MC, D'Antonio CM (1998) Impacts of biological invasions on disturbance regimes. *Trends Ecol Evol* 13:195–198
- Martin PH, Canham CD, Marks PL (2009) Why forests appear resistant to exotic plant invasions: intentional introductions stand dynamics and the role of shade tolerance. *Front Ecol Environ* 7:142–149
- Mattingly BW, Hewlate R, Reynolds HL (2007) Species evenness and invasion resistance of experimental grassland communities. *Oikos* 116:361–1170
- Maundu P, Tengnas B (2005) Useful trees and shrubs for Kenya. Technical handbook No. 35. World Agroforestry Centre, Nairobi, Kenya
- Milbau A, Nijs I (2004) The role of species traits (invasiveness) and ecosystem characteristics (invasibility) in grassland invasions: a framework. *Weed Technol* 18:1301–1304
- Moira CW, Glenda MW (2005) The invasion of two Eucalypt forests by *Pinus radiata* in the Blue Mountains, New South Wales, Australia. *Biol Conserv* 125:56–64
- Nunez MA, Pauchard A (2010) Biological invasions in developing and developed countries: does one model fit all? *Biol Invasions* 12:707–714
- Ortega YK, Pearson DE (2005) Weak vs. strong invaders of natural plant communities: assessing invasibility and impact. *Ecol Appl* 15:651–661
- Pielou EC (1975) *Ecological diversity*. Wiley, New York
- Pugnaire FI, Armas C, Valladares F (2004) Soils as mediator in plant–plant interactions in a semi-arid community. *J Veg Sci* 15:85–92
- Pyšek P, Pyšek A (1995) Invasion by *Heracleum mantegazzianum* in different habitats in the Czech Republic. *J Veg Sci* 6:711–718
- R Development Core Team (2009) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <http://www.R-Project.org>
- Rejmanek M, Richardson DM (1996) What attributes make some plant species more invasive? *Ecology* 77:1655–1661
- Richardson DM (1998) Forestry trees as invasive aliens. *Conserv Biol* 12:18–26
- Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol Evol* 17:170–176
- Standish RJ, Robertson AW, Williams PA (2001) The impact of an invasive weed *Tridascantia fluminensis* on native forest regeneration. *J Appl Ecol* 38:1253–1263
- Totland Ø, Nyeko P, Bjerknes AL, Hegland SJ, Nielsen A (2005) Does forest gap size affect population size, plant size, reproductive success and pollinator visitation in *Lantana camara*, a tropical invasive shrub? *For Ecol Manag* 215:329–338
- Vila M, Weiner J (2004) Are invasive species better competitors than native plant species? Evidence from pair-wise experiments. *Oikos* 105:229–238
- Walck JL, Baskin JM, Baskin CC (1999) Effects of competition from introduced plants on establishment, survival, growth and reproduction of rare plant *Solidago shortii* (Asteraceae). *Biol Conserv* 88:213–219
- Yurkonis KA, Meiners SJ (2004) Invasion impacts local species turnover in a successional system. *Ecol Lett* 7:63–769
- Yurkonis KA, Meiners SJ, Wachholder BE (2005) Invasion impacts diversity through altered community dynamics. *J Ecol* 93:1053–1061
- Zavaleta ES, Hulvey KB (2007) Realistic variation in species composition affects grassland production, resource use and invasion resistance. *Plant Ecol* 188:39–51