

Diversity, Disturbance Ecology, and the Ecological Characteristics of Commonly Exploited Timber Species – Recommendations for Peruvian Forestry

By ES

Introduction

The Peruvian forestry sector targets certain species for their high economic values for production as export commodities. The demand for these economically valuable species led to the development of highly selective logging practices that incorporate huge geographic areas in the search for only a few species. Studies regarding the ecological characteristics of the species extracted for timber are both lacking and under utilized by the timber industry for the purposes of sustaining future populations of the targeted species. The commercial extirpation of species like Mahogany and Tropical Cedar is a direct result of the combination of unsustainable harvest intensities and a lack of ecological knowledge. The diversity and heterogeneity of lowland Peruvian rainforests, which remains poorly understood, is critical to understanding rainforest functioning and to identifying areas of suitable habitat for many important species. The local, landscape, and regional environmental heterogeneity of the lowland Peruvian rainforests renders one overarching management strategy incapable of creating a sustainable forestry system. The recognition and incorporation of species-specific ecological constraints and characteristics into management plans are necessary steps to make the Peruvian forestry system both economically and environmentally sustainable. Therefore, knowledge of local diversity and heterogeneity needs to be the crux of forestry management plans in a new and reformed forestry system.

This paper is focused on providing general information on the multi-scalar diversity found in tropical forests, highlighting the most important disturbance dynamics present in the lowland forests of Peru, and identifying individual species that are targeted by the forestry sector. Information regarding how species interact amongst other species, how they regenerate, and how they are distributed is critical to understanding how they react to disturbance, and thus how their extraction should be managed. The information regarding species-specific ecologies should be incorporated into solutions designed to sustain the populations of over-exploited species. This information should ultimately be used to identify species more suited to sustainable management.

Methods

My approach to writing this paper was to find and analyze literature that examines the ecological themes associated with Peruvian Forestry. My research began as a general examination of the Peruvian Forestry system in order to determine the amount to which the system addresses rainforest ecology and ecological issues. In the beginning I searched for literature about the diversity and complexity of tropical rain forest ecosystems in our specific region of Amazonia. The topics examined in this research include all scales of diversity, forest community composition, and specific disturbance phenomenon. Next, I searched for literature on the ecology of commonly logged, economically valuable timber species. Although my findings on rainforest ecology, diversity, and tree specific ecology consisted the majority of my study, more analysis was needed to synthesize the ecological information into some kind of recommendation to Peruvian Forestry officials that highlighted the important ecological issues while providing possible solutions. After all, the research that our class is conducting needs to be informative, while concurrently providing some kind of solution to a system-wide problem.

Literature Review

The work of Pitman, Nuñez, and Condit was particularly important for my understanding of diversity and environmental heterogeneity in the neotropics. I relied on three studies by Pitman that focused upon the complexity and beta-diversity observed across the Amazon basin, and, in particular, in Peru and Ecuador. The work of Pitman was also instrumental to my findings on the role that disturbance plays in Amazon. Pitman's table that represents the classification scheme of rare species in the Amazon, which can be found as Figure 1 in the appendix, greatly contributed to my understanding of species composition and rarity. Nelson, Brokaw and Uhl made significant contributions to my analysis of forest blowdowns and gap dynamics respectively, with Nelson's article producing a particularly important map (Figure 2). Gullison, Salo, and Brown, all scholars who study Mahogany, Tropical Cedar, and other important but over-exploited species, studied the role that river bend migration plays in disturbance and contributed valuable information regarding the relationship between the form of disturbance and the ecology of Mahogany and Tropical Cedar. Laura Snook is another researcher who studies Mahogany regeneration and its relationship with river migration

and other disturbances. Two of her articles made significant contributions to my study. Nick Brown and James Grogan conducted other research concerning Mahogany that was incorporated into my paper. Nick Brown's research on the biogeography of Mahogany includes a figure in the appendix of this paper. Louis Putzel authored the only article concerning Shihuahuaco that made a significant contribution to the paper. His work should be recognized as one of the first and most extensive studies regarding the ecology and extraction of *Dipteryx spp.* Multiple authors contributed to each species-specific examination, but Edson Leite's article on *Amburana cearensis* and Mark Schulze research on *Tabebuia spp.* were of particular importance to their respective topics. Graphs from Mark Schulze's article appear in the appendix of this paper. Furthermore, many authors and researchers outside the realm of forest and rainforest ecology contributed to this paper, including avian biologist Donald Brightsmith and molecular ecologist J. R. Russell.

Analysis

Diversity

For many years, the common perception of neotropical rainforests was that their complexities made the ecosystem's structure and composition impossible to predict. This was due to the fact that local, isolated scales comprised most of the studies regarding the commonness and rarity of tree and species communities in the Amazon. Recent studies that explore tree species abundance and diversity at multiple scales, such as those conducted by Nigel Pitman, reveal that small proportions of common species typically dominate forest community composition by accounting for more than half the trees at local (1 ha), landscape (100,000 km²), and regional (10,000,000 km²) scales (Pitman, et al. 2001). These common species, with both high local densities and high landscape and regional frequencies, form an oligarchic forest structure that stretches across the Amazon basin (Pitman, et al. 2001). This study found that around 150 "common" species dominated forests plots in Ecuador and Peru, and 30% of these species were common species in both locations (Pitman, et al. 2002). Most of the tree species found in the study were at densities of less than one individual per hectare, but these locally and regionally rare species only accounted for a small minority of individual trees within each sampled area (Pitman, et al. 2001). In the lowland forests of Madre de Dios, Peru, none of the

sampled species were known to occur exclusively in Madre de Dios, only 15% of the species were restricted to one forest type, half the species occurred at plot densities greater than 1.5 trees per hectare, and a species' local abundance was positively correlated with the number of forest types where it was found (Pitman, et al. 1999). At least 69% of the named species found in the Madre de Dios plots were collected in Ecuadorian plots (Pitman, et al. 1999), which provides more evidence that the majority of trees in the Amazon represent species with cosmopolitan characteristics and broad geographic ranges. The rarest species sampled in Madre de Dios occurred at extremely low population densities (Pitman, et al. 1999), but their broad geographic range suggests their absolute population numbers are comparatively large at the regional scale of the Amazon. Furthermore, the clumped distributions of most tropical tree species can make local scales irrelevant when quantifying the rarity of an individual species. Figure 2 of Pitman, et al. 1999 provides an excellent, albeit simplified, classification scheme for rare tree species, and shows that, despite their dominance, common species are a small portion of overall diversity (Figure 1 in Appendix).

When comparing the plots sampled in Ecuador with those sampled in Peru, Ecuador exhibited greater overall species diversity, largely attributed to greater abundance of rare species, smaller-statured species, and niche specific and/or geographically-limited species (Pitman, et al. 2002). One factor contributing to this difference is climate, which subjects the plant communities in Peru to more extreme abiotic variables, such as drought and cold (Pitman, et al. 2002). A second factor, and a much stronger one regarding Pitman's study, is the higher density of trees per hectare found in the Ecuadorian forest. High tree density leads to the "mixing effect", which states the combination of dispersal limitation and weak competitive interactions among seedlings, two common characteristics of Amazonian plant taxa, over time leads a larger number of species per a given area and number of individuals (Pitman, et al. 2002). The mixing effect does well to explain the increased existence of rare species and less clumped species distributions in Ecuador (Pitman, et al. 2002). The two factors, mentioned above, that influenced diversity in the study show how biotic interactions are often more important in determining species distributions and diversity than abiotic constraints. Climate can be a limiting factor for species on regional and very large scales,

but is not as strong as biotic interactions in determining small landscape level forest structure. Greater rates of abiotic disturbance found in Ecuador did not contribute to greater diversity (Pitman, et al. 2002) in the study supports this conclusion.

Because the majority of tree species in the Amazon are relatively rare, environmental heterogeneity influences the presence, distribution, and abundance of most species, particularly habitat specialists (Pitman, et al. 2001). However, the common, oligarchic species found in both Peru and Ecuador can be found across a broad range of soil types and elevations, meaning they are less constrained by environmental heterogeneity. Therefore, because these common species make up more than half of the individual trees in a given area on average, small and regional scale environmental heterogeneity cannot exclusively explain the composition and structure of Amazonian trees. The realization that the forests of the Western Amazon are more homogenous in composition and structure than previously thought is crucial information for ecologists whose attempts to map forest types across the region are nearly impossible without the presence of oligarchic forest types.

Intermediate disturbance theory states that forests maintain maximum diversity when ecological disturbance is neither too frequent nor too infrequent, ensuring the survival of species with wide-ranging life histories and characteristics. Speciation, which results from intense inter-specific interaction, and limited dispersal theory, two biotic drivers of rainforest composition, do not explain aggregated species distributions common in Amazonia (Pitman, et al. 2002). How species respond to environmental heterogeneity is also important (Pitman, et al. 2002). Disturbance regimes in the Amazon contribute to environmental heterogeneity, and also influence species distributions at broad, regional scales because many tree species have regeneration ecologies adapted to forest disturbance. Individual disturbances exert their influence on forest composition at local scales. However, as indicated by Pitman, et al. 2002, more frequent disturbance regimes do not always result in expected outcomes for forest communities, meaning disturbance regimes in general may influence, but do not exclusively drive forest community composition in the Western Amazon. Therefore, in order to determine the extent to which disturbance regimes influence diversity, we need to examine the disturbances that occur in the lowland Amazon forests individually.

The primary agent of large-scale ecological disturbance in the Amazon is river-bend migration as a result of significant flooding events (Gullison, et al. 1996). In Peru, flooding and river disturbance plays a larger role than both wind (blowdowns) and fire, which are more prevalent in Central American rainforests (hurricanes) and tropical dry forests respectively (Gullison, et al. 1996). Primary succession on newly deposited riverine soils is a major mode of forest regeneration in the Peruvian Amazon, and is a major factor influencing and maintaining high beta-diversity (Salo, et al. 1986). Beta-diversity is summarized as how species composition changes with respect to distance, and is a central to understanding what controls diversity and species turnover at large scales (Pitman, et al. 2002). The wide variety of habitats and soil types present in floodplains that result from dynamic and meandering rivers creates significant beta-diversity of species in the parks and reserves of southeastern Peru, where small scale and landscape scale heterogeneity in both species composition and forest stand age is present (Salo, et al. 1986). This study also states that, in the absence of other physical features across the Amazon basin, river dynamics have been the primary drivers of allopatric speciation (specifically speciation driven by geographic separation and isolation) in the region's rainforests. The zonation of vegetation and forest types along floodplains maintains forests at different levels of succession, which not only fosters habitat diversity, but also the regeneration and growth of *Cedrela odorata* and other important keystone trees (Salo, et al. 1986). For example, localized disturbances, such as tree fall that results in canopy gaps, does not create the large areas of primary forest succession that we see with meandering rivers, which are often necessary for big-leaf Mahogany reproduction (Brown, 2003). In lowland rainforests where diversity is driven primarily by intense species interactions at local scales, abiotic and physical forces, like river dynamics, that create habitat heterogeneity help us examine species diversity at much broader scales.

At a much more local scale, forest blowdowns and severe wind disturbances caused by heavy thunderstorms help create habitat heterogeneity and diverse community structure in many regions of the Amazon basin (Nelson, et al. 1994). A study examining the geographical patterns of rainforest blowdowns in the Amazon by using remote sensing techniques produced maps that show Western Brazil, the area near the Peruvian,

Colombian, and Venezuelan borders with Brazil, has the highest frequency of blowdowns (Nelson, et al. 1994) (Figure 2 in Appendix). This region also happens to correspond with the part of the Amazon basin that receives the most annual rainfall and exhibits the least amount of annual temporal variability in precipitation (the dry season is not as pronounced) (Villar, et al. 2009). Therefore, blowdowns play a more significant role in the disturbance regimes of the lush, evergreen forests of Northeastern Peru than they do in the open evergreen and semi-deciduous forests of the Southern Peruvian Amazon, where higher seasonal variability and less overall precipitation lead to less disturbances caused by wind or thunderstorms. The majority of the blowdowns in the aforementioned study disturbed between 30 and 300 hectares, meaning that most were relatively small and localized (Nelson, et al. 1994). Although large blowdowns are very rare, if the disturbance is catastrophic enough to encourage pioneer and early successional plant communities in the affected area the blowdown can change forest composition for long periods of time. More importantly, the small, infrequent, and localized nature of wind disturbance regimes in the Amazon contributes to the heterogeneity of forest community composition and structure across larger areas.

The smallest and most localized disturbances that maintain species and community diversity in the Amazon are canopy gaps created by treefall. This disturbance provides the closest natural parallel to anthropogenic disturbance in the form of selective logging. Canopy gaps maintain diversity by providing areas of adequate light for the colonization of shade-intolerant pioneer species or for the release of previously suppressed shade-tolerant late-successional and climax species (Schnitzer & Carson, 2001). Canopy gaps also mitigate the force of competitive exclusion by better-adapted species because the stochastic nature of gap availability means gaps are most often colonized by chance (Brokaw & Bushing, 2000). This conclusion came from a study in Panama that found only 2.3% of canopy gap saplings originating from canopy trees in the forest, and that the tallest, fastest growing tree present in the gap was most likely to fill the canopy void (Brokaw & Bushing, 2000). Other studies indicate that tree growth in gaps is positively correlated with the height of understory tree saplings at the formation of the gap (Uhl, et al. 1988), which is further evidence that random chance and advance regeneration are very important to gap colonization. This evidence suggests that, even in

the context of a disturbance regime that creates frequent small-scale canopy gaps, chance recruitment of trees will eventually exclude pioneer species that are rare and do not regenerate well in areas of interior forest. However, since plant growth within canopy gaps also depends upon gap size, gap microhabitat, and gap age (Uhl, et al. 1988), canopy gaps do maintain both pioneer species density and diversity, especially in areas of high environmental heterogeneity. For example, a study conducted in Barro Colorado Island, Panama, showed pioneer species had significantly higher species density and richness in gap plots than in non-gap plots (Schnitzer & Carson, 2001). Although the number and density of shade-tolerant species far outnumbered those for pioneer species in gap plots, the presence of shade tolerant species highlights the importance of canopy gaps as refugia habitat for these species and for the maintenance of biodiversity (Schnitzer & Carson, 2001). The examined studies indicate the stochastic nature of canopy gaps allows several variables, including chance, physical gap characteristics, and the gaps biological history to influence forest structure and composition and maintain a certain level of species diversity.

Species

Big-leaf Mahogany, *Swietenia macrophylla*, widely regarded as the most valuable neotropical timber tree, is both the most studied species relevant to Peruvian forestry, and the timber species most in danger of commercial extirpation across the Amazon basin (Grogan and Barreto, 2005). The tree is a dominant, emergent canopy species that can reach up to 50 m in height. Mahogany is known for having heavy buttresses, which stabilize the tree and help it survive extreme wind events better than other species (Snook, 1993). It is a deciduous tree, which explains the species preference for more seasonal forest types, and it depends upon wind for initial seed dispersal (Gullison, et al. 1996). The broad geographical range of Mahogany is due to its ability to grow in many different soil and habitat types (Mayhew & Newton, 1998), and its ability to benefit from catastrophic disturbances including hurricanes, devastating floods, and fires.

In the Amazon, Mahogany has co-evolved to benefit from and possibly depend upon catastrophic disturbances such as blowdowns (wind), fires, and, in particular, flooding (Snook, 1996). This dependence is particularly strong in the dense evergreen forests of the central Amazon, where large disturbances are required to create the

expansive canopy gaps that are required by the shade-intolerant Mahogany for regeneration (Brown, 2003). For example, in northern Bolivia, an area characterized by semi-evergreen, seasonal rain forests, Mahogany regeneration is particularly correlated with major flooding events (Gullison, et al. 1996). Studies have linked Mahogany's shade intolerance and semi-drought tolerance to its successful regeneration in more open evergreen forests, like those in Eastern Peru, and the semi-deciduous forests that line the southern edge of the Amazon (Brown, 2003). This is mostly attributed to the fact that light penetration greatly increases from dense evergreen rain forests to open evergreen and semi-deciduous forests (Coomes & Grubb, 2000). Maps that display the geographical extent of Mahogany populations across the Amazon basin indicate existing populations primarily occur along the transition zone between open evergreen forests (including the Peru-Brazil borderlands region) and semi-deciduous forests in the Southern Amazon, which is consistent with the species' ecological characteristics and regenerative capabilities (Brown, 2003) (Map shown as Figure 3 in Appendix).

After major disturbances kill most other tree species in the disturbed area, Mahogany's ability to survive these types of disturbances means that it dominates seedling dispersal and regeneration in the newly formed gaps and clearings. This results in Mahogany establishing itself in even-aged stands intermixed with other species ranging from early successional, pioneer species to late successional species similar to Mahogany (Brown, 2003). However, many of these species lack the characteristic longevity that Mahogany exhibits (Snook, 1996), meaning once Mahogany becomes established and matures in a stand it will persist for a long time regardless of inter-specific competition. The catastrophic disturbances Mahogany depends upon for regeneration are both extreme and rare, which explains the species' heavy buttresses, relatively fast growth, and characteristic longevity. As noted by Snook (1996), the regeneration ecology of Mahogany, particularly its survival capabilities, help it maintain a broad geographical range. These same characteristics make Mahogany exceedingly rare due to its clumped, non-random distribution, which means it generally occurs in densities of less than 0.1 tree per hectare in Peru and across the region (Grogan and Schulze, 2008). Seed production for Mahogany is positively correlated with dbh (diameter at breast height), but the largest, most prolific seed trees also exhibit high variability in

annual fruit production (Snook, et al. 2005). The species shows a strong, positive correlation between annual fruit production annual basal area growth, showing that in years with good growing conditions Mahogany dedicates significant resources to reproduction (Snook, et al. 2005). This means that, to a certain extent, Mahogany reproduction and regeneration reacts to regional climactic trends, and therefore exhibits “boom” and “bust” years. For a multitude of reasons, fecundity included, mahogany does not establish the kind of extensive seed or seedling banks required to ensure regeneration in the absence of prolific seed trees (Snook, 1996).

Tropical Cedar (*Cedrela odorata*), also known as Spanish Cedar, stands behind only big-leaf Mahogany as the most exploited timber species in the neotropics and Amazon basin. The deciduous species is a habitat and climate generalist, but is most successful in seasonally dry forest types (Cintron, 1990). *C. odorata* is commonly associated with, but also less abundant than, big-leaf Mahogany because it has more exacting site regeneration requirements. This characteristic contributes to its rarity within its geographic range (Cintron, 1990). Populations of Spanish Cedar in the Amazon are widespread, but never common, exhibiting similar distributions to Mahogany and Shihuahuaco (Cintron, 1990). Similar to Mahogany, the seeds of Spanish cedar are disseminated during the dry season, vary in crop intensity from year to year, and lose their viability fairly quickly (Cintron, 1990). This mean the species is locally dependent on bumper crops from a few large, seed-bearing trees. In the Amazon basin, Spanish Cedar regenerates very successfully, but for a number of reasons, including competition and shallow rooting, it experiences high mortality rates among younger individuals. In Peru, specifically in the Madre de Dios province, remaining populations are commonly found in riparian zones (de la Torre, 2008). Ironically, this same study reveals that farmers in the region are responsible for the protection of this species in fencerows, fields, and forest fragments (de la Torre, 2008).

The demand for Shihuahuaco (*Dipteryx spp.*), known as cumarú or Brazilian teak in the international market, increased rapidly over the past few decades in response to continued international demand for tropical timber and the regional extirpation of species like Mahogany. *Dipteryx* species have large volumes, heavy buttresses, and can reach up to 60 m in height as canopy emergents (Putzel, et al. 2011). Studies indicate *Dipteryx*

species are both extremely slow growing and long-lived, with maximum adult ages of 1100 years estimated for *Dipteryx odorata*, a species common throughout Peru (Putzel, 2011). Shihuahuaco seeds, which mature in the dry season, are an important food source for bats, peccaries, and other herbivorous mammals. *Dipteryx* trees also provide critical long-term nesting habitat for several species of parrot and macaw in the Lowland forests of Peru (Brightsmith, 2005). Their ecological importance to mammals and birds, combined with their importance to the structure and gap dynamics of the forests, make Shihuahuaco *spp.* keystone species, critical to the ecological integrity of the forest. Unlike Mahogany, which relies on abiotic variables for seed dispersal, *Dipteryx* species depend upon mammals, in particular bats, to disperse their seeds and facilitate regeneration away from parent trees (Romo, et al. 2004, Putzel, et al. 2011). Also unlike Mahogany, *Dipteryx* species regenerate in both successional and mature forests, and in habitats ranging from floodplains to upland regions due to their large seeds and shade tolerant seedlings. High shade tolerance is a particularly advantageous trait that allows young *Dipteryx* trees to survive in the understory of mature forests for decades or centuries until a canopy disturbance allows enough light to release the smaller trees and encourage growth and maturation (Putzel, et al. 2011). The regenerative capabilities of *Dipteryx* allow it to have a broad geographical range, a fairly even distribution throughout its range, and individuals representing many different size and age classes where it is present in the forest. Their slow growth and characteristic longevity explain why species of *Dipteryx* exhibit high wood density and resistance to rot. These wood characteristics prized by the timber industry, which helps explain the recent spike in demand for shihuahuaco (Putzel, et al. 2011).

Ceiba pentandra, also known as both the Kapok tree and Lupuna, is a heavily buttressed, canopy-emergent tree that can reach 70 m in height (Dick, et al. 2007). The species is extremely fast growing (observed growth rates up to 2 m per year) and can mature and set seed in as little as 2 to 6 years (Dick, et al. 2007). Kapok commonly colonizes riverbanks, but is able to grow in both floodplain soils and *terra firme* soils that exist above the average inundation level. The preferred forest type of *Ceiba pentandra* on the eastern banks of the Ucayali River in the Peruvian Amazon is riverine forest (Parodi & Freitas, 1990). This forest type, which represents the final phase of primary riverine

succession, is also home to Spanish Cedar and big-leaf Mahogany in the Ucayali region. Although it is capable of self-fertilization, the Kapok tree depends upon bats and moths for pollination in the neotropics (Dick, et al. 2007). Because the reproduction of *C. pentandra* must occur at temperatures above 20 Celsius, the species is limited by elevation and does not exist above 1500 m (Dick, et al. 2007). Wind and water are the two major dispersal agents for Kapok tree seeds, which have cottony fibers that entangle the numerous, small, oily coated seeds (Dick, et al. 2007). The fibers, which give the species its silk-cotton tree nickname, and the oily seed surface allow for dispersal by both wind and water (Dick, et al. 2007). The species is relatively scarce across its range in Peru, and, for reasons not well understood, does not regenerate abundantly (Parodi & Freitas, 1990). *C. pentandra* used to be one of the most common tree species inhabiting the rich, alluvial soils that support the forests along the Peruvian Amazon (Gentry & Vasquez, 1988). Due to intensive extraction associated with the plywood industry, the species is now uncommon in Northern Peru (Parodi & Freitas, 1990).

Capirona, *Calycophyllum spruceanum*, (Rubiaceae family) is a valuable timber species in the Peruvian Amazon, and is widely regarded by local and indigenous Peruvian farmers as an ideal species for the production of lumber, charcoal, and firewood in agroforestry systems (Chabot, et al. 2004). Capirona is a fast-growing hardwood, and emergent pioneer species that can colonize a wide range of habitat and soil types, including alluvial floodplain areas, open fields, previously logged areas, and other disturbed sites (Montes, et al. 2003). At its largest, Capirona can attain a height of 40 m and a diameter of 90 cm (Chabot, et al. 2004). The species is limited by elevation, only growing below 650 m above sea level (Chabot, et al. 2004), but is able to grow in climates that range from 1800 mm to 4000 mm in annual precipitation (Russell, et al. 1999). Important traits of this species also include rapid maturation in the absence of competition (2 to 3 years), and dense and uniform wood characteristic of mature trees (Weber and Montes, 2005). Capirona primarily occupies river floodplain sites, where its numerous, winged and light-weight seeds can easily be distributed by both wind and water (Russell, et al. 1999). The morphology of Capirona seeds indicates that they are evolved to depend upon wind dispersal. However, the seeds also remain viable in water for several days, and research shows that downstream populations establish themselves

linearly along previous high flood levels, which indicates water is just as important as wind for *C. spruceanum* dispersal (Russell, et al. 1999). When Capirona is harvested, shoots rapidly grow out of the trunk at rates faster than growth rates of Capirona seedlings, and can be harvest up to five times before the stump is weakened and dies (Chabot, et al. 2004). The diameter of the tree stump, which is usually reflects the size of the stump's root system, is positively correlated with the height and growth rate of shoots, highlighting the relationship between root systems, water and nutrient availability, and the species' regenerative capabilities (Chabot, et al. 2004). Furthermore, in studies conducted on degraded lands previously used for agriculture near Pucallpa, Peru, *C. spruceanum* seedlings exhibited low mortality rates and successful growth (Soudre, et al.). Capirona's wide geographic distribution across the floodplains of the Peruvian Amazon, abundant regeneration, fast growth, and adaptability to anthropogenic disturbances means that its natural populations are not as threatened as other commonly logged species within its range.

Ishpingo, *Amburana cearensis*, is a small to medium sized, leguminous tree (height of 15 to 25 m) typically found within, but not restricted to, seasonally dry forest ecosystems across the Amazon Basin (Leite, 2005). In Peru, the species is not abundant, but exhibits a wide geographic distribution across Ucayali, Madre de Dios, Cusco, Puno, and the Brazilian state of Acre. Important populations of Ishpingo, for both the maintenance of genetic diversity and academic study, actually exist in cultivated regions where farmers protect the species (Leite, 2005). Ishpingo primarily occurs at elevations between 500 and 1000 m and in areas characterized by moderately hilly topography and deep, rich soils (Leite, 2005). Although the species has rather specific soil requirements, it is not known to form dense stands, and in fact exhibits low population density and abundance across its range (Leite, 2005). The seeds of this species are thought to be dispersed by wind and lose their viability quickly (Leite, 2005). Ishpingo seeds and seedlings are also subject to high predation rates in relation to other species (Mostacedo and Fredrickson, 1999), including well-documented seedling predation by a species of cricket (Leite, 2005). Ishpingo seedlings are shade intolerant and require clearings large enough to supply sufficient light for regeneration. In Bolivia, Ishpingo, which is logged intensively in the region due to the extirpation of Mahogany, scarcely regenerates within

both closed canopy forests and forests being selectively logged (Mostacedo and Fredrickson, 1999). The heartwood of Ishpingo, also referred to as Spanish Oak, resembles that of *Quercus spp.* (oaks), and the wood's characteristics are similar to those of teak (Leite, 2005). The reproductive biology, regeneration ecology, population structure and distribution of this species are very poorly documented in relation to its acknowledged high economic value (Leite, 2005). This lack of knowledge is particularly evident for the Peru-Brazil borderlands region relevant to my study.

Ipe, *Tabebuia spp.*, also referred to as the “New Mahogany”, are prized species for timber in the Amazon because of their dense and rot resistant wood (Schulze, et al. 2008). The two Ipes examined in this study are *T. impetiginosa* and *T. serratifolia*. Both of these species are canopy emergents attaining heights of up to 50 m. They are also both deciduous, shade-intolerant species with poorly understood reproductive ecologies (Schulze, et al. 2008). While little information exists on the regeneration of both species, particularly for *T. serratifolia*, in Bolivia, the absence of sufficiently large clearings or gaps created poor regeneration conditions for both species (Mostacedo and Fredrickson, 1999). Their seeds are also known to be small, winged, and most likely distributed by wind, and, much like Mahogany (Gullison, et al. 1996), *Tabebuia spp* do not establish seed banks because the seeds, which are dispersed at the onset of the rainy season to ensure successful germination, lose their viability after one season (Schulze, et al. 2008). Both *Tabebuia* species are widely distributed at low densities throughout the Amazon basin in seasonal forest types, with *T. impetiginosa* commonly found in the Pantanal and Cerrado regions of Brazil and *T. serratifolia* found at its highest densities in the transitional forests present in southwestern Brazil and southeastern Peru (Schulze, et al. 2008). Population structures of *Tabebuia* stands show that large, old adults are common, while seedlings and young trees are typically uncommon (Schulze, et al. 2008). This infers the species depends upon large gaps or clearings that are only created by significant disturbances. Slow growth, longevity, shade intolerance, and the lack of young individuals are all ecological characteristics also exhibited by Mahogany. The ecological similarities between *Tabebuia* and *S. macrophylla* are undeniable, and therefore both species face the same management issues and pressures associated with logging in the Amazon (Schulze, et al. 2008).

Knowledge/Information Issues

A readily apparent issue when attempting to study individual species utilized by the timber industry in Peru is the lack of consistency in documentation regarding certain species. For example, during my research, I encountered the common name Lupuna referring to two different species (*Chorisia integrifolia* and *Ceiba pentandra*). It was not until later in my research that I discovered several species of *Chorisia* are now considered *Ceiba* due to a study of taxonomic revision regarding *Ceiba* from 2003 (Gibbs and Semir, 2003). The sheer complexity, diversity, and size of the Amazon, along with the complex human and political geography, make it difficult to properly name and assign species to their appropriate taxonomic groups. Another difficult aspect of this project was simply finding studies relating ecological characteristics and timber extraction. The information that does exist is primarily regarding species that have already been over exploited, such as *S. macrophylla*, but for species that are currently at risk of commercial extirpation, like *Amburana* and *Tabebuia*, there is a huge gap in knowledge. Regeneration ecology, critical information that should be taken into account before extraction, is rarely studied for specific species found in the Peruvian Amazon. *Hura crepitans* and *Copaifera officinalis* are two more examples of species that need better documentation. With the proper information, management plans will be both locally (species level) and regionally (landscape and ecosystem level) sustainable.

Reflections, Recommendations, and Conclusions

Understanding the ecological characteristics of the exploited tree species in the Peruvian Amazon is important for ecologists, local people, and resource managers who want to create an ecologically and economically sustainable forestry system. Current management practices compromise the regenerative ecology of certain species and encourage a logging culture of over-exploitation and commercial extirpation. From the perspective of a forest manager, tree species with slow growth, low population densities, shade intolerance, and population structures with a large percentage of old trees provide an unfavorable situation for sustained timber management. Species with these characteristics include, but are not limited to, *S. macrophylla*, *Tabebuia spp.*, and *Amburana cearensis*. For example, the 30 year cutting cycle deemed possible because of reduced impact logging does not even come close to ensuring the population level

recovery necessary for sustainable management of species that exhibit slow growth, longevity, and regeneration dependent upon catastrophic disturbance (Schulze, et al. 2008). Under ideal conditions, in forest stands previously logged using reduced impact techniques, the population recovery of *Tabebuia spp* through seedling recruitment would take approximately 100 years (Schulze, et al. 2008). Furthermore, projected and observed seedling growth rates in logging gaps suggest that this recovery would actually take much longer (Schulze, et al. 2008) (Figure 4 in Appendix). Management practices that remove a high percentage of commercial-sized, seed-bearing individuals from a stand, as is common with *S. macrophylla*, directly compromises the ecological strategy of species like Mahogany, which form even-aged cohorts of trees that depend upon large, catastrophic disturbance to regenerate (Snook, 1996). These species occur in low densities at local, landscape, and regional levels means that the extraction of nearly all of the commercial sized timber effectively eliminates seed sources over large geographic areas (Snook, 1996). Under natural disturbance regimes, Mahogany, Ipe, and Ishpingo are adapted to survive the events that kill the majority of their competitors in a stand. The irony of current logging practices is that selective logging, especially logging that reduces overall forest impact, does not even come close to mimicking natural disturbances, such as river bend migration, that many species depend upon for successful regeneration. The disturbances created by logging are far too small, weak, and localized to create the conditions needed to stimulate Mahogany regeneration (Brown, 2003).

Based upon their ecologies, the logging *Swietenia macrophylla*, *Amaburana cearensis*, *Cedrela odorata*, *Tabebuia spp.*, and *Ceiba pentandra* must change in order to prevent the commercial extirpation and maintain future populations of these species. Current harvest selectivity and intensity undermines the regenerative capability of these trees. The most important change must be decreased logging intensity. As evidenced by *Tabebuia* in Figure 4, these species with similar characteristics simply cannot regenerate fast enough under the ecological conditions created by highly selective, intensive logging. Under natural conditions, all of these species regenerate infrequently and under rare circumstances. Ecologically, they are built to withstand the disturbances that other species cannot, but these types of disturbances are both rare and large, while selective logging creates frequent, but small disturbances. This regime overwhelmingly favors

pioneer species, habitat generalists, and the common species that comprise the majority of individual trees at localized scales. A possible solution to the problems associated with the sustainable management of species that exhibit longevity, slow growth, even-aged stands, and infrequent regeneration would be to leave all, large seed bearing individuals standing in the forest to ensure the continuation of seed sources. Another solution could be an attempt to mimic the natural catastrophic disturbance in areas where seed trees of these species exist. This would undoubtedly involve the extraction of a few individuals from the targeted species, but would largely involve the extraction of the other species found in the area. Mimicking natural disturbance would not be similar to clear cutting and slash and burn practices that devastate habitats in the Amazon, but instead would encourage successful regeneration. If management and logging is to continue to target the previously mentioned species three things must happen: (1) substantially decreased logging intensity, (2) large, seed-bearing individuals left standing, and (3) the disturbance created by logging resembles either a natural disturbance or a disturbance that results in successful regeneration for the targeted species.

For the two other species examined, *Calycophyllum spruceanum* and *Dipteryx spp*, hope does exist for sustainable management and logging development if this development is conducted properly. Capirona is more intriguing than Shihuahuaco because its ecological characteristics make it a pioneer hardwood species. This means it is a high quality wood that can be easily grown and managed both in plantations and naturally. I would highly recommend the development of this species for timber production on marginal and unproductive agricultural lands. This would not only maintain natural populations of Capirona, but would provide farmers with sustainable income on their less productive lands while simultaneously aiding the timber industry by simplifying the management of this species. A possible ecological problem exists with Capirona's dispersal and regenerative capacities, which would undoubtedly result in the invasion of Capirona along the forest edges surrounding a plantation. However, due to the multiple uses of this species, farmers and landowners could also manage this phenomenon by cutting these individuals to be sold as charcoal or firewood, providing the farmer with a more diversified income.

The single most important trait of Shihuahuaco is the shade tolerance exhibited by younger individuals, which means it is capable of regenerating abundantly in a closed-canopy forest. Despite Shihuahuaco's abundant regeneration, the harvest intensity of Shihuahuaco needs to be decreased in order to ensure that a sufficient number of adults are left in the forest to provide enough seed to facilitate regeneration. With a decrease in harvest intensity, there is no ecological constraint or reason why *Dipteryx* would not continue to regenerate. Due to the longevity exhibited by Shihuahuaco, I would also recommend that high percentages of trees with large dbh be left in the forest, because these trees act as seed sources for hundreds of years. Further aiding in the protection and sustainable management of Shihuahuaco is its standing as a keystone species within the forests where it is found. The ecological importance of these species to wildlife makes their populations the focus of conservation biologists in the international community. This attention undoubtedly lends itself useful for the protection of Shihuahuaco populations.

Literature Cited

- Brown, Nick, Steve Jennings, and Tom Clements. 2003. "The Ecology, Silviculture and Biogeography of Mahogany (*Swietenia Macrophylla*): A Critical Review of the Evidence." *Perspectives in Plant Ecology, Evolution and Systematics* 6 (1-2): 37-49
- Boivin-Chabot, Sara, Hank A. Margolis, and John C. Weber. 2004. "Variation in coppice shoot growth among provenances of *Calycophyllum spruceanum* Benth. in the Peruvian Amazon Basin." *Forest Ecology and Management* (198): 249-260
- Brightsmith, Donald J. 2005. "Competition, predation and nest niche shifts among tropical cavity nesters: ecological evidence." *Journal of Avian Biology* (36): 74-83
- Brokaw, Nicholas, and Richard T. Busing. 2000. "Niche versus chance and tree diversity in forest gaps." *TREE* 15(5): 183-187
- Condit, Richard, Nigel Pitman, Egbert G. Leigh, Jérôme Chave, John Terborgh, Robin B. Foster, Percy Núñez, et al. 2002. "Beta-Diversity in Tropical Forest Trees." *Science* 295 (5555): 666-669
- de, la Torre, Cesar López, Eliana Yglesias, and Jonathan P. Cornelius. 2008. "Genetic (AFLP) Diversity of Nine *Cedrela Odorata* Populations in Madre De Dios, Southern Peruvian Amazon." *Forest Ecology and Management* 255 (2): 334-339

Dick, C., Eldredge Bermingham, Maristerra R. Lemes, and Rogerio Gribel. 2007. "Extreme long-distance dispersal of the lowland tropical rainforest tree *Ceiba pentandra* L. (Malvaceae) in Africa and the Neotropics." *Molecular Ecology* (16): 3039-3049

Gentry, A. H. and R. Vasquez. 1988. "Where have all the Ceibas Gone? A Case History of Mismanagement of a Tropical Forest Resource." *Forest Ecology and Management* 23 (1): 73-76

Grogan, James, and Paul Barreto. 2005. "Big-leaf Mahogany on CITES Appendix II: Big Challenge, Big Opportunity." *Conservation Biology* 19(3): 973-976

Grogan, James, Stephen B. Jennings, R. Matthew Landis, Mark Schulze, Anadilza M.V. Baima, J. do Carmo A. Lopes, Julian M. Norghauer, L. Rogério Oliveira, Frank Pantoja, Diane Pinto, Jose Natalino M. Silva, Edson Vidal, Barbara L. Zimmerman. 2008. "What loggers leave behind: Impacts on big-leaf mahogany (*Swietenia macrophylla*) commercial populations and potential for post-logging recovery in the Brazilian Amazon." *Forest Ecology and Management* (255): 269-281

Gullison, R. E., S. N. Panfil, J. J. Strouse, and S. P. Hubbell. 1996. "Ecology and Management of Mahogany (*Swietenia Macrophylla* King) in the Chimanes Forest, Beni, Bolivia." *Botanical Journal of the Linnean Society* 122 (1): 9-34

Leite, Edson J. 2005. "State of Knowledge on *Amburana cearensis* (Fr. Allem.) A.C. Smith (Leguminosae: Papilionoideae) for genetic conservation in Brazil." *Journal for Nature Conservation* (13): 49-65

Mostacedo, Bonifacio C., and Todd S. Fredrickson. 1999. "Regeneration status of important tropical forest tree species in Bolivia: assessment and recommendations." *Forest Ecology and Management* (124): 263-273

Nelson, Bruce W., Valerie Kapos, John B. Adams, Wilson J. Oliveira, and Oscar P. G. Braun. 1994. "Forest Disturbance by Large Blowdowns in the Brazilian Amazon." *Ecology* 75 (3): 853-858

Parodi, J. L., and David Freitas. 1990. "Geographical Aspects of Forested Wetlands in the Lower Ucayali, Peruvian Amazonia." *Forest Ecology and Management* (33/34): 157-168

Pitman, Nigel C., A., John Terborgh, Miles R. Silman, and Percy Nuñez V. 1999. "Tree Species Distributions In An Upper Amazonian Forest." *Ecology* 80 (8): 2651-2661

Pitman, N., John W. Terborgh, Miles R. Silman, Percy Nuñez V., David A. Neill, Carlos E. Cerón, Walter A. Palacios, and Milton Aulestia. 2001. "Dominance and Distribution of Tree Species in Upper Amazonian Terra Firme Forests" *Ecology* 82(8): 2101-2117

Pitman, N., John W. Terborgh, Miles R. Silman, Percy Nuñez V., David A. Neill, Carlos E. Cerón, Walter A. Palacios, and Milton Aulestia. 2002. "A Comparison of Tree Species Diversity in Two Upper Amazonian Forests." *Ecology* 83(11): 3210-3224

Putzel, Louis, Charles M. Peters, and Mónica Romo. 2011. "Post-Logging Regeneration and Recruitment of Shihuahuaco (*Dipteryx* Spp.) in Peruvian Amazonia: Implications for Management." *Forest Ecology and Management* 261 (6): 1099-1105

Russell, J. R., J. C. Weber, A. Booth, W. Powell, C. Sotelo-Montes, and I. K. Dawson. 1999. "Genetic Variation of *Calycophyllum spruceanum* in the Peruvian Amazon basin, revealed by amplified fragment length polymorphism analysis." *Molecular Ecology* (8): 199-204

Sotelo-Montes, C., Hector Vidaurre, and John Weber. 2003. "Variation in stem-growth and branch-wood traits among provenances of *Calycophyllum spruceanum* Benth. from the Peruvian Amazon." *New Forests* (26): 1-16

Schulze, Mark, James Grogan, Chris Uhl, Marco Lentini, and Edson Vidal. 2008. "Evaluating *ipe* (Tabebuia, Bignoniaceae) logging in Amazonia: Sustainable management or catalyst for forest degradation?" *Biological Conservation* (141): 2071-2085

Salo, J., Risto Kalliola, Ilmari Hakkinen, Yrjo Makinen, Pekka Niemela, Maarit Puhakka, and Phyllis D. Coley. 1986. "River dynamics and the diversity of Amazon lowland forest." *Nature* (322): 254-258

Snook, Laura K. 1996. "Catastrophic Disturbance, Logging and the Ecology of Mahogany (*Swietenia Macrophylla* King): Grounds for Listing a Major Tropical Timber Species in CITES." *Botanical Journal of the Linnean Society* 122 (1): 35-46

Snook, Laura K., Luisa Camara-Cabrales, and Matthew J. Kelty. 2005. "Six Years of Fruit Production by Mahogany Trees (*Swietenia Macrophylla* King): Patterns of Variation and Implications for Sustainability." *Forest Ecology and Management* 206 (1-3): 221-235

Appendix

		GEOGRAPHIC RANGE:		Small	
		Large		Wide	Narrow
		HABITAT SPECIFICITY:			
		Wide	Narrow	Wide	Narrow
LOCAL POPULATION SIZE					
Large, dominant somewhere in Neotropics		Locally abundant in several habitats over a large geographical area	Locally abundant in a specific habitat over a large geographical area	Locally abundant in several habitats over a small geographic area	Locally abundant in a specific habitat over a small geographical area
Small, nondominant		Constantly sparse in several habitats over a large geographical area	Constantly sparse in a specific habitat over a large geographical area	Constantly sparse in several habitats over a small geographic area	Constantly sparse in a specific habitat over a small geographical area

FIG. 2. Rabinowitz's classification scheme for rare species (adapted from Rabinowitz [1981] with permission from John Wiley and Sons Limited).

Figure 1. Classification scheme for rare species (Pitman, et al. 1999).

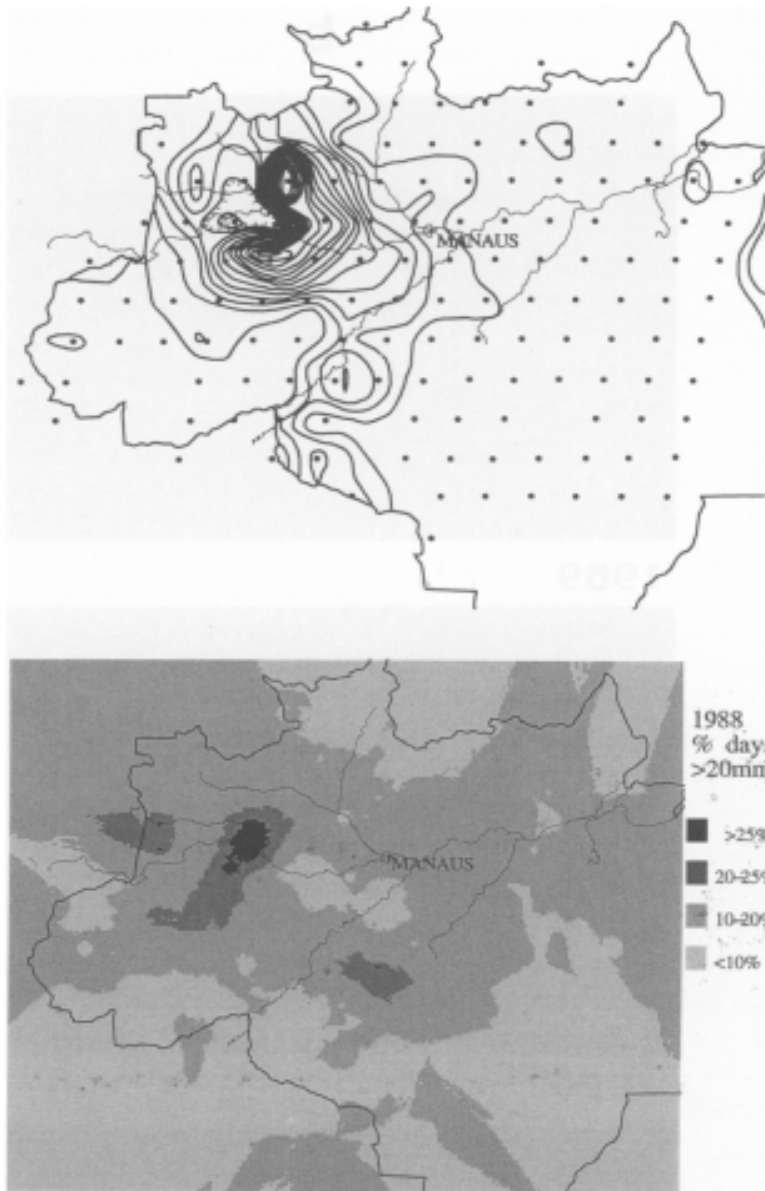


FIG. 2. The geographic distributions of blowdown occurrence and rainfall in the Brazilian Amazon showing the approximate coincidence of the zones of highest incidence of blowdowns and of greatest frequency of heavy rainfall. Top panel: distribution of large blowdowns expressed as square kilometres per Landsat scene, isolines range from 5 to 85 km² per scene at intervals of 5 km². Dots indicate centers of Landsat scenes surveyed. Scenes missing from the grid were not assessed because of cloud cover or predominance of nonforest vegetation. Bottom panel: distribution of heavy rainfall as percentage of days with > 20 mm of rainfall (J. Richey et al., *unpublished data*).

Figure 2. Geographic distribution and concentration of forest blowdowns in the Amazon (Nelson, et al. 1994).

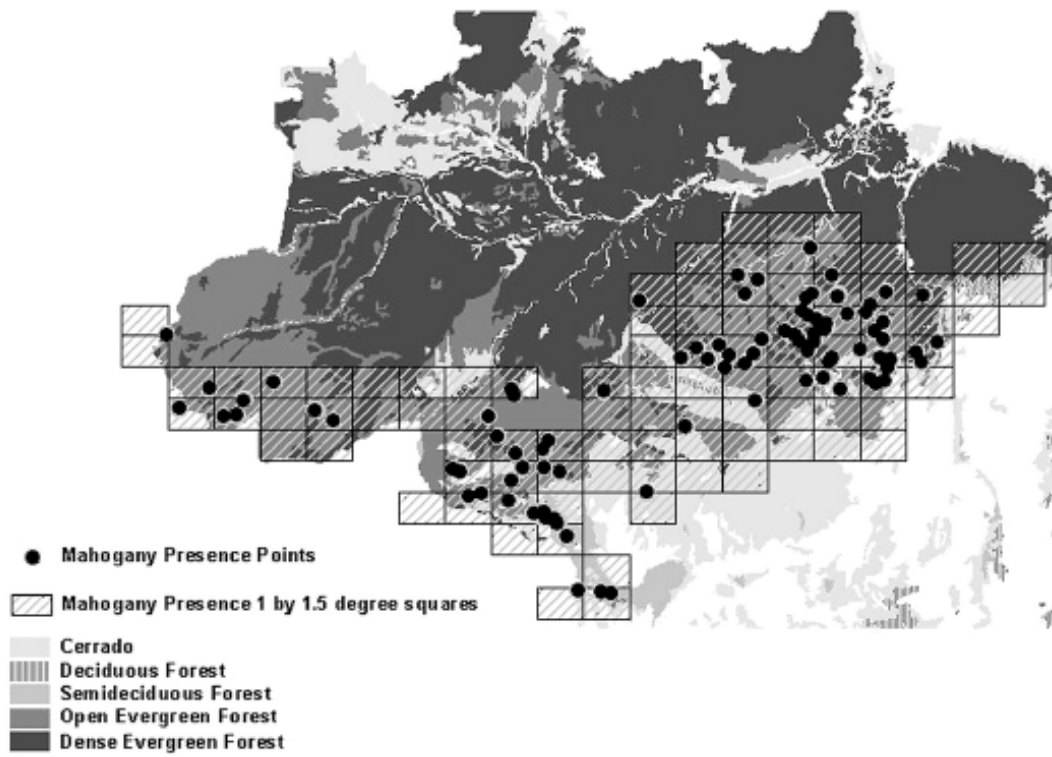


Fig. 5. Distribution of *Swietenia macrophylla* in the Amazon Basin in relation to forest types (taken from TRFIC 2000).

Figure 3. Map of Mahogany presence points overlaid on a base map of forest types (Brown, 2003).

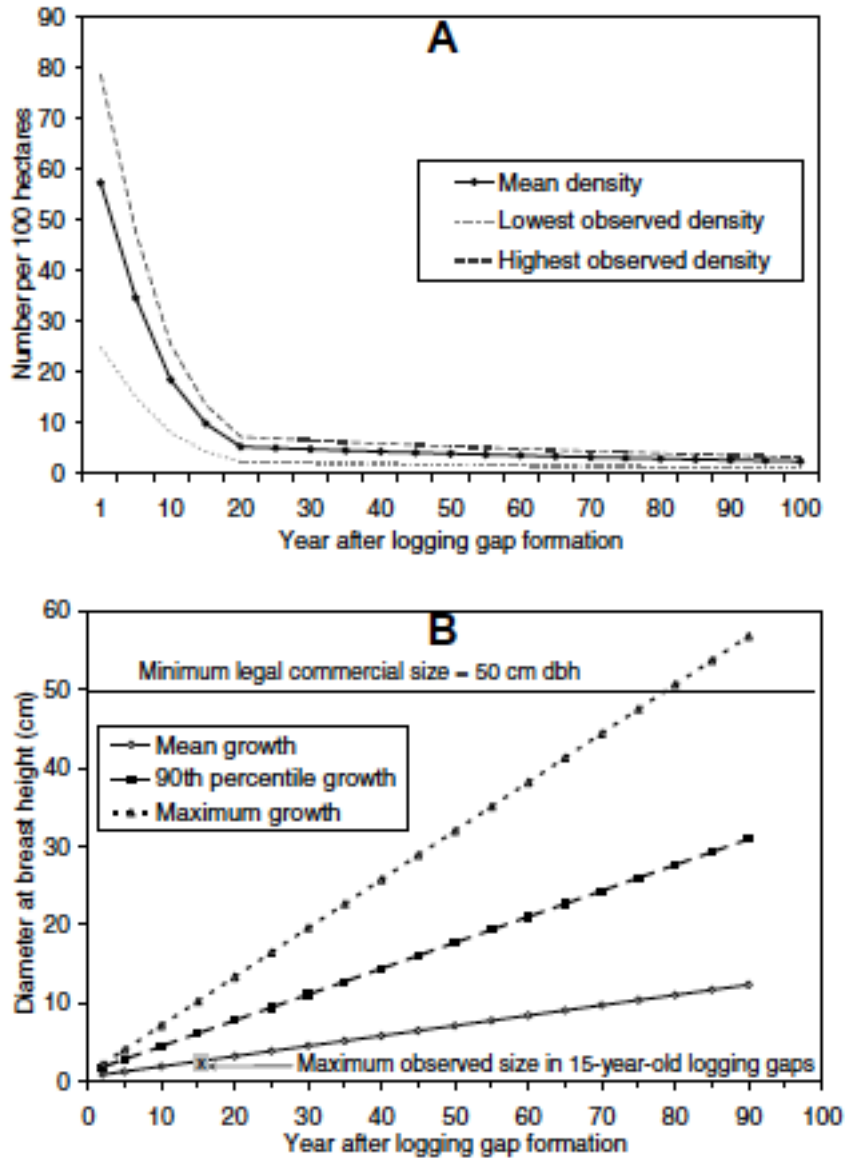


Fig. 3 – Projection of *Tabebuia* (A) survival and (B) recruitment in logging gaps based on observed sizes, densities, growth and mortality in 2-year-old logging gaps in RIL stands at three sites (A–C) in Pará, Brazil. The X in (B) represents the maximum observed size of a *Tabebuia* sapling observed in a survey of 180 15-year-old logging gaps.

Figure 4. Graphs showing projections and observed regeneration rates for *Tabebuia* (Schulze, et al. 2008).

Table 1. The species examined in this study and some of their ecological characteristics.

Scientific Name	Common Name	Shade Tolerance	Seed Dispersal	Elevation (m)	Habitat Preference	Max Height (m)	Deciduous	Growth	Notes
<i>Swietenia macrophylla</i>	Big-Leaf Mahogany	No	Wind, Water	lowland	seasonal forest	50	Yes	Slow	benefits from large disturbance
<i>Cedrela odorata</i>	Tropical Cedar	No	Wind, Water	lowland	riparian sites	n/a	Yes	Slow	high seedling mortality
<i>Dipteryx</i> spp.	Shihuahuaco	Yes	Bats, Mammals	n/a	all types	60	Yes	Slow	can live to 1100 years
<i>Ceiba pentandra</i>	Kapok Tree/Lupuna	No	Wind, Water	0 - 1500	floodplain sites	70	n/a	Fast	limited by temp - 20 C
<i>Calycophyllum spruceanum</i>	Capirona	No	Wind, Water	0 - 650	floodplain sites	40	n/a	Fast	Lumber, Charcoal, firewood
<i>Amburana cearensis</i>	Ishpingo	No	Wind	500 - 1000	seasonal forest	25	n/a	Slow	Legume, seed predation
<i>Tabebuia</i> spp.	Ipe	No	Wind	lowland	n/a	50	Yes	Slow	Similar to Mahogany