Title: Deforestation and the spread of invasive species

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Abstract

Over ninety percent of Madagascar's original forests have been deforested, and the population of Madagascar has doubled in the past forty years, further exacerbating problems of local, unsustainable forest use. While research on Madagascar's endemic species is common, less information is known about its non-native species and the increasing effects they have on local biodiversity as the forest becomes more degraded. This study aimed to fill this gap in knowledge. We collected data on human forest use and the presence/absence of five non-native plant species: *Mangifera indica,* (cultivated) *Albizia lebbeck* (cultivated), *Mucuna pruriens* (non-cultivated), *Lantana camara* (non-cultivated), *Tamarindus indica* (origin unknown) in and around the periphery of the Ankarana National Park, northern Madagascar. Data was collected systematically along transects across three different forest types which ranged low to high human disturbance.   We found that the presence of historically cultivated non-native species positively correlated with human disturbance. In contrast, historically non-cultivated species did not show this correlation to human disturbance levels. Our results indicate that anthropogenic modification of habitats could impacts the densities and spread of cultivated species. This study increases understanding of the negative effects that humans have on densities of non-native species in disturbed habitats, the effects of roads and human access points, and illustrates the importance of natural history knowledge of non-native species regarding their anthropogenic cultivation histories.

Introduction

The impacts of human disturbances and non-native species on biodiversity are of increasing concern (Morris 2010). Understanding the relationship between non-native plant species and the role anthropogenic disturbance plays in their dispersal and establishment is vital to conservation efforts and management practices. Studies have shown that non-native plant densities increase as distance to human populations decrease and levels of anthropogenic damage increase (Alston & Richardson 2006; Ervin et al. 2006), and that history of agricultural and logging use has impacted non-native plant densities (Brown & Gurevitch 2004; Hill et al. 2005). Research has also found that the history of human influence, including agricultural practices, timber extraction, and recreational use has a long-standing impact on non-native plant dispersal (Alston & Richardson 2006; Ervin et al. 2006). Studies have also shown that roads and human access points increase an ecosystems vulnerability to invasion from non-native plant species, but vulnerability varies with habitat type (Arevalo et al. 2010; Birdsall et al. 2012; Haider et al. 2010; Pollnac et al. 2012). While the potential for non-native species to disperse into disturbed habitats is relatively well known, studies that quantify how different disturbances affect plant densities is less researched (Binggeli 2003). More research is needed to understand the relative impacts different types of anthropogenic disturbances (i.e. roads, historical agricultural use, small scale human use) have on a region.

Madagascar, the fourth largest island in the world and adjacent to southern Africa, has been identified as a biodiversity hotspot (Mittermeier et al. 2000; Myers et al. 2000). With a population growth rate of 2.8% (World Bank Group 2012), Madagascar's biodiversity faces severe threats, as the potential for anthropogenic damage increases. The country of Madagascar went through an extensive deforestation period from 1895-1925 while colonized by the French,

in which approximately 75% of its primary forests were cleared (Jarosz 1993). It now retains only 9.9% of its original vegetation and is one of the top five biodiversity hotspots, containing 3.2% of the world's plant species and 2.8% of vertebrate species (Myers et al. 2000). Given that non-native species may have a negative impact on endemic biodiversity and community health (Gurevitch & Padilla 2004; Walsh et al. 2012), understanding non-native plant populations in the context of the country's anthropogenic habitat use is necessary to understand the potential impacts that these plants have on biodiversity.

The arrival of humans to Madagascar occurred relatively recently, with evidence of the first human inhabitants starting in 2300 BP (Before Present) (Kull et al. 2012). Prior to this migration, species were isolated and allowed to evolve without human influence (Irwin et al. 2010). This human migration facilitated the introduction of more than 1,200 non-native plant species to the island, either accidentally or for human profit (Philippe 2011), over 70% of which have now been determined to have been used by humans in some manner (Kull et al. 2012). Despite the large number of non-native plants in Madagascar (Kull et al. 2012), most botanical scientific research on the island focused on the island's endemic plant species (Binggeli 2003). While it is generally known that the species' are reacting negatively to disturbance (Irwin et al. 2010), further research could help better inform conservation efforts locally, and identify trends and similar threats throughout similar ecosystems (Binggeli 2003).

In this study, we attempted to analyze how human use of a forest area affected the densities and localities of non-native plant species. Specifically, we aimed to find whether small-scale human disturbances or human access points were the major driving force for the successful establishment and recruitment of non-native plant species within our study site. We predicted that - due Madagascar's, level of forest degradation, and established history of agricultural use -

our study site would show a correlation between the presence of non-native species and rates of human disturbance. Understanding this relationship can help aid management efforts and deter the spread of potentially harmful invasive species in an ecosystem.

Methods

Study Site

Our research took place across a gradient of habitat disturbance both inside and on the perimeter of the Ankarana National Park (12°57' S, 49°8' E) in northern Madagascar, established in 1956 (Wilson et al. 1989) . The site provided us access to three different forest types: primary forest (forest with little evidence of substantial anthropogenic disturbance), secondary forest (forest regenerating over an extended period of time after considerable deforestation), and degraded forest (forest extensively altered by recent and historic anthropogenic disturbances) (Sewall & Andriamanarina 2012).   Research was conducted in and around the eastern region of the park, near the village of Mahamasina. The region of Ankarana is known for its high levels of diversity and endemic flora and fauna, including endangered lemur species and habitat critical for numerous other rare plants and animals, (Fowler et al. 1989; Goodman & Benstead 2003;; Wilson et al. 1989). This area encompassing the park has a history of anthropogenic modification (Sewall & Andriamanarina in submission). The region of Ankarana continued to experience extensive deforestation from commercial timber extraction throughout the 1940's, and again for a brief period in late-1988 (Wilson et al. 1988).

The perimeter of the park continues to be affected by small-scale villager extractions, regional sapphire mining, and local agricultural practices including slash-and-burn methods

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(Cardiff & Befourouack 2003; Walsh 2002). Despite our understanding of the park's biodiversity and records of past human forest disturbance, no study had systematically measured deforestation across large areas of the park and attempted to link this data to the presence and densities of non-native species. Additionally, the use of data across a gradient of habitat degradation allowed us to compare the presence and densities of non-native plants across primary, secondary, and degraded forest.

Primary forest was located within the national park boundary and had only been slightly affected by ecotourism and a short period of commercial logging in the mid-1980s (Fowler et al. 1989; Wilson et al. 1988). Degraded forest was found outside of the park boundary, had a long history of anthropogenic use along the road that led from the east entrance of the park to the park boundary (Fowler et al. 1989; Wilson et al. 1988). Secondary forest was located between the primary and degraded forests and was both within and outside of the park boundary (Sewall & Andriamanarina in submission). The determinations for each forest type were based on previous classifications (Fowler et al. 1989; Wilson et al. 1988). There were marked height and species richness differences between all three forest types at our study site (Reuter et al. in submission).

Transects

We examined a total of .604 km^2 of land; .227 km^2 in both primary and degraded forests, and .015 km^2 in secondary forests. While we aimed to make each sample area equal, secondary forest was the least abundant forest type, and we examined all of the secondary forest that was accessible to us.

Straight line transects were made at predetermined angles lying across preexisting park roads and trails to stratify sampling of habitat. Each transect was separated by at least 100m from the

previous and was marked at 10m intervals. Our primary forest patch consisted of a long thin

corridor of forest patch, approximately 10km long varying from 200-400 m in width. Transects

within the primary forest began approximately 500 m into the forest and ended about 5 km into

the forest. Transects were laid perpendicular to a well-established tourist trail that ran through

the forest patch. Secondary and degraded forest transects were laid perpendicular to main roads

leading into the park. Due to permitting restrictions, we were not authorized to clear vines and

undergrowth, resulting in variable transect lengths, however the average lengths of the transects

did not differ significantly by forest type (Kruskal-Wallis ANOVA, Chi square: 2.5572, P =

0.2784). A total of 2.27 km of transect were marked in the primary forest (n=32, average

length= 70.94m, st. dev. = 41.69m) and 2.27 km in degraded forest type (n=26, average length

=87.31m, st.dev. 52.50m). A total of 1.50km of transect were marked in the secondary forest

(n=12, average length = 125m, st.dev. = 111.07m).

Quantifying Human Impact

To measure the density of habitat modification, we recorded all visible sources of

anthropogenic impacts to woody vegetation within a 5m radius along our transects. For analysis,

'human use' was classified into two categories: 1) *damage to a tree*, and 2) *removal of a tree*.

Damage to a tree included: the presence of machete marks, presence of "tops of trees", and

branches that had been removed by human tools, but still had the primary trunk intact. "Tops of

trees" referred to the branched, foliage of trees which was often cut off or stripped from the main

trunk of a tree, and left in the forest. *Removal of a tree* indicated that either a tree had been fully

removed so that only stumps remained, or that cut down tree trunks were found that had been

shaved of their bark (in preparation for movement) but abandoned. GPS points and relative

locations to the transect, were recorded for each instance of disturbance.

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Quantifying Non-Native Species

To determine the impact of anthropogenic human use on the presence and abundance of non-native plants, we surveyed for five non-native plant species within a 5m radius of all transects: *Lantana camara* (common name: Lantana), *Mucuna pruriens* (common name: Cow Itch), *Albizia lebbeck* (common name: Lebbeck), *Tamarindus indica* (common name: Tamarind) and *Mangifera indica* (common name: Mango). *A. lebbeck* and *M. indica* are both non-native plants that were cultivated in the region, but are now considered naturalized (Kull et al. 2012) while *M. pruriens* and *L. camara* are non-native plants that were accidently introduced into the Ankarana region. *T. indica* is a woody tree species whose origin is still debated (Binggeli 2003; Kull et al. 2012). *L. camara* is an herbaceous plant species with origins in the American tropics (Bhagwat et al. 2012). It was introduced to Madagascar in 1965 (Green et al), but it is now considered naturalized and invasive (Kull et al. 2012). *M. indica* is native to India and is thought to have been brought to Madagascar by Arab traders for cultivation in the tropics (Kull et al. 2012), it is now considered naturalized. *A. lebbeck* is a woody tree species originating in India (Khare 2007) brought to the island in 1815 for religious purposes (Binggeli 2003), and is now considered invasive in the region (Kull et al. 2012). *M. pruriens* is a herbaceous woody vine species that is thought to have originated in India and southeast China (Lim 2012), although its status as a native or introduced plant to Madagascar is debatable (Kull et al. 2012).

For the two tree species, we measured their perpendicular distance to transect, height, and diameter at breast height (DBH). We included saplings with a minimum height of 1m. All sampling was done by one pair of researchers to eliminate potential bias.

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Statistical Analyses

Significant differences in habitat modification and non-native plant density across forest types were calculated using non-parametric Kruskal-Wallis tests due to unequal variances and lack of normality within the dataset. If significance was present, post hoc Steel-Dwass multiple comparisons tests were used to make comparisons between forest types. Multiple regressions least squares analysis was done to determine correlation between habitat modification and presence of non-native plants at the transect level within degraded forests. Data was log transformed to achieve homogeneity of variances. Analyses were calculated using JMP10 statistical software (JMP 10). Zero inflated negative binomial models were used to rank and analyze correlations between densities of plant species and each type of disturbance within degraded forest.

Results

Human Disturbance:

Density of human forest use changed significantly across the three forest types ($p<0.0001$, $n=69$, $r^2=.30633$, Kruskal-Wallis Non-Parametric tests), with the average number of forest damage incidents increasing from 8.743 to 72.692 to 152.391 per hectare in the primary, secondary, and degraded forest, respectively. The secondary and degraded forests had significantly higher recorded densities of human forest use than the primary forest ($p = 0.0026$, $p < 0.0001$ Steel-Dwass All Pairs Non-Parametric tests). Although the mean density in the degraded forest was more than double that of secondary, there was no statistical significance between the densities of the two forest types ($p = 0.1575$, chi-square=34.1424, Steel-Dwass All Pairs Non-Parametric tests).

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The density of evidence for *removed trees* (evidence of complete tree removal including tree stumps and abandoned logs), was significantly different across all three forest types (p<0.0001, n=69 r^2=.309184 Kruskal-Wallis Non-Parametric tests). The primary forest had significantly less evidence for *removed trees* than the secondary forest (p<0.0001) and the degraded forest (p<0.0001, Steel-Dwass All Pairs Non-Parametric tests). Results were not statistically significant between degraded and secondary forests (p=0.1557, see figure 1). The mean density for evidence of *removed trees* in the primary, secondary and degraded forests were 2.480 (std dev=10.720); 55.829 (std dev =73.296); 119.623 (std dev 123.786) per hectare, respectively.

The density for evidence of *damaged trees* (anthropogenic damage to a tree, but not complete removal of the main trunk) was significantly different across all three forest types (p<0.0001, r^2=0.160916, n=69 Figure 1B, Kruskal-Wallis Non-Parametric tests). Again, the primary forest had significantly less evidence for *damaged trees* than the secondary (p<0.0001) and degraded forest (p=0.0188, Steel-Dwass All Pairs Non-Parametric tests). The densities of *damaged trees* were not significantly different between secondary and degraded forests (p=0.5642, Steel-Dwass All Pairs Non-Parametric tests Figure 1A). The mean density of evidence for *damaged trees* in the primary, secondary and degraded forests were 6.2624 (std dev=19.8361); 16.8621 (std dev =19.3407); 32.7677 (std dev = 40.4254) per hectare, respectively.

Analysis of historically cultivated plants:

Mangifera indica: The density of mango trees was significantly different across the three forest types (p<0.0001 r^2=0.196221, n=69; Figure 2A, Kruskal-Wallis Non-Parametric tests). Pair-wise

analysis showed that mango density was significantly lower in primary forest (mean =0.00, std dev 0.00) than both secondary (p=0.0223 mean=8.1650, std dev=16.3057) and degraded forest (p<0.0001, mean=17.1697, std dev=24.1870, Steel-Dwass All Pairs Non-Parametric tests). However, density estimates were not significantly different between the secondary and degraded forests (p=.2217)(Tables 1 and 2).

Albizia lebbeck: The density of lebbeck was significantly different across the three forest types (p<0.0016 r^2=0.19411, n=69; Figure 2B). The highest densities of this plant were found in the degraded forest (mean=28.5486, std dev=36.0893) and differed significantly from the primary forest (p=0.0016, mean=4.773, std dev =8.716), but did not differ significantly between the primary and secondary forest (p=0.1780, mean=8.3708, std dev=10.6064) or the secondary and degraded forest (p=0.2915) (Tables 1 and 2).

Tamarindus indica: The density of tamarind was significantly different across the three forest types (p<0.0034 r^2=0.04832, n=69; Figure 2B). The highest densities of this plant were found in the degraded forest (mean=38.7893, std dev=38.6812) and differed significantly from the primary forest (p=0.0032, mean=18.2733, std dev =55.7368), but did not differ significantly between the primary and secondary forest (p=0.5095, mean=17.6260, std dev=30.1122) or the secondary and degraded forest (p=0.1837) (Tables 1 and 2).

Analysis of historically non-cultivated plants:

Lantana camara: The density of the lantana plant was significantly different across all three forest types (p<.0001, r^2=0.170646, n=69, Kruskal-Wallis Non-Parametric tests) (Fig 2D). Pairwise analysis showed a significantly higher density of individuals in the degraded forest, with a mean density of 144.233 individuals/hectare (std dev=234.201), than both secondary

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(14.237 individuals/hectare, p=0.00247, std dev=34.515), and the primary forest (8.854

individuals/hectare, p=0.0060, std dev=44.396) (Table 1 and 2).

Mucuna pruriens: The density of the cow itch population was significantly different across all

three forest types (p<0.0001 r^2=0.24338, n=69, Kruskal-Wallis Non-Parametric tests) (Fig 2C,

Table 2). Pair-wise analysis showed a significantly higher density of individuals in degraded

forests (mean=188.455, std dev =266.978) than both primary (p<0.0001, mean=2.381, std

dev=13.258) and secondary forests (p=0.0002, mean=2.381, std dev=8.248, Steel-Dwass All

Pairs Non-Parametric tests). No significant difference was found in cow itch densities between

the primary and secondary forests (p=0.7884) (Table 1 and 2).

Correlating invasive species densities with anthropogenic forest use:

The densities of two cultivated non-native species were correlated to human forest use. Mango

density was positively correlated with the density of anthropogenic *tree damage* per hectare

(p=.045, r^2=0.24776, n=25, multiple regression analysis). Lebbeck was positively correlated with

the density of *removed trees* per hectare (p=0.0422, r^2=0.174895, n=25, multiple regression

analysis). Interestingly, mango densities were not significantly correlated with the density of

removed trees (p=0.8531 r^2=0.24776, n=25, multiple regression analysis) and lebbeck densities

were not significantly correlated with the density of *tree damage* (p=.189, r^2=0.174895, n=25,

multiple regression analysis). Tamarind showed no correlation with density of *tree damage*

(p=.9986, r^2=.015859, n=25) or *removed tree* (p=.6627, r^2=.015859, n=25).

Zero inflated negative binomial models showed that the highest predictor of cultivated plant

densities in our study was nearest human access point (p=.00003). This was also true when

mango and lebbeck species were analyzed independently (p=.000058 and p=0.00052,

respectively), however results indicate that tamarind species densities had a positive response to tree damage (p=0.0055) and the interaction between tree damage and human access point (p=0.0040), but did not significantly respond to nearest human access point alone (p=0.1554).

In contrast to the non-native plants with a history of cultivation, the densities of non-native without a history of cultivation were not correlated with human forest use. Multiple regressions analysis showed no significant correlation between density of *Mucuna pruriens* and the density of anthropogenic *tree damage* (p=0.7745, r^2=0.028064, n=25) or the density of *removed trees* (p=0.4663, r^2=0.028064, n=25). Likewise, multiple regressions analysis showed no significant correlation between density of *lantana* individuals and the density of tree damage (p=0.2932, r^2=0.1139, n=25) or density of removed tree (p=0.8259, r^2=0.1139, n=25).

Zero inflated negative binomial models indicated that nearest human access point was the most appropriate model for determining plant density in these plants as well. However the results do not indicate a significant correlation between the non-cultivated individuals and the presence of a human access point (p=0.2588). When analyzed individually, lantana species best fit with tree damage, but showed no significant correlation between density of plant and presence of tree damage (p=0.10). Cow itch species best fit the presence of trails, but did not show a significant correlation between presence of trails and density of cow itch individuals (p=1.00).

The presence of lebbeck saplings in the degraded forest were notably higher in degraded forests than both primary and secondary forests, but also showed a presence of adult individuals not present in primary and secondary forests (Fig 3). Mango saplings were also considerably high in degraded forests, as were overall densities, but showed a similar size distribution in secondary forests. No individuals were present in the primary forest (Fig 3). Tamarind sapling density was

notably higher in the degraded forests, but individuals of all size classes were present in each forest type.

Discussion:

Non-native plants with a history of cultivation:

Mango trees are thought to be able to thrive in the Ankarana region due to the area's extensive rainfall and distinct dry season. At our study site, we found it present in the secondary and degraded forests at approximately equal densities, though it was not present in the primary forest. That adult individuals were found in both the secondary and degraded forests, likely indicates that historical cultivation influenced its presence in the secondary forest types (potentially during the period of deforestation leading up to the creation of the park in the 1950's). However, mango saplings also found in these areas indicate that seeds are being dispersed and settling into the environment. Mango seed dispersal in this region is common due to extensive human use for nourishment and medicinal purposes (Rivierie et al. 2005); it is also a food source for several lemur and bat species in Madagascar (Long & Racey 2007; Simmen et al. 2005). The fruit is well-liked in the region and we were told that it is harvested and sold in local markets when in season. As the density of human anthropogenic use has increased, so has the density of mangoes within the degraded forests. Our results show that the best indicator for this species is nearest human access point. This may suggest that while local human use (small scale logging efforts) affects dispersal, dispersal may be more strongly affected by larger impacts (the presence of human created roads and trails). Also, it is likely that due to human preference for the fruit, both young and adult trees are not damaged or removed, further allowing their spread. Interestingly, the persistence and potential spread of mango in the perimeter region of the national park may

actually provide a much-needed seasonal food source for the locally endangered crowned and brown lemurs (*Eulemur coronatus* and *Eulemur sanfordi*), which reportedly eat the fruit. Native fruit sources for these lemur species may be decreasing around the perimeter of the park due to anthropogenic forest use (Reuter et al. in prep).

Lebbeck was present in higher densities, in areas with high human disturbance (degraded forest), and this was especially true for saplings. While lebbeck is often cultivated in many countries, it is also known for its rapid growth and ability to produce seeds in dry tropical regions (Singh et al. 2004). It is likely that lebbeck will continue to disperse with increased anthropogenic use, and may become invasive. Establishment of trails and roads may also assist the spread of this species. Future presence and spread of lebbeck may be facilitated by human use (it has been used for medicinal purposes in the Ankarana region) (Rivierie et al. 2005) and by local frugivorous animals (it has been documented to serve as a food source for lemurs) (Abhau 2007; Tarnaud 2004). It is unclear what effects lebbeck may have on the endemic biodiversity. It has been noted to be beneficial to the tropical dry landscapes by providing erosion control (Singh et al. 2004), and its presence near human access points may help prevent soil erosion in the park.

Tamarind densities increased in areas of human disturbance, but were also present in a noteworthy amount in the primary and secondary forests. This may be partially explained by the controversial status of the plant as a native or non-native species (Binggeli 2003; Kull et al. 2012; Labat & J. 2003). It is an easily cultivated plant, has a wide distribution range and can thrive in various environments (Richardson 2002). Its fruit is cited for various medicinal purposes, its wood for building (Bhadoriya et al. 2011), and it has also been noted to be an important food source for lemurs, especially in times of food scarcity (Freed 2012; Sauther & Cuozzo 2009).

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Non-native plants with no history of cultivation: Cow itch requires high levels of sunlight, which may be why it was not commonly seen in the primary or secondary forests; these forests both had a significantly higher canopy height than the degraded forest. Its growth is known to suppress neighboring plant species (Kobayashi et al. 2003) and it may prevent endemic species regrowth in the secondary and degraded forests after anthropogenic disturbance. While it has been documented for use in feeding livestock and aiding in other agricultural purposes in Central America (Buckles et al. 1998), there is no evidence of such a use in Madagascar, or how it arrived and established at our study site. We suspect that its local introduction was relatively recent (sometime in the early 2000's) and its densities may be increasing. We observed the plant at lower densities in 2006 (BJS, personal observation), and park agents indicated that the species was first observed a few years before that, after extensive fire damage in the area. However, we could not significantly correlate recent anthropogenic disturbance with the densities of cow itch, though this may be due to the recent nature of its introduction to the habitat. The common names of *M. pruriens* (cow itch and velvet bean) refer to its seed pod, whose hairs can cause mild to severe itching when close to the plant, or when touched. Several park agents, who assisted us in our work, cited this plant as dissuading them from working in certain perimeter/park border regions. In addition, this plant was cited by name by a park manager whose duties included managing park programs aimed at curbing illegal park use (such as wood extraction). This park manager indicated that the recent increase in cow itch densities and the severe itching the plant causes, as well as the lack of materials for clearing the plant, have made park management more difficult. Follow-up studies on this plant would be useful in determining whether it is spreading, whether its spread is linked to human forest use, how it is negatively impacting native species, and determining best management practices.

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Lantana is known to have spread in several tropical and subtropical forests, and is known to act as an invasive species (Heleno et al. 2013). It is known as a successful invader that excludes native plant seedling germination and survival (Sharma et al. 2005) and it does not thrive in canopied forests, but often does well in open, highly disturbed habitats and near paths and roads (Prasad 2012). While we did not see a significant correlation between local disturbance and plant presence, there was a significant trend of increasing density as forests became more degraded and the plant has been known to pose severe threats to neighboring national parks in Madagascar (Green et al. WWF). We observed lantana being consumed by *Hypsipetes madagascariensis*, a widespread bird species found in all three forest types. It has also been recorded being consumed by *Eulemur coronatus* and *Eulemur sanfordi* in an adjacent protected area (Freed 2012) which could possibly provide seed dispersal services to the plant. Humans have also been known to use this plant for medicinal purposes (Rivierie et al. 2005). This species may be of increasing concern in coming years if it out-competes native and endemic species, threatening the biodiversity of the area.

From our study, it is evident that the density of non-native species are higher in disturbed environments and continue to thrive in recovering secondary forests. This is especially the case with non-native plants that have been historically cultivated. Previous studies have indicated that these species have now become naturalized and spread without the aid of humans (Kull et al. 2012). These results signify the importance of preserving primary forest, as once an ecosystem is altered; non-native species have the potential to become established into these environments. The results of this research also suggest that, for these plant species, a significant variable in determining non-native plants success is its distance to a human access point. Like other studies, this study suggests that the presence of man-made roads and trails help to facilitate the spread of

non-native species and may help them become invasive. For cultivated individuals, the most important factor in determining plant densities was consistently nearest human access points, an important consideration when proposing management and conservation practices. Understanding how anthropogenic human use can facilitate non-native species introductions and spread is particularly important in biodiversity hotspots like Madagascar, where endemic plants compete with limited and diminishing natural resources. At our study site, the historically-cultivated species are continuing to thrive in their introduced habitats in both secondary and degraded forests. This seems to be because the environmental conditions are favorable to their survival, and endemic frugivores are acting as effective seed dispersers.

In the future, mango tree species will likely spread as they are favored by humans. However, this may help provide additional food sources to endemic frugivores. Lebbeck's high number of sapling individuals could indicate future increases in the species' densities, and it may become invasive. Tamarind's varying responses to human disturbance and density may indicate its spread, but because its origin is still debated, it is unclear what effects it may have on local biodiversity. Cow Itch and Lantana plants could both become invasive, and management strategies are needed specifically for Cow Itch as it impedes park management. The already high density of both these species is also cause for concern, as they have been previously cited as invasive plants in other regions of the world. While the primary forest is currently relatively free of these non-native plants, the same cannot be said for the secondary or the degraded forests. In the primary forest, this may be evidence of Biotic Resistance against non-native plants (Maron & Vilà 2001). For some of our focal non-native plants, the plant may already be so widespread that it is not clear whether anthropogenic disturbance increases their density and their likelihood of spread. Further studies in areas with longer histories with non-native species could examine in

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more detail, how both cultivated and non-cultivated non-native plants may have the potential to affect the endemic biodiversity of a region.

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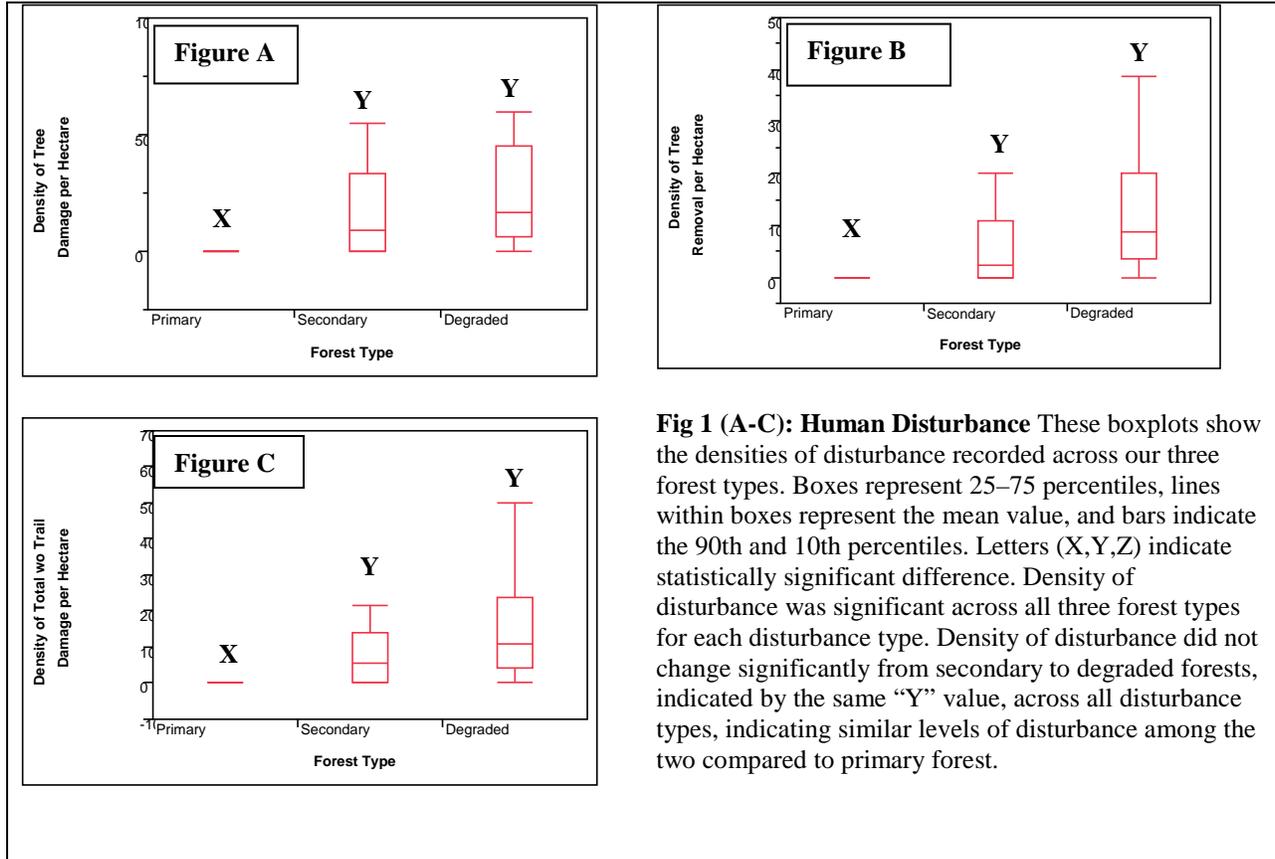**Figures and Tables**

Fig 1 (A-C): Human Disturbance These boxplots show the densities of disturbance recorded across our three forest types. Boxes represent 25–75 percentiles, lines within boxes represent the mean value, and bars indicate the 90th and 10th percentiles. Letters (X,Y,Z) indicate statistically significant difference. Density of disturbance was significant across all three forest types for each disturbance type. Density of disturbance did not change significantly from secondary to degraded forests, indicated by the same "Y" value, across all disturbance types, indicating similar levels of disturbance among the two compared to primary forest.

Figures and Tables

Table 1: Summary of Species Data per Forest Type – This table is a summary of non-native plant presence per forest type, known cultivation history, total individuals collected per forest type, mean densities, and standard deviations. P = Primary, S = Secondary, D=Degraded; C=Cultivated, NC=Not Cultivated.

Species Name	Presence per Forest Type				Sample Size per Forest Type			Mean Density of Individual/Hectare per Forest Type					
	P	S	D	C	P	S	D	P	Std Dev	S	Std Dev	D	Std. Dev
Mango	N	Y	Y	C	0	8	34	0.00	0.00	8.1650	16.3057	17.1697	24.1870
Albizia	Y	Y	Y	C	14	15	55	4.7773	8.7106	8.3708	10.6064	28.5486	36.0893
Tamarind	Y	Y	Y	C	30	93	32	18.2733	8.205	17.6260	13.399	38.7893	9.283
Lantana	Y	Y	Y	NC	6	31	235	8.854	44.396	14.237	34.515	144.233	234.201
Cow Itch	Y	Y	Y	NC	9	4	337	2.344	13.528	2.381	8.248	188.455	266.978

Table 2: Density of significance per forest type. *indicates significant difference between forest types. Significance is seen between primary and degraded forests for all forest types. No significant difference is seen between primary and secondary forests in lebbeck, tamarind and cow itch; however it is present in mango and lantana species. Significant differences are found between densities of lantana and cow itch species in secondary and degraded forests, but are not found for mango, tamarind and lebbeck individuals.

Level	Level	Mango	Lebbeck	Tamarind	Lantana	Cow Itch
Primary	**Degraded**	<.0001*	.0016*	.0032*	<.0001*	<.0001*
Primary	**Secondary**	0.0023*	.2915	.5095	.0060*	.7884
Degraded	**Secondary**	0.2217	.1780	.1837	.0247*	.0002*

Figures and Tables

Figure A — Mango Density Per Hectare vs Forest Type (Primary X, Secondary Y, Degraded Y)

Figure B — Albizia Density Per Hectare vs Forest Type (Primary X, Secondary XY, Degraded Y)

Figure C — Tamarind Density Per Hectare vs Forest Type (Primary X, Secondary XY, Degraded Y)

Figure D — Cow Itch Density Per Hectare vs Forest Type (Primary X, Secondary X, Degraded Y)

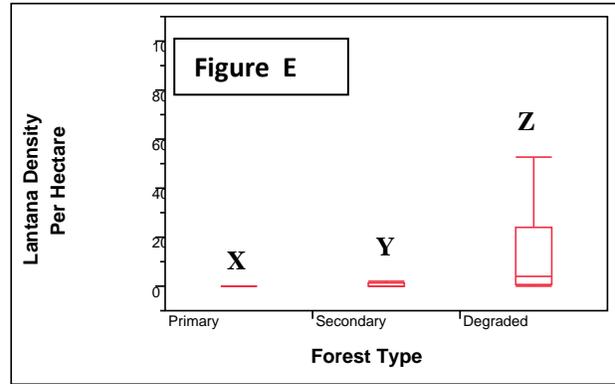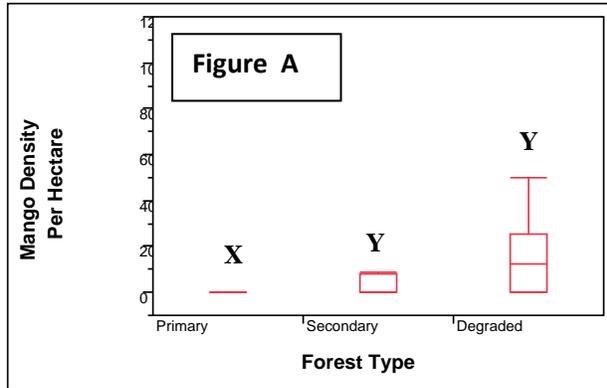Figure E — Lantana Density Per Hectare vs Forest Type (Primary X, Secondary Y, Degraded Z)

Fig 2 (A-E): Oneway Analysis of Density of Species per Forest Type

Boxplots performed on species density grouped per forest type (Primary n=32, Secondary n=12, Degraded n=25). Boxes represent 25–75 percentiles, lines within boxes represent the mean value, and bars indicate the 90th and 10th percentiles. Letters (X, Y, Z) indicate statistically significant differences. Density of individual species was significant across all three forest types for each species type. Figure A (X, Y, Y) indicates significant differences between primary and secondary forests and primary and degraded forests, but not between secondary and degraded forests. Figures B and C (X, XY, Y) indicate significant differences between primary and degraded forests, but no significant difference between either primary and secondary forests or secondary and degraded forests. Figure D(X, X, Y) indicate a significant difference between primary and degraded, and secondary and degraded but no significant difference between primary and secondary. Figure E (X, Y, Z) indicates significant differences between each forest type. All analyses were done using Steel-Dwass All Pairs Non-Parametric tests.
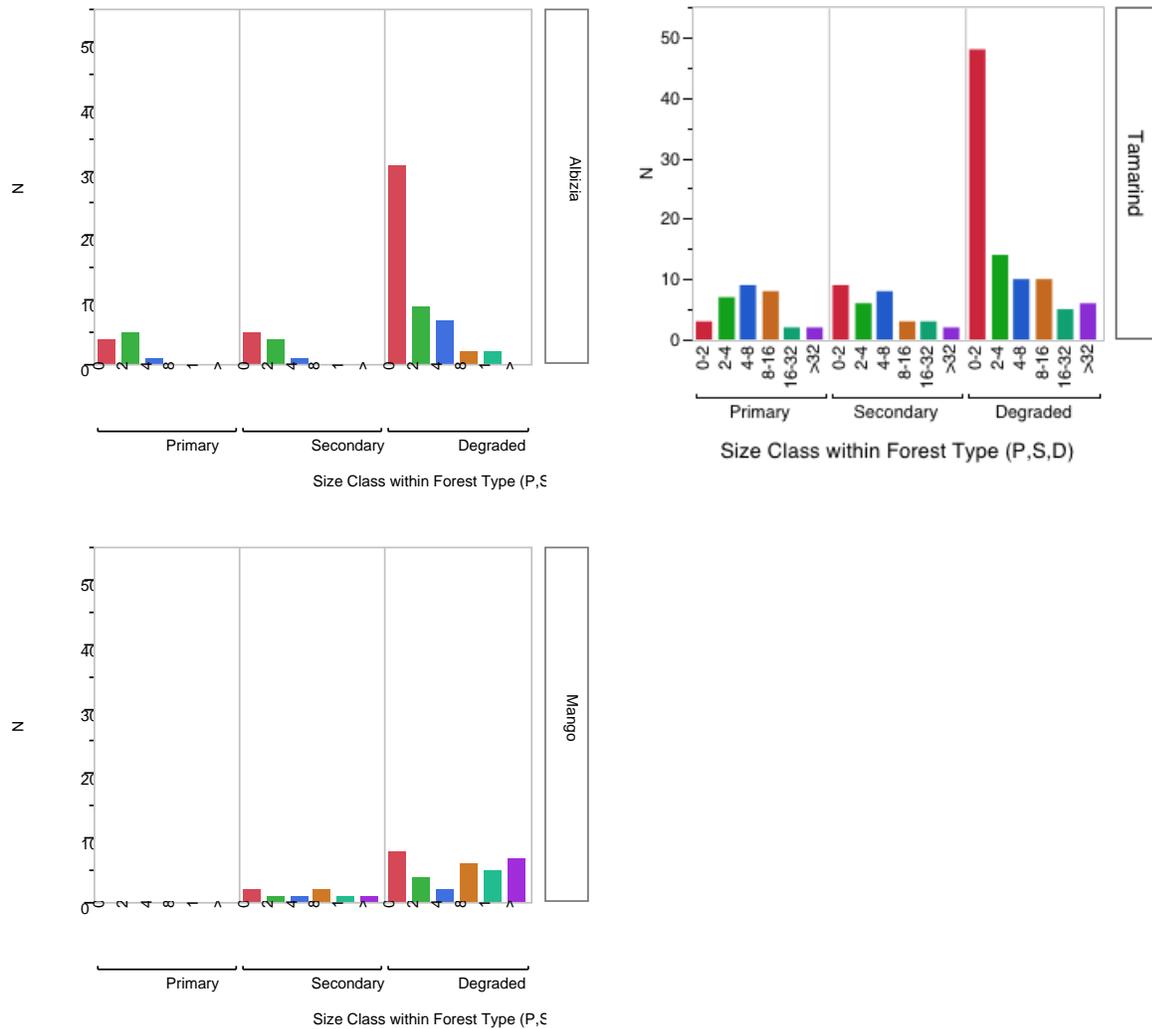
Figure 3 : These graphs show the distribution of tree size by DBH (cm) of the Lebbeck, Mango and Tamarind trees across the three forest types. On the x-axis are the log-scale size classes by forest type, and on the y-axis are the number of individuals belonging to a specific size class. Lebbeck abundance is highest in the degraded forest, and there are a large number of Lebbeck saplings in the degraded forest, as compared to the primary and secondary forest. In contrast, the Mango tree species is found only in the secondary and degraded forest. In addition, its abundances are higher in all size classes in the degraded forest, as compared to the secondary forest, and not just for saplings. Tamarind saplings were found in highest concentrations in degraded forest, but were present in all forest types. All class sizes were present in each forest type