

Spatio-temporal invasion dynamics of *Maesopsis eminii* in Amani Nature Forest Reserve, Tanzania

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ABSTRACT

Globally, invasive plant species cause negative impacts to human livelihoods and natural ecosystems, particularly in biodiversity hotspots. *Maesopsis eminii* invasion in Amani Nature Forest Reserve, Tanzania, was considered an ecological disaster in the 1980s. After > 50 years have elapsed since the species was first introduced in the reserve, there is yet little information available on its invasion progress. We assessed spatio-temporal invasion dynamics using forest inventory data collected in 1998 and resurveyed 60 (20 m × 50 m) sample plots in 2018. Among resurveyed plots, 30 had been invaded by *M. eminii* in 1998 and other 30 sample plots as control, which had no *M. eminii* in the year 1998. We also assessed vegetation cover change over a 20 year period between 1998 and 2018 using Landsat satellite images. Over the last 20 years, 23% of control plots were newly invaded by *M. eminii*. Tree species richness was 25% lower in invaded versus control plots ($U = 1490$, $z = 2.9$, $p = 0.04$). Large trees (DBH ≥ 31 –50 cm) of *Maesopsis eminii* were most abundant (62%) in invaded plots whereas small trees (DBH ≤ 10 cm) were most abundant (>50%) in control plots, indicating that the tree species might be prone to self-thinning. Woody species diversity was significantly lower in invaded (1.63 ± 0.49) vs control plots (1.87 ± 0.35 ; $t_{(58)} = -2.19$, $p = 0.03$). The number of *M. eminii* individuals ha^{-1} was positively associated with higher altitudes ranging above 800 masl ($\rho = 0.33$, $P = 0.011$) but there was no correlation with distance away from the forest reserve boundary ($\rho = 0.11$, $P = 0.394$;) nor with distance away from village centers ($\rho = -0.08$, $P = 0.502$). Change detection analysis indicated about 1,108 ha of non-forest vegetation had regrown into forest over the last 20 years, particularly in the south - western region of the reserve. The region included 4 sample plots newly invaded by *M. eminii*. We conclude that there is an increase in spatial distribution of *M. eminii* individuals between the year 1998 and 2018. Furthermore, *M. eminii* has low regeneration potential in already invaded sites of high invasive density and only slowly invading gaps in uninvaded sites.

1. Introduction

Biological invasion refers to a range expansion of species that were introduced intentionally or accidentally outside of their native or historic range, and that successfully spread in their new environment (McDougall et al., 2011). It is mentioned as one of the major global causes of ecosystem degradation (Liebhold et al., 2017). It is the second largest driver of biodiversity declines after anthropogenic activities (Vardien et al., 2012). The negative impacts of biological invasions are predicted to increase even further under future climatic change conditions (Thapa et al., 2018). Furthermore, the global cost caused by

invasion events sums to about US\$ 400 billion per year, assessed by crop damage, ecosystem function damage, loss of crop yields as well as investment into control and management methods (Borghesio, 1995; Chornesky and Randall, 2003). There is an urgent need to identify invasive species distribution as well as spread, particularly in Tanzania, a fragile biodiversity hotspot (Lyimo et al., 2009).

In sub-Saharan Africa, invasive plants have increased rapidly in numbers, with dire consequences not only for agriculture, livestock productivity and water security, but also for fisheries, wildlife conservation and human health (Boy and Witt, 2005). The spread of invasive plant species is damaging livelihoods, particularly in rural areas,

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aggravating poverty and hampering economic development, while at the same time irreversibly compromising biological diversity (Boy and Witt, 2005). In Ethiopia, for instance, the evergreen mesquite shrub (*Prosopis juliflora*) has formed impenetrable shrubby thickets, invading watercourses, lowering the water-table and, hence, starving other plants of moisture and nutrients, creating what is known as “green deserts” (Boy and Witt, 2005; Mehari, 2015). As another example, *Lantana camara*, now considered to be the most destructive of all widespread terrestrial invasive plants, is present in no fewer than 60 countries across sub-Saharan Africa (Shackleton et al., 2017). In Tanzania, there has been a substantial increase in biological invasions and spread of invasive plant species since the 1960s (Lyimo et al., 2009). Forest-threatening invasive species, particularly *Maesopsis eminii*, *Cedrela odorata*, *Prosopis juliflora* and *Acacia mearnsii* are replacing their native counterparts (CMEAMF, 2007; Kilawe et al., 2018). Many of these species have severely disrupted forest ecosystem processes, thereby hampering the provisioning of ecosystem services that societies depend upon. *Maesopsis eminii* is a tree species in the family Rhamnaceae, commonly known as umbrella tree (Mugasha et al., 2000). It occurs naturally in a band across Africa from Kenya to Liberia between 8°N and 6°S, where it is mainly found on the fringes of submontane forests between rainforest and savannah zones (Binggeli, 1998). The species is an early successional tree species when introduced, which easily adapts and colonizes forest gaps (Dawson et al., 2008). Within the area of its natural distribution it is found in the lowlands and extending into submontane forest up to 1800 masl (Mugasha et al., 2000).

Maesopsis eminii has been used in plantations in the lowland and grows best at altitudes from 600 to 900 masl and under mean annual rainfall of 1200–3600 mm, tolerating a dry season of up to four months (Hall, 2009). *Maesopsis eminii* was introduced in the East Usambara Mountains around the 1910s for plant growth experiments (Binggeli and Hamiltonn, 1993). Large scale planting in the 1960s and 1970s to fill logged forest gaps helped its spread into the endemic and species-rich natural forests (Binggeli and Hamiltonn, 1993). In Amani Nature Forest Reserve, *M. eminii* has been regarded as an invasive due to its fast growth rates and prolific seed production, which impoverished the natural understory scrub and herb vegetation of the forest ecosystem and changed the canopy structure and species composition (Musila, 2006) while the same species is native in Lake Victoria basin, northern Tanzania (Binggeli and Hamiltonn, 1993; Burgess et al., 2005; Hall, 1993). A recent study has shown higher mortality and retrogressive recruitment of *M. eminii* in its original area of introduction (Kilawe et al., 2018). However, up to now, there is no adequate information on the spatio-temporal dynamics of *M. eminii* invasion in the Amani Nature Reserve. Relatively dense stands of *M. eminii* have been observed in Amani Nature Forest Reserve and nearby forest reserves (Frontier Tanzania, 2001). The species is also becoming dominant in nearby agroforestry systems (Hall et al., 2011). At the beginning of this century, 15% of Amani Nature Reserve contained *M. eminii* with floristically impoverished understory vegetation, little regeneration of primary forest trees and poor animal, plant and soil fauna diversity (Frontier Tanzania, 2001). Although the invasion of *M. eminii* in Amani has raised recent concerns that it may dominate a significant area of the forest and impacts biodiversity and other ecosystem services, there is no updated information on the current spatial distribution of *M. eminii*, which is crucial for invasive species spreading quickly, particularly for predictions on future spread (Hernández et al., 2014; Pyšek and Hulme, 2005; Thapa et al., 2018).

We assessed the spatial and temporal dynamics of *M. eminii* in the Amani Nature Forest Reserve, Tanzania (Pyšek and Hulme, 2005). Based on Hall et al., (2011) and Kilawe et al., (2018), we hypothesized that *M. eminii* spread and recruitment has declined between 1998 and 2018 and expected to observe spatial differences in its expansion. We

also examined forest vegetation cover changes between 1998 and 2018 using Landsat satellite images complemented by field surveys. We quantified the current distribution, species richness and population structure and basal area of *M. eminii* in the study area along ground transects and in vegetation plot assessments. We anticipated higher species richness in sample plots which are not invaded by *M. eminii* and more invasive trees common close to village land and higher elevations. We also expected population structure of *M. eminii* to differ between sample plots with *M. eminii* and those without.

2. Methodology

2.1. Study area

Amani Nature Forest Reserve (ANFR) is located along 5°14'10" – 5°04'30" S and 38°30'34" – 38°40'06" E at 190 masl to 1,130 masl within north-eastern Tanzania (Fig. 1). The Nature Reserve, situated at the foothills of the East Usambara Mountains, forms the largest single block of forest with 8,360 ha in size (Hall et al., 2011). It is a catchment of Sigi River with sub-montane forest vegetation, lowland and plantation forests that were gazetted as a nature and biosphere reserve in 1997 (Frontier Tanzania, 2001). Its proximity to the Indian Ocean ensures high annual rainfall ranging from 600 mm to 3,000 mm and relatively stable mean temperature ranging 15 °C to 23 °C (EAMCEF, 2013). Amani Nature Forest Reserve is part of a “biodiversity hotspot”, named by Conservation International and an Endemic Bird Area (EBA), both of the sub-montane and lowland forests (Stattersfield et al., 1998). Amani forest contains 71 species of vertebrates, which are near-endemic to the Eastern Arc Mountains, and of these, nearly half are found in the lowland Coastal Forests (Mugasha et al., 2000).

In 2000, the East Usambara mountain, part of which is the Amani Nature Forest, was designated as a man and biosphere reserve (BR) by UNESCO (Kijazi et al., 2014). According to the programme, the goal of the East Usambara man- and biosphere reserve is for conservation of biological diversity, maintenance of ecosystem functions, place for learning of natural systems and traditional forms of land-use, sharing of knowledge and the co-operation in solving natural resource problems (Hokkanen, 2002). Other biosphere reserves recognized by UNESCO in Tanzania are the Lake Manyara National Park and the Serengeti-Ngorongoro ecosystem.

Maesopsis eminii has accounted for >6% of large trees in pristine forest, 30% in secondary forest and 50% in agroforestry systems of this area (Hall et al., 2011). The spread of *M. eminii* into the forest impoverishes the understory scrub and herb vegetation, altering the canopy structure and species composition, thereby modifying the regeneration environment of native species (Burgess et al., 2007). It further changes fauna species composition, and elevates soil pH (Binggeli, 1989; Binggeli and Hamiltonn, 1993; Burgess et al., 2005; Dawson et al., 2009; Hall, 1993). In agroforestry systems surrounding the forest reserve, the invasive species is used as shade tree in cardamom (*Elettaria cardamomum*), cinnamon (*Cinnamomum verum*), tea (*Camellia sinensis*) and cocoa (*Theobroma cacao*) plantations (Epila et al., 2017; Hall et al., 2011). The Forest Reserve is surrounded by twenty villages (URT, 2017), with almost half of the population located in the villages south and south-west of the reserve and about 10% living in two enclaves in the forest (Frontier Tanzania, 2001; Shoo and Songorwa, 2013; URT, 2017; Fig. 1). Communities bordering the ANFR practice small holder agriculture and cash crops (Engel, 2011). A recent survey has indicated persistent problems of timber harvesting and pole cutting, even though the people are aware of the forest conservation needs (URT, 2017).

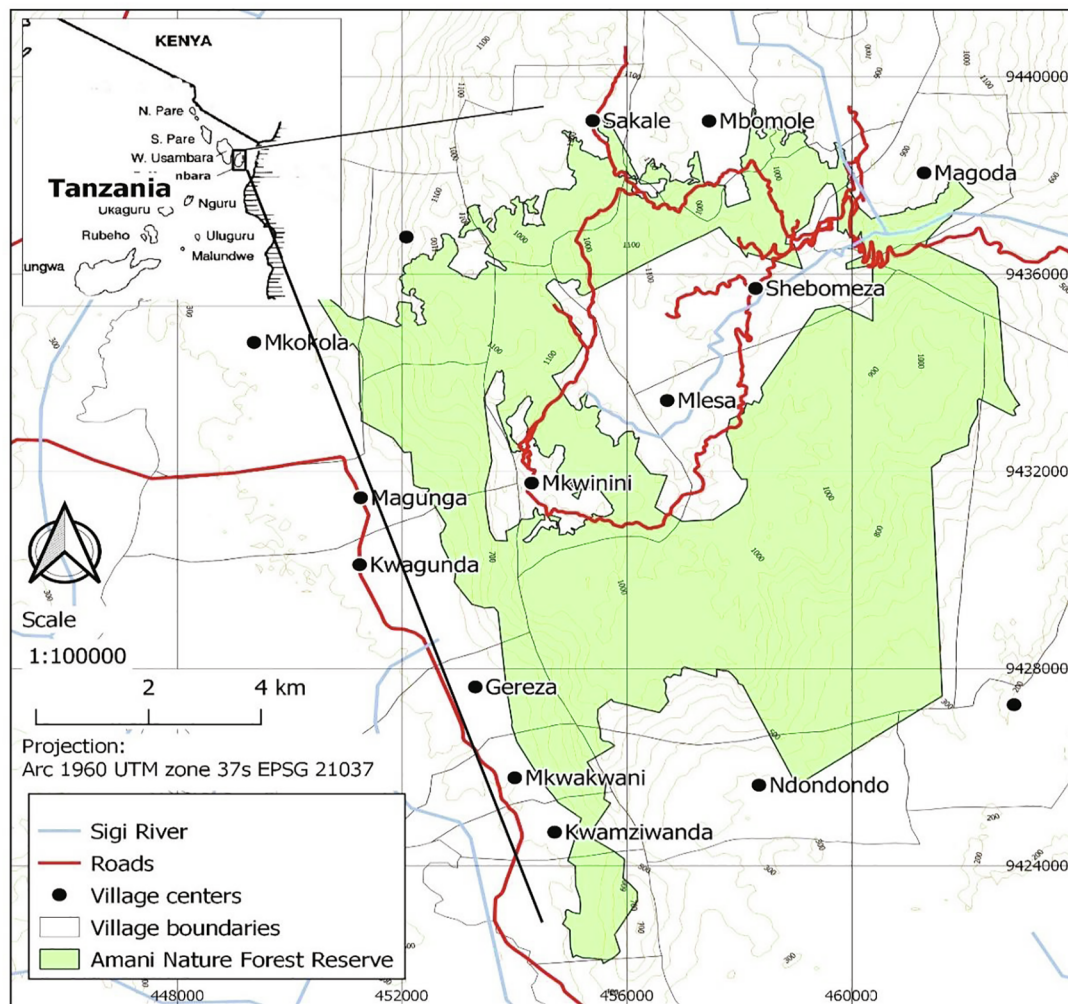


Fig. 1. Map of East Usambara mountains showing the location of Amani Nature Forest Reserve (Modified from Frontier Tanzania, (2001).

2.2. Data collection

Our forest survey adopted a study design by Frontier Tanzania (2001), and we resurveyed the same transects and plots that had been established in 1998. We surveyed the current distribution of *M. eminii* relative to other native tree species along fourteen straight line transects, 900 m apart from each other and of various lengths ranging from 0.6 km to 11 km (Frontier Tanzania, 2001). The transect lines were orientated from West to East to facilitate maximum sampling of the altitudinal variation. Vegetation sample plots were 20 m × 50 m at every 450 m along each transect. We surveyed a total of 60 plots out of 181 (33%) that had been established in 1998. We investigated 30 plots invaded already in 1998 by *M. eminii* and 30 plots that had not been invaded in 1998 (control). Resurveyed invaded and control plots were randomly distributed within the entire forest reserve, inclusion and exclusion criteria comprised of infestation status by *M. eminii* and accessibility (Fig. 2).

In each sample plot, we identified all tree species and measured diameter at breast height (DBH) for *M. eminii* trees. We also laid 10 m × 10 m sub-quadrats to assess regeneration in each sample plot, in which we identified all tree species and measured *M. eminii* trees with DBH below 10 cm (hereafter called saplings). Elevation and location of each sample plot were recorded together with woody species richness, abundance and relative density. We calculated tree species diversity in each sample plot using Shannon-Wiener index (Hitimana et al., 2004; Kijazi et al., 2014) and mapped the distribution of *M.*

emini.

Remote Sensing data of forest vegetation cover for the years 1998 and 2018 were obtained from United States Geological Survey (USGS) Earth Explorer satellite imagery archive. Landsat- 5-TM of October 1998 and Landsat-8-OLI of November 2018 were selected. Preference to Landsat imagery was due to their relatively high resolution (30 m × 30 m) and appropriate spectral designed suitability for vegetation cover analysis (Table 1).

Prior to classification, the Landsat images were re-projected to Arc UTM 1960, Zone 37S. Images were pre-processed for more direct association between the biophysical phenomena on the ground and the acquired data (Coppin et al., 2002). During image pre-processing, the Landsat layers were stacked together; clipped and radiometric calibration and image enhancement were applied. Radiometric calibration involved conversion of per pixel value to radiance and to convert radiance to reflectance, performed in Environment for Visualizing Images (ENVI) version 5.3 software (Key and Benson, 2006). Pixel-based vegetation cover classification was performed in ENVI 5.3. We used multispectral bands; 1–5 and 7 of the Landsat- 5- TM and bands 2–7 of Landsat 8 OLI images. Spectral band combination of RGB (Red, Green, Blue) color composite and true colors composite used band 4, 3 and 2 for Landsat 5 TM and band 5, 4 and 3 for Landsat 8 OLI. This band combination were clearer and different vegetation types could be easily separated. Prior to image classification, we categorized land cover into two classes: forest and non-forest. Forest was defined as a continuous stand of trees with no evidence of farming or settlement (Kilawe et al.,

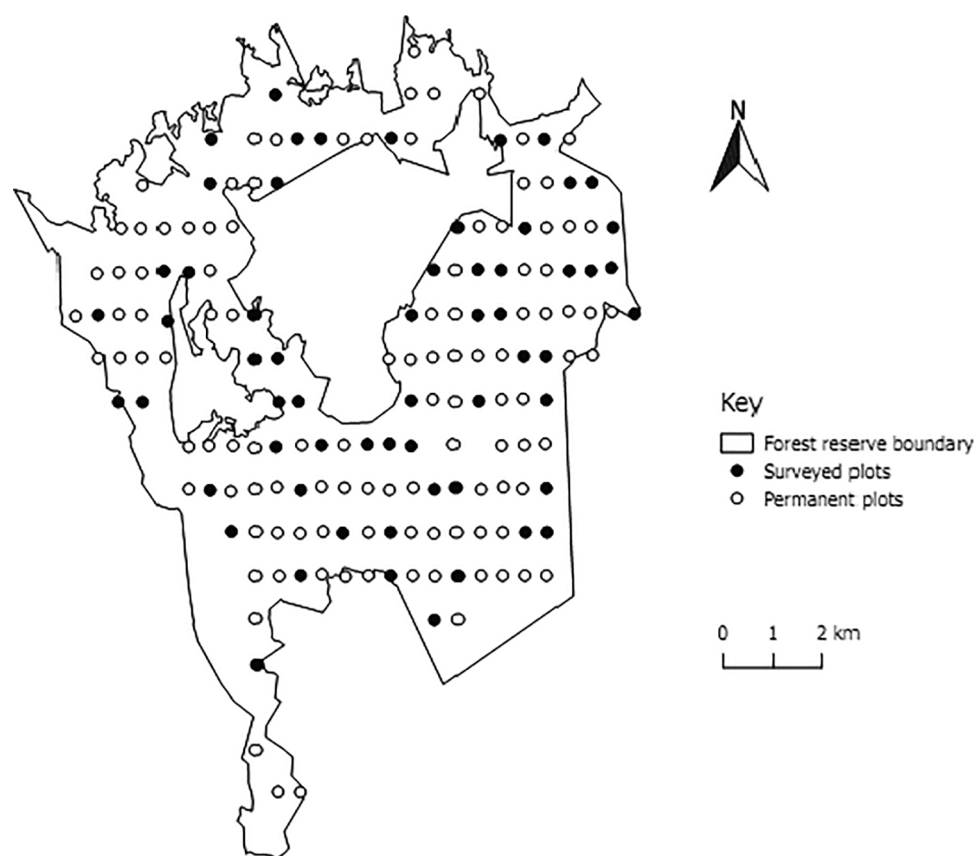


Fig. 2. Amani Nature Forest Reserve map showing permanent sample plots established (white circles) and surveyed in 1998 by Frontier Tanzania (2001) and plots revisited during this study (black circles) to monitor the spread of *Maesopsis eminii* ($n = 60$).

Table 1

Landsat Imagery properties downloaded for forest vegetation cover classification.

Type	Sensor	Path/Row	Acquisition date	Cloud cover (%)
Time 1	Landsat 5 TM	166/064	21/10/1998	0.00
Time 2	Landsat 8 OLI	166/064	15/11/2018	0.36

2018). All other cover types were defined as non-forest including but not limited to grassland, open land, agricultural fields, settlements, grassland, infrastructure and other areas of land covered with trees less than 5 m tall. Training samples for each land cover class were drawn from the images, a minimum of 50 samples for each class was considered adequate. Differentiation of classes was based on image color, tone and texture by using different spectral band combination such as true colors composite, infrared and vegetation analysis using band 4:3:2 for Landsat 5 TM and band 5:4:3 for Landsat 8 OLI where forest appear as red and non-forest as green, gray, blue or black. Land cover classification was performed in ENVI using support vector machine classifier (SVM), which is considered to give high classification accuracy (Wulder et al., 2008). We used an error matrix to assess and measure the accuracy of vegetation cover map (Wulder et al., 2008, Congalton, 1991). Every classified map was assessed by randomly collecting 254 ground truthing points for the year 2018 and 290 points for the year 1998 from respective unclassified images and assigning classes to each point based on visual interpretation. A confusion matrix was run to compare classes to the classified images based on Wulder et al. (2008).

2.3. Data analyses

Vegetation cover changes between 1998 and 2018 were captured

through change detection analysis of Satellite images. We performed Change Workflow post classification change detection in ENVI 5.3 software and produced maps and statistics indicating the area that had been converted from forested to non-forested vegetation and vice versa. Ground forest inventory and survey data were summarized, categorized and analyzed using both inferential and descriptive statistics. Individual tree species were identified at plot, species and family levels. Individual tree species were characterized in terms of species richness, abundance, density (no of trees/hectare) and diameter at breast height (DBH) classes. Species diversity in the surveyed area was presented using Shanon Wiener index while differences in species richness and DBH classes were compared using Mann-Whitney U test. The relationship between *M. eminii* density and elevation gradient, distance from forest edge, village centers and species richness were determined using Spearman's Rank order correlations. Prior to analysis, all data were tested for normality using Shapiro Wilks test. Statistical analyses were carried out in IBM SPSS version 20 and OriginPro 2015 software.

3. Results

3.1. Vegetation cover changes between 1998 and 2018

Our land cover classification indicated that forest cover had increased from 5,701 ha (68%) in 1998 to 6,778 ha (81%) in 2018 (Fig. 3). Change detection analysis indicated that 1,077 ha (13%) of non-forested vegetation cover, mostly in the south-western part and in the boundary area of the reserve, had been converted to forest while only 55 ha (1%) had been converted to non-forested vegetation over the past 20 years (Fig. 3). Overall, Producer and User accuracy assessment results for 1998 and 2018 classified vegetation cover maps reached between 95% and 100%.

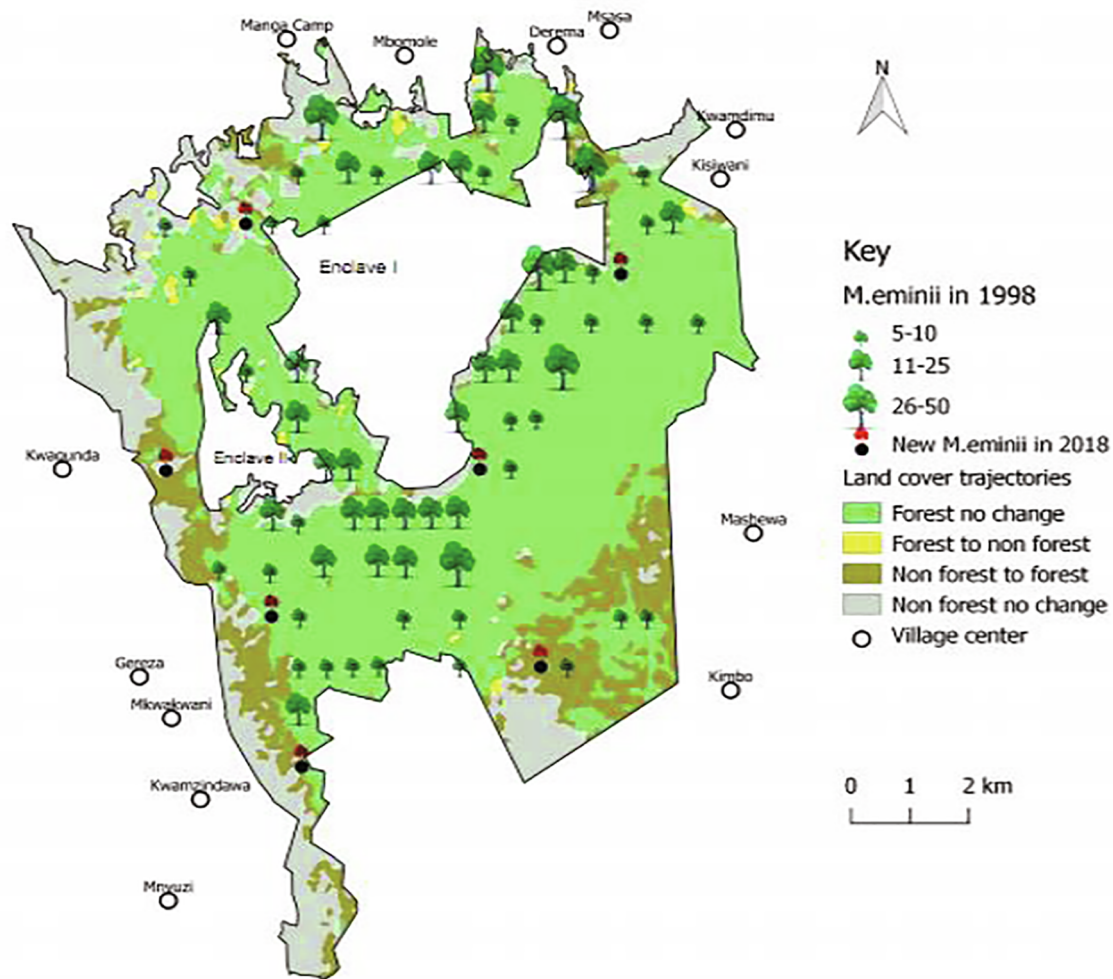


Fig. 3. Amani Nature Forest Reserve cover change map indicating vegetation class changes (forest vs non-forest) between 1998 and 2018, villages surrounding forest reserve and current (2018) distribution of the invasive species *Maesopsis eminii*, with the size of tree symbols representing different numbers of *M. eminii* trees within the sampling plot, tree symbols with red color and black dot indicates newly invaded plots. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

3.2. Change in *Maesopsis eminii* distribution

Out of 30 control sample plots that had not contained *M. eminii* in 1998, this species had invaded seven new sample plots (23%) while all plots that had been invaded in 1998 still contained same *M. emini* in the year 2018. Three of the seven newly infested vegetation sample plots were located in the south-western region of the nature forest reserve, adjacent to highly populated villages namely Kwagunda, Gereza, Mkwakwani and Kwamzindawa and Mnyuzi (Fig. 3). Half of the entire local human population in Amani is located in these villages, south and south west of the forest reserve (URT 2017). We found that *M. eminii* currently occupies 86 plots (48%) as compared to 79 plots (44%) in 1998 and out of 181 permanent sample plots in the entire forest reserve (Fig. 3). Our field survey data concurred with remote sensing data as 3 plots out of 7 newly invaded sample plots were recorded within the areas that were classified as “converted into forest”. There was an increase of *M. eminii* individual trees by 4% in the surveyed plots from 1998 to 2018 (Figs. 3 and 5).

3.3. Tree species richness and abundance

We recorded a total of 721 and 642 individual trees in invaded and control sample plots, respectively. In invaded plots, *M. eminii* species was the most dominant species with 206 individuals (29%), followed by

Cephalospathela usambarensis and *Allablankia stuhlmanii* with 87 (12%) and 65 (9%) individual trees, respectively. In control plots, the most abundant species were *C. usambarensis*, *A. stuhlmanii* and *N. buchananii*, covering 74 (12%), 69 (11%) and 62 (10%) individual trees, respectively (Fig. 4). Despite of variation in species abundance, the mean number ($\pm$ SD) of *M. eminii* per plot between invaded (0.4 ± 0.99) and control sample plots (36 ± 0.47) did not differ statistically ($t_{(118)} = 0.31$, $p = 0.761$). Control plots hosted 60 different tree species while we found only 46 tree species in invaded plots (appendix 1). We recorded a significant difference ($U = 1490$, $z = 2.9$, $p = 0.04$) in tree species richness between invaded and control sample plots. Control plots contained more native species such *C. usambarensis*, *A. stuhlmanii*, *N. buchananii*, another invasive tree *C. odorata* and many others (appendix 1). The Shannon-Wiener diversity index differed slightly but significantly between invaded (1.63 ± 0.49) and control plots (1.87 ± 0.35 ; $t_{(58)} = -2.19$, $p = 0.033$).

The cumulative mean number of *M. eminii* individuals did not differ between 2018 (0.41 ± 0.56) from that in 1998 (0.35 ± 0.52 ; $t_{(118)} = 0.51$, $p = 0.611$) but it was slightly higher in 2018 as compared to 1998 (Fig. 5).

3.4. Population structure of *Maesopsis eminii*

In invaded plots, mean DBH of *M. eminii* revealed a bell shaped

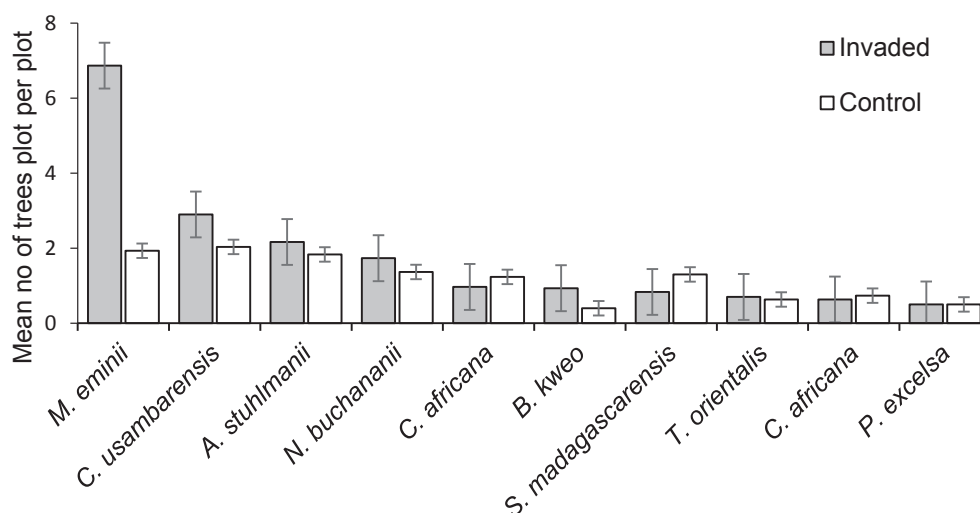


Fig. 4. Mean ($\pm$ SD) number per plot of 10 trees species in *M. eminii* invaded plots and control plots in the Amani Nature Forest Reserve. Also see appendix I for complete list of tree species in invaded and control plots. Control plots are those plots which had no *M. eminii* during 1998 survey by Frontier Tanzania, (2001).

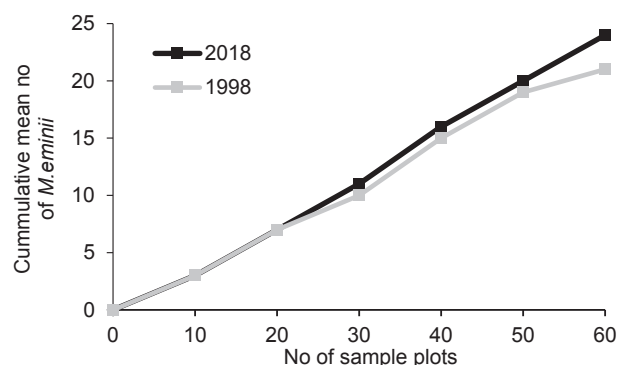


Fig. 5. Changes in the mean number of *M. eminii* stems between 1998 and 2018 in 60 (invaded and control plots) vegetation sample plots.

structure with few saplings (2%), while large trees (DBH = 31–50) contributed 62% and very large trees (DBH > 50 cm) occupied about 5% (Fig. 6a). In control plots, *Maesopsis eminii* had 26% saplings and 51% pole-sized (DBH 11–20) trees while mature (DBH > 30) trees contributed 23% (Fig. 6). Despite of this variation, we did not find a significant difference in mean DBH size between invaded plots (16.6 ± 13) and control sample plots (9.5 ± 11 ; $t_{(10)} = 1.02$, $p = 0.34$).

The number of *M. eminii* individuals ha^{-1} was positively associated

with higher altitudes ranging above 800 masl ($\rho = 0.33$, $P = 0.011$) but there was no correlation with distance away from the forest reserve boundary ($\rho = 0.11$, $P = 0.394$;) nor with distance away from village centers ($\rho = -0.08$, $P = 0.502$). However, tree species richness in general dropped slightly with increasing distance away from village centers ($\rho = -0.26$, $P = 0.047$; Fig. 7).

4. Discussion

4.1. Change in *Maesopsis eminii* distribution

Against our expectations that *M. eminii* would spread and recruitment would decline between 1998 and 2018 we found an increase in spatial distribution of *M. eminii*. Like other invasive tree species, this increase in *M. eminii* individuals was associated with changes in vegetation cover from non-forested to forested patches. This is in line with Hernández et al. (2014), who reported that invasive forest trees tend to increase their spatial range, particularly along disturbed forest edges, boundaries and gaps. We found a 13% increase in forested land since 1998, which mainly occurred in the western and northern areas at elevations below 600 masl. These areas had large proportions of non-forested land, which might be attributed to a locally large human population in villages bordering the forest reserve, intensive tree harvesting and ineffective forest management before gazettement in 1997 (Hall, 1993; Miller, 2013). This increase in forested land concurred with

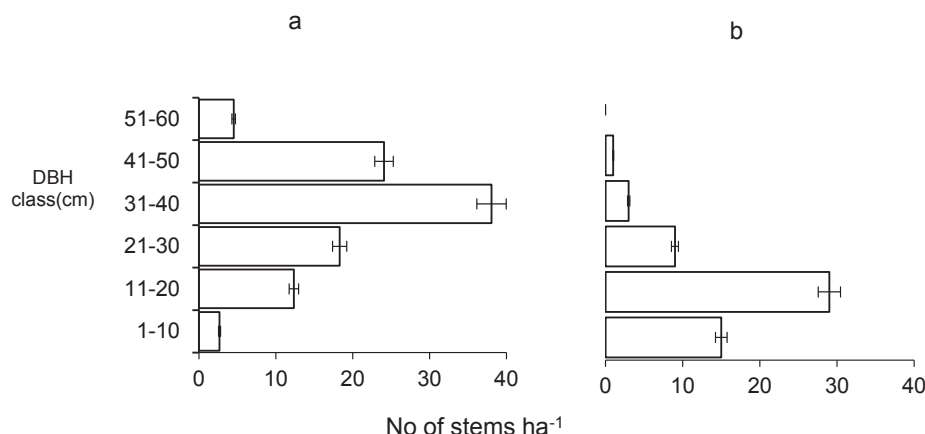


Fig. 6. Mean ($\pm$ SE) Diameter at Breast Height (DBH) distribution indicating population structure of *M. eminii* in (a) invaded plots and (b) control plots.

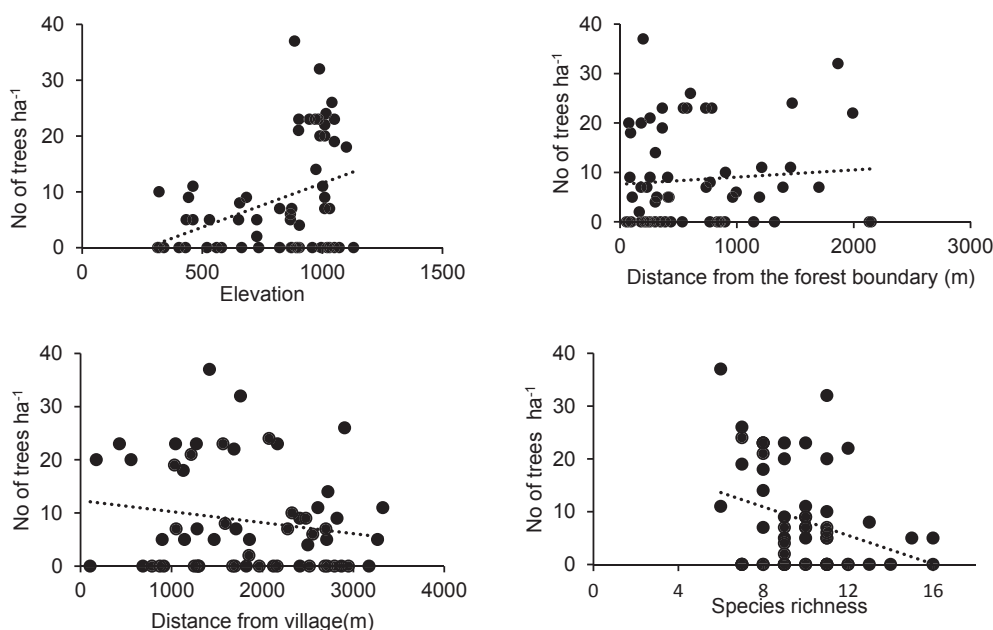


Fig. 7. Spearman's Rank Order Correlation between the number of *Maesopsis eminii* trees ha^{-1} and elevation gradient, distance from the forest boundary, distance from village centers and species richness variation in each sample plot ($n = 60$) in ANFR in 2018.

the local increase in occurrence of *M. eminii*. Agreeing with our expectation, we recorded a 23% increase in occurrence of *M. eminii* in 2018 compared to the year 1998. The increase in occurrence was recorded away from the point of introduction of *M. eminii* in the North, below the Amani rest house and as part of collection of the Amani Botanic Garden (Mugasha, 1981). A large-scale spread of the invasive in the 1970 s probably followed industrial logging and subsequent planting of *M. eminii* to restock the logged sites (Viisteensaari et al., 2000). These plantations provided a massive seed source of *M. eminii*, particularly in the established forest gaps. *Maesopsis eminii* has now also been reported to the nearby forests such as Nilo nature forest reserve (Frontier Tanzania, 2002), Mtai forest reserve and Bombo East Forest reserve (Kijazi et al., 2014), where it might be threatening the natural plant biodiversity. *Maesopsis eminii* spread escalated in the 1990s, when a high industrial activity and an increasing human population were observed in communities surrounding Amani Nature Forest Reserve (Frontier Tanzania, 2001; Hamilton and Bensted-Smith, R(edts), 1989). As a result, lowlands, forest on estate land and boundaries had been destroyed on a large scale to create plantations of sisal (*Agave sisalana*), exotic trees such as teak (*Tectona grandis*), *Grevillea robusta*, *Eucalyptus* species, *Cedrela odorata* and other agricultural crops (Hamilton and Bensted-Smith, R(edts), 1989). These activities created forest gaps, which facilitated progressive invasion and spread of *M. eminii*, particularly in Amani Nature Forest reserve (Binggeli, 1989).

In other areas, where *M. eminii* has been taken beyond its natural range, similar patterns of invasion have been noted. While studying spontaneous regeneration associated to invasiveness, Bongers and Tennigkei (2010) reported that *M. eminii* had been introduced in at least twelve countries outside its natural range. Out of these twelve countries, beside Tanzania mainland, spontaneous regeneration associated with invasiveness of *M. eminii* was viewed with major concern in Puerto Rico and Pemba island (Bongers and Tennigkei, 2010). Beentje, (1992) reported the success in *M. eminii* colonization of gaps and open areas in Ngezi forest in Pemba island, where seeds had been dispersed from stands planted in the 1980s. In these areas, a dramatic land-use change, fragmented nature of the forest, and the dependence of invasive species for both commercial and local agriculture likely contributed to the spread and naturalization of this invasive plant species (Hulme et al., 2013). Similar patterns are reported for the invasive species

Prosopis juliflora and *Cedrela odorata* in Sudan and eastern Africa, where it has exhibited vigorous growth and very wide ecological adaptability in poor soils, deforested and desertification areas (Abdulahi et al., 2017; Chornesky and Randall, 2003).

During our study, we did not find newly invaded sample plots in the closed, natural and undisturbed forests. This shows that the invasive species mainly takes advantage of disturbed sites. Further, the lack of new *M. eminii* seedlings in our plots of mature, dense stands of *M. eminii* is probably due to poor recruitment in the absence of adequate, large-scale disturbance that can create required gap size and probably enough light for germination of *M. eminii* seeds and seedling survival, leading to self-thinning (Mwendwa et al., 2019). In addition to anthropogenic effects also natural causes, e.g., tree falls can create small gaps, which contributes to dynamics of *M. eminii* (Kilawe et al., 2018). A similar ecological strategy on its spread and colonization ability was noted in other areas, where *M. eminii* is not invasive and occurs naturally, i.e., in West Africa, Togo and Nigeria, Congo and southern Sudan, southern Uganda, north-western regions of Tanzania and western Kenya (Hall, 1993). In these regions, *M. eminii* has been reported to be unable to directly invade intact forests, possibly due to a combination of fire-sensitivity and sensitivity to competition, particularly for light (Ani and Aminah, 2006). Naturally, *M. eminii* is fire-sensitive and cannot establish in dense grass communities but its vigorous early growth outcompetes other trees and shrubs (Binggeli, 1989). Similar to many other trees, *M. eminii* exhibits the "Gulliver effect", where juveniles that are suppressed by repeated topkill can be trapped in the grass flame zone for many years, resulting in a demographic bottleneck (Oliveras and Malhi, 2016).

4.2. Tree species richness and abundance

The higher species richness we found in control plots compared to invaded sample plots might be contributed by a high density of *M. eminii* individuals. This is supported by Binggeli, (1998) who linked presence of *M. eminii* in East usambara with displacement of native species such as *A. stuhlmanii*, *A. obtusifolia*, *E. usambarensis* and *G. suaveolens* in East Usambara. Similarly, Binggeli and Hamilton, (1993) found a reduced representation in *M. eminii* rich forest of many endemic tree taxa. Suppression and displacement of native and endemic species

is a typical manifestation of invasive tree species. Invasive plants have the capacity to alter the stability and productivity of forest biodiversity globally (Liebholt et al., (2017)). This mechanism facilitates exclusion of native plant species via either direct or indirect competition for resources such as water, nutrients and light. This may result in total extinction of native plant species and cascading influences on many endemic species of the forest ecosystem.

4.3. Population structure of *Maesopsis eminii*

Our analysis of the diameter size distribution in invaded plots showed increase of *M. eminii* individuals from lower DBH class to higher class. This shows that invasive species *M. eminii* has low regeneration potential and its natality is decreasing. According to Saxena and Singh (1984) population structure representing lower number of saplings indicates future decline in population. Low regeneration of *M. eminii* provides space for regeneration and increase of shade-tolerant native species such as *C. usambarensis*, and *A. stuhlmannii* are increasing in matured *M. eminii* stands as reported in Kilawe et al., (2018); and Viisteensaari et al., (2000). Unlike in the invaded plots, the study observed population structure with higher seedlings and saplings than mature individuals. Most of the seedlings and saplings were recorded in the open gaps, edges and forest boundaries indicating that the species were recruiting in these sites. A population structure characterized by a high number of seedlings, saplings, and young trees indicates the high regeneration potential of this invasive (Paul et al. (2018)).

Similar demographic structure has been recorded in other invasive tree species in other regions. In the Atlantic forest in Brazil, a fast growing invasive tree species *S. parathyba* were found with higher proportion of seedlings and juveniles in uninvaded sites than in invaded sites (Sampaio-e-Silva et al., 2015). Another study in Northeastern Thailand by Marod et al., (2012) reported an invasive tree *L. leucocephala* with DBH class distribution fitting a negative exponential growth curve with large number of trees in the small size class particularly on clear cut patches, open gaps and edges. This seem to be a general phenomenon for many invasive tree species which enhances positive net gain that expands future stable population. The findings may help in management and preventing further spread of invasive species by removing seedlings and saplings as early in their stage of growth as

possible, before they become reproductively mature.

5. Conclusion

We conclude that *M. eminii* still encroaches due to a combination of disturbance incidences, mainly forest gaps and vegetation structure. We propose that *M. eminii* is at a later stage of invasion with lower regeneration potential, particularly in high density *M. eminii* stands and, thus, might be replaced by other native understory species such as *Cephalosphaela usambarensis*, *Newtonia buchananii* and *Belschmedia kweo*. Our study, therefore, highlights areas of easy management potential to reduce this invasive. We further recommend future comparative studies of the genetic differentiation as well as biophysical factors between Amani Nature Forest Reserve, where *M. eminii* is invasive, and other areas such as lake Victoria basin, Bukoba and southern Uganda, where *M. eminii* is not invasive. This will help to ascertain whether the species has undergone rapid evolutionary change, loss of genetic variation (founder effects), hybridization or adaptation to novel environments (Hamrick and Godt, 1996). Comparative studies on biophysical factors will show any differences in environmental factors, presence or absence of natural enemies, competitors and destructive diseases. Overall, we highlight that the species should be managed in its early invasion stage and that future man-made gaps should be quickly replanted with native species.

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CRediT authorship contribution statement

Beatus A. Mwendwa: Conceptualization, Methodology, Writing - original draft, Data curation, Project administration. **Omega E. Kaaya:** Methodology, Software, Formal analysis, Visualization, Data curation. **Charles J. Kilawe:** Supervision, Writing - review & editing, Visualization. **Anna C. Treydte:** Funding acquisition, Supervision, Writing - review & editing.

Appendix 1. – Species abundance in invaded and control sites

Family	Species	Species abundance	
		Invaded plots	Control plots
Rhamnaceae	<i>Maesopsis eminii</i>	206	58
Myristicaceae	<i>Cephalosphaela usambarensis</i>	87	61
Clusiaceae	<i>Allablankia stuhlmannii</i>	65	55
Mimosaceae	<i>Newtonia buchananii</i>	52	41
Cannabaceae	<i>Celtis africana</i>	29	37
Lauraceae	<i>Beilschmedia kweo</i>	28	12
Anacardiaceae	<i>Sorindea madagascarensis</i>	25	39
Cannabaceae	<i>Trema orientalis</i>	21	19
Boraginaceae	<i>Codia africana</i>	19	22
Chrysobalanaceae	<i>Parinari excelsa</i>	15	15
Meliaceae	<i>Khaya anthotheca</i>	13	13
Rubiaceae	<i>Sericanthe odoratissima</i>	12	12
Fabaceae	<i>Albizia gummifera</i>	11	9
Meliaceae	<i>Cedrela odorata</i>	10	11
Moraceae	<i>Mesogyne insignis</i>	9	9
Lauraceae	<i>Ocotea usambaransensis</i>	8	7
Sapindaceae	<i>Blighia unijugata</i>	7	15
Chrysobalanaceae	<i>Parinari curatellifolia</i>	7	6
Euphorbiaceae	<i>Ricinodendron heudelotii</i>	6	7
Rubiaceae	<i>Rothmania manganjae</i>	5	7
Phyllanthaceae	<i>Bridelia micrantha</i>	4	6
Malvaceae	<i>Cola usambarensis</i>	4	12
Lauraceae	<i>Cryptocarya liebentiana</i>	4	6
Rubiaceae	<i>Leptactina benguelensis</i>	4	4

Urticaceae	<i>Myrianthus holstii</i>	4	28
Rosaceae	<i>Prunur african</i>	4	11
Anacardiaceae	<i>Rhus natalensis</i>	4	9
Combretaceae	<i>Terminalia sambesiaca</i>	4	4
Clusiaceae	<i>Garcinia volkensii</i>	3	7
Hypericaceae	<i>Harungana madagascariensis</i>	3	5
Euphorbiaceae	<i>Macaranga capensis</i>	3	7
Euphorbiaceae	<i>Sapium ellipticum</i>	3	7
Olaceae	<i>Strombosia scheffleri</i>	3	6
Leguminosae	<i>Acacia polyacantha</i>	2	5
Apocynaceae	<i>Dictyophleba lucida</i>	2	5
Moraceae	<i>Ficus lutea</i>	2	4
Apocynaceae	<i>Landolphia lucida</i>	2	5
Anacardiaceae	<i>Lannea schimperi</i>	2	4
Bignoniaceae	<i>Markhamia lutea</i>	2	4
Fabaceae	<i>Milletia usambarensis</i>	2	4
Lauraceae	<i>Phyllanthus inflatus</i>	2	5
Myrtaceae	<i>Eucalyptus tereticornis</i>	1	3
Malvaceae	<i>Grewia platyclada</i>	1	3
Chrysobalanaceae	<i>Maranthes goetzeniana</i>	1	3
Celastraceae	<i>Maytenus acuminata</i>	1	3
Celastraceae	<i>Maytenus holstii</i>	1	4
Fabaceae	<i>Albizia petersiana</i>	0	1
Euphorbiaceae	<i>Alchornea hirtella</i>	0	1
Icacinaeae family	<i>Alsodeiopsis schumannii</i>	0	2
Gentianaceae	<i>Anthocleista grandiflora</i>	0	2
Moraceae	<i>Antiaris toxicaria</i>	0	2
Aphloiaceae	<i>Aphloia theiformis</i>	0	2
Moraceae	<i>Aulacocalyx diervilleoides</i>	0	2
Cannabaceae	<i>Celtis philippensis</i>	0	1
Agavaceae	<i>Dracaena steudneri</i>	0	1
Putranjivaceae	<i>Drypetes gerrardii</i>	0	1
Leguminosae	<i>Erythrophleum guineense</i>	0	1
Rubiaceae	<i>Oxyanthus speciosus</i>	0	2
Olaceae	<i>Rytigynia schumannii</i>	0	2
Rutaceae	<i>Teclea amaniensis</i>	0	3

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2020.118102>.

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