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THE CULTIVATION AND MANAGEMENT OF *CHAMAEDOREA* PALMS IN THE UNDERSTORY OF A TROPICAL RAIN FOREST IN MEXICO

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ABSTRACT

The cultivation of nontimber forest products in forest understories is being promoted in many tropical regions in order to conserve habitat and provide income for rural communities. This study describes the management of plantations of the palm *Chamaedorea hooperiana* Hodel in an area of primary rain forest in southeastern Mexico and assesses how management affects forest structure and composition, understory light availability and patterns of seedling establishment. Compared to unmanaged forest, plantation sites were found to have significantly lower density and diversity of woody species in smaller size classes (≤10 cm dbh). Analyses of hemispherical photographs revealed that canopy openness and light availability were significantly greater in plantations than in unmanaged forest. A trend towards higher proportions of shade-intolerant species of canopy tree seedlings in plantations may reflect these altered light conditions. The conservation implications of these ecological changes are discussed in the context of community composition and forest regeneration.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (continued)

CHAPTER I

Introduction

Tropical ecosystems are currently facing unprecedented rates of habitat degradation and species loss (Wilson 1999). This biological crisis is largely due to pressure from a growing human population coupled with the implementation of destructive land uses such as cattle ranching, unsustainable timber extraction and industrialized agriculture (Anderson 1990a). In response to the widespread depletion of biological resources in tropical forests, many nations and conservation organizations have promoted the establishment of national parks and protected areas. Alcorn (1995) notes, however, that despite the presence of protected areas of forests, most of the biodiversity in the tropics exists, and will continue to exist, in areas occupied by humans. Land management in tropical regions must therefore cope with the seemingly paradoxical problem of maintaining biodiversity and supporting a burgeoning human population.

Although nearly all forest reserves in the tropics are surrounded by a matrix of forested and deforested land under human management, the interactions between areas of managed forest and adjacent protected areas are not well understood. Still, integrating this surrounding matrix with the conservation of protected areas has become the basis for the widespread establishment of Biosphere Reserves in both temperate and tropical regions. Biosphere Reserves designate various zones of protection, consisting of a central zone of strict preservation surrounded by so-called "buffer zones," in which a variety of land uses are practiced by local communities. The theory behind the biosphere reserve model is to employ sustainable land practices in the buffer zone that integrate habitat conservation with economic development. In practice, however, management in buffer zones ranges from potentially sustainable practices such as the extraction of nontimber forest products and small-scale shifting agriculture to large-scale forest conversion for cattle ranching and agriculture. Despite the relative ubiquity of the Biosphere Reserve design, its overall effectiveness at conserving forested areas is still debatable (e.g., Duffy et al. 2001; Hayes et al. 2002).

This study examines some of the ecological consequences of the management of forest resources in an area of tropical wet forest in the buffer zone of the Los Tuxtlas Biosphere Reserve (LTBR) in southeastern Mexico. Specifically, I examine the practices involved in the establishment of plantations of the palm, *Chamaedorea hooperiana* Hodel, in the understory of primary forest. People of many communities within the buffer zone of the LTBR depend on the harvest of the leaves and seeds of several *Chamaedorea* species as well as other nontimber forest products (NTFPs) as a major source of income. Historically, NTFPs have been harvested primarily from wild plant populations. Recently, however, many people have begun to establish small-scale plantations of NTFP crops in the understories of primary and secondary forest surrounding their communities. Although the forest canopy is left intact to provide the crops with shade, plantation owners clear much of the understory and midstory vegetation in order to increase light availability and thereby increase crop productivity. Despite the growing prevalence of NTFP cultivation in the Los Tuxtlas Biosphere Reserve and elsewhere in Mexico and Central America, to date there are no studies that have examined how the establishment of plantations may alter the structure, composition and patterns of regeneration in tropical forests.

OBJECTIVES

The objective of this study is to characterize the management of plantations of *Chamaedorea hooperiana* Hodel in the understory of an area of primary wet tropical forest located within the buffer zone of the Los Tuxtlas Biosphere Reserve and to quantitatively evaluate the effects of these practices on forest structure and composition, light availability and woody seedling establishment. The data are presented in two chapters. In Chapter II I describe the practices involved in the establishment and maintenance of plantations and compare forest structure and species composition of plantations with neighboring areas of unmanaged forest. In Chapter III, I compare the patterns of understory light availability and canopy openness between plantations and unmanaged forest using hemispherical photographs of the forest canopy. I then explore how changes in light availability may be reflected in differences in seedling composition between plantation and forest sites and considers the potential implications of plantation management for patterns of forest succession. Finally, for the concluding chapter, I draw upon the findings of the previous chapters and discuss the implications for conservation, management and future research.

LITERATURE REVIEW

1. Nontimber Forest Products

Nontimber forest product (NTFP) harvesting has received much attention for its potential as a sustainable and economically viable form of land use in many ecosystems (see Plotkin and Famolare 1992). The term NTFP collectively refers to plant resources other than timber, such as seeds, leaves, fruits, fibers, resins, oils, latex and herbs, that are extracted from the local environment both for subsistence and market economies.

Although much research has assessed the economic feasibility of harvesting and marketing these resources for local people (Peters et al. 1989; Godoy and Bawa 1993; Hedge et al. 1996; Marshall et al. 2003), large gaps still exist in our understanding of the ecological consequences of their removal (Ticktin 2004). For instance, while many studies advocate the conservation value of NTFPs (Peters et al. 1989; Anderson 1990b; Gomez-Pompa and Kaus 1990; Peters 1990), others have reported unsustainable harvesting (Hall and Bawa 1993; Salafsky et al. 1993; Murali et al. 1996). To ensure that NTFP exploitation can live up to its potential for biodiversity conservation, it is crucial that our understanding of the ecological effects of management be further developed.

The current body of literature suggests that sustainable extraction of NTFPs may have little influence on ecological relationships when compared with other forms of land use (Hall and Bawa 1993). Research that has applied quantitative ecological methods to evaluate the impacts of NTFP harvesting has primarily been restricted to the population dynamics of single species that are being exploited (Ticktin 2004; but see Salick et al. 1995). A common method has been to model harvested plant population dynamics by measuring mortality and movement between various life stages (Peters 1991; Hall and Bawa 1993; Ticktin et al. 2002; Endress et al., in press). Continued population growth under harvest pressure is interpreted as evidence of minimal ecological impact. However, while these studies establish a strong baseline for single populations, they do not take into account the ways in which management may affect the myriad of other biotic and abiotic factors interacting in ecological communities.

Evaluating the sustainability of NTFP extraction is further complicated by variation in management practices. Just as very few studies have considered ecological effects of NTFP management beyond the population level (e.g., Salick et al. 1995), few have also considered the ecological consequences of differences in management practices (but see Ticktin et al. 2002; Ticktin and Johns 2002; Endress et al., in press). Although variation in NTFP extraction may be apparent when comparing distinct management strategies (e.g., harvesting from wild populations vs. plantations), there can also be considerable variability in the ways that different harvesters exploit the same resource. Therefore, it is necessary for NTFP studies to take into account both how different practices may affect different ecological processes and how the variation among harvesters employing the same management strategy may affect the degree of ecological impact.

Recently, government agencies and non-government organizations have begun to promote the cultivation of NTFPs in the understories of forested areas in order to increase the economic resource base for rural communities and reduce harvest pressure on wild populations (Gunatilleke et al. 1993; Sugandhi and Sugandhi 1995; Ratsirarson et al. 1996; Carpentier et al. 2000). Although the cultivation of domesticated crops, such as coffee and cacao, below planted and naturally occurring canopy trees has received relatively wide attention (e.g., Beer et al. 1997; Moguel and Toledo 1999; Rice and Greenberg 2000; Bandeira et al. 2002), no studies to date have examined the management practices involved in the cultivation of NTFPs in forest understories. Ecological research on other agroforestry systems demonstrates that declines in the structural complexity of vegetation are associated with significant declines in the diversity of birds (Thiollay 1995; Greenberg et al. 1997a; Greenberg et al. 1997b; Calvo and Blake 1998), mammals (Estrada et al. 1994; Gallina et al. 1996), and arthropods (Estrada et al. 1998; Perfecto et al. 1997; Perfecto and Vandermeer 2002). NTFP cultivation may also have significant effects on the ecological community due to plantation owners manipulating vegetation in the forest in order to increase light availability for understory crops. In addition to the potential impacts on community diversity due to structural changes, there may also be changes in forest composition due to the alteration of light conditions in the forest understory.

2. The Ecology of Light in Tropical Forests

Despite the myriad interacting ecological factors affecting woody species composition in tropical forests, light has received singular attention due to its major role as a limiting resource for plant growth and survival (Augspurger 1984; Chazdon et al. 1996; Whitmore 1996; Kobe 1999) and to its potential influence over the patterns of forest regeneration (Clark and Clark 1992; Clark et al. 1996). The ecological focus on light has traditionally centered on the dynamics of tree-fall gaps and comparisons of gap/non-gap environments in tropical forests. Light gaps have been shown to influence the photosynthetic responses of plants (e.g., Chazdon 1986), root dynamics (e.g., Sanford 1989), and nutrient cycling (e.g., Vitousek and Denslow 1986) in tropical forests. Light gaps also release shade-tolerant tree seedlings and saplings from suppressed growth rates in the forest understory (e.g., Uhl et al. 1988; Viana 1990), allow for the establishment of shade-intolerant pioneer species (Brokaw and Scheiner 1989) and remove competition from understory shrubs that cannot survive in direct sunlight (Hubbell 1998). Furthermore, observations that certain tree species are restricted to light gaps while other species establish beneath the forest canopy have formed the basis for traditional ecological classifications based on shade-tolerance (e.g., Swaine and Whitmore 1988;

Whitmore 1989) and fueled discussions of niche partitioning along light gradients in tropical forests (Ricklefs 1977; Denslow 1980; Brokaw 1985).

Debate over the extent of light partitioning among tropical tree species continues to be a central issue driving research on tropical community diversity. Two major models have been suggested to explain the maintenance of the high diversity of tree species in tropical forests. The gap-partitioning hypothesis maintains that species are able to coexist due to niche partitioning along resource gradients created by tree-fall gaps of varying size (Denslow 1980; Denslow 1987). The prevailing alternative proposed by Hubbell et al. (1999) asserts that extreme dispersal limitation of propagules among tropical tree species essentially eliminates competition for suitable recruitment sites. Thus, Hubbell et al. (1999) argue that species abundances are determined not by competitive interactions for limited resources, but by stochastic events that allow for the persistence of competitively inferior species.

The gap-partitioning model is partially supported by experimental research showing that changes in light conditions result in different responses among species of tropical tree seedlings in terms of growth and survival (Augspurger 1984; Kobe 1999; Hall et al. 2003), leaf dynamics and morphology (Popma and Bongers 1988; Bongers and Popma 1990) and root development (Tyree et al. 1998). However, long-term research has shown species composition and diversity to be largely independent of gap formation (Lieberman et. al. 1995; Hubbell et al.1999), and direct evidence of niche partitioning along light gradients within and among gaps is still lacking (Brown and Jennings 1998; Brokaw and Busing 2000). In addition, light gap partitioning does not seem to explain the coexistence of the majority of tree species in tropical forests which are shade-tolerant and capable of establishment in the low-light levels of the forest understory (Hubbell 1998). On the other hand, although the dispersal limitation model provides a cogent null hypothesis capable of explaining the sympatric distributions of ecologically similar tree species, evidence of niche partitioning along light gradients in woody seedlings (Kobe 1999, Montgomery and Chazdon 2002), saplings (Clark and Clark 1992; Poorter and Arets 2003) and adult trees (Terborgh and Matthews 1999) contradicts the model's basic assumption that species are competitively equal.

Given that the spatial and temporal variability of light in gaps is likely too unpredictable to allow for adaptive differentiation among species (Wright 2002) and that the largest contribution to regrowth in light gaps comes from advance regeneration (Uhl et al. 1988), the competitive hierarchy among gap regrowth may simply be determined by the size of individuals already established when the gap occurs (Brown and Jennings 1998; Brokaw and Busing 2000). This paradigm maintains that only the tallest seedlings and saplings in the advance regeneration will experience increased growth rates in the event of a canopy opening. Thus, competitive interactions occurring among seedlings and saplings in the understory may be significant in establishing the size-hierarchy of advance regeneration, which would then determine the competitive superiority of individuals at the time of gap formation (Connell 1989; Brown and Jennings 1998). However, while biologists have long recognized the significance of spatial and temporal variation in understory light microenvironments for plant growth (e.g., Pearcy 1983; Chazdon 1986; Chazdon 1988), research has only recently begun to consider how this fine-scale variation of light conditions may influence community dynamics (but see Lieberman et al. 1989).

To date, several studies have quantified the microscale variation in the light regimes beneath intact forest canopies (e.g., Clark et al 1996; Montgomery and Chazdon 2001). However, relating the patterns of light availability to the composition of woody seedlings and saplings has proven difficult (MacDougall and Kellman 1992; Clark et al. 1996; Nicotra et al. 1999). More promising has been recent research demonstrating niche partitioning among seedlings and saplings of shade-tolerant tropical tree species along fine-scale gradients of light in the forest understory (Montgomery and Chazdon 2002; Poorter and Arets 2003). These studies provide direct evidence that the competitive hierarchy of species can shift along small-scale variations in understory light conditions due to their differing abilities for growth and survival. They also lend strong support to the hypothesis that forest composition may be influenced by competitive interactions among the advance regeneration before gap formation. In the context of this study, these findings suggest that if NTFP plantations do indeed alter understory light environments, they may also indirectly influence forest composition.

CHAMAEDOREA PALMS

Distribution and Ecology

Chamaedorea Willd. is a large genus of understory palms, comprising approximately 130 species, whose range extends from Mexico through Central America to northern South America. In Mexico, it is the largest palm genus, containing approximately 50 species, 14 of which are endemic to the country (Hodel 1992). In the Los Tuxtlas Biosphere Reserve, the seeds and leaves of several species of *Chamaedorea* are collected from wild and cultivated populations in areas of primary and secondary forest surrounding communities (see Table 1.1). The two most widely cultivated and exploited species are *C. elegans* Mart. and *C. hooperiana* Hodel. Both species are dioecious and have similar flowering and fruiting phenology, with most plants producing inflorescences between December and February and fruits between October and November (F. Ramirez, pers. comm.). *C. hooperiana* is endemic to the Sierra de Santa Marta and considered threatened whereas the range of *C. elegans* extends throughout Mexico, Guatemala, and Belize (Hodel 1992).

Economic Importance

The popularity of *Chamaedorea* palms for ornamental plantings began in the late 19th century, which first initiated a trade in seed collection. The collection of leaves for use in the floriculture industry began around the 1950s. Currently, approximately 20 species of *Chamaedorea* are commercially exploited by the horticultural and floricultural industries for their leaves, seeds and whole plants. Although commercial greenhouses and plantations in Florida, Hawaiʻi, and California supply most of the trade in whole *Chamaedorea* plants, the majority of leaves and seeds are still supplied from palm populations in their native ranges. For example, in 1998, *Chamaedorea* leaves imported from Mexico and Guatemala represented approximately 14% of the 2.2 billion cut stems of foliage sold in the United States (CEC 2003). Historically, the leaves and seeds of *Chamaedorea* species have been gathered from wild populations in Mexico and Central America; however, the practice of cultivating palms in the understory of forests and coffee plantations has been growing widely over the past 10 years (CEC 2003).

The harvesting of *Chamaedorea* palms in most rural communities in Mexico and Guatemala tends to be a sporadic activity due to the slow production of leaves and annual fruiting phenology of most species; thus it is often supplemented by other economic activities, such as coffee and maize production. Still, in the Mexican state of Veracruz alone, 872 tons of *Chamaedorea* leaves were collected in 1999, for a total revenue of 9,679,200 pesos (≈ $770,000 USD; CEC 2003). However, producers of palm products (i.e., harvesters and small-scale plantation owners) only receive 7% of the final US wholesale price (Table 1.2; CEC 2003). In the Los Tuxtlas Biosphere Reserve, palm harvesters earn between 12-15 pesos (≈ $1-1.2 USD) per gross (144) of leaves, depending on the species. On an average day of work, a palm harvester generally gathers between 8-12 gross of leaves (G. Lopez, pers. comm.). Producers then deliver the leaves to local or regional collectors who sort, pack and distribute the palm leaves to Mexican retailers and US wholesalers who earn 180 pesos per gross (≈ $14 USD/gross; CEC 2003).

The Cultivation of Chamaedorea *palms*

The high demand for palm leaves and seeds has led both government agencies and non-government organizations to promote the cultivation of *Chamaedorea* palms in forested areas by people in rural communities throughout Mexico (F. Ramirez, pers. comm.). There are both advantages and disadvantages of shifting from wild harvesting to the cultivation of *Chamaedorea* palms in plantations. One of the benefits is a larger, more consistent resource base that can be managed closer to communities. As discussed above, harvesting from wild populations is sporadic and often entails hiking long distances through dangerous terrain. Another potential advantage is that plantations may relieve harvesting pressure on wild populations and increase populations of threatened species, such as *C. hooperiana*. However, the establishment of plantations is a relatively new practice and, currently, harvesters and plantation owners are still exploiting wild populations both for leaves and seeds (C. Trauernicht, pers. obs.). Finally, plantations provide better conditions for monitoring and regulation than do wild populations, which makes plantations good candidates for marketing programs that certify sustainable production of forest goods (CEC 2003).

The potential of plantations to reduce the overexploitation of wild *Chamaedorea* populations may be a double-edged sword. If plantation management replaces the practice of wild harvesting, there may be less incentive to conserve areas of native forest. This tradeoff may be balanced by the current practice of planting *Chamaedorea* palms and other NTFP species in the shade of native forest trees. However, the potential to incorporate palm cultivation into agroforestry systems such as coffee, cacao and timber production may further reduce the incentive for forest conservation. Moreover, the ecological effects of *Chamaedorea* cultivation in the shade of forest trees have not been previously assessed. While the practice maintains continuous canopy cover, plantation owners clear much of the understory and midstory vegetation in order to increase light availability and reduce competition for cultivated species. Thus, plantations may not support the same assemblages of understory plants and animals as unmanaged forest. Furthermore, the alteration of the light conditions in plantations may have significant implications for patters of forest regeneration, as discussed in the previous section.

STUDY SITE

This research was conducted in the buffer zone of the Los Tuxtlas Biosphere Reserve (LTBR) in southeastern Mexico in an area of primary forest adjacent to the community of Adolfo Lopez Mateos, located at about 18° 24' N, 94° 58' W (Figure 1.1). The LTBR, established in 1998, encompasses several extinct volcanoes surrounding the city of Catemaco on the gulf coast of southeastern Veracruz. Mean annual temperature in the area is approximately 24° C and mean annual precipitation is between 3000-4000 mm with a dry season from December to May (Soto and Gama 1997).

Adolfo Lopez Mateos is located approximately 18 km east of the city of Catemaco at an elevation of 200 m. To the east of the community the Sierra de Santa Marta, an extinct volcanic crater, rises to an elevation of 1700 m. The terrain surrounding the community is dominated by Cerro El Marinero to the southeast and an abrupt ridge to the north, both of which rise steeply to about 900 m. To the northwest, the coastal plain below Lake Catemaco runs into the Gulf of Mexico, visible from the hills above the community.

The 30 families of Lopez Mateos hold rights to the lands to the east of the community, adjacent to the protected zone of the LTBR that encompasses the crater of the Sierra de Santa Marta. Most of the land to the west of Lopez Mateos has been converted to large-scale cattle pastures by neighboring communities. However, land use in the area to the east of the community primarily consists of small parcels that have been cleared for maize, cattle and coffee in addition to areas of primary and secondary forest that contain plantations of several species of *Chamaedorea* palms. The community also runs an ecotourism project and has set aside over 100 hectares as a community reserve. This study was conducted in the relatively extensive area of tropical high evergreen rain forest (e.g., Bongers et al. 1988) above the community on the slopes of Cerro El Marinero.

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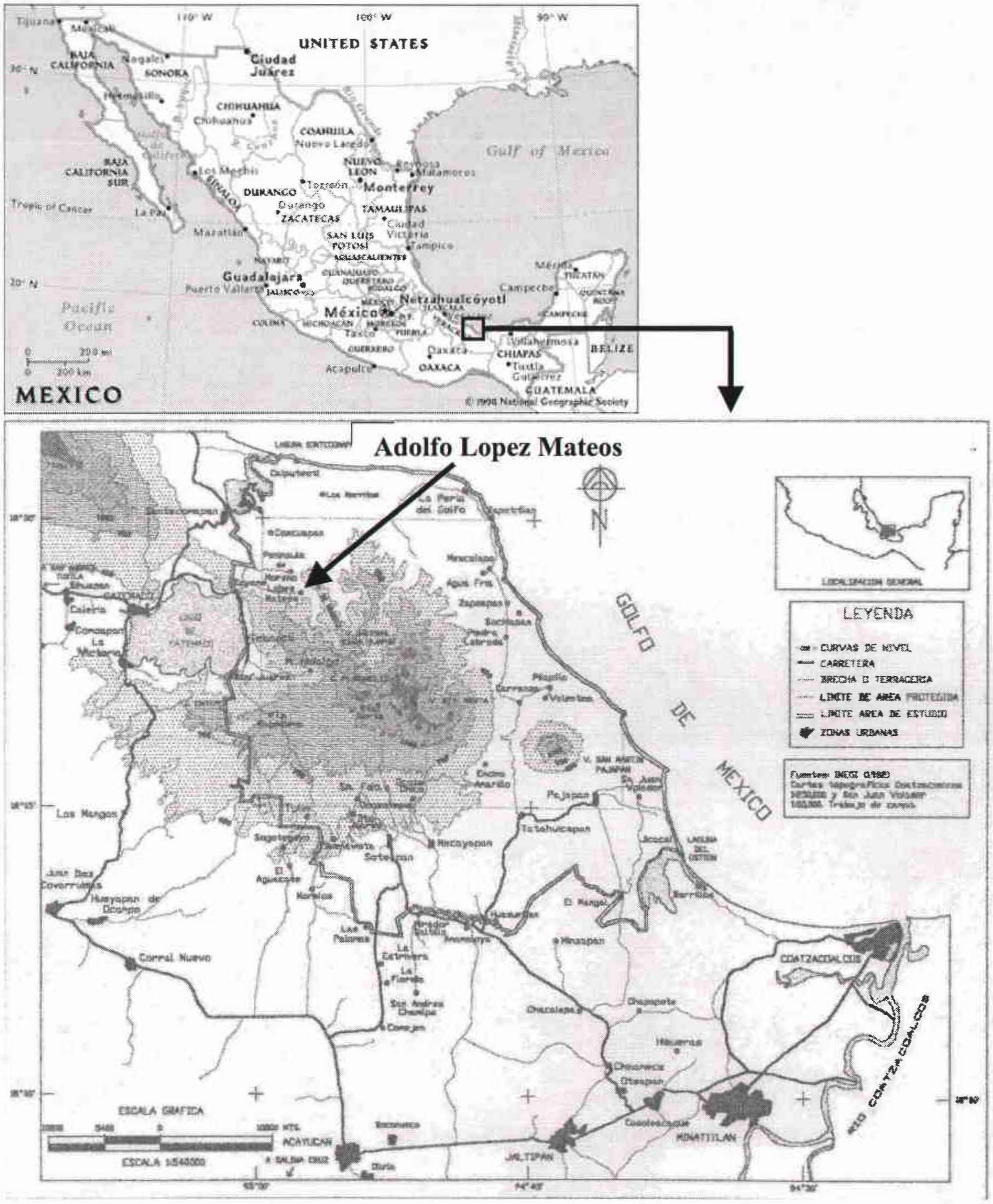

Figure 1.1. Map of the study site.

Table 1.1. Species of *Chamaedorea* palms exploited in the Los Tuxtlas Biosphere Reserve.

Species	**Parts of plant exploited**
C. alternans H.A. Wendl.	leaves, seeds
C. elegans Mart.	leaves, seeds
C. eliator Mart.	leaves, seeds
C. ernesti-augustii H.A. Wendl.	leaves, seeds
C. hooperiana Hodel	leaves, seeds
C. liebmanii Mart.	leaves, seeds
C. oblongata Mart.	leaves, seeds
C. pinnatifrons (Jacq.) Oerst.	leaves, seeds
C. tenella H.A. Wendl.	seeds, whole plant?
C. tepejilote Liebm.	leaves, seeds
C. tuerckheimii (Dammer) Buuret	seeds, whole plant

Table 1.2. Prices paid for *Chamaedorea* leaves at each level of the distribution chain in Mexico (CEC 2003).

Level	**Price (pesos/gross)**
Producer (e.g., harvester)	12-15
Local Collector	14
Regional Collector	16
Mexican Wholesaler	30
Mexican Retailer/US wholesaler	180

CHAPTER II

The Management of *Chamaedorea* Plantations and the Effects on Plant Community Structure and Composition

INTRODUCTION

Nearly all of the reserves and protected areas in the tropics are surrounded by a matrix of managed landscapes. Management in these areas can range from large-scale conversion of forest to cattle pasture or large-scale agriculture to less intensive uses such as nontimber forest product extraction and small scale shifting agriculture. Biologists are just beginning to consider the relationships and interactions between these managed zones and the adjoining protected areas. Despite the importance of reserves and protected areas for biological conservation, the majority of the world's biodiversity exists and will continue to exist in areas occupied by humans (Alcorn 1995). Therefore, in order to effectively conserve these ecosystems, we must understand how the various forms of land use affect the biological processes and diversity in these managed areas.

The harvesting of nontimber forest products (NTFPs) has received much attention for its potential as a sustainable and economically viable form of land use in many ecosystems (Peters et al. 1989; Anderson 1990; Gomez-Pompa and Kaus 1990; Peters 1990; Plotkin and Famolare 1992). The term NTFP collectively refers to plant resources other than timber, such as seeds, leaves, fruits, fibers, resins, oils, and latexes that are extracted from the local environment both for subsistence use and market economies. In addition to harvesting from wild populations, the planting of non-domesticated NTFP crops in the understories of forests is being promoted both as a conservation strategy to protect wild populations and as an economic development plan for rural communities

(Gunatilleke et al. 1993; Sugandhi and Sugandhi 1995; Ratsirarson et al. 1996; Carpentier et al. 2000). This practice is particularly widespread with the cultivation of domesticated plants such as coffee and cacao grown under planted or naturally occurring canopy trees (Beer et al. 1997; Moguel and Toledo 1999; Rice and Greenberg 2000; Bandeira et al. 2002).

The majority of ecological research on NTFP management has been devoted to understanding the effects of extraction on wild populations of economically important species (Peters 1991; Hall and Bawa 1993;Ticktin et al. 2002). Yet the management practices involved in NTFP cultivation differ considerably from wild population management and subsequently have different ecological implications. In order to assess the sustainability of NTFP plantations, we must consider not only the effects of management on the NTFP resource itself, but also on other ecological aspects such as community structure, species interactions and diversity. For example, many studies have examined how other agroforestry systems, such as coffee and cacao plantations, support various faunal assemblages, asserting that plantations with complex vegetative structure can play an important role in biodiversity conservation (Thiollay 1995; Gallina et al. 1996; Greenberg et al. 1997a ; Greenberg et al. 1997b; Perfecto et al. 1997; Calvo and Blake 1998). However, despite the growing numbers of plantations of non-domesticated NTFPs being established in forest understories, no research to date has examined the effects of plantation management on the structure and composition of plant communities (Ticktin 2004).

The goals of this chapter are: 1) to describe the management practices and decisions involved in the establishment and maintenance of NTFP plantations and 2) to assess the ecological implications of these practices by comparing the community structure and composition of plantations with that of unmanaged areas of forest. In order to accomplish this, I conducted a case study of four plantations of the understory palm *Chamaedorea hooperiana* Hodel established in an area of primary rain forest in southern Mexico. *C. hooperiana* is endemic to the Los Tuxtlas region of Veracruz and is considered to be vulnerable to extinction because its natural range is largely restricted to wet montane forests above 600 m (Hodel 1992). *C. hooperiana* and several other species of native understory palms are valued for their leaves and seeds which are harvested and marketed both locally and internationally in the horticulture and floriculture industries.

CHAMAEDOREA PLANTATION MANAGEMENT

One of the key factors making the study of NTFP management so difficult is the variation in land management practices. Rarely is this issue addressed in the literature (but see Ticktin et al. 2002; Ticktin and Johns 2002; Endress et al., in press), though it is arguably a confounding factor in any NTFP study. This variability becomes apparent from simply visiting different *Chamaedorea* plantations. Whereas some plantations are difficult to distinguish from the surrounding forest, others are quite conspicuous with very open understories and patchier canopy cover. This range of conditions reflects the wide array of factors that are taken into consideration both at the outset of plantation establishment as well as later on during routine maintenance. The variation in decision-making largely depends upon the ecological knowledge and foresight of the plantation owner and can be compounded by others who are often hired to help with the work.

In Mexico, the process by which NTFP plantations are established and maintained is called *limpiando*, translated literally as "cleaning". This consists of clearing out much of the understory and midstory vegetation while leaving the larger canopy trees standing in order to provide shade. Although the NTFP species being managed are normally shade tolerant, slow-growing understory plants (such as *Chamaedorea* palms), increasing the amount of light in plantations increases resource production (Ticktin et al. 2003; F. Ramirez, unpublished data). This concept is well understood by plantation owners and is the primary reason for removing the smaller trees and shrubs beneath the canopy.

Decisions about what plants to remove depend on several factors. First, plantation owners maintain that economically valuable timber trees are invariably spared. In addition, the majority of naturally occurring *Chamaedorea* palms as well as *Reinhardtia gracilis* are spared because their leaves are also economically valuable. Beyond that, it is the existing canopy structure that largely determines how much thinning is required below. For example, if a canopy tree has a particularly large crown, the majority of the trees below it will be removed. On the other hand, with patchier canopy cover, smaller trees will be spared in order to maintain some shading. Another important factor mentioned by plantation owners that governs which trees are spared is leaf morphology. Large leaves can cover and kill NTFP seedlings when shed. Therefore, there is often selection against trees with large leaves (e.g., *Cecropia* spp., some palms).

After the initial clearing of the understory and midstory, the debris is not burned but rather left to decompose naturally. Once the debris has decomposed sufficiently, NTFP seedlings are outplanted into the plantation understory. In the case of *Chamaedorea* palms, seeds are collected from adults in existing plantations and wild populations and germinated in *viveros,* or shaded growing beds, near the homes of plantation owners. Once they have reached a certain size (≈10 cm in height), the palm seedlings are placed in bags and carried out to the plantations for outplanting. For some NTFP species, such as *Aechmea magdelenae*, plants can be propagated vegetatively in plantations by collecting clones from existing populations (Ticktin et al. 2003).

Although higher light increases the production of economically valuable species, plantation owners note that it also increases the rate at which herbaceous plants reestablish in plantations. Thus, there is a balance between the amount of clearing done at the time of plantation establishment and the frequency of routine maintenance work. This periodic maintenance consists of simply cutting back the understory herbaceous regrowth amidst the NTFP species. In plantations with very open canopies, this may be required every six months whereas in those with denser canopy cover it may be only annually or even less frequently.

OBJECTIVES

My specific objectives are to address the following questions: 1) Does the management of NTFP plantations have different effects on community structure and composition (vegetative cover, plant diversity, stem density, basal area) for different life history stages and assemblages of plant species when compared to unmanaged forest? The establishment of NTFP plantations entails the removal of much of the understory and midstory vegetation in order to increase light availability for planted species. Thus, I hypothesized that the structure and composition of plantations would be most different from areas of unmanaged forest among the smaller size classes, including shrubs, saplings and certain species of palms.

2) To what extent are naturally occurring, economically valuable plant species spared when plantations are established and how may this affect the densities of these

species in plantations vs. forest sites? Many plantation owners maintain that when clearing plantation understories, they leave saplings of timber species and certain native palm species that are also valued for their leaves (*Chamaedorea alternans, C. elegans, C. eliator, C. ernesti-augustii, C. oblongata, C. pinnatifrons, C. tepejilote* and *Reinhardtia gracilis*). I therefore hypothesized that there would be no difference in the densities of palm species between plantations and areas of unmanaged forest. However, given the focus of management practices on removing woody plants in order to increase light levels, I still expected the density of timber saplings to be reduced in plantations.

3) What are the conservation implications of both the changes in community composition and the management of naturally occurring, economically valuable species? For this discussion, I draw upon studies of other agroforestry systems in order to address the potential consequences of changes in the structural complexity of the vegetation in plantations of *C. hooperiana*.

METHODS

This research was conducted in the buffer zone of the Los Tuxtlas Biosphere Reserve (LTBR) in southeastern Mexico in an area of primary forest adjacent to the community of Adolfo Lopez Mateos, located at about 18° 24' N, 94° 58' W. The LTBR, established in 1998, encompasses several extinct volcanoes surrounding the city of Catemaco on the gulf coast of southeastern Veracruz. Mean annual temperature in the area is approximately 24° C and mean annual precipitation is between 3000-4000 mm with a dry season from December to May (Soto and Gama 1997).

Adolfo Lopez Mateos is located approximately 18 km east of the city of Catemaco at an elevation of 200 m. To the east of the community the Sierra de Santa

Marta, an extinct volcanic crater, rises to an elevation of 1700 m. The terrain surrounding the community is dominated by Cerro El Marinero to the southeast and an abrupt ridge to the north, both of which rise steeply to about 900 m. To the northwest, the coastal plain below Lake Catemaco runs into the Gulf of Mexico, visible from the hills above the community.

The 30 families of Lopez Mateos hold rights to the lands to the east of the community, adjacent to the protected zone of the LTBR that encompasses the crater of the Sierra de Santa Marta. Most of the land to the west of Lopez Mateos has been converted to large-scale cattle pastures by neighboring communities. However, land use in the area to the east of the community primarily consists of small parcels that have been cleared for maize, cattle and coffee in addition to areas of primary and secondary forest that contain plantations of several species of *Chamaedorea* palms. The community also runs an ecotourism project and has set aside over 100 hectares as a community reserve. This study was conducted in the relatively extensive area of tropical high evergreen rain forest (e.g., Bongers et al. 1988) above the community on the slopes of Cerro El Marinero.

In order to identify and characterize the management decisions that govern both the establishment and the maintenance of palm plantations, I relied on informal discussions with plantation owners both in the community and in the field. I spoke with ten out of the fourteen plantation owners in Adolfo Lopez Mateos, all males between the ages of 22 and 80.

To compare the vegetative cover and community structure and composition of NTFP plantations with unmanaged forest, I selected four locations that each contained an area of plantation (0.5-1 ha with understory plantings of *Chamaedorea hooperiana* Hodel) surrounded by an area of primary forest (without planting). The experimental design therefore consisted of four blocks, each containing a plantation site paired with an adjacent forest site of similar size, inclination and slope aspect. Of the four blocks, Blocks 1 and 2 were located at approximately 300 m in elevation and Blocks 3 and 4 were located at approximately 500 m in elevation. All were situated on steep slopes ranging from about 30 to 45 degrees. Block 1 had an easterly slope aspect and Blocks 2, 3 and 4 had northerly slope aspects. The plantations in Blocks 2, 3, and 4 were established in 2001 and the herbaceous understory vegetation in their understories was cleared 1-3 months before data sampling. The plantation in Block 1 was established in 1999 and its owner had not cleared the understory vegetation for over a year.

In each plantation and forest site, 12 plots were established for a total of 96 plots across all blocks (4 Blocks x 2 treatment x 12 plots; Figure 2.1). Maps of each site were sketched based on measurements of plantation area and the corresponding, adjacent area of unmanaged forest. Plot locations were then randomly selected using an x-y coordinate system. Each plot consisted of a 3x2 m quadrat circumscribed by a 10 m diameter circular plot (see Figure 2.1). The 3x2 m quadrat was established in order to measure vegetative cover as well as to assess seedling density and composition for a separate portion of the study. The 10 m diameter plots were used to assess the composition and structure of woody plants and palms and covered a sampling area of 942.4 m^2 per site. In order to avoid confounding effects of plantation edges and existing tree fall gaps, a minimum distance of 10 m was maintained between adjacent plots and no plot was placed less than 10 m from a tree fall gap edge or less than 5 m of a plantation edge.

Vegetative cover measurements were taken at 24 points within each of the 3x2 m plots for a total of 288 points per site. Four transects were randomly placed running parallel to the long edge of the plot and cover was measured at 6 points along each transect at 0.50 m intervals beginning at 0.25 m and ending at 2.75 m. Vegetative cover was measured from ground level to 1.8 m using a string with a weighted plumb. At each sample point, I recorded the number of contact points between the string and surrounding plant individuals and noted the life form of each individual. I also recorded the presence or absence of overhead cover above 1.8 m using a densitometer.

In order to analyze community structure and diversity I recorded the identity and stem diameter at breast height (dbh; @1.3 m) of all woody individuals ≥1 cm dbh within each 10 m diameter circular plot. In addition, I recorded the height and identity of all palms and cycads ≥0.20 m high.

ANALYSIS

For analyses of species richness, diversity, stem density, basal area, and vegetative cover, I pooled data from the 12 plots in each plantation and forest site. I used completely randomized blocks design ANOVAs (Sokal and Rohlf 1995) to make comparisons between plantation and forest sites when assumptions of normality and homogeneity of variances were met. When original data sets did not meet these assumptions, I either used transformed data that did meet the assumptions or I employed the nonparametric Friedman's test. In order to assess differences within life history stages and species assemblages for species richness, diversity, and stem density, analyses were made using the following groups: 1) all species, including all palms and cycads ≥0.20 m in height and all woody plants ≥1 cm dbh, 2) all woody species, 3) woody understory including all individuals <10 cm dbh, 4) woody individuals ≥10 cm dbh, 5) woody individuals ≥ 20 cm dbh, 6) shrub species (e.g., adults rarely exceeding 10 cm dbh), 7) all palms and cycads, and 8) wild palms and cycads, specifically excluding the planted *Chamaedorea hooperiana* individuals in the plantations.

Richness was determined using total species counts for each site. Diversity was evaluated using Simpson's index (sensitive to changes in abundant species) and Brillouin's index (sensitive to changes in rare species). Both were calculated based on the relative abundances of each species (see Krebs 1999 for formulae). Density was calculated as the number of stems per hectare.

In addition to the life stage groupings, I made species-specific comparisons of density between plantation and forest sites for the midstory palm, *Astrocaryum mexicanum*, and the economically valuable understory palm species, which included *Reinhardtia gracilis* and all *Chamaedorea* species recorded in the study site. I also made density comparisons between plantation and forest sites for timber saplings, which included all individuals of timber species <10 cm dbh. In addition to comparisons of the overall density of timber saplings, I compared the relative abundance of timber saplings (proportion of the # of timber saplings to total saplings in each site). Basal area (m^2/ha) was calculated from measurements of stem diameter at breast height (1.3 m) for all woody individuals within the 10 m diameter plots. Of the life history groups described above, basal area was only analyzed for those containing woody species.

Percent vegetative cover was calculated as the percentage of hits to total sample points for the following groups: 1) overhead cover (above 1.8 m), 2) overall cover (below 1.8 m), and on a per life form basis (all below 1.8 m) for 3) palms and cycads,

4) herbaceous plants (including ferns), 5) woody plants, and 6) vines and lianas. Since percent overhead cover was based on presence or absence of canopy cover, values fell between 0-100%. For percent cover in the understory, I recorded multiple hits at each sample point and therefore values could have been greater than 100%. In addition to analyses using completely randomized blocks design ANOVAs, I also ran nested ANOVAs on percent understory cover for all groups that met the required assumptions of normality and homogeneity of variances. This enabled me to compare the variation in cover between management types with the variation among sites.

Community structure analyses based on size class distributions were performed separately for woody species and palms and cycads. I tested the independence of size class distributions on management type (plantation vs. unmanaged forest) using the log-linear model of goodness of fit (Sokal and Rohlf 1995). Because these analyses included a multitude of species with differing life history traits, size classes were assigned based on 10 cm dbh increments for woody species and 1 m height increments for palms and cycads. In order to increase resolution for the smaller, more abundant individuals, the first two size classes for both species groups are based on smaller increments. Therefore, 8 size classes were used for woody species based on dbh: 1) 1-4.9 cm, 2) 5-9.9 cm, 3) 10-19.9 cm, 4) 20-29.9 cm, 5) 30-39.9 cm, 6) 40-49.9 cm, 7) 50-59.9 cm, and 8) ≥60 cm. For palms, 7 size classes were used based on height: 1) 0.2-0.4 m, 2) 0.5-0.9 m, 3) 1.0-1.9 m, 4) 2.0-2.9 m, 5) 3.0-3.9 m, 6) 4.0-4.9 m, and 7) ≥5.0 m.

RESULTS

Community Structure and Composition

Forest sites were significantly greater in overall species richness than plantation sites. When broken down into life history groups, richness was greater in forest sites for all woody species, woody understory species, shrubs, and woody individuals ≥10 cm dbh (Figure 2.2). Species richness did not significantly differ between forest and plantation sites for woody individuals ≥ 20 cm dbh, all palms and wild palms.

According to Brillouin's diversity index, the overall diversity of forest sites was greater than plantation sites. Looking at life history groups, diversity was greater in forest sites for all woody species, shrubs and woody individuals ≥10 cm (Figure 2.3). The Brillouin's indices for the woody understory also indicate that forest sites tend to be more diverse than plantations (F=7.99, P=.0664, df=1). As with species richness, no differences between forest and plantation sites were found for woody individuals ≥20 cm dbh, all palms and wild palms.

In contrast to Brillouin's index, Simpson's index of diversity proved less sensitive to differences in species diversity between forest and plantation sites. The only significant difference between sites was for the woody understory (Figure 2.4).

The overall density of stems in the forest sites was also significantly greater than in plantation sites. Analyses of life history groups show stem density to be greater in forest sites for all woody species, woody understory, shrubs, as well as wild palms (Figure 2.5). No significant differences in stem density were found between forest and plantation sites for the groups including woody individuals ≥10 cm dbh, woody individuals ≥20 cm dbh and all palms and cycads.

The densities of the seven non-cultivated *Chamaedorea* species and *R. gracilis* did not significantly differ between forest and plantation sites (Figure 2.6). In contrast, large differences in mean densities were found between plantation and forest sites for both *A. mexicanum* and *C. hooperiana*. Whereas *A. mexicanum* densities are significantly greater in forest sites, the density of *C. hooperiana* is significantly greater in plantation sites (Figure 2.7).

For timber saplings (<10 cm dbh) overall density was significantly greater in forest than in plantation sites while the relative abundance (proportion of timber saplings to total saplings) was significantly greater in plantation sites (Figure 2.8).

The distribution of basal area among size classes illustrates differences between forest and plantation sites among the smaller size classes (Figure 2.9). The woody understory (<10 cm dbh) of forest sites had significantly greater basal area than the understory of plantation sites (F=211.22, P<0.005, df=1). No significant differences were found for all woody individuals, woody individuals ≥10 cm dbh and woody individuals ≥20 cm dbh.

Although the forest sites had higher average percent vegetative cover than plantation sites, no significant differences were found among any of the groups tested (Figure 2.10). The results using nested ANOVAs for overall understory, herbaceous cover, and woody cover show that there were significant differences among sites within treatments (plantation vs. forest) and no significant differences between plantation and forest sites (Table 2.1). For the cover of palms and cycads, there were neither significant differences among sites nor between treatments.

The difference in the community structure of woody species between forest and plantation sites illustrates the reduction of smaller size classes in plantations (Figure 2.11). The log-linear analysis for woody species demonstrated that size class distribution is dependent upon management type (forest vs. plantation; $G=222.6$, $P<0.0001$, $df=28$). Examining the community structure of palms in plantations illustrates a scarcity of individuals in larger size classes when compared with forest sites (Figure 2.12). Log-linear analysis of palm community structure also found that size class distribution is dependent upon management type ($G=838.7$, $P<0.0001$, $df=20$).

DISCUSSION

Through this case study I intended to describe the decisions that govern the management of NTFP plantations and to assess their ecological implications by comparing the community structure and composition of plantations with that of unmanaged forest. It is clear that the management practices involved in the establishment of understory NTFP plantations are largely directed at removing both the understory and midstory vegetation in order to increase light for the species being planted. The results from the quantitative analyses also clearly illustrate that the greatest differences between plantation and forest sites are found within these lower strata.

Structure

Comparing the size class distributions of forest and plantation sites presents a fairly comprehensive picture of how the establishment of plantations changes the community structure of woody species. Whereas there was very little difference between plantation and forest sites among individuals larger than 20 cm dbh, the density of individuals in the smaller size classes was significantly reduced in plantations. Similarly, there were significant differences between plantations and forest sites for almost all other variables analyzed, including species richness, diversity, basal area, among woody species <10 cm dbh and no differences among larger trees (≥20 cm dbh).

In contrast, for palm community structure, the size class distribution in plantations is concentrated in the smaller size classes with very few individuals >3 m tall. This difference may be due entirely to the replacement of *Astrocaryum mexicanum*, the most abundant palm in forest sites, with *C. hooperiana* (normally restricted to areas >600 m though one forest site had a wild population at 300 m). Whereas adults of *C. hooperiana* as well as the other *Chamaedorea* species rarely reach heights greater than 3 meters (with the exceptions of *C. tepejilote* and *C. eliator*, neither of which were very abundant), the height of *A. mexicanum* adults normally exceeds 5 meters. This shift in species dominance may have ecological implications due to changes in the 3-dimensional structure in plantation understories as well as differences between *C. hooperiana* and *A. mexicanum* in crown structure, growth form (e.g., clonal growth in *C. hooperiana*), resource use, and species interactions.

The result of these changes in the community structure of woody species and palms is a simplification of the understory and midstory of plantations which may have implications for assemblages of species other than plants. Studies of other agroforestry systems point to the importance of complexity in plant community structure in maintaining diversity levels close to that in forested areas. For instance, several studies note that more structurally complex agroforestry systems tend to support a greater diversity of bird species than simplified systems (Thiollay 1995; Greenberg et al. 1997a; Greenberg et al. 1997b; Calvo and Blake 1998). In addition, reduction in the structural complexity of vegetation in agroforestry systems has been associated with reductions in mammal diversity (Estrada et al. 1994; Gallina et al. 1996) and even arthropod diversity (Estrada et al. 1998; Perfecto et al. 1997; Perfecto and Vandermeer 2002).

Plant Diversity

The discrepancies between Brillouin's and Simpson's indices of diversity suggest that rare species are being lost with the establishment of plantations. Whereas Simpson's index is sensitive to differences in the most abundant species, Brillouin's index is more sensitive to differences in rare species (Krebs 1999). In a diverse tropical forest such as that in the Los Tuxtlas region, the reductions in stem density encountered in plantations would likely result in a loss of the rarer species first. Thus, in this case, Brillouin's index was more effective than Simpson's index in illustrating the effects of plantation establishment on plant diversity.

The decrease in species diversity in the smaller size classes found in this study suggests a potential problem for the conservation of shrub species whose adult sizes rarely exceed 10 cm dbh. NTFP plantations are likely to have little effect on the reproductive output of larger tree species because management practices do not appear to affect the forest overstory. Therefore, despite losses of saplings in the smaller size classes, there still may exist the potential for regeneration of canopy trees, if given the chance to grow, due to the persistence of large adults as seed sources in plantations. However, since the understories of plantations are continually removed, populations of shrub species may become fragmented or even eliminated locally. Further research is required in order to fully understand the implications this may have for the conservation of these species, yet it suggests the importance of maintaining a forested matrix around plantations in order to sustain shrub populations.

Vegetative Cover

Despite the tendency for percent cover to be greater in forest sites, the differences between forest and plantation sites were not significant. This is surprising given the great reduction of understory plant density in plantation sites. However, these results may be explained in part by the great degree of variation among sites as indicated by the results of the nested ANOVAs. These differences among plantation sites may be a reflection of the variability inherent in management practices. For example, in the plantation that had not been cleared for over a year, overall, woody and herbaceous cover were actually greater than in the corresponding forest site. This observation corroborates claims made by local plantation owners that vegetative regrowth is faster in palm plantations due to elevated light levels.

Economically Valuable Species

The results from this study indicate that economically valuable NTFPs, namely the naturally occurring *Chamaedorea* species and *Reinhardtia gracilis*, were spared when plantations are established and maintained. In contrast were the large reductions of *Astrocaryum mexicanum* in plantations. Although *A. mexicanum* is generally valued as a food source (both flowers and palm hearts are eaten), it is considered a nuisance in plantations due to its spine-encrusted trunk and its large leaves that can fall and cover planted seedlings.

For timber species, although plantations had a higher proportion of timber saplings relative to total saplings than forest sites, this must be interpreted with caution due to the overall reduction of timber sapling density in plantations. The practice of leaving timber saplings may have the potential to sustain the populations of valuable tree species in plantations, however, the number of saplings currently spared is likely too small to effectively maintain populations. Further long-term research would be required to determine whether selection for timber species within NTFP plantations at this small of a scale has the potential to alter future forest composition.

Limitations

This study reveals some consistent trends in the structural and compositional changes associated with the establishment and maintenance of NTFP plantations. At the same time, the variation encountered in the analyses illustrates the importance of taking into account the variation among sites with different NTFP management practices and land use histories. While an analysis of the ecological knowledge of plantation owners is well beyond the scope of this study, it is clear that this knowledge ultimately governs which plants will be removed and which will be spared in NTFP plantations. The human variable complicates the design and analysis of ecological studies by making replication difficult, in addition to complicating the implementation of more sustainable management practices. Some studies are beginning to overcome this problem through experimental manipulations of NTFPs that simulate local management practices (Ticktin et al. 2002, Endress et al., in press).

Despite the substantial changes to forest structure and composition, NTFP plantations are less ecologically destructive than large-scale clear cutting for agriculture and pasture because the forest canopy remains intact. Still, it is difficult to surmise the long-term consequences of plantation management due to the limited temporal scope of this study. With continual clearing of the forest understory, regeneration is effectively stopped unless the plantation is abandoned. Interestingly, one of the only reasons owners will abandon a plantation or an area of a plantation, is when the NTFP species, which require some shade for survival, are exposed to full sunlight due to a tree fall gap. In the event of a canopy opening in a plantation, the composition of secondary growth may be altered by the reduction of advanced regeneration in the plantation understory. In addition, differences in abiotic factors brought about by the alteration of the forest structure, such as increases in light and temperature, may influence the assemblages of tree seedlings that are able to establish in plantations between clearings. The implications that these indirect effects of plantation management may have on the process of forest regeneration are explored in more detail in the following chapter.

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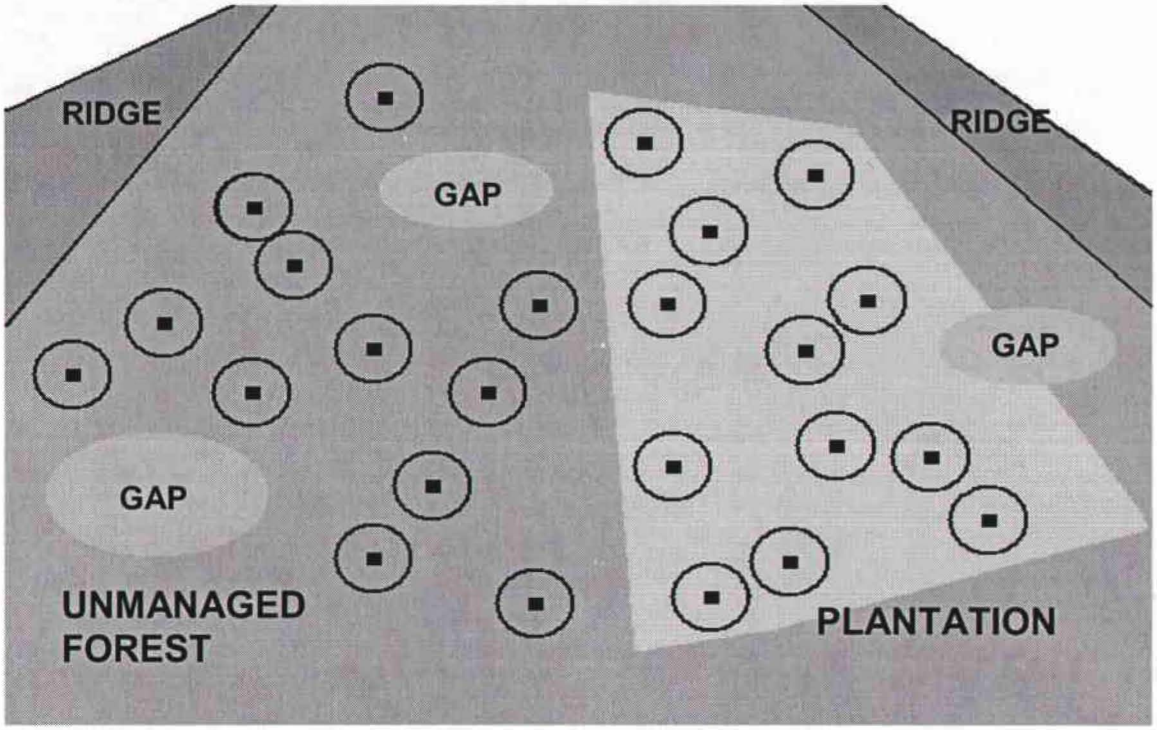

Figure 2.1. Diagram of sampling design for plantation and forest sites in a single block. Black squares are 3x2 m plots and circles are 10 m diameter plots.

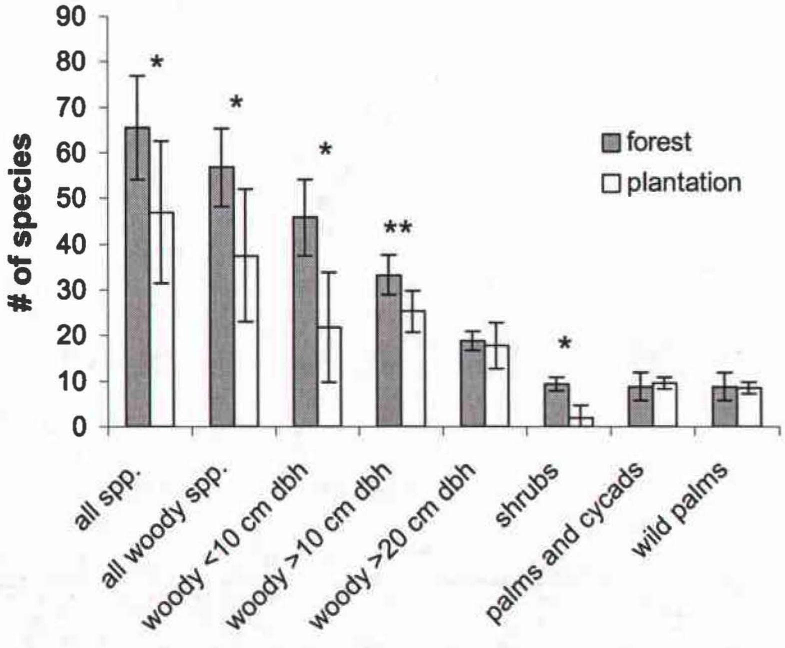

Figure 2.2. Mean species richness for forest and plantation sites for all life stage groups and species assemblages analyzed. Error bars represent one standard deviation. (*significant difference at P<0.05; **significant difference at P<0.005)

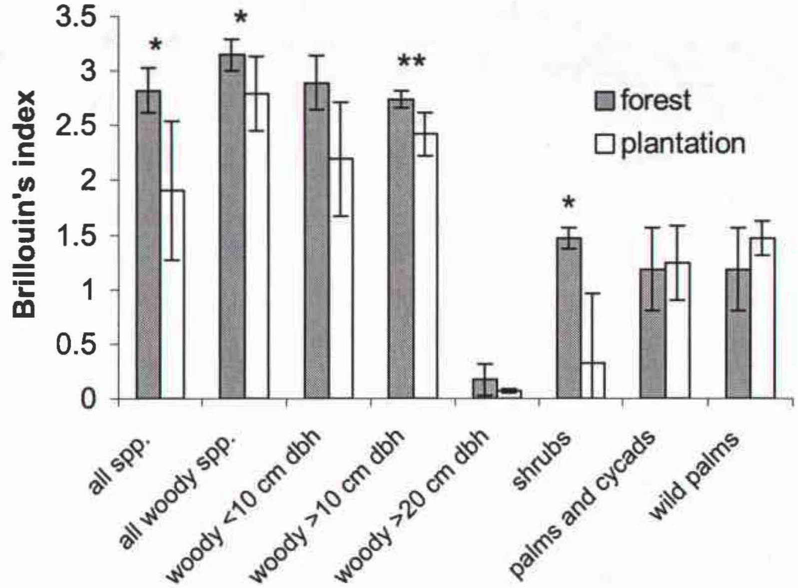

Figure 2.3. Mean values of Brillouin's index of diversity for forest and plantation sites for all life stage groups and species assemblages analyzed. Error bars represent one standard deviation. (*significant difference at P<0.05; **significant difference at P<0.005)

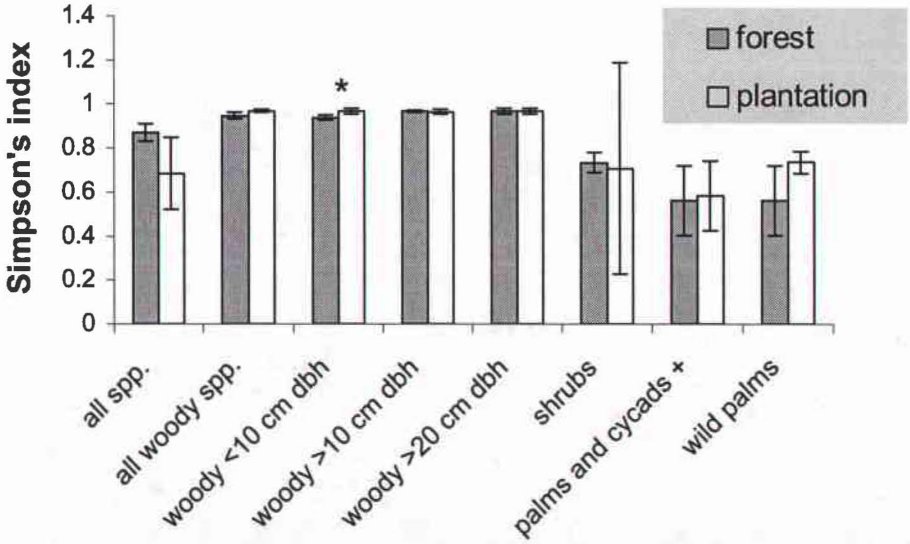

Figure 2.4. Mean values of Simpson's index of diversity for forest and plantation sites for all life stage groups and species assemblages analyzed. Error bars represent one standard deviation. (*significant difference at P<0.05; $^+$Data arcsine transformed)

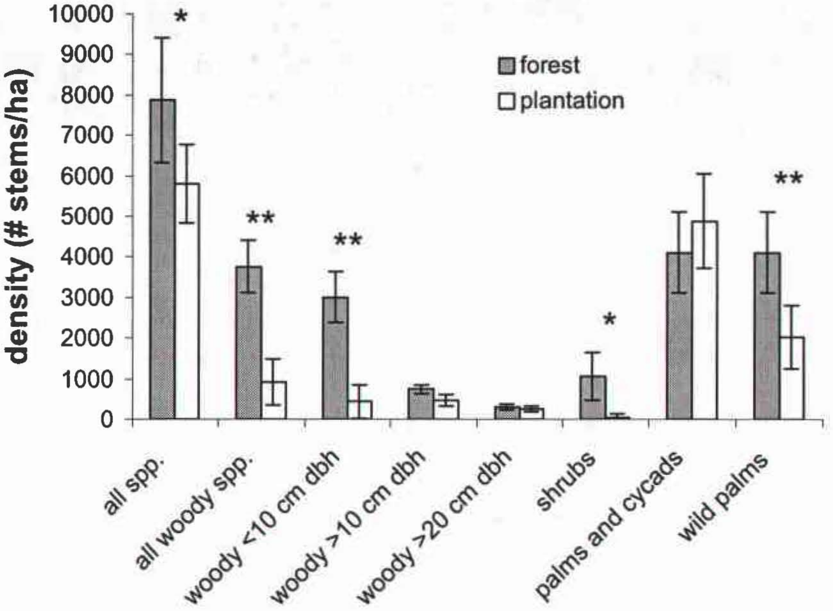

Figure 2.5. Mean stem densities for forest and plantation sites for all life stage groups and species assemblages analyzed. Error bars represent one standard deviation. (*significant difference at P<0.05; **significant difference at P<0.005)

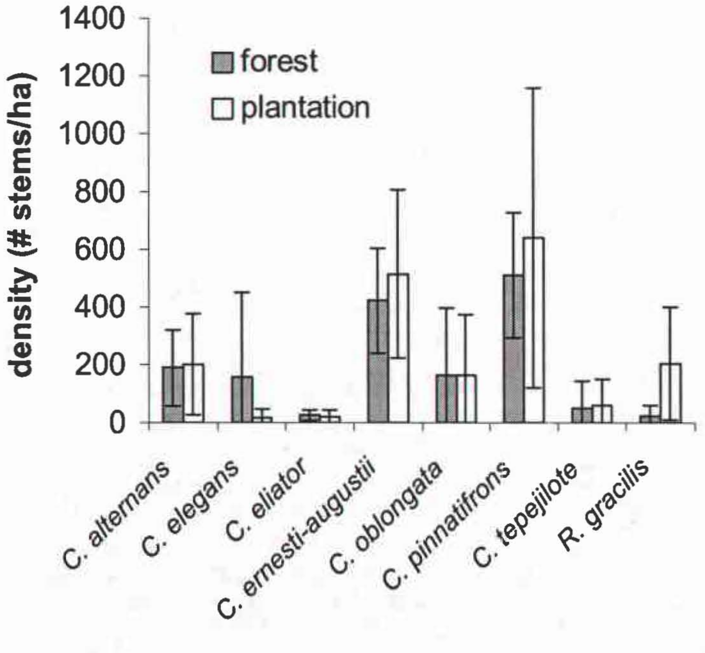

Figure 2.6. Mean stem densities for forest and plantation sites for the economic palm species *Reinhardtia gracilis* and the seven native *Chamaedorea* species not being cultivated in plantations. Error bars represent one standard deviation. No significant differences were found between forest and plantation sites.

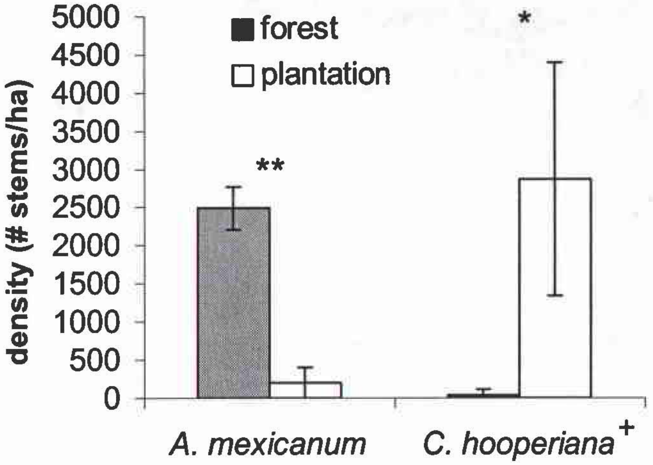

Figure 2.7. Mean stem densities for forest and plantation sites for the palm species *Astrocaryum mexicanum* and *Chamaedorea hooperiana*. Error bars represent one standard deviation. (*significant difference at $P<0.05$; **significant difference at $P<0.005$; $^+$Data log transformed)

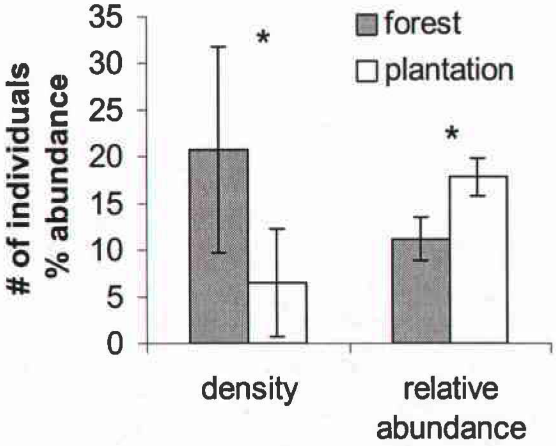

Figure 2.8. The mean density (total count of timber saplings) and relative abundance (proportion of timber saplings to all saplings) of timber species saplings (<1 cm dbh) in plantation and forest sites. Error bars represent one standard deviation. (*significant difference at $P<0.05$)

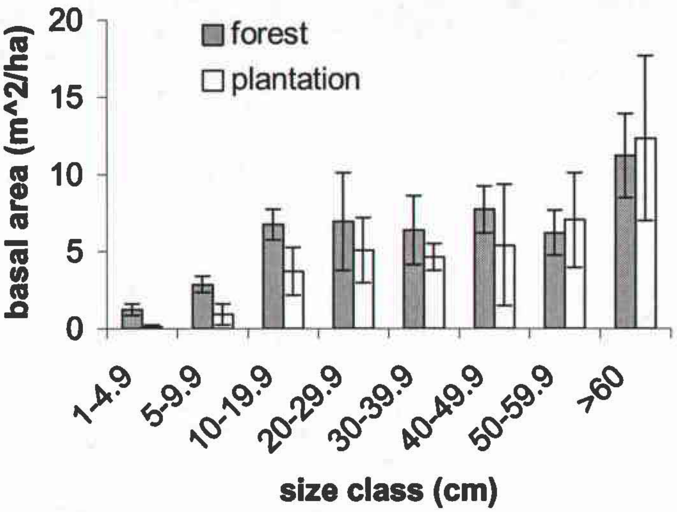

Figure 2.9. The distribution of mean basal area across the size classes of woody species (based on dbh) for forest and plantations sites. Error bars represent one standard deviation.

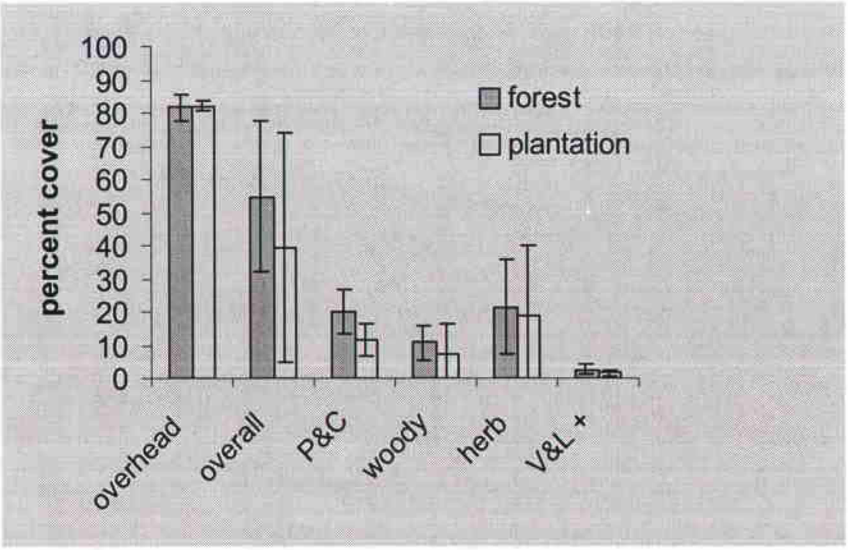

Figure 2.10. Mean percent vegetative cover for forest and plantation sites. Overhead refers to overhead cover above 1.8 m and overall refers to total percent cover of the understory below 1.8 m. The other groups refer to understory cover based on life form: P&C=palms and cycads, herb=herbaceous plants, woody=woody plants, and V&L=vines and lianas. No significant differences were found among the groups. ($^+$Data log transformed)

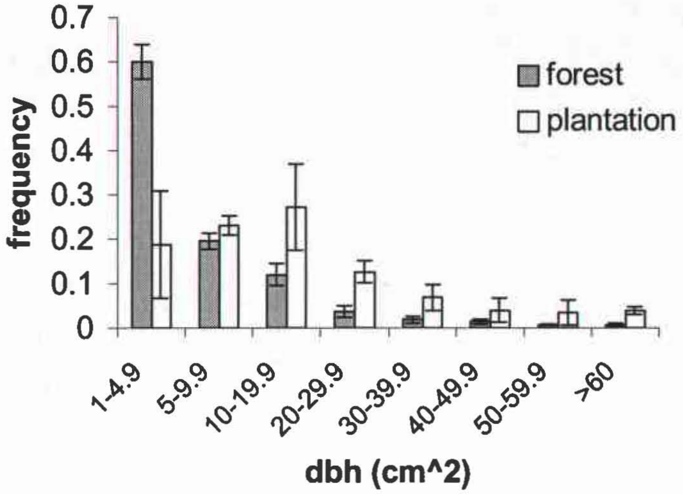

Figure 2.11. The size class distribution of woody species (based on dbh) for forest and plantation sites. Error bars represent one standard deviation.

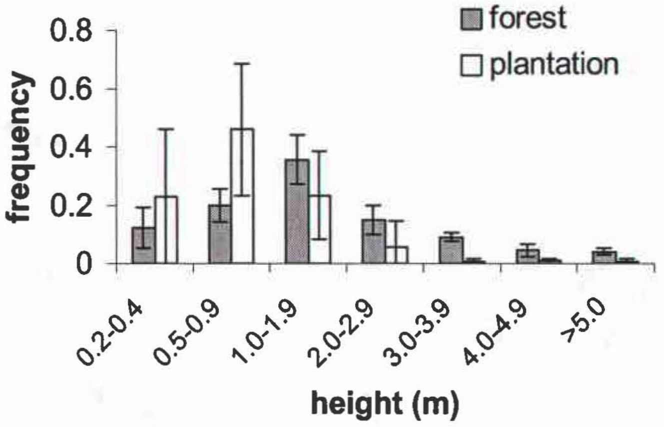

Figure 2.12. The size class distribution of palms and cycads (based on height) for forest and plantation sites. Error bars represent one standard deviation.

Table 2.1. Results from the nested ANOVAs for percent vegetative cover.

Life Form Grouping		df	F Value	P Value
overall cover	Treatment/site	1	0.54	0.4895
	Site/error	6	12.52	<0.0001
	Overall	7	21.04	<0.0001
palm and cycad cover+	Treatment/site	1	3.19	0.1245
	Site/error	6	1.85	0.0984
	Overall	7	2.43	0.0253
woody cover+	Treatment/site	1	0.82	0.3998
	Site/error	6	11.28	<0.0001
	Overall	7	11	<0.0001
herbaceous cover+	Treatment/site	1	0.15	0.7129
	Site/error	6	16.48	<0.0001
	Overall	7	14.48	<0.0001

+Data log transformed

CHAPTER III

The Understory Light Environment of *Chamaedorea* Plantations and Implications for Patterns of Regeneration

INTRODUCTION

A large proportion of the remaining tracts of tropical forests in the world are located in protected reserves surrounded by lands managed by local communities. While much of the forest in these landscapes has been converted for large-scale cattle and agricultural production (Anderson 1990), many areas still consist of small-scale landholdings that incorporate managed patches of primary and secondary forest (Gomez –Pompa and Kaus 1990; Alcorn 1995). The exploitation of these forest patches for both timber and nontimber resources is becoming an important component of many conservation and development programs in rural communities (Sugandhi and Sugandhi 1995; Carpentier et al. 2000). However, as is often the case in tropical regions, many of these management programs are being implemented without a sound understanding of the potential impacts on the ecological relationships and processes necessary for the conservation of these habitats. In the previous chapter, I demonstrated how the establishment and maintenance of crops of *Chamaedorea* palms in the understory of primary rain forest in southeastern Mexico directly affect the community structure and composition of the forest understory and midstory. In this chapter, I explore how the manipulation of forest structure in palm plantations affects light conditions in the forest understory and then consider the implications of these changes for patterns of forest regeneration.

Light is a major factor affecting the growth and survival of plants (Augspurger 1984; Chazdon et al. 1996; Whitmore 1996; Kobe 1999) and influencing patterns of forest regeneration (Clark and Clark 1992; Clark et al. 1996). Although research on the role of light in forest dynamics has traditionally focused on tree fall gap succession (e.g., Denslow 1980, 1987; Brokaw 1985; Uhl et al. 1988), these studies have largely overlooked the potential significance of the microscale variation of light conditions in the forest understory (Lieberman et al. 1989; Clark et al 1996; Montgomery and Chazdon 2001). More recent studies have demonstrated that differences in competitive abilities among seedlings and saplings of shade-tolerant tree species lead to niche partitioning along fine-scale light gradients in tropical forest understories (Montgomery and Chazdon 2002; Poorter and Arets 2003). These findings suggest that relatively small changes in light availability may influence community composition and subsequent patterns of forest succession.

OBJECTIVES

The primary objective of this chapter is to determine whether the management of plantations of *Chamaedorea hooperiana* Hodel alters the patterns of light availability in the forest understory. Specifically, I compare the light environment in palm plantations with neighboring areas of unmanaged forest using hemispherical photographs. While the forest canopy is left intact in plantations of *Chamaedorea* palms and other understory NTFPs in order to provide crops with some shade, plantation owners clear much of the understory and midstory vegetation to increase light availability and thereby increase crop production (see Chapter II). Increases in the leaf production of *Chamaedorea* palms have been demonstrated among plantations with higher light availability (F. Ramirez, unpublished data); however, to date no study has characterized how the understory light environment varies between plantations and unmanaged forest and what the ecological implications of these differences may be.

The secondary objective of this study is, therefore, to explore how differences in light conditions may be reflected in differences in the types of canopy and subcanopy tree seedlings regenerating in plantations versus unmanaged forest. *Chamaedorea* plantations can be expected to alter seedling establishment if at least one of two conditions are met: 1) most of the previously established seedlings are removed when the plantation understory is cleared, and/or 2) the altered light environment in plantations affects the competitive interactions among woody seedlings that subsequently establish. In order to test the first condition, I compared seedling density and seedling size class distribution in plantations versus forest sites based on measurements of height and crown area. I explored the second condition by comparing proportions of shade-tolerant and shade-intolerant species between plantation and forest sites. In addition, I examine how well the combined influences of light availability and seedling community composition define the differences between plantation and forest sites using multivariate discriminant analysis. Establishing a causal relationship between light environments and seedling composition is well beyond the scope of this research due to the scarcity of physiological data on tropical tree species, the longevity of seedling life stages (Clark and Clark 1992; Hubbell 1998), and the limited duration of this study. However, exploring shifts in seedling community composition may provide a better understanding of the ecological significance of any differences found in plantation light environments.

Assessing the effects of NTFP plantation management on understory light conditions is also important because the influence of light on seedling composition may have implications for patterns of forest succession. Research on gap-phase regeneration in tropical forests has demonstrated that the majority of gap regrowth consists of the advanced regeneration of seedlings and saplings that establish before canopy gaps occur (Uhl et al. 1988). Although plantation owners routinely clear the understory vegetation amidst NTFP crops and essentially arrest the process of regeneration, sections of plantations are abandoned in the event of a tree fall gap due to high mortality of NTFP species exposed to full sunlight. As regeneration proceeds in these abandoned gaps, the composition of the vegetative regrowth would largely consist of the advanced regeneration that has established since the last time the plantation was cleared. Thus, if NTFP plantations alter the composition of tree seedlings due to changes in the understory light environment, they are likely to influence the composition of the vegetation that regenerates with the eventual occurrence of a canopy opening.

METHODS

This research was conducted in the buffer zone of the Los Tuxtlas Biosphere Reserve (LTBR) in southeastern Mexico in an area of primary forest adjacent to the community of Adolfo Lopez Mateos, located at about 18° 24' N, 94° 58' W. The LTBR, established in 1998, encompasses several extinct volcanoes surrounding the city of Catemaco on the gulf coast in the state of Veracruz. Mean annual temperature in the area is approximately 24° C and mean annual precipitation is between 3000-4000 mm with a dry season from December to May (Soto and Gama 1997).

Adolfo Lopez Mateos is located approximately 18 km east of the city of Catemaco at an elevation of 200 m. To the east of the community the Sierra de Santa Marta, an extinct volcanic crater, rises to an elevation of 1700 m. The terrain surrounding the community is dominated by Cerro El Marinero to the southeast and an abrupt ridge to the north, both of which rise steeply to about 900 m. To the northwest, the coastal plain below Lake Catemaco runs into the Gulf of Mexico, visible from the hills above the community.

The 30 families of Lopez Mateos hold rights to the lands to the east of the community, adjacent to the protected zone of the LTBR that encompasses the crater of the Sierra de Santa Marta. Most of the land to the west of Lopez Mateos has been converted to large-scale cattle pastures by neighboring communities. However, land use in the area to the east of the community primarily consists of small parcels that have been cleared for maize, cattle and coffee in addition to areas of primary and secondary forest that contain plantations of several species of *Chamaedorea* palms. The community also runs an ecotourism project and has set aside over 100 hectares as a community reserve. This study was conducted in the relatively extensive area of tropical high evergreen rain forest (e.g., Bongers et al. 1988) above the community on the slopes of Cerro El Marinero.

To assess differences in the light environments and the canopy tree seedling composition of NTFP plantations with unmanaged forest, I selected four locations that each contained an area of plantation (0.5-1 ha with understory plantings of *Chamaedorea hooperiana* Hodel) surrounded by an area of primary forest (without planting). The experimental design therefore consisted of four blocks, each containing a plantation site paired with an adjacent forest site of similar size, inclination and slope aspect. Of the four blocks, Blocks 1 and 2 were located at approximately 300 m in elevation and Blocks 3 and 4 were located at approximately 500 m in elevation. All were situated on steep slopes ranging from about 30 to 45 degrees. Block 1 had an easterly slope aspect and Blocks 2, 3 and 4 had northerly slope aspects. The plantations in Blocks 2, 3, and 4 were established in 2001 and the herbaceous understory vegetation in their understories was cleared 1-3 months before data sampling. The plantation in Block 1 was established in 1999 and its owner had not cleared the understory vegetation for over a year.

Hemispherical photos and seedling measurements were taken at twelve, 3x2 m plots established in each forest and plantation site for a total of 96 plots across all blocks (4 blocks x 2 sites x 12 plots; Figure 3.1). Maps of each site were sketched based on measurements of plantation area and the corresponding, adjacent area of unmanaged forest. Plot locations were then randomly selected using an x-y coordinate system. In order to reduce spatial autocorrelation between sample points and to avoid confounding effects of plantation edges and existing tree fall gaps, a minimum distance of 10 m was maintained between adjacent plots and no plot was placed less than 10 m from a tree fall gap edge or less than 5 m of a plantation edge.

At the start of the wet season (June 2003), canopy photographs were taken at the center point of each plot, at 1 m above the ground, using a Nikkor 8-mm hemispherical lens mounted on a Nikkon FM10 camera body. At each sample point, the camera lens was leveled and the camera body aligned with true north using a handheld compass. All photographs were taken either under overcast skies or within one hour after sunrise or before sunset to minimize the effects of light reflection off leaves.

In order to assess canopy tree seedling composition and size structure, all seedlings <50 cm in height were counted and identified in each of the ninety-six 3x2 m plots. Therefore the total sampling area was 72 m^2 in each site. For each individual seedling, stem height was measured and crown area was determined from measurements of crown diameter at the widest point and along the axis perpendicular to the first measurement.

Woody species composition was determined by counting, identifying and measuring the dbh of all woody individuals ≥1 cm dbh in 10 m diameter circular plots that circumscribed each 3x2 m plot. This resulted in a total sampling area of 942.5 m^2 per site.

ANALYSIS

Hemispherical Photographs

Photographic negatives were digitized using a Hewlett-Packard scanner. I used the program Gap Light Analyzer version 2.0 (Frazer et al. 1999) to compute percent site openness and total transmittance. Both of these analyses incorporated the topographic data and geographic position of each sample point, but I did not obtain data for region-specific model parameters based on local atmospheric conditions. Percent site openness is the percentage of open sky visible from below the forest canopy. Total transmittance predicts the average photon flux density ($mol/m^2/d$) of direct and diffuse solar radiation transmitted by the canopy per day based on calculations of the solar path over each sample point during the course of the year. In order to assess the relationship between measurements, I performed correlations between percent site openness and total transmittance.

To assess differences in light conditions, I examined the frequency distribution of light availability (total transmittance) and canopy openness (percent site openness) among forest and plantation sites. The most effective method for demonstrating differences in light conditions is through analyses of frequency distribution as opposed to analyses of means of light availability (Chazdon and Fetcher 1984; Brown and Parker 1994; Nicotra et al. 1999). Therefore, I tested the independence of light distribution on management type (plantation vs. unmanaged forest) using the log-linear model of goodness of fit (Sokal and Rohlf 1995). I calculated the overall G statistic comparing the distributions of plots among categories of canopy openness (for percent site openness) and light availability (for total transmittance) between plantation and forest sites. In addition, I calculated G statistics for the distribution of plots within each category in order to determine which categories were responsible for any overall differences between plantation and forest sites.

Categories of light availability and canopy openness were determined by dividing the total range of values for percent site openness and total transmittance into three equal groups. This enabled me to examine differences between plantations and forest sites in the lower and upper categories and to avoid error among potentially overlapping values in the middle range due to low accuracy of hemispherical photographs in closed canopy conditions (Whitmore 1993). For percent site openness the categories were: 1) 1.8-7.5%, 2) 7.6-13.3%, and 3) 13.4-19.1%. For total transmittance the categories were: 1) 0.5-4.0 mol/m^2/d, 2) 4.1-7.5 mol/m^2/d, and 3) 7.6-11.2 mol/m^2/d.

Seedling Size and Density

I also used log-linear analysis of goodness of fit (Sokal and Rohlf 1995) to compare the frequency distributions of seedling size between plantation sites and forest sites. I performed two analyses to test for the independence between management type (plantation vs. forest) and seedling size class. The first analysis used size classes based on seedling stem height and the second used size classes based on crown area. Because these analyses included many species with differing life history traits, stem height size classes were assigned based on 5 cm increments from 0-50 cm. Due to its wide range of sizes (0.1-1335.3 cm^2), crown area size classes were based on 20 cm^2 increments between 0.1-200 cm^2 and then on 100 cm^2 increments from 200.1 to the final category of >600 cm^2. Given the difference in age and management history of the plantation in Block 1, I also plotted the frequency distributions of seedling height and crown area for each plantation site in order to examine whether management differences were reflected in seedling size class structure. Finally, differences in seedling density between forest sites and plantation sites were assessed using a randomized complete blocks ANOVA.

Seedling Community Composition

In order to look at patterns of seedling establishment in the context of light environments, I grouped the species of canopy tree seedlings into two functional groups using the ecological classifications based on shade-tolerance as outlined by Swaine and Whitmore (1988) and Whitmore (1989). Under this system, shade-tolerant, non-pioneer species are defined as those that are capable of germinating and establishing in low light, closed-canopy conditions while shade-intolerant, pioneer species are those that require direct exposure to sunlight in order to germinate. I compiled a list of functional group classifications for 41 of the 62 recorded species of canopy and subcanopy tree seedlings using the available scientific literature (Appendix B). These classifications were based both on data on physiological characteristics and seed ecology as well as anecdotal references made by biologists concerning habitat preferences. For the remaining species not discussed in the literature, I relied on observations made by local plant experts (see Appendix B).

I performed separate sets of analyses using, first, a list of species classifications based solely on evidence from the literature and, second, a combined list that included literature classifications and classifications made by local experts. Using each of these species lists I used randomized complete blocks ANOVAs to examine differences between plantation and forest sites in the proportion species per functional group to the total number of species recorded. Due to the inclusion of unclassified species in the total count for comparisons using the literature classifications, separate analyses were made for the proportions of shade-tolerant and shade-intolerant species. In the analyses using combined literature and local classifications, all species were classified as either shade-tolerant or shade-intolerant. Therefore separate analyses of each functional group were redundant and only the ANOVA results for the proportion of shade-intolerant species are discussed. Due to the differences in the management history of the plantation in Block 1 (see Methods section), I also carried out these same sets of analyses excluding this block.

To investigate whether the differences between plantation and forest sites in the functional group proportions of seedlings were due to differences in the composition of the overstory (i.e., the available local seed sources), I performed the same set of tests described above on all adult individuals (≥20 cm dbh) of the same 62 species recorded for seedlings that were sampled from the 10 m diameter plots within each site. Only adults ≥20 cm dbh were used in the analysis because the density of woody individuals <20 cm dbh is significantly reduced in plantation sites due to management practices (see Chapter II).

Multivariate Discriminant Analysis

I performed a canonical analysis of discriminance (CAD) in order to examine how well the differences between plantation plots and forest plots are explained by the variation among the multiple variables measured in this portion of the study. This type of analysis combines two or more variables into linear equations based on each variable's ability to discriminate between a priori defined groups (McGarigal et al. 2000). These equations, known as canonical functions, thereby maximize the between-group variation relative to within-group variation. The ability of the variables to discriminate between groups can then be examined by reclassifying the sampling entities (e.g., plots) based on predictive classification equations derived from the canonical functions and comparing the predicted classifications with the original data.

In order to avoid redundancy (i.e., multicollinearity) in the data set, I performed pairwise correlations for all combinations of variables being considered for the CAD. I then ran a one-way ANOVA for each variable involved in a high correlation ($r^2>0.7$), using plantation vs. forest as the treatment effect. From each correlated pair of variables, the one with the lowest F value was eliminated from the data set (McGarigal et al. 2000). I then used SAS to perform a CAD to discriminate plantation plots from forest plots using a canonical function derived from the following five variables: percent site openness, seedling density, seedling richness, the proportion of shade-intolerant seedling species (based on literature and local expert classifications) and the proportion of "established" seedlings >20 cm in height (e.g., Nicotra et al. 1999). Plots were also reclassified by SAS using a quadratic classification function based on the canonical function from the CAD. Finally, a *Tau* statistic was calculated that provides a measure of the predictive power of reclassifications relative to the random assignment of sampling entities among groups (McGarigal et al. 2000).

RESULTS

Light Availability and Canopy Openness

Percent site openness and total transmittance were positively and significantly correlated ($r^2=0.862$, $P<0.0001$). Log-linear analyses showed that for percent site openness (PSO) and total transmittance (TT), the overall distribution of light categories was dependent on management type (PSO: G=12.59, $P<0.005$, df=2; TT: G=8.83, $P<0.05$, df=2). The distributions of both percent site openness and total transmittance exhibit the same pattern, with higher percentages of forest plots falling into the darker, less open categories, relatively equal distributions within the middle categories, and higher percentages of plantation plots falling into higher light, more open categories (Figures 3.2 and 3.3). For percent site openness, only 2% of the forest plots fell into the most open category compared to 20.8% of the plantation plots. This difference was significant (G=4.82, $P<0.05$, df=1). For total transmittance, 62.5% of the forest plots fell into the lowest light category versus 33.3% of the plantation plots. This difference was also significant (G=4.12, $P<0.05$, df=1).

Seedling size and density

Seedling size class distributions based on seedling height and crown area showed that plantations have a higher proportion of seedlings in the smaller size classes than forest sites (Figures 3.4 and 3.5). Log-linear analyses of the size class frequency distributions showed that seedling size class distribution was dependent on management type (plantation vs. forest) for both seedling height ($G=136.12$, $P<0.0005$, $df=35$) and crown area ($G=136.73$, $P<0.0005$, $df=42$). The plantation in Block 1 had a higher proportion of seedlings in the larger size classes than the other plantations (Figure 3.6). While the Block 1 plantation had a more even distribution across the larger size categories of crown area, the difference from the other plantations is not as pronounced as for height (Figure 3.7). Although average seedling density was greater in plantation sites (mean=2.83 individuals/m^2) than in forest sites (mean=1.91 individuals/m^2), there was no significant difference in seedling density ($F=2.21$, $P=0.2339$, $df=1$).

The proportion of shade-intolerant species was not significantly different between plantation and forest sites using both the literature classification and the combined literature and local expert classifications (Figure 3.8). There was a trend indicating a higher percentage of shade-intolerant species in plantation sites. When Block 1, which contains the older and less intensively managed plantation, was removed from the analysis using the combined classifications, the proportion of shade-intolerant seedling species was significantly greater in plantation sites than in forest sites (Figure 3.9).

The proportion of shade-intolerant species of trees ≥20 cm dbh did not significantly differ between forest and plantation sites (Figure 3.10). There was a trend indicating a higher proportion of shade-intolerant species in forest s than in plantation sites. The functional group proportions of adults thus exhibit the opposite pattern found among seedling functional groups.

Multivariate Discriminant Analysis

The overlap of plantation and forest plot classifications based on the canonical function was evident in the distribution of canonical scores by group (Figure 3.11). The results of the canonical analysis of discriminance indicated that only 27.6% of the total variation in the derived canonical function is explained by differences between plantation plots and unmanaged forest plots. However, comparisons between the actual and predicted plot classifications showed that 78.1% of plots were classified correctly by the quadratic classification procedure. The *Tau* statistic of 0.563 suggests that the classification power based on the variables is approximately 56% better than random assignment. Among all misclassified plots, a slightly higher percentage of plantation plots (23%) than forest plots (21%) were placed into the wrong group. Among the misclassified plots for plantation sites, the site in Block 1 contained 6 plots, the Block 2 site contained 4 plots, the Block 4 site contained 1 plot, and the Block 3 site contained no misclassified plots.

The canonical structure coefficients derived for each variable indicate that percent site openness was the most important component of the canonical function, followed by the proportion of seedlings >20 cm in height, the proportion of shade-intolerant seedling species and seedling density, in decreasing order of importance (Table 3.1). The low structure coefficient for seedling richness indicates that it was not correlated with the canonical function. The class means on the canonical function show that plantation plots were positively correlated with the canonical structure coefficients and forest plots were negatively correlated with the coefficients (Table 3.1). Thus, the variables with positive coefficients (percent site openness, the proportion of shade-tolerant seedling spp. and seedling density) tended to be greater in magnitude in plantation plots. Similarly, variables with negative coefficients (proportion of seedlings >20 cm ht.) were greater in magnitude in forest plots.

DISCUSSION

The primary objective of this chapter was to examine how the management of NTFP plantations, specifically plantations of *Chamaedorea* palms, affects patterns of light in the forest understory. The secondary objective was to examine the extent to which any differences in the light environment may be reflected in patterns of seedling composition between plantation and forest sites. The results of this study illustrate that the frequency distribution of light availability among plantation sites is different than forest sites. The results from the patterning of seedling composition, however, are less conclusive.

Patterns of Understory Light Distribution

The management of the *Chamaedorea* plantations examined in this case study appears to be altering light conditions in the forest understory. Analyses of percent site openness and total transmittance illustrate that the proportion of plots falling into more open and higher light categories is greater in plantations than in forest sites. This trend is also supported by the dominance of percent site openness in the canonical function used to discriminate between plantation and forest plots in the multivariate analysis. Thus, although the forest overstory is left intact (see Chapter II), the felling of smaller trees and shrubs (<20 cm dbh) below the canopy in *Chamaedorea* plantations appears to increase the proportion of sites in the forest understory that have greater canopy openness and light availability.

Although comparisons between hemispherical photographs and quantum sensors have shown that predictions of photon flux density (e.g., total transmittance) from hemispherical photographs tend to have low accuracy under closed-canopy conditions (Clark et al. 1996; Nicotra et al. 1999), the use of frequency distributions in this case likely provides a robust analysis. By dividing the light levels into three categories, I was able to focus the analysis on the upper and lower limits of the range of light values (total transmittance) and thus reduce the error due to the potential overlapping of inaccurate predictions in the middle range of values. Moreover, canopy photographs are useful in revealing larger patterns in canopy structure and the distribution of canopy openings (Whitmore 1993; Clark et al. 1996; Nicotra et al. 1999). Since the objective of this research was to compare the general patterns of light availability and canopy openness across plantation and forest sites rather than to characterize the small-scale variation within each site, hemispherical photography provided a method of measuring light conditions that was both logistically feasible and adequate for the purpose of the study.

Altered Light Environments and Seedling Composition

Although it appears that plantation management alters light conditions, the ecological significance of these changes is much more difficult to demonstrate. Some studies have suggested that light availability in the forest understory directly affects seedling growth and survival (e.g., Augspurger 1984; Whitmore 1996) as well as seedling community composition due to differential responses to light gradients (Kobe 1999; Montgomery and Chazdon 2002; Hall et al. 2003). As discussed earlier, any differences in plantation seedling composition due to light would depend both on whether the majority of seedlings establish after plantation understories are cleared (i.e., once light patterns are different) and whether different assemblages of species regenerate in the altered light conditions. In addition, it is also necessary to demonstrate that differences in seedling composition between plantations are not simply a reflection of differences in the composition of adult trees.

Though it is impossible to ascertain whether the seedlings present in the plantations at the time of sampling had established since the last clearing, the proportions of seedling individuals in the larger size classes for height and crown area were significantly lower in plantations than in forest sites. It is difficult to assess seedling age simply from size due to slow and variable growth rates (e.g., Hubbell 1998). However, the differences in size class distributions between plantation and forest sites indicate that the larger, potentially more-established seedlings are being reduced in plantation sites. This pattern in plantation seedling distribution may simply reflect a tendency for plantation owners to overlook smaller seedlings and remove the larger individuals while clearing the understory. However, seedling density between plantation and forest sites was not significantly different, suggesting that any recruitment sites created by the removal of larger individuals are soon occupied by new seedlings. Moreover, the tendency towards higher seedling densities in plantations may indicate that management actually increases the number of potential recruitment sites in the forest understory.

The results from this study suggest a tendency for higher proportions of shade-intolerant species to establish in *Chamaedorea* plantations than in forest sites. Although this trend may be attributable to differences in the composition of adult trees, the lower proportion of shade-intolerant adults in the plantation overstories suggests that seedling composition is not merely reflecting the composition of local seed sources. Thus, it is possible that the greater frequency of higher light environments in plantation understories may create more suitable recruitment sites for shade-intolerant seedling species, which would have a competitive advantage over shade-tolerant species in the altered light conditions. Nevertheless, these results must be interpreted with caution given the scarcity of data on the physiological characteristics of tropical tree species and the complexity of tropical tree life histories (e.g., Clark and Clark 1992).

The potential for plantation management to alter seedling assemblages may have subtle, yet long-term effects on patterns of future forest succession and composition. When areas of NTFP plantations are abandoned in the event of a canopy disturbance, the vegetative regrowth in the gap may largely consist of the advanced regeneration of seedlings that have established since the last time the plantation was cleared (e.g., Uhl et al. 1988). The results from this study suggest that the composition of advanced regeneration growing into gaps in plantations may consist of a higher percentage of shade-intolerant species than surrounding forest sites. Moreover, if the understory and midstory are cleared for cultivation once the canopy gap has been filled by faster growing pioneer trees, shade-tolerant species that may require multiple gap events to reach maturity may not be able to complete their life cycles (e.g., Clark and Clark 1992). This shift in successional patterns may ultimately favor a disproportionately lower percentage of the local tree species diversity given that most species in tropical forests are shade-tolerant (Brokaw and Scheiner 1989; Hubbell 1998).

The fact that the differences in seedling composition between plantation and forest are more pronounced when Block 1 is removed from the analysis is particularly interesting in that it demonstrates the variation inherent in plantation management and its potential ecological consequences. The owner of the plantation in Block 1 maintains that he does not clear the vegetation as often or as thoroughly as in other plantations in order to preserve soil humidity. The less frequent and less intensive clearing in this plantation leads to higher proportions of larger seedlings. A larger number of plots in the plantation of Block 1 were also misclassified as forest plots by the discriminant analysis compared to the other plantation sites. Variation in human management complicates quantitative studies such as this one due to the lack of controlled, replicable treatment conditions. This emphasizes the need for controlled experimental approaches in NTFP research (Ticktin et al. 2002; Endress et al., in press). It is also indicative of the range of ecological impacts that plantation management can have and underscores the necessity of collaboration with local harvesters and plantation owners in order to develop and implement more sustainable practices (e.g., Alcorn 1995).

Limitations and Directions for Future Research

Demonstrating a causal relationship between light availability and seedling composition is beyond the scope of this study. The analysis and discussion of the seedling composition presented here are based on static community structure data collected over the course of a single field season. Thus it is not possible to relate changes in environmental conditions to shifts in seedling survival, mortality and species abundances or to make strong predictions about future patterns of community composition. Yet the trend towards higher proportions of shade-intolerant species of canopy tree seedlings in plantations suggests that management practices may alter seedling community assemblages. Although the dichotomous species classification scheme of shade-tolerant vs. shade-intolerant has been criticized for being ecologically crude (e.g., Brown and Jennings 1998), it provides a useful baseline from which to make preliminary explorations of the ecological effects of forest management.

There are other limitations to be considered due to the complexity of ecological communities. Although light availability in tropical forests is likely to be the most important variable influencing plant growth and survival (Whitmore 1996), some studies suggest that single factors are inadequate to explain community composition (Rees and Brown 1992; Meiners and Handel 2000). Altered patterns of seedling composition in NTFP plantations may simply be due to reduced levels of above- and below-ground competition from understory vegetation when plantations are cleared (e.g., Wright 2002). There may also be different patterns of seed dispersal in plantations due to the more open midstory and understory affecting bird and mammal assemblages (e.g., Gallina et al. 1996; Calvo and Blake 1998). In addition, the periodic disturbance of plantation clearing may favor the survival of certain species of seedlings over others, such as those capable of resprouting due to underground seed reserves (Dalling and Harms 1999).

There are many ways in which future research can contribute to a more complete understanding of the ways in which NTFP plantations and other management practices affect community composition. First, studies on the intricate competitive interactions occurring among so-called shade-tolerant species in the forest understory have only begun to reveal the degree to which light can influence the composition of woody seedlings (e.g., Montgomery and Chazdon 2002; Poorter and Arets 2003). These studies illustrate the need to further explore the extent of niche partitioning among apparently ecologically similar species in order to improve both our knowledge of community dynamics and our ability to predict the effects of forest management. In addition, although management practices may alter numerous environmental variables, some of these variables may influence ecological processes more strongly than others. Thus, it is necessary to test the potential additive and interactive effects of multiple factors, such as herbivory, nutrient limitation, and competition, that affect seedling recruitment and survival (Whitham et al. 1991). Finally, although assessing the impacts of forest management on community dynamics is difficult due to environmental stochasticity and the patchy distributions of most tropical tree species, a comparison of the patterns of gap-phase succession between forest and plantation sites may provide at least a preliminary understanding of the longer-term repercussions of plantation management. However, it is still necessary to examine management effects in the temporal context of natural successional processes. Fortunately, human-managed systems easily lend themselves to long-term research through community-based resource monitoring in collaboration with local harvesters and landowners.

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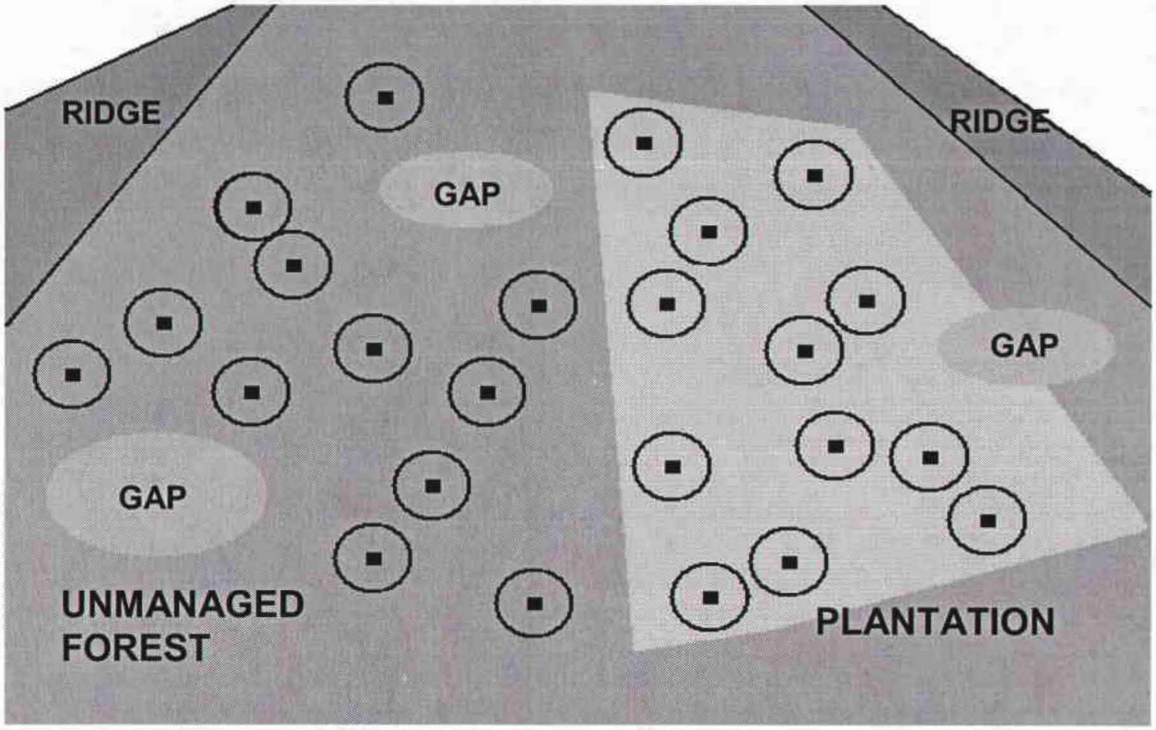

Figure 3.1. Diagram of sampling design for plantation and forest sites in a single block. Black squares are 3x2 m plots and circles are 10 m diameter plots.

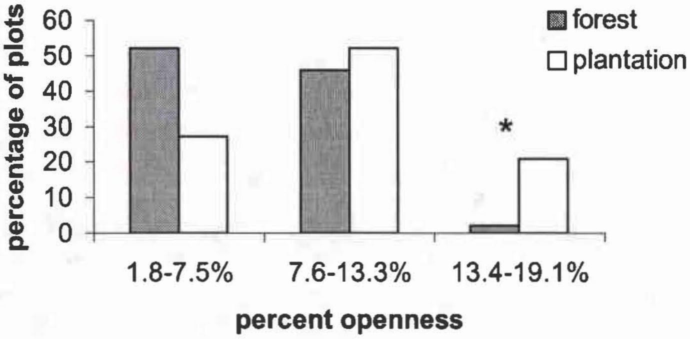

Figure 3.2. The distribution of canopy openness among plantation plots vs. forest plots. (*significant within-category difference at P<0.05)

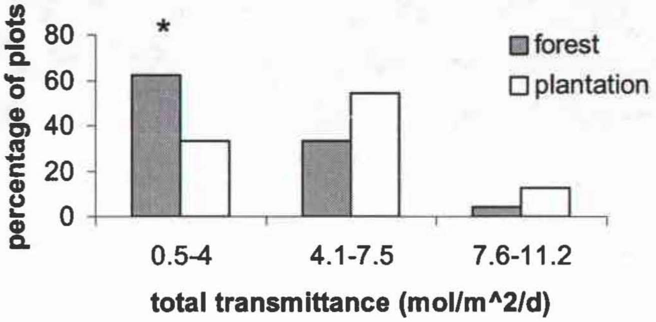

Figure 3.3. The distribution of total light transmitted by the canopy among plantation plots vs. forest plots. (*significant within-category difference at P<0.05)

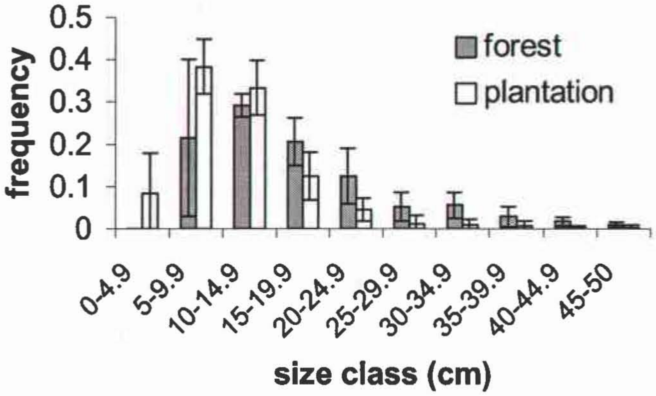

Figure 3.4. Mean distribution of seedling size class for plantation sites vs. forest sites based on stem height. Error bars represent one standard deviation.

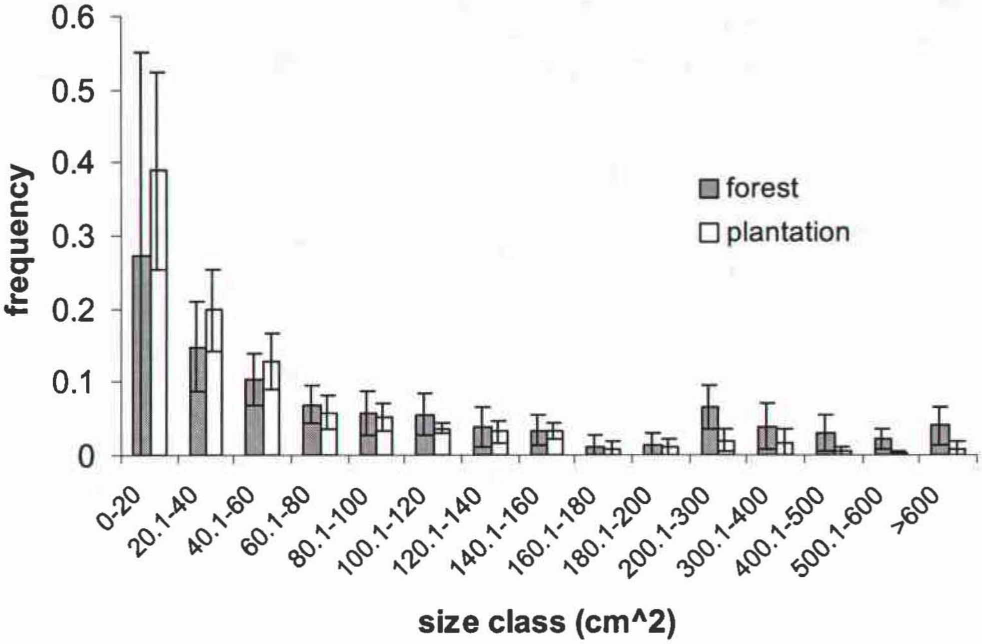

Figure 3.5. Mean distribution of seedling size class for plantation sites vs. forest sites based on crown area. Error bars represent one standard deviation.

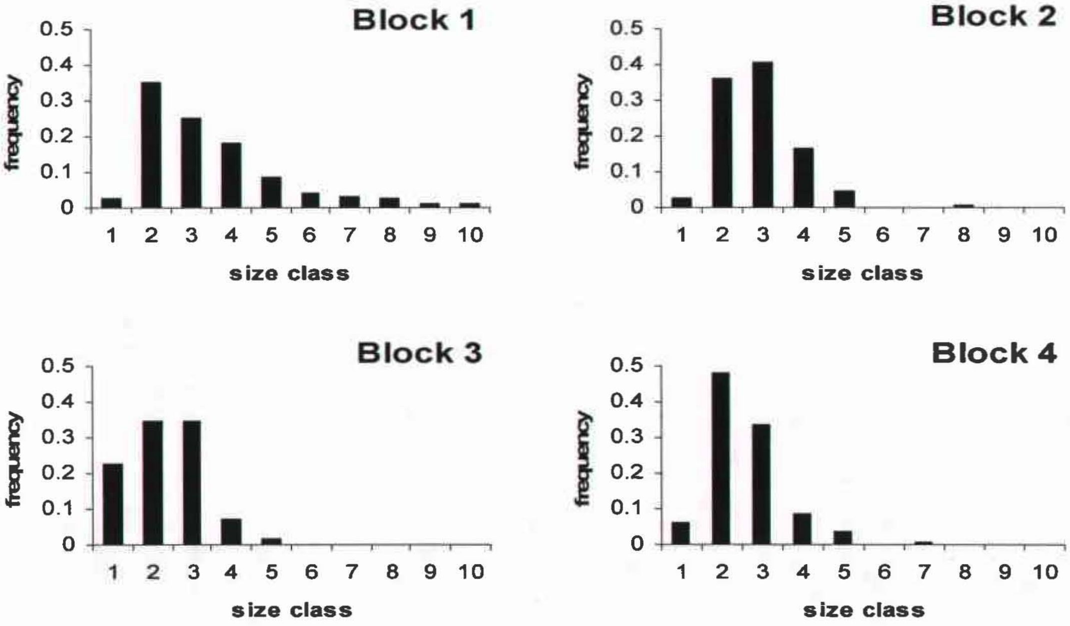

Figure 3.6. Seedling size class distribution for each plantation site based on stem height. Size classes are assigned by 5 cm increments from 0-50 cm

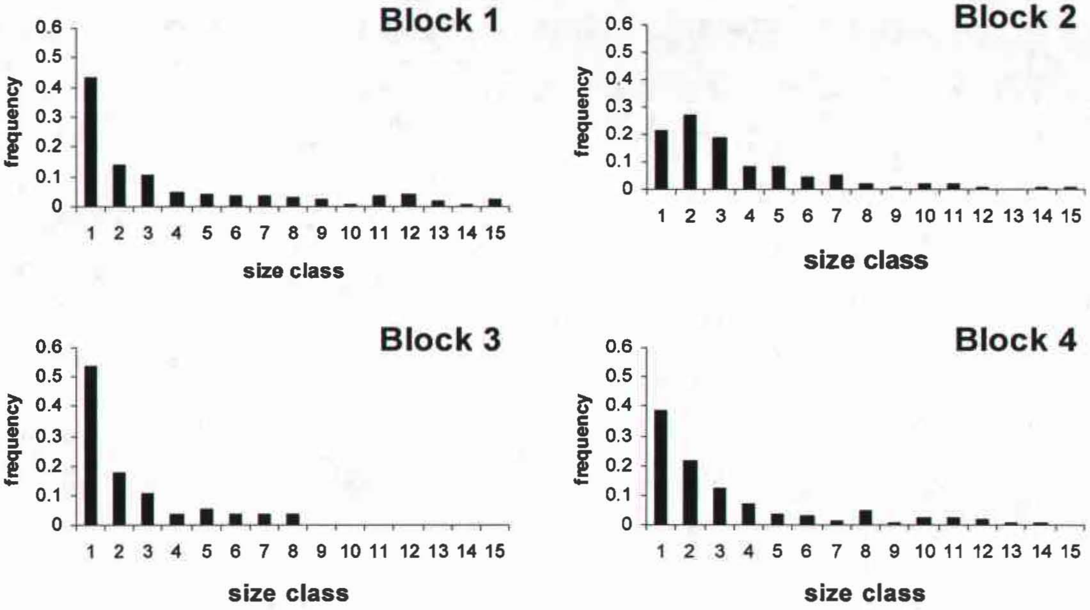

Figure 3.7. Seedling size class distribution for each plantation site based on crown area. Classes 1-10 are based on 20 cm^2 increments from 0-200 cm^2. Classes 11-15 are based on 100 cm^2 increments from 200.1 cm^2 to the final category of >600 cm^2.

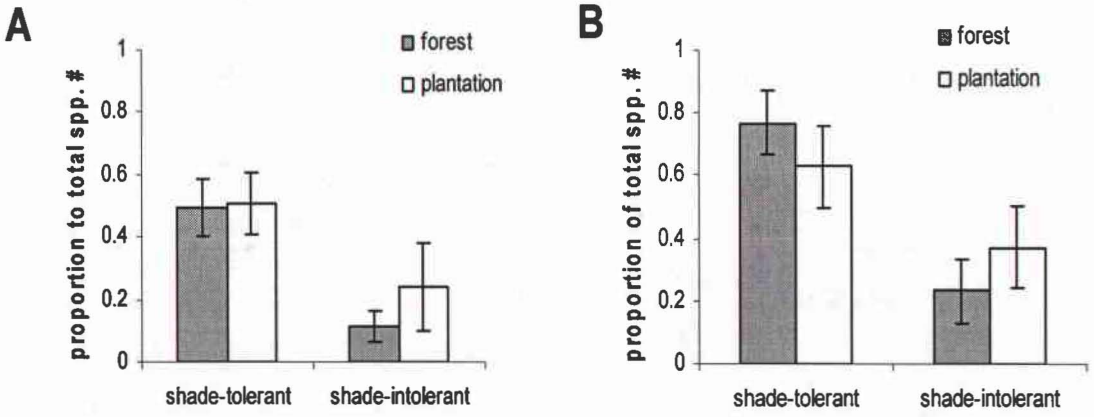

Figure 3.8. Mean proportion of each functional group (shade-tolerant and shade-intolerant) for canopy tree seedling species in plantation and forest sites. A) Proportions of species classified in the scientific literature to total species (including unclassified spp.) B) Proportions using all species (combining spp. classified in literature with spp. classified by local experts). Error bars represent one standard deviation.

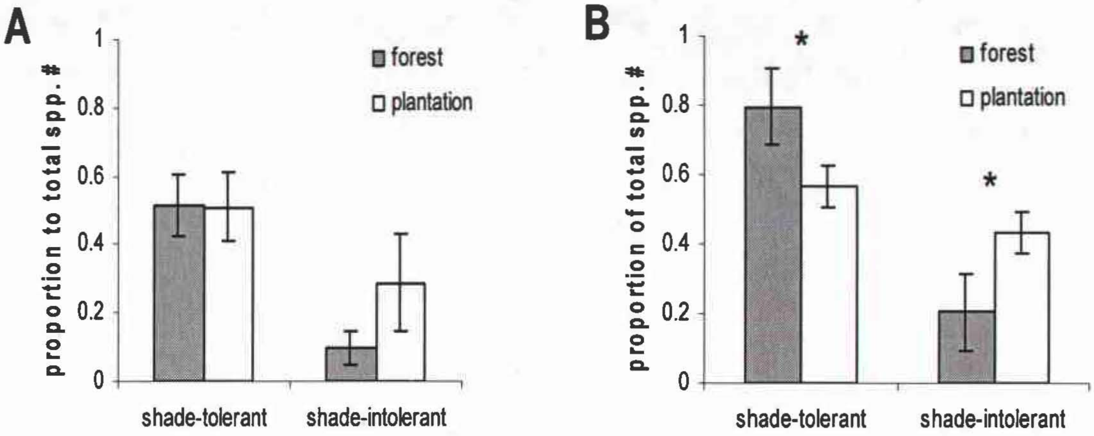

Figure 3.9. Mean proportion of each functional group (shade-tolerant and shade-intolerant) for canopy tree seedling species in plantation and forest sites excluding Block 1. A) Proportions of species classified in the scientific literature to total species (including unclassified spp.) B) Proportions using all species (combining spp. classified in literature with spp. classified by local experts). Error bars represent one standard deviation. (*significant difference at P<0.05)

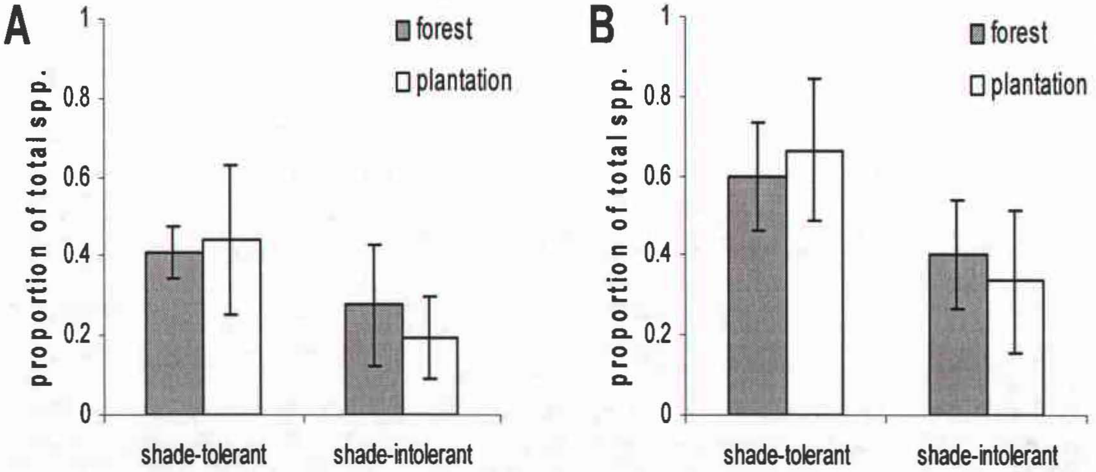

Figure 3.10. The mean proportion of each functional group (shade-tolerant and shade-intolerant) for adult tree species (>20 cm dbh) in plantation and forest sites. A) Proportions of species classified in the scientific literature to total species (including unclassified spp.) B) Proportions using all species (combining spp. classified in literature with spp. classified by local experts). Error bars represent one standard deviation.

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Frequency
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   ----------------------------------------------------------------------------------------------
          -4        -3        -2        -1         0         1         2         3         4
                                       Canonical Score Midpoint
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Figure 3.11. Histogram of canonical scores for forest plots (1) and plantation plots (2) derived from canonical analysis of discrimination based on the following variables: percent canopy openness, seedling richness, seedling density, the percentage of shade-intolerant seedling species, and the percentage of seedlings greater than 20 cm in height.

Table 3.1. Canonical structure coefficients for the variables used in the canonical analysis of discriminance and class means on canonical variables for each group.

Variable	**Coefficient**
Percent site openness	0.726816
Proportion of seedlings >20 cm ht.	-0.678387
Proportion of shade-intolerant seedling spp.	0.440768
Seedling density	0.266944
Seedling richness	-0.063302

Group	**Class Mean**
Forest	-0.611196
Plantation	0.611196

CHAPTER IV

Conclusions

The intention of this study was to develop a broader understanding of the ecological effects of *Chamaedorea* palm cultivation in the understory of tropical forests, a management practice that is currently being promoted as a potential "alternative to deforestation" (Anderson 1990) over a wide region of Mexico's humid tropics and parts of Central America. Although assessing the long-term environmental impacts of *Chamaedorea* cultivation in the forest understory is beyond the scope of this study, the results illustrate some of the more immediate ways in which the management of *Chamaedorea* plantations affects forest structure and composition as well as the light conditions in the forest understory.

The initial and most evident ecological effects of plantation management are due to the process that plantation owners call *limpiando*, which literally translates from Spanish as "cleaning." Plantation owners are well aware of the fact that the productivity of *Chamaedorea* crops in the forest understory is limited by light availability (F. Ramirez, unpublished data). Therefore, in order to increase crop productivity, much of the vegetation beneath the forest canopy, including herbs, shrubs, seedlings, saplings, and small midstory trees, is cut and felled before palms are planted and cleared on a periodic basis once palms are established.

ECOLOGICAL IMPACTS OF *LIMPIANDO*

My initial findings quantify the deliberate results of the process of *limpiando*. This study demonstrates how the stem density of woody species less than 10 cm dbh is significantly reduced in plantations when compared to unmanaged forest. It also illustrates that, as a result of these structural changes, the frequency of sites with greater canopy openness and light availability is higher in *Chamaedorea* plantations than in areas of unmanaged forest.

The process of *limpiando* also results in changes in species composition that are not necessarily the direct intent of plantation owners. The most immediate result of plantation management is the reduction in the species diversity among the smaller size classes of woody species. In addition, while the overall density and diversity of palm species does not differ between plantations and unmanaged forest due to plantation owners sparing economically important species, there is a large decline in the density of *Astrocaryum mexicanum,* which is the most abundant palm in unmanaged forest. Although less conclusive, the trend towards higher proportions of shade-intolerant species of canopy tree seedlings in plantations suggest that the changes in light conditions may indeed be ecologically significant and have longer-term consequences for community composition. For the purposes of this study, shade-intolerant species are those trees that require exposure to sunlight in order to germinate and establish as opposed to shade-tolerant species whose seedlings can establish in the shade of the forest canopy (e.g., Swaine and Whitmore 1988; Whitmore 1989).

The reduction in species diversity among the smaller size classes of woody species in plantations may have serious implications for populations of understory and midstory plants. When plantation owners clear the forest understory for palm cultivation, they may end up fragmenting and/or eliminating local populations of herbs, shrubs and midstory trees that rarely grow larger than 10 cm dbh. Species of larger canopy and subcanopy trees are likely not to be immediately affected by this reduction due to the persistence of adults of the plantation overstory. However, the continued existence of understory and midstory plant species may depend on the availability of forested areas with unaltered understories. While a relatively extensive area of unmanaged forest surrounds the *Chamaedorea* plantations examined in this study, the populations of understory and midstory plants may be declining near communities with more intensified cultivation of nontimber forest products (NTFPs). Given the patchy distributions of many tropical plant species (e.g., Hubbell 1998), these species may become a conservation concern even in areas with less intensive cultivation.

The potential for plantations to favor higher proportions of shade-intolerant species of tree seedlings suggests there may also be more subtle changes in community composition due to increases in understory light availability. The implications of a possible shift in the assemblage of seedling species are not immediately apparent, especially since repeated clearings of the understory by plantation owners essentially halt the regeneration of woody species. However, the process of regeneration resumes when areas of plantations are abandoned in the event of a tree fall gap due to high mortality of *Chamaedorea* palms exposed to direct sunlight. Thus it is important to consider the potential consequences that changes in the species composition of the seedling community may have for patterns of forest succession.

If management favors the establishment shade-intolerant tree seedlings, there may be eventual shifts in the composition of plantation overstories towards higher proportions of shade-intolerant, pioneer trees given the fact that advanced regeneration comprises the majority of the vegetative regrowth in gaps (Uhl et al. 1988). Furthermore, as canopy openings in plantations initially fill in with faster-growing pioneer trees (Whitmore 1991) the understory and midstory may be cleared again for cultivation before the shade-tolerant tree species reach maturity, as this may require multiple gap formations (Clark and Clark 1992). Therefore, with the turnover of the existing plantation canopy over the long-term, management practices may potentially leave an ecological "footprint" consisting of a higher proportion of shade-intolerant species and since the majority of tropical tree species are shade-tolerant (Brokaw and Scheiner 1989; Hubbell 1998), an overall reduction in canopy tree diversity.

EFFECTS OF MANAGEMENT VARIATION

The process of *limpiando*, as described in this study, may be expected to result in very noticeable and relatively consistent changes to forest structure. In reality, however, while the boundary between managed and unmanaged forest is quite clear in some plantations, it can be difficult to distinguish in others (see Figures 4.1 and 4.2). This difference shows how the process of *limpiando* varies among plantation owners and also how this variation results in different degrees of ecological impact. For example, in this study, the different management history of the plantation in Block 1 is reflected in differences in seedling size class distribution and functional group proportions when compared to the other plantations. Although this variability in management can be a confounding factor in observational studies such as this one, it is also indicative of the range of ecological knowledge that local harvesters and landowners use to experiment with and modify various techniques in order to meet their individual needs (e.g., Alcorn 1984; Ticktin and Johns 2002). Recent research has begun to explore the variation in knowledge and management by incorporating local practices into experimental designs that assess the ecological effects of NTFP harvesting (Ticktin et al. 2002; Endress et al. in press). Unfortunately, studies such as these that integrate human variability remain uncommon, despite the wide applicability of this approach in ecological research on human-managed systems.

There may also be ways in which the potential impacts of plantation management on species diversity may be lessened through changes in management practices. In order to compensate for the significant declines in the diversity of understory and midstory plant species due to plantation establishment, it may be necessary to designate areas of forest among NTFP crops in which the understory vegetation remains unaltered. Variation in topography, such as very steep slopes and ravines, may provide refugia for understory and midstory plant species; however, some NTFPs such as *Chamaedorea* palms can be planted along relatively extreme topographic gradients (on slopes of up to 48° in this study). Moreover, relative to the number of studies on the ecology of larger canopy tree species (e.g., Denslow 1987; Clark and Clark 1992; Lieberman et al. 1995; Hubbell 1998), research on shrubs and understory trees in tropical forests is relatively limited (but see Martinez-Ramos et al.1988; Oyama 1990). Thus, our overall knowledge of the ecology and the extent of habitat required for the persistence of these species needs to be expanded.

In order to better assess the potential of integrating NTFP cultivation with habitat conservation, it is necessary to consider the effects of plantation management across different habitat types and using different species. This research only provides evidence from a single case study of plantations of *Chamaedorea hooperiana* being cultivated in an area of primary wet tropical forest. While there were significant changes in forest structure and community diversity in these plantations, the ecological effects of management may be less pronounced in other systems. For example, light availability may be naturally higher in areas of secondary forest or in drier, more deciduous forests, and NTFP cultivation in these areas may therefore require less manipulation of the forest structure. In addition, while the productivity of most understory species is likely to be highly limited by light availability (Chazdon et al. 1996), variation in the photosynthetic responses among different NTFP species may make some species better suited for the low light conditions in primary forest. For example, one plantation owner mentioned plans to cultivate *Chamaedorea ernesti-augustii* because he feels its productivity is superior to other species under low light. Thus, it may be possible to further reduce the extent of understory and midstory clearing in plantations by selecting NTFP species that are best suited for natural environmental conditions.

POTENTIAL FOR FOREST CONSERVATION

The cultivation of nontimber forest products in the forest understory may help to alleviate some of the problems associated with the exploitation of wild populations, such as resource depletion through over-harvesting (e.g., Salafsy et al. 1993; Murali et al. 1996). Harvesting from wild populations of NTFP species often only provides a sporadic source of income and involves traveling long distances from communities across dangerous terrain. In contrast, NTFP crops can provide a larger and potentially more reliable resource supply that relieves harvest pressure on wild populations and can be cultivated near communities. However, the economic importance of wild populations may create a larger incentive to conserve areas of primary forest than the cultivation of NTFPs in plantations, which can also be established in agroforestry systems and secondary forest. Thus, if the resource supply from NTFP plantations were to completely supersede the contribution of wild populations, the connection between habitat conservation and economic development may be weakened.

Any human-managed system will have ecological impacts. However, it is readily apparent that some management practices are more disruptive than others in affecting local ecological processes and species diversity. With land development in the tropics largely dominated by large-scale conversion of forest for cattle and agricultural production, the cultivation of nontimber forest products in the forest understory offers a promising land use alternative in terms of habitat conservation. On the other hand, while harvesters exploiting wild NTFP populations may also manipulate the forest understory and midstory to some extent, the effects of NTFP plantations on the forest community are likely to be more intensive than harvesting from wild populations. However, because they provide more stable incomes for rural communities, it is likely that plantations will supplant the economic importance of wild populations for the market supply of many NTFPs. Given the growing prevalence of NTFP cultivation, it is imperative that the ecological impacts of management be further explored.

FUTURE RESEARCH

Although this study provides limited evidence of a shift towards higher proportions of shade-intolerant species establishing in plantations versus unmanaged forest, this observation must be further explored with longer-term studies that follow the survivorship of seedlings. In most areas, NTFPs have only been in cultivation over the past 10 years, thus, it is unlikely that compositional changes due to management are currently reflected in the forest overstory. However, we can at least begin to assess the potential long-term effects of management on canopy tree assemblages by examining the vegetative composition in areas of plantations that are in the gap and building phases of regeneration. If NTFP cultivation does appear to affect patterns of forest succession, it may be possible for plantation owners to selectively manage the advanced regeneration of tree seedlings in order maintain populations of shade-tolerant species (e.g., Viana 1990; Mesquita 2000). For example, this study provides strong evidence that economically valuable palm species are spared when plantations are cleared, and some plantation owners maintain that seedlings and saplings of timber species are also spared. However, the density of timber species less than 10 cm dbh is still significantly reduced in *Chamaedorea* plantations.

While this case study on *Chamaedorea* plantations provides some preliminary data on the effects of NTFP cultivation on the forest community, the more critical questions relate to the effects of management on successional processes operating on temporal scales much larger than the scope of this study. Our understanding of forest dynamics, especially in the tropics, has advanced enormously through research based on long-term monitoring of large plots and populations of multiple species (e.g., Clark and Clark 1992; Hubbell et al. 1999). Unfortunately, nearly all of these studies take place in a small number of protected reserves, which makes extrapolation to human managed landscapes difficult. The fact that the majority of the world's biological diversity exists in ecosystems occupied by humans (Alcorn 1995) points to the necessity of establishing research projects of similar scope that can examine the effects of management in the context of natural successional processes. Moreover, collaborating with the landowners and harvesters who have a stake in the natural resources being studied can greatly facilitate long-term monitoring and data collection (e.g., Bawa 1999). In the end, it is the flexibility and resourcefulness with which local people adapt management practices to meet individual needs that hold promise for modifying these strategies to best meet the objectives of forest conservation.

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Figure 4.1. Plantation of *Chamaedorea* hooperiana in established in an area primary forest above the community of Adolfo Lopez Mateos, Veracruz, Mexico.

Figure 4.2. Plantation of *Chamedorea hooperiana* in an area of older (>20 yrs) secondary forest near the community of Adolfo Lopez Mateos, Veracruz, Mexico.

APPENDIX A

ANOVA Tables for Chapter II

ANOVA results for the analyses presented in Chapter II. Treatment refers to comparisons of management type (*Chamaedorea* plantations vs. unmanaged forest). Block refers to the among block differences for the 4 study blocks. All statistical comparisons were made using completely randomized blocks design ANOVAs unless otherwise specified. See the Methods section of Chapter II for more detailed descriptions of the categories being tested. Significant P Values (P<0.05) for treatment effects are in bold type.

SPECIES RICHNESS		**df**	**F value**	**P value**
overall	Treatment	1	48.32	**0.0061**
	Block	3	25.19	0.0125
	Overall	4	30.97	0.0090
all woody individuals	Treatment	1	27.32	**0.0136**
	Block	3	9.37	0.0493
	Overall	4	13.86	0.0282
woody understory <10 cm dbh	Treatment	1	54.86	**0.0051**
	Block	3	9.09	0.0514
	Overall	4	20.53	0.0162
woody individuals >10 cm dbh	Treatment	1	76.80	**0.0031**
	Block	3	22.90	0.0143
	Overall	4	36.37	0.0071
woody individuals >20 cm dbh	Treatment	1	0.40	0.5720
	Block	3	4.83	0.1141
	Overall	4	3.72	0.1543
shrubs	Treatment	1	33.64	**0.0102**
	Block	3	2.07	0.2831
	Overall	4	9.96	0.0444
palms and cycads	Treatment	1	0.53	0.5195
	Block	3	4.29	0.1312
	Overall	4	3.35	0.1740
wild palms	Treatment	1	0.06	0.8240
	Block	3	4.29	0.1312
	Overall	4	3.24	0.1811

SIMPSON'S INDEX		**df**	**F value**	**P value**
Overall	Treatment	1	5.60	0.0988
	Block	3	1.28	0.4231
	Overall	4	2.36	0.2535
all woody individuals	Treatment	1	4.54	0.1229
	Block	3	0.41	0.7592
	Overall	4	1.44	0.3978
woody understory <10 cm dbh	Treatment	1	20.71	**0.0199**
	Block	3	2.21	0.2653
	Overall	4	6.84	0.0731
woody individuals >10 cm dbh	Treatment	1	0.74	0.4540
	Block	3	1.88	0.3081
	Overall	4	1.60	0.3651
woody individuals >20 cm dbh*	Treatment	1	S=1	0.3170
shrubs	Treatment	1	0.01	0.9230
	Block	3	0.93	0.5244
	Overall	4	0.70	0.6426
palms and cycads†	Treatment	3	0.05	0.8346
	Block	1	2.50	0.2357
	Overall	4	1.89	0.3142
wild palms	Treatment	3	6.38	0.0858
	Block	1	1.99	0.2935
	Overall	4	3.08	0.1909

*Friedman's nonparametric test used

†Data arcsine transformed

BRILLOUIN'S INDEX		**df**	**F value**	**P value**
overall	Treatment	1	12.57	**0.0382**
	Block	3	2.34	0.2511
	Overall	4	4.90	0.1112
all woody individuals*	Treatment	1	S=4	**0.0460**
woody understory <10 cm dbh	Treatment	1	7.99	0.0664
	Block	3	1.75	0.3280
	Overall	4	3.31	0.1764
woody individuals >10 cm dbh	Treatment	1	13.65	**0.0344**
	Block	3	2.04	0.2864
	Overall	4	4.94	0.1101
woody individuals >20 cm dbh	Treatment	1	0.56	0.5319
	Block	3	3.88	0.2117
	Overall	4	3.05	0.2618
shrubs	Treatment	1	16.50	**0.0269**
	Block	3	1.62	0.3509
	Overall	4	5.34	0.1001
palms and cycads	Treatment	1	0.18	0.6965
	Block	3	6.02	0.0873
	Overall	4	4.56	0.1215
wild palms	Treatment	1	3.79	0.1469
	Block	3	2.98	0.1970
	Overall	4	3.18	0.1846

*Friedman's nonparametric test used

STEM DENSITY		**df**	**F value**	**P value**
Overall	Treatment	1	13.86	**0.0338**
	Block	3	4.41	0.1273
	Overall	4	6.77	0.0740
all woody individuals	Treatment	1	124.61	**0.0015**
	Block	3	4.64	0.1197
	Overall	4	34.63	0.0076
woody understory <10 cm dbh	Treatment	1	140.96	**0.0013**
	Block	3	5.07	0.1078
	Overall	4	39.04	0.0064
woody individuals >10 cm dbh	Treatment	1	6.39	0.0856
	Block	3	0.36	0.7874
	Overall	4	1.87	0.3174
woody individuals >20 cm dbh	Treatment	1	1.88	0.2638
	Block	3	1.81	0.3185
	Overall	4	1.83	0.3234
shrubs	Treatment	1	10.38	**0.0485**
	Block	3	0.78	0.5785
	Overall	4	3.18	0.1846
palms and cycads	Treatment	1	1.46	0.3134
	Block	3	1.84	0.3152
	Overall	4	1.74	0.3383
wild palms	Treatment	1	68.75	**0.0037**
	Block	3	11.71	0.0366
	Overall	4	25.97	0.0116

BASAL AREA		**df**	**F value**	**P value**
all woody individuals	Treatment	1	2.77	0.1945
	Block	3	1.59	0.3571
	Overall	4	1.88	0.3152
woody understory <10 cm dbh	Treatment	1	211.22	**0.0007**
	Block	3	11.66	0.0368
	Overall	4	61.55	0.0033
woody ind. >10 cm dbh	Treatment	1	1.35	0.3286
	Block	3	1.41	0.3919
	Overall	4	1.40	0.4079
woody ind. >20 cm dbh*	Treatment	1	S=1	0.3170

*Friedman's nonparametric test used

PALM DENSITY		**df**	**F value**	**P value**
Astrocaryum mexicanum	Treatment	1	452.24	**0.0002**
	Block	3	4.03	0.1413
	Overall	4	116.08	0.0013
Chamaedorea alternans	Treatment	1	0.01	0.9166
	Block	3	0.73	0.5969
	Overall	4	0.55	0.7139
Chamaedorea eliator	Treatment	1	0.30	0.6238
	Block	3	1.09	0.4732
	Overall	4	0.89	0.5610
Chamaedorea elegans	Treatment	1	1.17	0.3593
	Block	3	1.55	0.3642
	Overall	4	1.45	0.3953
Chamaedorea ernesti-augustii	Treatment	1	0.82	0.4316
	Block	3	4.61	0.1206
	Overall	4	3.67	0.1572
Chamaedorea hooperiana †	Treatment	1	16.85	**0.0262**
	Block	3	0.33	0.8069
	Overall	4	4.46	0.1248
Chamaedorea oblongata	Treatment	1	0.06	0.8240
	Block	3	413.39	0.0002
	Overall	4	310.06	0.0003
Chamaedorea pinnatifrons	Treatment	1	0.14	0.7305
	Block	3	0.33	0.8040
	Overall	4	0.29	0.8708
Chamaedorea tepejilote	Treatment	1	0.31	0.6140
	Block	3	1.13	0.4606
	Overall	4	0.93	0.5468
Reinhardtia gracilis	Treatment	1	2.90	0.1869
	Block	3	0.74	0.5957
	Overall	4	1.28	0.4731

†Data log transformed

TIMBER SAPLINGS		**df**	**F value**	**P value**
Density	Treatment	1	25.19	**0.0152**
	Block	3	8.59	0.0554
	Overall	4	12.74	0.0317
Relative Abundance	Treatment	1	10.84	**0.0460**
	Block	3	0.16	0.9139
	Overall	4	2.83	0.2093

VEGETATIVE COVER		**df**	**F value**	**P value**
canopy cover	Treatment	1	0.00	0.9656
	Block	3	0.92	0.5256
	Overall	4	0.69	0.6448
overall understory cover	Treatment	1	2.03	0.2493
	Block	3	6.50	0.0793
	Overall	4	5.38	0.0991
understory palm cover	Treatment	1	5.75	0.0960
	Block	3	1.82	0.3174
	Overall	4	2.80	0.2117
understory woody cover	Treatment	1	0.71	0.4615
	Block	3	2.94	0.2001
	Overall	4	2.38	0.2512
understory herbaceous cover	Treatment	1	0.71	0.4615
	Block	3	2.94	0.2001
	Overall	4	2.38	0.2512
understory vine and liana cover[†]	Treatment	1	2.36	0.2217
	Block	3	1.60	0.3541
	Overall	4	1.79	0.3297

[†] Data log transformed

APPENDIX B

Functional Group Classifications

Species of canopy tree seedlings are classified into functional groups according to shade tolerance based on a review of available literature and discussions with local experts.

Family	Species	Group	References
Actinidaceae	*Saurauia scabrida* Hemsl.	2	a
Anacardiaceae	*Spondias radlkoferi* J.D. Smith	2	c, g, h
	Tapirira mexicana Marchand	2	o
Annonaceae	*Cymbopetalum bailloni* R.E. Fries	1	b, j, y
	Cymbopetalum penduliflorum (Dunal) Baillon	1	a
	Guatteria amplifolia Triana & Planch.	2	a
	Rollinia mucosa (Jacq.) Baill.	2	a
Araliaceae	*Dendropanax arboreus* (L.) Decne. & Planchon	2	h, j, l
Bignoniaceae	*Tabebuia guayacan* (Seeman) Hemsl.	1	h
Bombacaceae	*Bernoullia flammea* Oliver	2	q
	Quararibea yunckeri Standl.	1	a
Boraginaceae	*Cordia megalantha* Blake	1	r
	Cordia stellifera I.M. Johnston	2	a
Burseraceae	*Bursera simaruba* (L.) Sarg.	2	j, p, q, s, w
Cecropiaceae	*Cecropia obtusifolia* Bertol.	2	c, h, j, k, p, q, s, t, w
Clusiaceae	*Calophyllum brasiliense* Camb.	1	f, h, m, p
	Garcinia intermedia (Pittier) Hammel	1	j, q
Ebenaceae	*Diospyrus digyna* Jacq.	1	j
Elaeocarpaceae	*Sloanea medusula* Shumann & Pittier	2	a
	Sloanea petenensis Standley	2	a
Euphorbiaceae	*Alchornea latifolia* Sw.	2	c
	Croton draco Schlecht.	2	j, k
Fabaceae	*Cynometra retusa* Britton &Rose	1	q
	Dialium guianense (Aublet) Sandw.	1	j, p
	Dussia mexicana (Standley) Harms	1	j, q
	Inga sp. 1	1	a
	Inga sp. 2	1	a
	Inga thibaudiana DC.	2	x
	Ormosia panamensis Benth.	2	a
	Pithecellobium macrandrium J.D. Smith	2	p
	Platymiscium pinnatum (Jacq.) Dugand	1	e
Icacinaceae	*Calatola laevigata* Standley	1	h, q

Family	Species	Group	References
Juglandaceae	*Alfaroa* sp.	1	a
Lauraceae	*Nectandra ambigens* (Blake) Allen	1	h, q, s, w
	Ocotea sp.	1	a
	Persea schiedeana Nees	2	j
Malvaceae	*Hampea nutricia* Fryx.	2	q
	Robinsonella mirandae Gomez-Pompa	2	k, q
Meliaceae	*Guarea glabra* Vahl	1	h
	Guarea bijuga var. *glabra*	1	a
	Trichilia moschata Sw.	1	p
	Trichilia pallida Sw.	1	q
Moraceae	*Brosimium alicastrum* Sw.	1	j, k, q, s, t
	Ficus yoponensis Desv.	2	h,g
	Poulsenia armata (Miq.) Standley	1	h, s, h, t
	Pseudolmedia oxyphyllaria J.D. Smith	1	h, j, s, t
Myristicaceae	*Virola guatamalensis* (Hemsl.) Warb.	1	a
Myrtaceae	*Eugenia acapulcensis* Steud.	1	a
	Eugenia lindeniana Berg	1	a
	Pimenta dioica (L.) Merr.	1	j, p
Nyctaginaceae	*Neea psychotroides* J.D. Smith	1	q
Polygonaceae	*Coccoloba hondurensis* Lundell	2	a
Proteaceae	*Roupala borealis* Hemsley	1	a
Rutaceae	*Zanthoxylum caribaeum* Lam.	2	j
Sapindaceae	*Cupania glabra* Sw.	2	y
	Cupania macrophylla A. Rich.	2	a
Sapotaceae	*Pouteria reticulata* (Engl.) Eyma	1	u
Staphyleaceae	*Turpinia occidentalis* (Sw.) G. Don	1	h, k
Sterculiaceae	*Sterculia apetala* (Jacq.) Karst.	1	h, n
Tiliaceae	*Heliocarpus appendiculatus* Turcz.	2	k, q, s, v
	Trichospermum galeottii (Turcz.) Kosterm.	2	a
Vochysiaceae	*Vochysia guatemalensis* J.D. Smith	1	i

Group 1 = shade-tolerant; capable of forming banks of seedlings beneath closed canopy
Group 2 = shade-intolerant; requiring light for germination.

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APPENDIX C

ANOVA Tables for Chapter III

ANOVA results for the analyses of functional group proportions (shade-intolerant and shade-tolerant spp.) of seedling and adult canopy tree communities presented in Chapter III. Treatment refers to comparisons of management type (*Chamaedorea* plantations vs. unmanaged forest). Block refers to among block differences for the 4 study blocks. All statistical comparisons were made using completely randomized blocks design ANOVAs. Analyses based on literature classifications use the proportion of classified species to total species (including unclassified species). In the analyses using combined literature and local classifications, all species were classified as either shade-tolerant or shade-intolerant. Therefore separate analyses of each functional group would be redundant and only the ANOVA results for the proportion of shade-intolerant species are presented. See the Methods section of Chapter III for more detailed descriptions of the categories being tested. Significant P Values (P<0.05) for treatment effects are in bold type.

SEEDLING FUNCTIONAL GROUPS		**df**	**F value**	**P value**
Proportion of shade-intolerant spp. (literature classifications)	Treatment	1	1.72	0.2815
	Block	3	0.25	0.8551
	Overall	4	0.62	0.6803
Proportion of shade-tolerant spp. (literature classifications)	Treatment	1	0.02	0.8967
	Block	3	0.09	0.9586
	Overall	4	0.08	0.9849
Proportion of shade-intolerant spp. (literature and local classifications)	Treatment	1	2.27	0.2287
	Block	3	0.63	0.6420
	Overall	4	1.04	0.5066
Proportion of shade-intolerant spp. excluding Block 1 (literature classifications)	Treatment	1	3.37	0.2075
	Block	2	0.22	0.8187
	Overall	3	1.27	0.4685
Proportion of shade-tolerant spp. excluding Block 1 (literature classifications)	Treatment	1	0.00	0.9783
	Block	2	0.04	0.9624
	Overall	3	0.03	0.9926
Proportion of shade-intolerant spp. excluding Block 1 (literature and local classifications)	Treatment	1	30.48	**0.0313**
	Block	2	5.04	0.1656
	Overall	3	13.52	0.0697

ADULT FUNCTIONAL GROUPS		**df**	**F value**	**P value**
Proportion of shade-intolerant spp. (literature classifications)	Treatment	1	4.40	0.1268
	Block	3	9.62	0.0476
	Overall	4	8.32	0.0565
Proportion of shade-tolerant spp. (literature classifications)	Treatment	1	0.66	0.4748
	Block	3	3.05	0.1924
	Overall	4	2.45	0.2438
Proportion of shade-intolerant spp. (literature and local classifications)	Treatment	1	0.07	0.4724
	Block	3	2.63	0.2239
	Overall	4	2.14	0.2788