BIOTROPICA
THE JOURNAL OF THE ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION

BIOTROPICA 0(0): 1–10 2016 10.1111/btp.12370

Forest degradation and invasive species synergistically impact *Mimusops andongensis* (Sapotaceae) in Lama Forest Reserve, Benin

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ABSTRACT

Harvesting of Non-Timber Forest Products (NTFPs) can threaten target species, especially those with limited distribution and density. Exploited species also face threats from habitat fragmentation, fire, and invasive species. We assessed the impact of human disturbances and invasive species on the population of a key multipurpose NTFP species, *Mimusops andongensis*, in Lama Forest reserve (Benin). The densities of adult trees and regenerative stems decreased with increasing degradation. *Mimusops andongensis* contributed less to total tree density with increasing human disturbance. There were significantly fewer *M. andongensis* recruits with increasing cover of invasive *Chromolaena odorata*. Smaller diameter individuals predominated in non-degraded and moderately degraded sites while in degraded sites, the structure showed a negative exponential trend with the density of small diameter individuals being less than two trees/ha. Larger individuals were also rare in degraded sites. The low density of both mature trees and seedlings in degraded sites may undermine the long-term viability of *M. andongensis*, despite existing protection against NTFP harvesting and other anthropogenic pressures. Management should emphasize facilitating recruitment subsidies and limiting the presence of *C. odorata*.

Abstract in French is available with online material.

Key words: anthropogenic pressure; biological invasion; demographic structure; diameter class distribution; Non-Timber Forest Products.

Around the world, rural dwellers near forests make use of many products known as non-timber forest products (NTFPs). NTFPs play important roles in rural households' diets, health, energy, economy, culture, and other aspects of rural well-being (Shackleton *et al.* 2007, 2011, Vedeld *et al.* 2007, Babulo *et al.* 2009, Mutenje *et al.* 2010). The widespread importance of and demand for NTFPs potentially pose many threats to the species from which they are extracted. The realization and severity of such potential threats is context specific, being the result of interacting social, economic, and biological variables (Ticktin & Shackleton 2011). Additionally, many NTFP species also face multiple pressures such as changing land use, altered fire regimes, increased herbivory from domestic livestock, and competition from invasive species. Individually, such pressures are known to alter population structures (Sinsin *et al.* 2004, Ticktin 2004, Shackleton *et al.* 2009), dynamics (Endress *et al.* 2006, Gaoue & Ticktin 2010), productivity (Sinha & Bawa 2002), and life history (Gaoue *et al.* 2013). However, our understanding of the effects of multiple stressors on NTFP population demography is limited (see Mandle & Ticktin 2012, Ticktin *et al.* 2012).

Forest degradation can be defined as 'changes within forests that negatively affect the structure or function of the stand or site over many decades, and thereby lower the capacity to supply products and/or ecosystem services' (WWF 2015). Apart from harvesting of NTFPs, other disturbances that can lead to such changes in forest include the clearing of forest lands for tree plantations and farmlands, unsustainable logging, and uncontrolled fires. However, forest degradation driven by logging and conversion into cultivated lands is the main threat faced by many forest species (WWF 2015) and represents additional major perturbation for many NTFP species. Forest degradation driven by logging and conversion into cultivated lands can lead to the loss of adults and recruits (Shanley & Luz 2003) as well as shifts in their distribution through loss of natural habitats (Broadbent *et al.* 2008). The loss of habitat through conversion of forest lands to agricultural lands is the primary cause of species population decline and extinction (*e.g.,* Bradshaw *et al.* 2009). Through loss of individuals and shifts in distribution, forest degradation exacerbates the harvesting pressures on many NTFP species populations, with consequent conservation implications (Sinsin & Sinadouwirou 2003, Yosi *et al.* 2011).

Another threat to the population dynamics and viability of many indigenous species is the colonization of disturbed and degraded habitats by invasive species (de Rouw 1991, Ticktin *et al.* 2006). The International Union for Conservation of Nature (IUCN) considers invasive species to be the most significant threat to biodiversity after habitat degradation and believes that their impacts may be permanent (Environment Canada 2012). In southwestern Ivory Coast, in degraded areas with prolonged cultivation where repeated weeding has inhibited the germination of fallow tree seeds, *Chromolaena odorata* thicket has hindered the

Received 9 June 2015; revision accepted 8 June 2016.
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establishment of dominant forest tree species (de Rouw 1991). The same has been suggested for *Lantana camara* in South Africa and India (Ticktin *et al.* 2012, Shackleton *et al.* 2013). Ticktin *et al.* (2006) also recorded that invasive species hindered population density and recruitment of several harvested NTFP species in Hawaii.

Previous studies have investigated the impacts of forest degradation (*e.g.,* Shanley & Luz 2003) and invasive species (*e.g.,* Zachariades *et al.* 2009), but few have considered the synergistic effects of these pressures. Such studies are needed to guide decisions for sustainable management and future conservation strategies. In this study, we assessed the synergistic impact of forest degradation and invasive species on the population abundance and structure of a multipurpose NTFP species, *Mimusops andongensis* Hiern (Sapotaceae), in Lama Forest reserve in Benin, West Africa. *M. andongensis* has been much exploited by people near the forest (for details, see Methods). Moreover, Lama Forest reserve has been degraded through extraction of NTFPs, wood and conversion into cultivated lands. Indeed, for many decades before the full protection of the forest in 1988, local people surrounding it exploited resources for their daily needs and cleared portions for agricultural activities (National Office of Wood [ONAB] 2011). This facilitated the colonization of degraded areas by *Chromolaena odorata* (Bonou *et al.* 2009), which competes with the regeneration, although until recently, no action was taken to control it (ONAB 2011). *Chromolaena odorata* (L.) King & Robinson (Asteraceae, Eupatorieae) is a perennial shrub originating in subtropical and tropical America and is nowadays widespread in subtropical and tropical areas worldwide, especially in degraded or open areas. This plant is a potential competitor for light and soil nutrients, especially for regenerative stems (Zachariades *et al.* 2009, Koutika & Rainey 2010).

This study investigated how the coupling of forest degradation and invasion of *C. odorata* in Lama Forest reserve affects the population abundance and structure of *M. andongensis*, an important NTFP species. We addressed the following questions: (1) how do forest degradation and invasion by *C. odorata* individually impact the population abundance and structure of *M. andongensis* in Lama Forest reserve? and, (2) is the impact of forest degradation and *C. odorata* invasion additive? We hypothesized that: (1) adults and recruits of *M. andongensis* decrease with increasing degradation; (2) *C. odorata* decreases regeneration of *M. andongensis*; and (3) forest degradation would have a more severe impact on the population of *M. andongensis* in the context of *C. odorata* invasion.

METHODS

Study species.—*Mimusops andongensis* is a medium-sized (~20 m tall) tropical tree species that occurs naturally in West and Central Africa from Senegal and Guinea-Bissau to Cameroon, Congo Brazzaville, Democratic Republic of Congo and Angola (Burkill 1985, Lemmens 2005). It is found in diverse habitats, ranging from dense forest to woodlands and savannas, but most frequently in gallery and riparian forests along watercourses. *Mimusops andongensis* is a key multipurpose NTFP species. It has been used in many West African countries such as Nigeria, Niger, Benin, and Ivory Coast for local healthcare (leaves, bark, roots, latex, young stems), alimentary (fruits, bark) and fuelwood needs (wood, young stems) (Assogbadjo 2000, Lokonon 2008). The wood is used for construction, charcoal production, carving and the manufacturing of grain stores, pirogues (boats), musical and field instruments, and hunting and fishing traps (Burkill 1985, Lemmens 2005, Lokonon 2008, Soro *et al.* 2010). In Benin, the species can mainly be found in Lama Forest reserve, which is the largest remnant of dense semi-deciduous forest in the country and represents a particular type of dense semi-deciduous forest based on its floristic diversity (Djego 2003). Due to its multipurpose uses and limited distribution, *M. andongensis* has been classified as an endangered and vulnerable species according to IUCN criteria, respectively, in Benin and Togo (Kokou & Kokutse 2007, Neuenschwander *et al.* 2011).

Study area.—We conducted the study in Lama Forest reserve, located in southern Benin between 6°56′ N and 2°08′ E at an altitude of 50–60 m asl (Fig. 1). Lama Forest has been protected by law since 1946 as a forest reserve, but the absence of a management plan allowed local farmers in search of fertile soils to extract NTFPs and wood, and to clear portions of the forest for agricultural fields. The original forest was thereby fragmented, with only 2500 ha of forest remaining in 1987. In 1988, farmers were evicted from the forest. A zoning plan was implemented, allowing the full protection of a portion of natural forest at the core of the reserve named 'Noyau central' for biodiversity conservation and scientific research.

The climate is characterized by two rainy seasons (one long from mid-March to mid-July and one short from mid-September to mid-November) alternating with two dry seasons (one long from mid-November to mid-March and one short from mid-July to mid-September). The mean annual rainfall is 1100 mm, the mean temperature varies between 25 and 29°C, and the dominant soils are clayed vertisols (Specht 2002).

The original vegetation was dense semi-deciduous forest, but has been strongly modified by various anthropogenic activities. Currently, four vegetation types have been identified in the 'Noyau central' (Bonou *et al.* 2009): (1) the typical non-degraded dense forest, where the most common species with large diameters and heights are *Afzelia africana* and *Ceiba pentandra*, followed by *Diospyros mespiliformis*, *Dialium guineense,* and *Mimusops andongensis*; (2) the degraded dense forest dominated by *Cynometra megalophylla*, characteristic of permanent humid zones; (3) the old preforest fallow, where the most common species are *Lonchocarpus sericeus* and *Albizia zygia* along with *C. pentandra*, *Ficus sur*, and to a lesser extent *Anogeissus leiocarpa*; and (4) the young preforest fallow, where the dominant species are *L. sericeus* and *A. leiocarpa*.

Regarding the abovementioned characteristics, we denoted three forest degradation levels, namely, non-degraded sites (for typical non-degraded dense forest) with no or very limited human pressure, moderately degraded sites (for degraded dense forest) with low human pressure and degraded sites(for old preforest

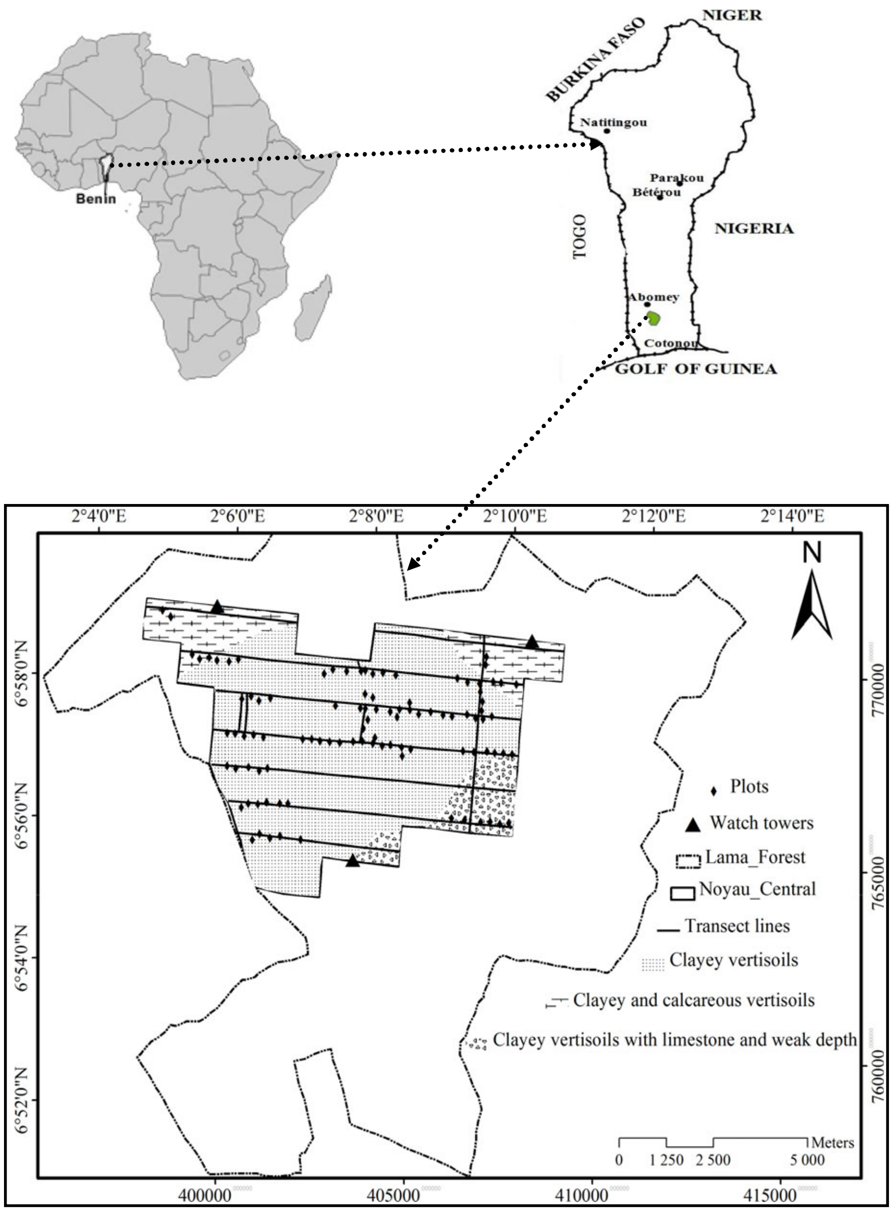

FIGURE 1. Location of Lama Forest reserve and the Noyau central.

fallow) with severe human pressure. We excluded young preforest fallow from this study, because old and young fallows represent the same level of degradation; only the time since degradation differs. Threats from NTFP harvesting, logging, and land clearance for fields are combined in each pressure level. However, the increasing anthropogenic pressure in this study from non-degraded sites to degraded sites is mainly due to the extent of land clearance for fields, which typically overrides the more selective pressures on harvesting of individual trees of *M. andongensis.*

STUDY DESIGN AND DATA COLLECTION.—To assess the structure of *M. andongensis* populations in the 'Noyau central' of Lama Forest reserve, we sampled a total of 77 rectangular plots (50 × 30 m), with 39 plots in non-degraded sites, 17 in moderately degraded sites, and 21 in degraded sites. We set the plots randomly at least 200 m apart (Laurance *et al.* 2002) following the transect lines plotted in the forest reserve (Fig. 1).

In each plot, we enumerated all *M. andongensis* individuals with dbh ≥10 cm and recorded their diameter at 1.3 m above the ground (dbh) using a forester tape and their height using a clinometer. We also measured the diameter of all other tree species with dbh ≥10 cm. We sampled ten 5 × 5 m subplots within each plot to visually estimate *Chromolaena odorata* cover and to assess *M. andongensis* regeneration by counting poles (dbh 5–10 cm), saplings (diameter at ground collar <5 cm and height ≥1 m), and seedlings (diameter at ground collar <5 cm and height <1 m).

DATA ANALYSIS.—We tested the impact of forest degradation on *M. andongensis* by analyzing variations in densities, dbh, height of trees with dbh ≥10 cm, and their contribution to the overall tree stand of the forest in density and basal area, using an ANOVA fixed-effect model with one factor (degradation, with three levels). We also analyzed mature trees (individuals with dbh ≥13.9 cm; G. Sinasson, unpubl. data on the species phenology) and regeneration densities across degradation levels. We established size class distributions for each forest degradation level by grouping individuals into 5-cm diam. classes. We analyzed the observed structures and adjusted them to a Weibull theoretical distribution (Agresti 1990, Caswell 2001). Weibull distribution can take many shapes depending on the value of the shape parameter (c) (Johnson & Kotz 1970,

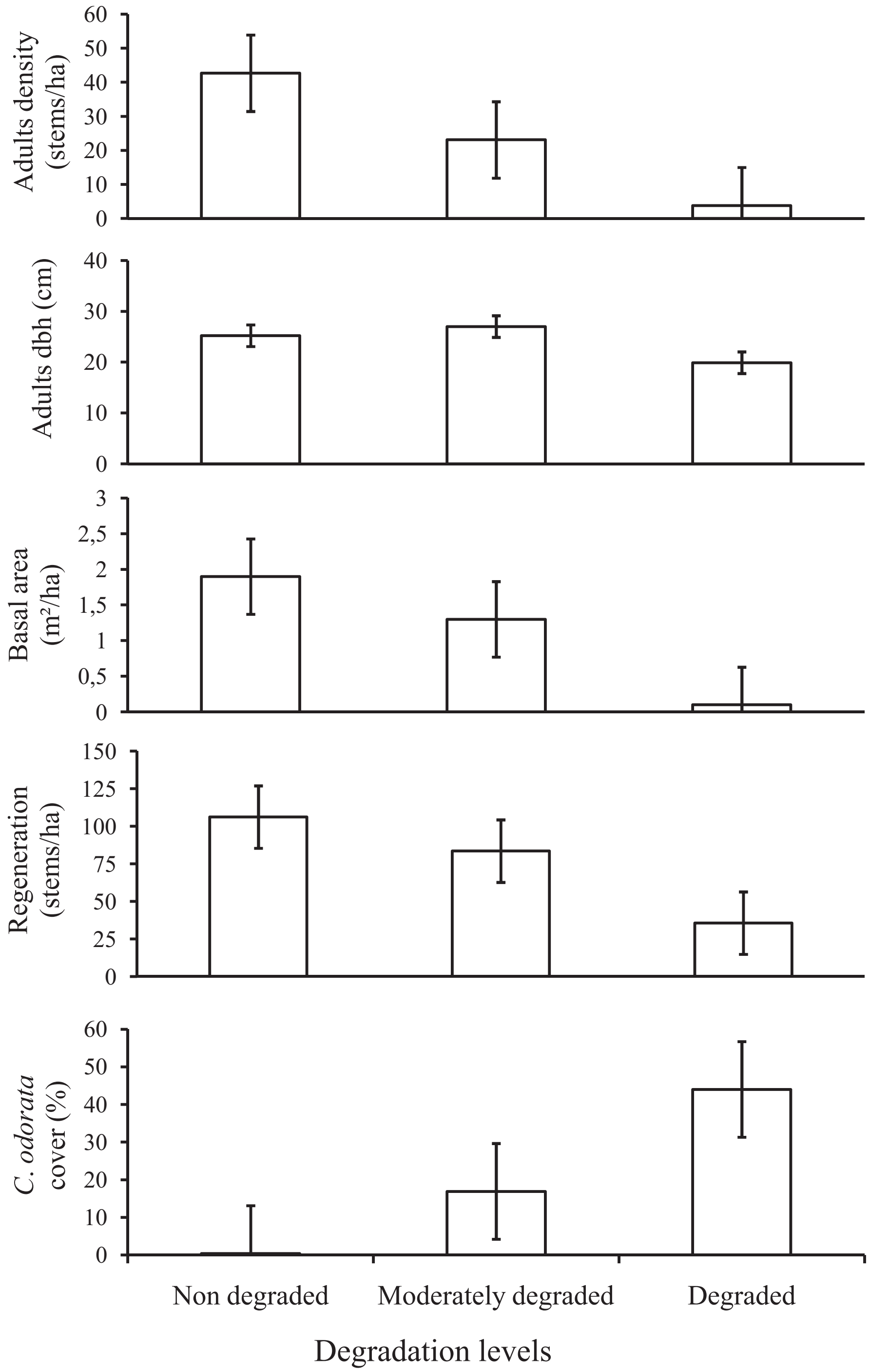

FIGURE 2. Stem density, dbh, basal area, regeneration density of *M. andongensis,* and *C. odorata* cover according to degradation levels (mean ± SE).

Rondeux 1999). We performed Log-linear analysis using SAS to test if the diameter structures were different between degradation levels.

We also assessed variation in *C. odorata* cover between degradation levels via an ANOVA fixed-effect model with one factor (degradation, with three levels). We tested its impact on *M. andongensis* regeneration (diameter at ground collar <5 cm) using GLM Poisson. We tested the synergistic impact of forest degradation and invasive species on *M. andongensis* regeneration number (diam. at ground collar <5 cm) using ANCOVA. *C. odorata* cover and degradation level were the continuous and categorical variables, respectively. We performed the analyses using R 3.1.2 (R Development Core Team 2014).

RESULTS

Dendrometric characteristics according to human pressure levels.—The density of adult trees varied significantly from 42.7 ± 35.0 stems/ha in non-degraded sites to 3.8 ± 11.0 stems/ha in degraded sites ($F_{2,74}$ = 10.67, P < 0.0001; Fig. 2). Similarly, the density of mature trees varied significantly from 33.2 ± 23.7 stems/ha in non-degraded sites to 2.5 ± 7.1 stems/ha in degraded sites ($F_{2,74}$ = 11.02, P < 0.0001). The proportional contribution of *M. andongensis* to the overall tree density of the forest in non-degraded sites was twice as high as in moderately degraded sites and eight times higher than in degraded sites ($F_{2,74}$ = 10.7, P < 0.0001).

The basal area of *M. andongensis* ($F_{2,74}$ = 12.59, P < 0.0001) and the contribution to basal area ($F_{2,74}$ = 11.38, P < 0.0001) decreased significantly with increasing human pressure (Fig. 2). Differences in mean diameter were not significant between sites, ranging from 27.0 ± 10.3 cm in moderately degraded sites to 19.9 ± 6.2 cm in degraded sites ($F_{2,74}$ = 1.14, P = 0.3, Fig. 2). Similarly, the mean height did not significantly differ between sites ($F_{2,74}$ = 0.87, P = 0.6), ranging from 17.6 ± 4.7 m in degraded sites to 15.6 ± 5.6 m in moderately degraded sites.

The regeneration density differed significantly between different sites ($F_{2,74}$ = 3.77, P = 0.03) and was higher in non-degraded sites (106.2 ± 117.2 stems/ha) and moderately degraded sites (83.5 ± 140.0 stems/ha) than in degraded sites

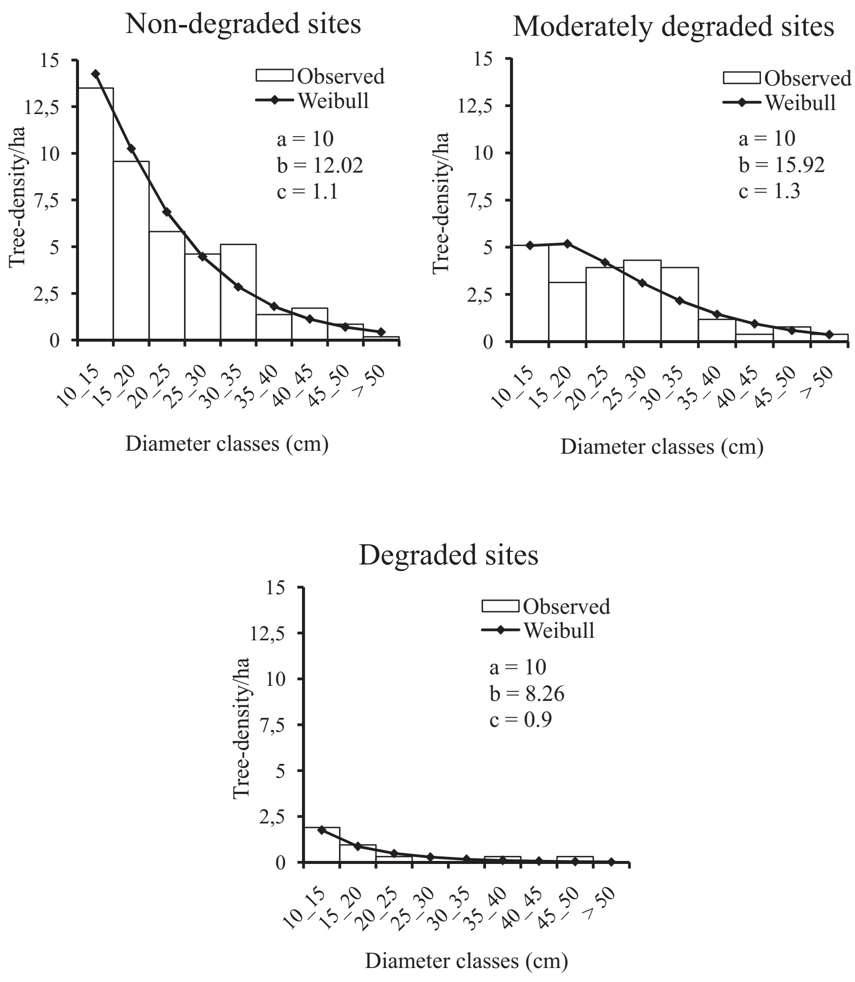

FIGURE 3. Diameter size class distributions of *M. andongensis* in the different degradation levels.

(35.6 ± 105.2 stems/ha; Fig. 2). Regeneration stems were found in 77 percent of plots in non-degraded sites, 64 percent in moderately degraded sites, and only 14 percent in degraded sites. *Chromolaena odorata* cover differed significantly between sites ($F_{2,74}$ = 55.97, P < 0.0001), being highest (44.0%) in degraded sites and lowest in non-degraded sites (Fig. 2).

DIAMETER SIZE CLASS DISTRIBUTIONS ACCORDING TO HUMAN PRESSURE LEVELS.—The diameter size class distribution of trees in the different sites were largely inverse J-shapes, characteristic of multi-species populations (Fig. 3). However, the log-linear analysis showed a difference between the degradation levels (χ^2 = 27.19, P = 0.04). The structures in non-degraded and moderately degraded sites were characterized by the relative dominance of young individuals or small diameters (1 < c < 3.6). In degraded sites, the structure was exponentially declining (c-value close to 1), with some diameter classes absent. This value of the shape parameter is characteristic of populations with high regeneration potential but with significant decreases in individuals in the subsequent dbh classes. The 10–15 cm dbh class was the most abundant in the three populations, with ~32, 22, and 50 percent of individuals in non-degraded, moderately degraded and degraded sites, respectively. However, the density of this dbh class was low in degraded sites (<2 trees/ha).

RELATIONSHIP BETWEEN *C. ODORATA*, FOREST DEGRADATION LEVEL, AND MIMUSOPS REGENERATION DENSITY.—There was a significant negative relationship between *C. odorata* cover and the number of individuals of dbh <5 cm in Lama Forest reserve (χ^2 = 23.13, df = 1, P < 0.0001; Fig. 4). We found a significant synergistic impact of forest degradation and *C. odorata* cover on the species regeneration (dbh <5 cm) density ($F_{3,73}$ = 3.10, P = 0.03; Table 1). However, the impact of degradation level alone on regeneration (dbh <5 cm) was not significant ($F_{2,76}$ = 0.97, P = 0.4; Table 1), while the impact of *C. odorata* cover while taking into account degradation levels was ($F_{1,76}$ = 7.36, P = 0.008; Table 1). Regeneration density decreased with increasing *C. odorata* cover, with a similar slope irrespective of the degradation level (Fig. 5).

TABLE 1. *Results from ANCOVA realized between* Mimusops andongensis *regeneration,* Chromolaena odorata *cover, and degradation levels.*

Source	DF	Type III SS	Mean squares	*F*-value	Pr >F
Model	3	60.43	20.14	3.1	0.03
Error	73	474.74	6.50		
Corrected total	76	535.17			
Degradation level	2	13.31	6.66	1.02	0.36
C. odorata cover	1	47.86	47.86	7.36	0.008

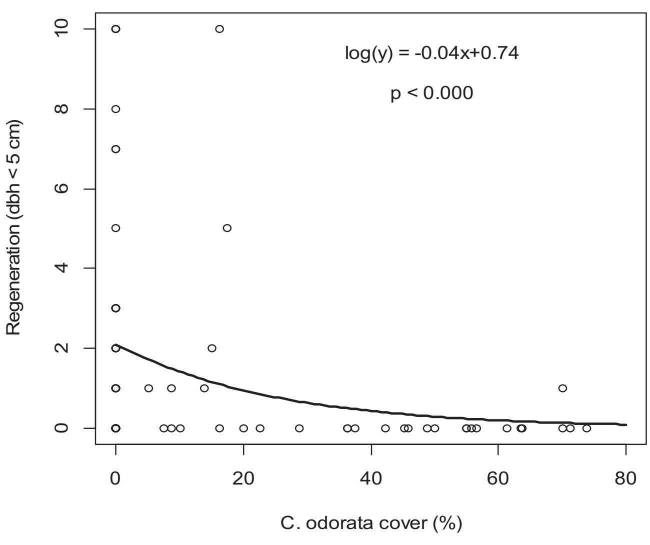

FIGURE 4. Relationship between *C. odorata* cover and *M. andongensis* regeneration (dbh <5 cm) in Lama Forest reserve.

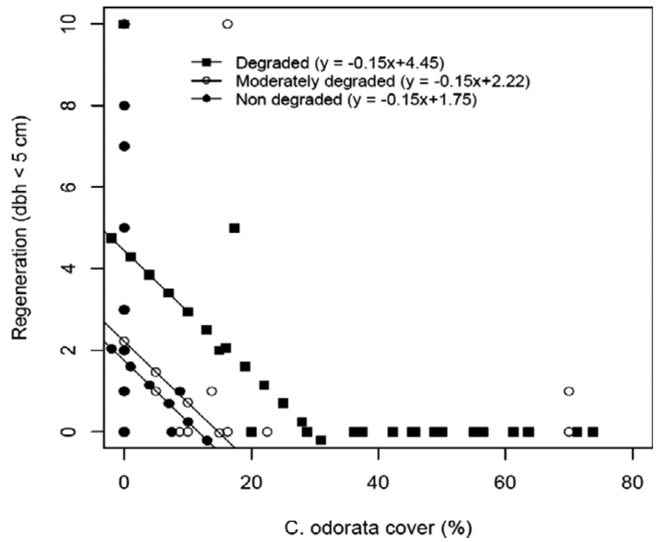

FIGURE 5. Relationship between *C. odorata* cover and *M. andongensis* regeneration (dbh <5 cm) according to degradation levels.

DISCUSSION

IMPACT OF FOREST DEGRADATION AND INVASIVE SPECIES ON POPULATION STRUCTURE.—The abundance, size, population structure, and regeneration of *M. andongensis* were negatively impacted by increasing anthropogenic pressures. Indeed, adult individuals were present in 92 percent of sample plots in non-degraded sites, 71 percent of moderately degraded sites, and only 14 percent of degraded sites. This corresponds with a declining density and basal area declined with increasing degradation. The difference between sites is due to the increasing extent of forest degradation, mainly due to land clearing for agricultural activities, and potentially exacerbated by *C. odorata* suppressing regeneration. Land clearing for agricultural activities represents the most important cause of the decrease in density of forest tree species and complementary threats to many NTFP tree species (Sinsin

et al. 2004, WWF 2015). Previous work showed a declining density of tamarind (*Tamarindus indica*) from riparian forests to farmlands in Benin (Fandohan *et al.* 2010) while in western Nepal, the overall tree density and diameter were lower in disturbed and harvested sites than in protected sites (Thapa & Chapman 2010). In contrast to our expectations, there was no significant difference in the average diameter between degradation levels. The same trend was obtained for the mean height. This may be due to selective logging of large trees in moderately degraded and degraded sites and to the abundance of small trees in non-degraded and moderately degraded sites.

The highest regeneration densities were found in non-degraded and moderately degraded sites. The same trend was observed by Fandohan *et al.* (2010), who recorded a lower regeneration density of tamarind in habitats with high human pressure than in areas with low or medium pressure. The difference in regeneration density may also be explained by the lower density of sexually mature trees (individuals with dbh ≥13.9 cm; G. Sinasson, unpubl. data) in degraded sites than in the other sites. Indeed, a low density of sexually mature trees, resulting in low seed number, can weaken regeneration. The scarcity of tamarind regeneration in farmlands has been linked to the reduction of mature tree density in Benin, the authors arguing that land clearing, fire, and removal of mature trees may significantly affect seedling establishment and thereby threaten population viability (Fandohan *et al.* 2010). Similarly, the rarity of *Dipteryx odorata* seeds due to their collection in the Tapajos National Forest in Brazil has depleted young individuals (Herrero-Jauregui *et al.* 2012). However, it is unknown what might be the threshold density requirement. The low density of regeneration in more degraded sites may also be due to competition with invasive species. We found a significant negative relationship between *C. odorata* cover and the density of regeneration, suggesting the invasive species may compete with recruits, as has been reported in other contexts. For example, indigenous forest seedlings are suppressed by the invasive shrub *Lantana camara* (Jevon & Shackleton 2015), and removing *C. odorata* in a degraded forest in Ghana allowed the development and growth of indigenous tree species seedlings (Honu & Dang 2000). Invasive species impact natural regeneration mainly through not only direct competition for available resources but also through allelopathy (Orr *et al.* 2005, Adams & Engelhardt 2009). For example, *Microstegium vimineum* reduces the recruitment of native woody species by colonizing disturbed environments in moist forests in southern United States (Oswalt *et al.* 2007). Similarly, *Elaeagnus umbellate* can affect the recruitment of common successional species, such as *Acer saccharinum*, *Populus deltoides*, and *Platanus occidentalis,* through allelopathy (Orr *et al.* 2005). Invasive species can also disrupt existing ecological associations (such as mycorrhizal associations) on which native tree species regeneration depend or reduce the density of arbuscular mycorrhizal fungi (Smith & Read 2008).

Other factors, such as biotic and abiotic characteristics and predation, also influence the regeneration density of plant species. Physiological traits of a tree species can affect the production of fruits or viable seeds from which young individuals emerge, since these characteristics determine the success in plant reproduction (Maharjan *et al.* 2011). Adverse ecological or climatic conditions can hinder seed germination and seedling development and growth (Wiegand *et al.* 2000). Trees infection resulting in the production of infested seeds can also hinder seed germination (G. Sinasson, personal field germination assays). Nonetheless, the scarcity of mature trees due to anthropogenic pressure, along with *C. odorata* cover, remains a significant factor explaining the weakness of the regeneration in degraded areas. Forest tree species can regenerate and overcome the impact of *C. odorata* if there are enough seeds in invaded areas (de Rouw 1991). Moreover, tree seedlings can survive in unfavorable conditions created by *C. odorata* (Honu & Dang 2002).

We found a significant difference in the diameter size class distribution between degradation levels, with more degraded sites showing a negative exponential trend. The first class size (dbh 10 - 15 cm) is the most abundant in the three degradation levels. However, its density was very low in degraded sites (nearly two stems/ha). The low presence of trees with dbh 10–15 cm in more degraded sites, even after 25 years of strict protection of Lama Forest, may be linked to the low density of regeneration, as they come from sapling growth (Assogbadjo *et al.* 2009). Trees with dbh more than 15 cm were also scarce in degraded sites (less than 1 stem/ha) while in non-degraded and moderately degraded sites, they were more abundant. The degradation of the forest by increasing human pressure in degraded sites probably explains the rarity of individuals with dbh >15 cm. Trees with dbh >15 cm probably represent sexually mature individuals likely to produce seeds for regeneration. Thus, the rarity of such individuals may account for the low regeneration density in more degraded sites. However, this dbh size is to be confirmed by ongoing studies on the phenology of the species.

Implications for species management and conservation.—Forest degradation and invasion by alien species are the two most important threats not only to NTFP species but to many other forest tree species as well (WWF 2015). Thus, understanding how these two factors simultaneously impact tree species is of great importance for biodiversity conservation.

Our findings showed significant synergistic impact of degradation levels and invasive species on the regeneration (dbh <5 cm) of the study species and confirmed that both factors significantly affected the population abundance and structure of NTFP tree species. We also found a decreasing density of mature trees with increasing degradation. Moreover, the invasive species cover increased with increasing forest degradation. As the low presence of seeds due to the reduction of mature trees can also justify the scarcity of regeneration (Fandohan *et al.* 2010), our results suggest that emphasis should be placed not only on protecting forests against further human pressures (de Rouw 1991) but also on increasing the availability of seeds (and thus the future availability of mature trees) and on eliminating competing invasive species. Similar conclusions have been drawn by Ticktin *et al.* (2012), who suggested that management focused only on the interruption of fruit harvest in Indian protected areas is not effective for

conservation of *Phyllanthus emblica* or *P. indofischeri*. For *M. andongensis* in Lama Forest reserve, after more than 25 years of protection, we observed its almost complete absence from most degraded sites and no regeneration of the species in plots lacking its trees.

The observed negative relationship between invasive species cover and regeneration density suggests invasive species may threaten the long-term viability of *M. andongensis*. Even if the seeds are dispersed into degraded areas, competition with invasive species may hinder the recolonization of degraded areas. Invasive species suppress the regeneration of other tree species (Ticktin *et al.* 2012, Shackleton *et al.* 2013, Jevon & Shackleton 2015), and their impacts may be manifest in the long term as recruitment dwindles. This could result, in time, in relatively even-aged stands of mature individuals, which are undesirable because of their increased potential for age-related phenomena such as death and threats that affect a large proportion of the population (Elena *et al.* 1992). In addition, populations with low recruitment become vulnerable to other pressures such as fires and diseases, which result in mortality of stems and recruits (Marod *et al.* 2004, Vieira & Scariot 2006). Climate change may also increase the incidence of, and susceptibility to fires and diseases (Moser *et al.* 2010), as well as the aggressiveness of invasive species (Willis *et al.* 2010). The impact of invasive species may be more severe in situations of low adult densities and recruitment, as we found in the degraded sites.

Overall, our study highlights the importance of taking into account multiple pressures when studying the impacts of anthropogenic pressure on population demography and structure of key or threatened species, given that they may have complementary impacts. Understanding simultaneous effects can also enhance and target appropriate interventions to conserve species at risk (Mandle & Ticktin 2012, Ticktin *et al.* 2012). Most studies on the impact of human pressure have dealt separately with the two factors examined in our study (Oswalt *et al.* 2007, Herrero-Jauregui *et al.* 2012). *Chromolaena odorata* is not the only factor hindering and limiting the regeneration of forest tree species in degraded areas. The absence of mature trees due to forest degradation, along with factors preventing seed germination or development of recruits, may strongly limit the survival of population of tree species. Consequently, forest managers should also focus on the availability of seeds and perhaps consider human-assisted natural regeneration and introduction of seedlings (for species with scarce seeds) rather than focusing only on eliminating invasive species (Honu & Dang 2000). Thus, studies on the sylviculture of local species may be of great importance. Vegetative propagation tests could help grow species in agroforestry systems to sustain their use by local communities and for conservation. Furthermore, integration of useful species while planning forest management may be useful for population conservation.

ACKNOWLEDGMENTS

We thank M. Hounsa, H. Kanlissou, C. Affoukou, and local communities for their help during fieldwork, A. Natta for support, and K. Schreckenberg for her comments on an earlier version of this manuscript. We are also grateful to F. Azihou and W. Bonou for their assistance with statistical analyses. This work was supported by International Foundation for Science grant D/5467-1 to KGSS and, OWSD and SIDA through a Postgraduate Fellowship to KGSS. Anonymous reviewers provided useful comments that improved the manuscript.

DATA AVAILABILITY

Data deposited in the Dryad Repository: http://dx.doi.org/10.5061/dryad.d1m02 (Sinasson *et al.* 2016).

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