Effect of Exotic Canopy on Understory Species Composition in Degraded Subtropical Dry Forest of Puerto Rico

By

Freddie O. Pérez Martínez

A thesis submitted in partial fulfillment of the requirements for the degree of: MASTER OF SCIENCE in Agronomy

UNIVERSITY OF PUERTO RICO MAYAGÜEZ CAMPUS 2007

Approved by:

Edwin Más, MS Member, Graduate Committee

Jesús Danilo Chinea, Ph.D. Member, Graduate Committee

Ramón I. Torres, Ph.D. Member, Graduate Committee

Skip J. Van Bloem, Ph.D. President. Graduate Committee

Bryan R. Brunner, Ph.D. Representative, Graduate Studies

Miguel Muñoz Muñoz, Ph.D. Head, Department of Agronomy and Soil Date

Date

Date

Date

Date

Date

ABSTRACT

Most of the forest in the dry zone of Puerto Rico is relatively young secondary forest dominated by exotic species. This pattern is the result of the abandonment of lands that were intensively used for agriculture and other human activities in the first half of the 20th century. Because many of these exotic species are nitrogen fixers and have a wide range of invasive capacities they may interfere with the regeneration of native species. The study of the species composition of understory provides insight to the generations of trees and shrubs that will dominate the canopy as natural succession progresses. The purpose of this work research was to measure the species composition, species richness, and diversity of the understory of forests with canopies dominated by exotic species and compare it with native forest in southwestern Puerto Rico. Fifty-four belt transects of 2 x 50 m were established along different parts of the study area, 27 in forest dominated by exotics and 27 in native forest. Physical and descriptive measurements were taken on saplings (0.50 m - 2.0 m), seedlings (0-0.50 m) and canopy trees. Results indicate that native sites had a higher number of species in the canopy, sapling and seedling levels. The canopy and seedling levels of native sites showed higher diversity than in exotic-dominated sites. At the sapling level there was a similar number of species between the two forest types. The species that dominated the native forest understory were not the same that were found in areas dominated by exotics. The amount of individuals from exotic species decreased as time since abandonment increased. This study suggests that the areas that have canopies dominated by exotics facilitate the conditions for colonization by some native species but not in the pattern as in nativedominated areas. Based on the overall results I predict that native species would be emerging in the canopy of areas that are dominated by exotics but it will take longer to dominate as they do on natural native forest areas.

RESUMEN

La mayor parte de la zona boscosa en la zona seca de Puerto Rico es bosque secundario relativamente joven dominado por especies exóticas. Este fenómeno es el resultado del abandono de las tierras que fueron utilizadas intensivamente para agricultura y otras actividades humanas a principios del siglo XX. Como consecuencia del uso intensivo de estas tierras, las especies exóticas han colonizado estas áreas y han cambiado los patrones de la regeneración. Dichas especies son fijadoras del nitrógeno y tienen una amplia gama de capacidades invasoras por lo que estas podrían interferir con el desarrollo de las especies nativas. El estudio de la composición de especies es una representación verdadera de la posible futura generación de árboles y arbustos que podrían crecer, establecerse y dominar estas áreas en las siguientes etapas de la sucesión natural. Por lo tanto, el propósito de este trabajo fue medir la composición, la riqueza y la diversidad de especies de sotobosque de áreas dominadas por exóticas y compararlas con bosques dominados por especies nativas en el suroeste de Puerto Rico. Un total de cincuenta y cuatro transectos fueron establecidos a lo largo de diferentes partes del área del estudio, 27 en el bosque dominado por exótic as y 27 en bosque nativo. Se identifico y se midió la altura de los individuos juveniles (0.50 a 2.0 metros de altura), plántulas (0-0.50 metros de altura) y árboles del dosel en transectos de coreas de 2 metros de ancho por 100 metros de largo. Los resultados indicaron diferencias significativas en la riqueza de especies de los tres niveles, y ninguna diferencia significativa en diversidad en juveniles pero diferencia en la diversidad de las plántulas. Las especies que dominaron el bosque nativo no fueron las mismas que las encontradas en las áreas dominadas por exóticas. Además el porciento de individuos exóticos, en el sotobosque disminuyó a medida que el tiempo después del abandono aumentaba. Este estudio sugiere que las áreas que tienen doseles dominados por exóticas tiene la capacidad de facilitar las condiciones para el crecimiento de ciertas especies nativas pero no de la misma forma que las áreas dominadas nativas lo están haciendo. Podemos predecir que las especies nativas serán reintroducidas naturalmente a las áreas donde las especies exóticas dominan pero tomara más tiempo para que estas puedan dominar estas áreas como ocurre en bosques secos nativos.

DEDICATION

- To my dear daughter, Beira Rahé, and my wife, Rosemarie, who served as inspiration in this journey; life. They have been my primary source of happiness, strength and joy during all these years.
- To my parents Alfredo and Nilsa for their love and support.
- To my cousin, José, whose help is unconditional every time.
- To other members of my family for their support and guidance.
- To the great many friends I have met along the way and had made the difference in my life.
- To my friends and peers at the University of Puerto Rico at Mayagüez and Utuado.
- Finally, to God and Mother Nature who inspires me quite often every morning, and to whom I am grateful for the many things given to me.

ACKNOWLEDGEMENT

I would like to express my special appreciation and gratitude to my major professor, Dr. Skip van Bloem, first for accepting me on his team, and for his help and commitment to this work. He believed in me, and put great trust in me during the development of this investigation. I am also grateful to Dr. Jesus Danilo Chinea, Dr. Ramon Torres, Prof. Edwin Más and Dr. Bryan Brunner for their guidance and always positively critical comments about my academic work.

My special appreciation and gratitude goes to my friend Brett Wolfe, without whom the field work would have been much more difficult. Brett, thanks a lot for the many ideas and time you put into it. Also I want to thanks Jose Javier Vargas Almodovar, Ricardo Santiago García, Jose G. Martínez Rodríguez and Ramón Agosto for their continuous help in the field and review of previous drafts of this work. To Jorge Betancourt, Oscar Abelleira, Armando Feliciano, Edgardo de la Torre, Arcides Morales and Papo Vives for the many times they helped in the field work. To my wife, Rosemarie, for the review and corrections in this manuscript.

I want to thank the PR DRNA and the staff at Guanica Forest, especially to Miguel Canals for support in the identification of plants and access into the forest. Also landowners who provided access to other forest stands: E. Maciula, and Conservation Trust. I am also thankful to Dr. Gary Breckon, Director of the Herbarium of the University of Puerto Rico at Mayagüez who helped me identify unknown botanical samples. Also to Roy Ruíz Vélez for assistance working with the maps and aerial photos.

Finally, I would like to thank the staff of the Agronomy and Soils Department, Agricultural Experimental Station in Mayagüez and the Agricultural and Biosystems Engineering Department, especially Gloria Aguilar, for their help with transportation and support during the time this investigation took place.

This project was funded by a USDA - McIntire-Stennis grant to Skip J. Van Bloem.

LIST OF TABLES......viii LIST OF FIGURES.....ix LIST OF APPENDICES.....x INTRODUCTION......1 LITERATURE REVIEW......4 Land Use History......4 Effect on Native Seed Dispersal and Survivorship......5 Overview of the Study Area......9 -Peñuelas......10 -Guanica.....11 -Cabo Rojo......12 -Canopy Coverage......13 -Richness and Diversity......13 -Similarity and Species Composition.....14 - Effects of Exotic Canopy and Age since Abandonment in Sapling and Seedling Individuals......14 -Hypothesis Testing.....15

TABLE OF CONTENTS

RESULTS	16
General Description	16
Canopy Coverage and Density	17
Species Richness and Diversity	19
Species Similarity and Composition	21
Effects of Exotic Canopy and Age since Abandonment in Sapling and Seed	iling
Individuals	27
DISCUSSION	
Patterns of Species Composition	30
Native Species Regeneration	31
Invasion and Continuous Growth of Exotic Species	32
Patterns in Rare Species Across the Landscape	34
Possible Effects of Land Use and time since Abandonment	34
Management Implications	35
CONCLUSIONS	36
RECOMMENDATIONS	37
BIBLIOGRAPHY	38
APPENDICES	41

LIST OF TABLES

Table 1. Description of all paired sites including physicalinformation, location, elevation, age and descriptiveinformation of each sites
Table 2. Overall composition for each vegetation layer
in each of the 9 pairs of sites used in this study. Pair numbers are the same as in Table 1 and Figure 1
Table 3 . Similarity index of sapling and seedling categories between each pair of native and exotic canopy dominated areas
Table 4. Importance values and presence of all the species found in the study
Table 5. List of the native specie found in the understory(sapling and seedling) of exotic sites and its main seed dispersal agents

LIST OF FIGURES

Figure 1. Map of study area including the sample points. Paired plot are numbered. Each pair of sites included one exotic and one native canopy forest. Life zones are delimited according to Ewel and Withmore (1973). Although pair #2 is outside of the area delimited as dry zone, it is in dry forest according to Helmer (unpublished data)
Figure 2. Comparison if canopy coverage (A), sapling density and seedling density (B) between native and exotic canopy dominated areas. Canopy coverage is denoted as the percentage of coverage in each forest cover. Different letters above the
boxes show significant difference between each forest cover
Figure 3. Comparison of richness in native and exotic canopy dominated sites and between the three levels in each forest cover type. Different letters show significant difference (p<0.05) between forest cover and within forest layers in
each forest cover
Figure 4. Accumulation species area curves for native (A) forest understory (saplings and seedlings) and exotic (B) forest understory
Figure 5. Comparisons between Shannon diversity index (H`) between native and exotic canopy dominated areas and between each of the three categories in each forest cover. Different letters show significant difference (p<0.05) between forest cover and within forest layers in each forest cover
Figure 6. Comparison of the Sorensen similarity index between canopy and understory in the native and exotic canopy dominated areas. Letters show significant difference between each height level in the two forest covers
Figure 7. Importance values of all species in canopy, sapling and seedlings categories in the native (A) and exotic (B) canopy dominated areas. Y-axis is in log scale to expand low end of x-axis and separate lines. Note different scale on x-axis
Figure 8. Relation between the % of exotic canopy coverage and the percentages of native and exotic sapling (A) and seedling (B) individuals. Dashed lines represent the 50% of the values to show distribution of individuals

Figure 9. Relationship between age since abandonment and	
the percentage of exotic individuals in the sapling (A) and	
seedling (B) categories	29

LIST OF APENDICES

APPENDIX I. Aerial photo of pair #1: Peñuelas. Native site
is inside private land, south of road #2 and the exotic site is
near a cell phone tower system. Native site is illustrated by a
blue dot and exotic site is illustrated by a red dot41
APPENDIX II. Aerial photo of pair #2: Tallaboa. Native site
is located on a hill and exotic site is an alluvial valley. Native site
is illustrated by a blue dot and exotic site is illustrated by a red
dot42
APPENDIX IV. Aerial photo of pair #4. Guanica Forest.
Native site is located in an old forest and exotic site is located at the
site of and old baseball field. Native site is illustrated by a blue
dot and exotic sites is illustrated by a red dot
APPENDIX IV. Aerial photo of pair #4. Guanica Forest. Native
site is located in an old forest and exotic site IS located where the
community that is observed in the photo was settle. Native site is
illustrated by a blue dot and exotic sites is illustrated by a red dot44
APPENDIX V. Aerial photo of pair#5. Guanica Forest. The native
site (left photo) was located at the east part of Guanica Forest. The
main human activity was charcoal production. The exotic site
(rigth photo) was locate near Playa Tamarindo and the area was a
cattle farm. Native site is illustrated by a blue dot and exotic site is
illustrated by a red dot45
APPENDIX VI. Aerial photo of pair #6.The native site was
located in an area of charcoal production and the exotic was at
•
the site of an old golf course. Native site is illustrated by a blue dot and exotic sites is illustrated by a red dot
dot and exotic sites is illustrated by a red dot46
APPENDIX VII. Aerial photo of pair #7. Playa Santa, Guanica.
Native site was inside an area of charcoal pits and the exotic site was
located in an old cattle farm. Native site is illustrated by a blue dot
and exotic site is illustrated by a red dot
APPENDIX VIII. Aerial photo of pair #8. Yauco. The native site
was located nn a hill where charcoal production was a common
practice and the exotic site was on an old tobacco farm. Native site is
illustrated by a blue dot and exotic site is illustrated by a red dot
ADDENIDIVIN A avial what a of main #0. Cabo Dais Native site was
APPENDIX IX. Aerial photo of pair #9. Cabo Rojo. Native site was
located in an old uncut forest and the exotic site was on an old cattle
farm. Native site is illustrated by a blue dot and exotic site is

illustrated by a red dot	49
APPENDIX X Analysis of Variance (ANOVA) for block design for the percentage of canopy in native and exotic canopy coverage sites. Post-hoc comparisons between sites were	
done using a Tukey test	50
APPENDIX XI. Analysis of Variance (ANOVA) for block design	
for the logarithm of sapling density in native and exotic	
canopy coverage sites. Post-hoc comparisons between cover types and pairs were done using a Tukey test	51
APPENDIX XII Analysis of Variance (ANOVA) for block design	
for the logarithm of seedling density in native and exotic canopy	
coverage sites. Post-hoc comparisons between cover types and pairs were done using a Tukey test	52
APPENDIX XIII Analysis of Variance (ANOVA) for block design	
for the number of species in the canopy level between native	
and exotic canopy coverage sites. Post-hoc comparisons between cover types and pairs were done using a Tukey test	53
APPENDIX XIV Analysis of Variance (ANOVA) for block design	
for the square root of the number of species in the sapling level between native and exotic canopy coverage sites. Post-hoc	
comparisons between cover types and pairs	
were done using a Tukey test	54
APPENDIX XV Analysis of Variance(ANOVA) for block design	
for the number of species in the seedling level between native	
and exotic canopy coverage sites. Post-hoc comparisons between cover types and pairs were done using a Tukey test	55
cover types and pans were done using a rakey test	
APPENDIX XVI Analysis of Variance(ANOVA) for block design	
for the diversity in the canopy level between native and exotic canopy coverage sites. Post-hoc comparisons between cover types and pairs	
were done using a Tukey test	56
APPENDIX XVII Analysis of Variance(ANOVA) for block design	
for the diversity in the canopy level between native and exotic canopy	
coverage sites. Post-hoc comparisons between cover types and pairs	
were done using a Tukey test	57
APPENDIX XVIII Analysis of Variance(ANOVA) for block design	
for the diversity in the seedling level between native and evotic canony	

for the diversity in the seedling level between native and exotic canopy coverage sites. Post-hoc comparisons between cover types and pairs

were done using a Tukey test	58
APPENDIX XIX List of species and importance values of Pair #1	59
APPENDIX XX List of species and importance values of Pair #2	60
APPENDIX XXI List of species and importance values of Pair #3	61
APPENDIX XXII List of species and importance values of Pair #4	63
APPENDIX XXIII List of species and importance values of Pair #5	64
APPENDIX XXIV List of species and importance values of Pair #6	65
APPENDIX XXV List of species and importance values of Pair #7	67
APPENDIX XXVI List of species and importance values of Pair #8	68
APPENDIX XXVII List of species and importance values of Pair #9	69

INTRODUCTION

The forest dynamics of the Caribbean island of Puerto Rico have significantly changed in the last two centuries. During the colonization by the Europeans the island was almost completely covered by forest and it remained that way during the first three centuries of Spanish rule (Wadsworth, 1950). Then, in the 19th and first half of the 20th century, forest areas were reduced to almost 5% by clearing land for sugarcane, tobacco and coffee plantations. Deforestation reached a peak in the middle of 1900's when the economy changed from agriculture to industry. As a consequence, agricultural fields were abandoned and forests have reclaimed this land (Birdsey and Weaver, 1987). As a result of this change, today, forest covers about 35% of the island area.

One of the most affected and disturbed forest areas was the tropical dry forest on the south coast of the island (Murphy and Lugo 1986) due to the conversion of these lands to agricultural fields, urbanization, industrial development, cattle production and many other uses. Approximately 96% of original dry forest was converted to agricultural lands. The remaining 4% that was left intact represents only about 5,000 ha (Murphy et al., 1995). Although there are no recent studies that quantify the percentage of the area that is relatively young forest in succession, a simple glance at the region suggests that mature forest is rare in areas where there is no protection. The abrupt abandonment of these fields from one or more of the intensive uses mentioned above has caused this type of succession.

The age of this developing forest, particularly in dry forest, may vary depending on when these fields were abandoned and the type of activities that were carried out in those areas. According to Lugo (2004), after the abandonment of a field and as an effect of the type of land use, exotic species (*Leucaena leucocephala, Prosopis juliflora,* and *Albizzia sp.*) dominate these areas for 30 to 40 years, at which time native species began to grow in the understory. This pattern results in a forest with open canopy (less than 30 years) dominated by exotic species and a more closed canopy forest (more than 60 years) dominated by native species. Forests between 30 to 60 years of age have transitional succession where exotics and natives develop together. This leads to a more diverse forest, in terms of species composition, because of the growth of the two types of species in the same space. Exotic species are particularly likely to colonize areas where the soil structure is severely disturbed (i.e., agricultural and bulldozed areas).

The introduction of these exotic species results in considerable changes in the structure and species composition of tropical forest. These changes have resulted in young forest with canopy coverage dominated by exotics and less native species growth. Although the long term effects of these species are not yet understood, they may have significant consequences on the patterns of native species regeneration, wildlife habitat (especially birds), and biochemical and nutrient cycles (D`Antonio et al., 2001).

Recent studies suggest that the way regeneration occurs will depend on the frequency, intensity and scale on which the disturbance happened (Guariguata and Oestertag, 2001). It has been demonstrated that the composition of relatively young forest will be dominated by exotic species in wet and moist forest (Aide et al., 2000, Chinea 2002) and the same pattern appears to be true in young dry forest which is dominated by *Prosopis juliflora* and *Leucaena leucocephala*, among other species. It is not clear if the native forest that will develop after the young forest dominated by exotics will have the same composition, structure and resistance to natural disturbance that older forests have. The answer to this question is very important to determine if it is better to manage young forest regeneration or if it is better to let it regenerate naturally. Several studies that have addressed this question have been conducted in Puerto Rican moist and wet forest but few have been done in the dry zone.

The species composition of understory is crucial in describing the regeneration capacity and possible species composition of tree communities in dry forest through secondary succession. However, data of this type is practically nonexistent (Castilleja, 1991). Studies of understory species composition in different areas undergoing secondary succession in dry forest will give information about the species composition, structure, and resistance to natural disturbance. These studies also can provide guidelines for silvicultural techniques, particularly in reforestation of degraded areas of dry forest. **The goal of this project is to evaluate, identify and compare the species composition of forest understory of areas dominated by exotic and native species in dry forests of southwestern Puerto Rico.**

OBJECTIVES

The general objective of this study was to evaluate the effects of forests dominated by exotic species on the composition of understory in tropical dry forests of southwestern Puerto Rico. The specific objectives were:

- 1) To evaluate and compare the species composition and diversity of forest understory under exotic and native canopy dominated forest.
- 2) Evaluate and compare the similarities between canopy and understory species.
- To determine variability of understory species composition across southwestern Puerto Rico.

LITERATURE REVIEW

Land Use History

With the exclusion of some patches, forest was the predominant vegetation in Puerto Rico at the time of the Europeans' arrival (Wadsworth, 1950). However, their impact changed the landscape. Southern Puerto Rico was one of the most heavily impacted areas. At the time of the Spanish control (19th century) the extraction of wood for construction was common (Wadsworth, 1950) throughout the region because of the hardwoods that were present. Later in the early twentieth century sugarcane cultivation and refineries were expanded over the region and with it, the population movement to the coast (Scarano, 2000). This increase in population and sugarcane cultivation had a direct effect on the forest because of the demand for products, especially charcoal, as the main fuel for cooking and sugar refineries. Subsistence agriculture and cattle production were other common practices in the area. By the 1940's most of the dry forest was cut and just 5% of the entire south coast was intact forest (Wadsworth, 1950). Since 1950 a shift in the Puerto Rican economy from intensive agriculture to manufacturing has led to a natural forest recovery in the area. Now forest covers 23.2% of the dry forest zone (Ramjohn, 2004), within several fragments in the area with Guanica State Forest as one of the biggest portions. The other 76.8% is distributed in agricultural land (croplands and cattle production) and urban areas (commercial, recreational, public use, industrial and residential).

Effects of Land Use

Most of the Puerto Rican tropical dry forest has been heavily disturbed or eliminated (Murphy and Lugo 1986) due to the conversion of these lands to agricultural fields, urbanization, industrial development, cattle herding and many other uses. The abrupt abandonment of these fields from one or more of these intensive uses has caused most forest stands in the dry zone of Puerto Rico to be relatively young secondary forest. The vegetation in this developing forest is mainly a mix of exotic species such as *Leucaena leucocephala* and *Prosopis juliflora* (Ramjohn, 2004).

According to some studies, sites recovering from agricultural usage and cattle production have lower native plant diversity than those recovering from cutting for charcoal production or low density grazing (Ramjohn, 2004 and Molina Colon, 1998). In a study of forest composition of different land uses in the Guánica Forest, Molina Colón (2006) found a distinct difference between areas that had been used for agriculture, housing and charcoal production. Only charcoal land use had similar structural and species composition as uncut forest, while the others supported a species-poor community dominated by exotic species (mainly *L. leucocephala*). *L. leucocephala* dominated both tree and sapling size classes after 50 years since abandonment. In a separate study of dry forest fragments in southwestern Puerto Rico (Ramjohn, 2004), areas of regrowth (areas with less than 25% of old growth) and edges of uncut forest patches were mainly dominated by *L. leucocephala*.

Exotic Species Invasion Capacities

The two most common exotic species that have invaded SWPR are *Leucaena leucocephala* and *Prosopis juliflora*. *L. leucocephala*, which is mainly dispersed by wind, is a nitrogen-fixing legume and a shade-intolerant species with a broad capacity of germination and growth that allows it to colonize the most marginal areas of dry zone, such as abandoned crop lands and pastures, forest edges, burned sites and road sites (personal observation). *P. juliflora*, is a common pasture tree and its seeds are dispersed by cattle (Janzen, 1986). Active pasture can develop a continuous canopy of monodominant *P. juliflora* (personal observation).

Dry forests exhibit conditions that may permit the introduction and persistence of these two species. For example, the leaf area index of dry forests is much lower than in wetter forests (Murphy and Lugo, 1986) resulting in a more open canopy. This increases the amount of sunlight reaching the forest floor that can help exotic pioneer species grow in native forests. Also, native dry forest species rely more on vegetative or asexual reproduction than by seed, as opposed to exotic species, which often have high germination rates and high seed viability (Ray and Brown, 1995). Thus, disturbances like agricultural use that disrupt soils will tend to limit regeneration of native species, and exotic species may be able to persist longer due to higher levels of sunlight on the forest floor.

Effect on Native Seed Dispersal and Survivorship

Leucaena leucocephala is dry fruited and thus, unattractive to frugivorous birds and bats (Little et al., 1974). This factor may substantially reduce external native seed inputs because birds and bats would not enter *L. leucocephala* areas. Castilleja (1991) found that, while there was enough light for seed germination below the forest canopy, and seedling density correlated inversely with canopy cover, seedling survival through the dry season was dependent on dry season canopy cover. In the same way, Ray (1993) found that seedlings planted under shade cloth survived better than seedlings planted in the direct sun. As a consequence, it seems

reasonable to assume that native species will not regenerate well under *L. leucocephala* canopy. Some authors have postulated that one of the reasons of the failure of *L. leucocephala* forest in increasing species richness is that seedling survivorship through the dry season is low under its fairly open deciduous canopy.

International Examples of Invasiveness of Exotic Species

L. leucocephala has been shown to be an invasive colonizer species in other tropical ecosystems around the world. For example, in Guam and Saipan an erosion control practice was implemented after the devastation of World War II using *L. leucocephala*. This species was broadcasted aerially in fields that had been strongly disturbed to accelerate regeneration so that erosion could be controlled. After fifty years, the northern part of the island was dominated by this early successional exotic species and native forest flora was restricted in distribution (D'Antonio et al. 2001). Although the shortage of native forest areas in the island area could be related to the forest degradation by war, *L. leucocephala* colonized those areas leading to no progression of natural succession processes.

In a study of succession conducted on St. John in U. S. Virgin Islands, Ray (1993), and Ray and Brown (1995) found that a 33-year-old abandoned pasture supported a community mono-dominated by *L. leucocephala*, while a 50-year-old site supported a richer community mainly dominated by *B. succulenta*. Similar successional patterns had been observed on abandoned agricultural land in Dominican Republic (Roth, 1999). After 29 years since the cessation of agricultural activity, dry forest supported species-poor forests dominated by *L. leucocephala* in the canopy and its understory. Only one native species was found on the area.

Succession in Other Life Zones of Puerto Rico

Recent studies on species composition of wet and moist forests in Puerto Rico concluded that successional stages on abandoned agricultural fields are much different from natural disturbances. Regeneration on these fields takes a longer time in comparison to other disturbances due to the elimination of remnant vegetation, roots or soil seeds banks (Chinea 2002, Aide et al., 2000). On the other hand, when some roots or remnant vegetation are left after disturbance, regeneration occurs more rapidly, in the case of dry forest (Murphy et al., 1995) by resprouting mechanisms. Due to this factor, forests that grow on old agricultural fields may be dominated by exotic tree species because they have a higher percentage of seed viability and better mechanisms of seed dispersal and, therefore, can invade and colonize these areas faster than native species (Aide 2002, Chinea, 2002, Murphy et al., 1995).

In a study conducted by Aide et al. (2000) in moist and wet forests of P.R., the pattern of secondary succession was determined by studying the woody vegetation in 71 abandoned pastures and forest. The forest structure (height, basal area, biomass, and species richness) on abandoned agricultural lands was found to return to native forest after a period of 40 years. However, the species composition of these new forests was much different than in native forests, even after 77 years. The most common trees in old growth native forests were rarely found in sites recovering from agricultural use. Exotic species such as *Spathodea campanulata* and *Syzygium jambos* were some of the most common species in secondary forest. They concluded that the long term impact of these exotics in the development of Puerto Rican forest will depend on life history characteristics of each species. When a species can develop and persist throughout all stages of succession it could remain in old forest and become a permanent part of forest flora. What is not understood is if the growth of these species can change the patterns of native growth, energy flux, nutrient cycles and wildlife habitat.

As the distance to remnant forest stands increased, the presence of native tree species on old fields decreased (Chinea, 2002). In the municipality of Humacao, P.R., forest structural and compositional changes along sites that were abandoned in different times were compared. Chinea's findings are similar to what Aide et al. (2000) obtained from their study, where similar structural characteristics of old forest were obtained after a period of 40 years, but these were different than the-70 year old-forest species composition because of the growth of exotic species. Recolonization of old agricultural fields takes longer than from other disturbances and young forests that develop are dominated by exotic tree species.

In a study conducted by Parrota (1995) in the north coast of Puerto Rico, the patterns of understory colonization were evaluated in a 4.5 year old plantation of *L. leucocephala*. It was found that the density of woody tree individuals found beneath *Leucaena* was 50% higher than the density found in the understory of stands dominated by *Casuarina equisetifolia* and *Eucalyptus robusta*. The results indicate that overstory species selection in plantations can exert significant influence on subsequent patterns of colonization by secondary forest species and is an important consideration in the design for catalyzing succession in degraded deforested areas.

Actual Situation in P.R. Dry Forest

A lot of studies have been conducted in the tropical moist and wet forest of Puerto Rico and other parts of the world that address the pattern of regeneration after various and uses. Although many conclude that the regenerative power of Neotropical forest vegetation is clearly high (Guariguata and Ostertag, 2001) the presence of exotic species remains in the tropical forest until it reaches 40 to 50 years old (Aide et al., 2000, Chinea, 2000). The presence of exotic species will diminish depending on the type and characteristics of the exotics that remain. The factors that may prolong their presence and may vary according to the exotic species are growth, dispersal and response to shade. These conclusions can be applied to dry forest although there is little direct evidence that species would behave the same due to the different environmental conditions found in dry forests (light, precipitation, evapotranspiration and temperature). Since these conditions can be different, some authors share the conclusion that more research needs to be done (D`Antonio et al. 2001 and Murphy et al., 1995) on the way that the effect of this exotic species affected the native flora and forest regeneration.

MATERIALS AND METHODS

Overview of the Study Area

This study was carried out in the subtropical dry forest region of Puerto Rico as delineated by Ewel and Whitmore (1973): a coastal strip between approximately 18°N 66° 35'W and 18°N 67° 12'W. All the sites were located west of the city of Ponce and were situated in the towns of Peñuelas, Yauco, Guanica and Cabo Rojo (Figure 1). Mean annual rainfall ranges from a minimum of about 600 to a maximum of 1000 mm (Ewel and Whitmore, 1973) and it is received mostly between late August and mid-November with a shorter rainy season in April and May. Annual potential evapotranspiration exceeds 1200 mm and mean annual temperature is about 25°C (Murphy and Lugo, 1986). The area consists of alluvial valleys scattered among low hills. Soils are developed from tertiary limestone and the most abundant soil orders are the Mollisols, Aridisols and Entisols.

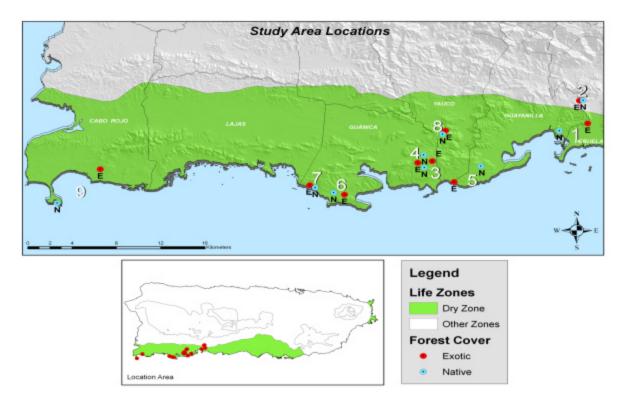


Figure 1. Map of study area including the sample points. Paired plots are numbered. Each pair of sites included one exotic and one native canopy forest. Life zones are delimited according to Ewel and Whitmore (1973). Although pair #2 is outside of the area delimited as dry zone, it is in dry forest according to a new analysis of life zones (Helmer, unpublished data). Design assisted by Roy Ruiz at Department of Water Resources in UPRM.

Study Sites

Nine different pairs of sites in the towns of Peñuelas, Guanica, Yauco and Cabo Rojo were selected to make this study (Table 1). Each pair of sites included one exotic and one native canopy forest. Edaphic and topographic conditions varied between some pairs of sites. However, sites were chosen to be close together to minimize physical variation as much as possible. Field sites were selected previously with aerial photos to distinguish the exotic-dominated canopy and the native-dominated canopy. Areas with exotic-dominated canopies were identified based on the fact that all agricultural land identified in the 1936 and 1950 photos that were closed forest in recent aerial photos were to be dominated by exotics (this was empirically confirmed).

Forest Elevation Slope									
Pair	Sites	Cover	Location	Land Use	Age	(MSL)	(°)	Latitude	Longitude
1	Peñuelas	Native	Private Farm Cellular	Charcoal Pits Construction of	80	96.8	15-35	18° 0' 26.25" N	66° 45' 32.70"
1	Peñuelas	Exotic	Antennas Land	roads	40	82.9	0-25	18° 0' 52.61" N	66° 44' 5.18" \
				Extraction of					
2	Tallaboa	Native	Private Land	Wood	80	167.0	0-25	18° 2' 15.38" N	66° 44' 19.72"
2	Tallaboa	Exotic	Private Land	Cattle Production	40	121.7	0-5	18° 2' 13.83" N	66° 44' 31.05"
3	Main Plot	Native	Guanica Forest	Charcoal Pits	80	161.0	0-15	17° 58' 14.19" N	66° 52' 27.02"
3	Granados	Exotic	Guanica Forest	Farm land	50	163.9	0-10	17° 58' 37.18" N	66° 52' 2.90" \
4	La Hoya Baseball	Native	Guanica Forest	Charcoal Pits	80	149.8	0-10	17° 58' 59.16" N	66° 52' 29.11"
4	Park	Exotic	Guanica Forest	Community	50	194.2	0-5	17° 58' 30.99" N	66° 52' 46.96"
5	Magueyes	Native	Guanica Forest	Charcoal Pits	80	82.9	0-10	17° 58' 19.43" N	66° 49' 33.50"
5	Tamarindo	Exotic	Guanica Forest	Cattle Production	50	6.7	0-5	17° 57' 22.77" N	66° 50' 55.53"
6	La Jungla Golf	Native	Guanica Forest	Charcoal Pits	80	21.02	0-20	17° 56' 43.56" N	66° 57' 5.04" \
6	Course	Exotic	Guanica Forest	Sports	35	10.3	0-5	17° 56' 36.60" N	66° 56' 31.71"
7	La Jungla	Native	Guanica Forest	Charcoal Pits	80	12.7	0-20	17° 57' 1.45" N	66° 58' 2.05" \
7	La Jungla	Exotic	Guanica Forest	Cattle Production	50	7.0	0-5	17° 57' 9.83" N	66° 58' 19.02"
8	Yauco	Native	Private Farm	Charcoal Pits	80	171.8	15-40	18° 0' 13.43" N	66° 51' 30.98"
8	Yauco	Exotic	Private Farm	Farm land	35	81.2	0-15	18° 0' 26.09" N	66° 51' 21.87"
9	Cabo Rojo	Native	Public Land	Charcoal Pits	80	0.0	0-5	17° 56' 3.77" N	67° 11' 13.94"
9	Cabo Rojo	Exotic	Private Farm	Cattle Production	35	32.6	0-15	17° 58' 5.17" N	67° 9' 2.62" W

Table 1. Description of all paired sites including physical information, location, elevation, age and descriptive information of each site.

-Peñuelas

Pair #1 was selected in a hilly area in Peñuelas. The exotic-canopy forest site was near an installation system of cellular phone relay antennas located in road #384, 400 meters from road #2. The area was cut for the construction of electrical antennas around 1970. Soils of this area were identified as Mollisols, and the dominant series is Aguilita which consists of very deep, well drained, alkaline, moderately permeable soils on ridge tops, summits and side slopes in uplands and limestone hills. The native forest site is situated on a hill on the other side of road #2, 500 meters from road #127. This site was the property of one of the managers of the nearby sugarcane fields, and, as viewed in the aerial photos, the area was forest land in 1936.

The 2nd pair of sites was located in land owned by "Fideicomiso de Parques" which is called Tallaboa. The valleys of the areas were used for cattle production and intensive agriculture until the 1960's and now exotic tree species dominate the area. Some of lower hills were abandoned in the beginnings of the 1900's and are mostly dominated by native trees. The area is mostly dominated by rocky and alluvial soils identified as Mollisols, with Aguilita the predominant soil series.

-Guanica

Three pairs of sites were selected in Guanica State Forest. One native forest site was previously evaluated by Murphy and Lugo (1986) and its pair (exotic forest) was nearby in an abandoned baseball park (Pair #4). The native area was used for extraction of charcoal and had a combination of alluvial and rocky soils classified as limestone rock land, which consist of calcareous rock deposits with a thinner later of organic soil. The exotic area was a baseball park that belonged to a community that was settled in the area until 1950's. Soils of this area are within the order of the Aridisols and, specifically, the most dominant series is La Covana. Another pair (Pair #3) of sites was selected in two other areas, the native forest called "La Hoya" and the exotic canopy dominated forest near a road called "Los Granados". Both areas have alluvial and rocky soils classified as Aridisols and were in the soil series La Covana. Los Granados was extensively used for agriculture until the 1950's and La Hoya had areas that were used for charcoal production or were apparently old growth forest.

Pair # 5 was situated in areas near the beach. The native site was located at the end of road Lluberas in the east of Guanica Forest. This site was used for charcoal pits and, as viewed in the aerial photo it was forest in 1936. Its pair was located near Tamarindo beach. This site was

used for cattle production 50 years ago. Soils of the area were rocky calcareous formations and alluvial soils identified as Aridisols of which the predominant soil series was La Covana.

Another two pairs (Pairs #6 and #7) of sites were located in the area of "La Jungla" near Playa Santa. This area included two native forest sites, which were used for charcoal production, and an exotic forest which was used for cattle production (Pair #7). The other exotic forest (Pair #6) was an old go lf course near the community of Ensenada along road #325. According to Lugo *et al.* (1996) this area was abandoned after 1970. The soils of all the sites were mostly alluvial deposits identified as Mollisolls and Entisols, specifically, in the Pozo Blanco and Pitahaya series.

-Yauco

An area near the Yauco city dump was selected to be another pair of sites (Pair # 8). The exotic site was located on tobacco farm abandoned 35 years ago. It was hilly and had alluvial soils identified as Mollisols and Entisols, specifically, as the Aguilita and Pitahaya series. The native site was located in the lower part of a mountain and as it appeared in the 1936 aerial photo it is an old forest.

-Cabo Rojo

An area near the Cabo Rojo Lighthouse was sampled as a native canopy dominated forest (Pair #9). The soils of this site were rocky limestone. Some patches of this forest area were used for charcoal extraction. Its exotic pair was located close to road 303 near the Cabo Rojo city dump. This area was used for cattle production and the soils were a combination of rocky formations with some alluvial areas identified as Mollisols and Entisols, specifically, within the soil series San German and La Pitahaya.

Transects and Measurements

Field work was carried out from June 2006 to February 2007. In each area six belt transects were installed (600 n^2 per area); three transects under each canopy. A total of 54 transects were assessed from June 2006 to June 2007. The presence of native and exotic tree species was determined by an exhaustive census of belt transects in exotic-canopy forest and native-canopy forest. Three transects per site were established to span the variation of vegetation growth and topography in each area. The belt transects were composed of a straight line of 50 meters length and 2 meters width. Inside each transect three subplots of 5 by 2 meters were

randomly selected to sample the smallest individuals (<50cm tall seedlings). All juvenile trees with a height between 0.5 and 2 meters and a diameter at breast height (1.3 m) of less than 2.5 cm were measured and identified along the entire transect. Canopy coverage was estimated by a line transect of 50 meters running down the middle of the belt transect. Crown length was determined by measuring the point where each edge of a crown intersected with the line transect. The measurements of tree canopy coverage (trees with dbh>2.5cm) were determined by the estimation of the canopy length in the straight line of the transect. Established transects were mapped and tagged for study in future years. Site characteristics for each transect were noted (i.e. soil surface condition, topography, aspect and others) to determine patterns between vegetation types and physical environment. Species were identified following Lioger and Martorrel (2000).

Statistical Analysis and Indexes Calculations

Data was analyzed with the program Infostat/Professional (2005). A Shapiro-Wilks test was used to verify the normality of the variables. Distribution was tested using a Levene Test (p= 0.05). Data were analyzed with ANOVA for a complete randomized block design, having each pair of sites as a separate block. The following variables violated assumption of ANOVA and were transformed prior to analysis: sapling density (log transform), seedling density (log transformed), canopy diversity (exponent), and sapling richness (square root). Differences between sites were determined using post-hoc multiple comparisons (Bonferroni test).

-Canopy Coverage

Percent of canopy coverage was calculated using the formula:

$$Canopy \ Coverage = \left(\frac{crown \ length \ of \ each \ tree}{length \ of \ tran \sec t}\right) * 100$$

Comparisons of canopy coverage were made between: 1) native and exotics canopy types and 2) each site.

-Densities

Densities of saplings (sap/ha) and seedlings (seed/m²) were calculated using the following formulas. The seedling density was calculating dividing between the sum of the areas of the three subplots $(30m^2)$.

Sapling Density =
$$\left(\frac{\text{total of saplings}}{100m^2}\right) * 100$$

Seedling Density =
$$\left(\frac{\text{total of seedlings}}{30m^2}\right)$$

-Richness and Diversity

Species richness was compared between: 1) the three levels (canopy, saplings and seedlings) in each forest cover, and 2) native and exotic sites.

Diversity was estimated for each exotic and native understory of all the sites using the Shannon Diversity Index (Brower et al., 1990). The density of each species was used as proportions in the formula of this index, which is:

> $H' = -\sum [p_i * (Log(p_i))]$ $p_i = proportion of the total number of individuals ocurring in species i$

H` from each site and size class were used to compare the diversity between:

1) understory (saplings and seedlings) of native and exotic dominated canopies and 2) canopy, saplings and seedlings in each forest cover.

Species area curves were used to evaluate if the diversity of species was completely captured. This evaluation gives an outline of the coverage of the area study in terms of diversity. If the diversity of the study area was not covered more area is needed to be covered if other studies are going to be made in the area.

Similarity and Species Composition

To compare differences in species composition of each native and exotic site a Sorensen similarity index (Brower and Zar, 1990) was used between: 1) canopy and sapling species, 2) canopy and seedling species and 3) understory of native sites and understory of exotic sites.

$$S.I. = 1 - \left(\frac{\sum |x_i - y_i|}{\sum (x_i + y_i)}\right)$$

where x_i is the density of the species i in one level and

y_i is the density of that species in the other level

An evaluation of the dominance of the species was done calculating the importance values of each species that was found in the understory and canopy. This parameter was calculated using as follows:

Sap. and Seed. I.V. =
$$\left(\frac{frequency + density}{2}\right)$$

Canopy I.V. = $\left(\frac{frequency + density + coverage}{3}\right)$

where the frequency was the proportion of the number of transects where the species was present to the total number of transects. The density was the proportion of the number of individuals of each species to the total number of individuals (number of crowns in the case of the importance values for the canopy). Coverage, in the case of the importance value of the canopy, was the proportion of the total coverage of each species to the total coverage of all species.

Effects of Exotic Canopy and Age since Abandonment in Sapling and Seedling Individuals

To evaluate the effects of the exotic canopy on the proportion of native and exotic individuals in the understory, a regression analysis was conducted between the percentage of exotic coverage in the canopy and the native and exotic individuals in the understory. I also tested for the relationship between the percentages of exotic individuals with the time since abandonment from human activity.

Hypothesis Testing

To comply with all the objectives of this research, nine hypotheses were tested according to the structure of the data to discern significant differences.

These hypotheses were:

Ha₁: canopy coverage is higher in native-canopy dominated areas.

Ha₂: sapling density is higher in native-canopy dominated areas.

Ha₃: seedling density is lower in native forest areas.

Ha₄: for species richness, native-dominated canopy areas will have higher numbers of species, in each of the three levels of vegetation, than exotic-dominated canopy areas.

Ha₅: species richness will be higher in the canopy level than in the two other levels in the two forest cover areas.

Ha₆: diversity is higher in native forest areas and in the canopy level.

Ha₇: there is more similarity between the canopy and its understory in native dominated areas than in exotic areas.

 $Ha_{8:}$ as the percentage of exotics in the canopy gets higher the percentage of exotics in the understory will diminish.

Ha₉: as the age since abandonment increases the percentages of exotic individuals decreases while native individuals increase in the understory

RESULTS

General Description

A total of 3728 seedlings and 4676 saplings were measured and identified in this study. Thirty-four percent (1276) of the seedlings were found in native-canopy dominated sites and 65% (2452) were found in exotic canopy dominated sites. By contrast, in the sapling class 54% (2527) were found in native canopy dominated sites and 46% (2149) were found in exotic canopy dominated sites. Of all the saplings and seedlings found in the native canopy dominated sites, 2.5% and 10.2% respectively were exotic. In the exotic canopy sites, exotics account for 23.7% and 32.7% of the total of sapling and seedling categories, respectively.

In the overall study 85 species were found in the three levels (canopy, sapling and seedlings). Of this total, 6 species were identified as exotics and two of them (*L. leucocephala* and *P. juliflora*) were more common. In the native-dominated canopy areas 62, 63 and 50 species were found in the three levels (canopy, sapling and seedlings) and in the exotic sites 51, 51 and 35 species were found in canopy, sapling and seedlings, respectively.

Table 2.Co	mposition for each v	egetation laye	in each o	f the 9 pairs o	of sites used	in this
study. Pair	numbers are the san	ne as in Table 1	l and Figu	re 1.		
•				# Spacing in 0	02	

					# Species in 0.03 ha			H		
Pair	Canopy Type	Canopy Coverage (%)	Sapling Density (sap./ha)	Seedling Density (seed./m)	Can.	Sap.	Seed.	Can.	Sap.	Seed.
1	Native	210	9366	19.2	24	29	23	1.12	1.1	0.49
1	Exotic	131	4266	9.3	8	15	7	0.44	0.9	0.12
2	Native	155	7867	2.5	17	22	17	1.04	1.1	1.07
2	Exotic	160	3566	16.6	12	21	14	0.77	1.2	0.39
3	Native	131	1733	4.2	30	25	4	1.2	0.8	0.25
3	Exotic	166	23600	19.9	22	29	18	1.11	1	0.5
4	Native	189	10900	4.6	26	33	21	1.18	1.1	0.92
4	Exotic	140	10100	4.9	18	17	11	0.85	0.8	0.43
5	Native	132	5800	2.7	20	18	5	1.15	0.8	0.5
5	Exotic	172	14400	2.4	13	21	6	0.9	1.1	0.08
6	Native	130	9666	2.8	23	28	24	1.15	0.8	1.03
6	Exotic	164	8700	10.3	9	19	7	0.63	0.9	0.38
7	Native	136	8700	2.5	24	28	24	1.2	0.9	1.03
7	Exotic	172	3100	0.6	7	14	7	0.62	0.9	0.62
8	Native	165	11966	2.5	27	26	15	1.21	0.9	0.7
8	Exotic	168	3600	15.7	14	13	9	0.77	0.6	0.09
9	Native	105	2633	1.4	10	10	9	0.9	0.9	0.88
9	Exotic	130	300	2.0	12	17	10	0.78	1	0.74

Canopy Coverage and Density

Average canopy cover in native forest was 132.8 % (Fig. 2A), which did not differ from that 142.9% found in exotic forest (df=1, F=0.59, p=0.44). None of the paired sites showed differences among the others (Table 2) (df=8, F=1.01, p=0.44). Overall sapling and seedling density was 8659 sapling/ha and 2.3 seedling/m² respectively. In the comparisons of sapling and seedling density (Fig. 2B) no differences were found between native and exotic sites (sapling; df=1, F=0.81, p=0.37; seedling; df=1, F=0.01, p=0.90). A difference was found in the comparisons of each of the pairs (df=8, F=4.25, p=0.0008), where two of the pairs had higher sapling density (# 4 and #5; Table 2).

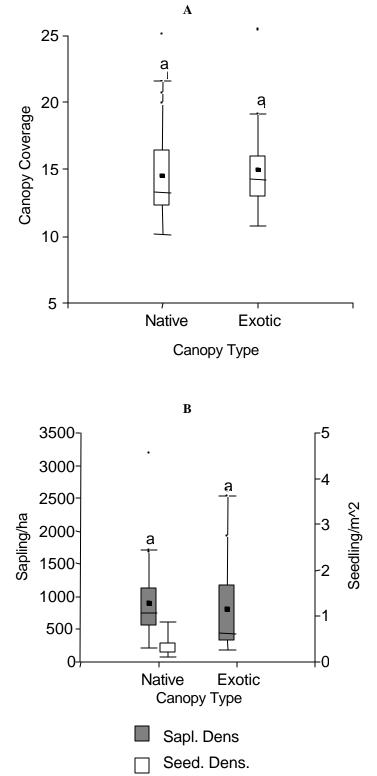


Figure 2. Comparison of canopy coverage (A), and sapling and seedling density (B) between native and exotic canopy dominated areas. Canopy coverage is denoted as the percentage of coverage in each forest cover. Different letters above the boxes show significant differences between each forest cover.

Species Richness and Diversity

Native sites had higher species richness in the canopy than exotic sites. Native forest had six more species (Fig. 3), on average, than exotic sites (df=1, F=68.8, p=0.0001). In addition pair #5 had a higher number than the other pairs (df=8, F=3.78, p=0.0019). Native saplings had four more species than saplings in exotic canopy dominated sites (df=1, F=10.01, p=0.0028). There was no difference (p>0.05) in the number of species in the saplings among each pair of sites (Table 2).

On average, native sites also had four more species (ld=1, F=28.85, p=0.0001) in the seedling category than exotic sites (Fig. 3). Also there were differences in three of the pairs of sites (#1, #2 and #4) in which the number of seedling were significantly higher than the other sites (df=8, F=3.34, p=0.0045).

In native sites the numbers of species in the canopy and in the sapling category were 4 to 6 species higher than the seedling category (Fig. 3). In exotic sites the number of species in the sapling level was significantly higher than those in the canopy and the seedling levels (Fig. 3).

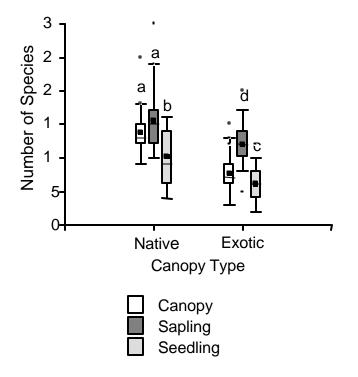


Figure 3. Comparison of richness in native and exotic canopy dominated sites and between the three levels in each forest cover type. Different letters show significant difference (p<0.05) within forest layers in each forest cover and forest layers between forest types.

Accumulation species-area curves of the sapling and seedling categories of native and exotic dominated areas show that the study covered a representative portion of the diversity of understory of southwestern Puerto Rico (Fig. 4). Although the two curves do not acquire an asymptote, it is satisfactory for the goals of this study.

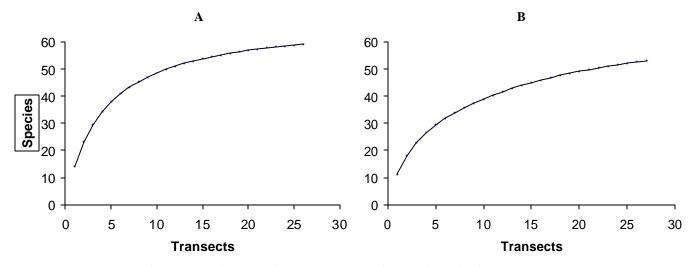


Figure 4. Accumulation species area curves for native (A) forest understory (saplings and seedlings) and exotic (B) forest understory.

The Shannon diversity index in native sites was 43% higher than in exotic sites (df=1, F=2.32. p<0.05) (Fig. 5). When comparing all the sites results show that pair #4 had higher diversity (df=8, F=32.33, p<0.05) than all the other pairs in the study area (Table 2). The comparison between the sapling diversity did not show any difference (df=1, F=0.75, p=0.39) between the two forest types (Fig. 5) nor between any of the paired sites in the study area (df=8, F=1.49, p=0.19). The diversity in the seedling category (Fig. 5) was 29% higher (df=1, F=22.51, p=0.0001) in native sites than in exotics areas. Pair #2 (Table 2) had higher diversity (df=8, F=4.30, p<0.0005) than the others pairs.

Comparisons between the diversity of canopy trees, saplings and seedlings of each forest type showed similar patterns as species richness (Fig, 5). Results show that in the native sites saplings and canopy categories had similar diversity between each other (p>0.05) but higher diversity than the seedling category (p<0.05). In the exotics sites the sapling category had the highest diversity while diversity in the canopy was higher than in the seedlings category (p<0.05)

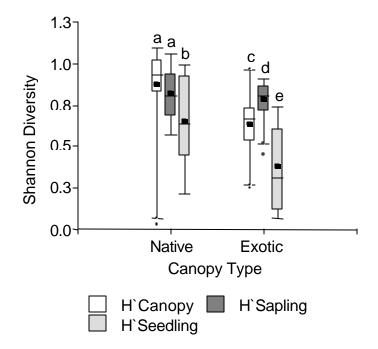


Figure 5. Comparisons between Shannon diversity index (H) between native and exotic dominated areas and between each of the three categories in each forest cover. Different letters show significant difference (p<0.05) within forest layers in each forest cover and forest layers between forest types.

Species Similarity and Composition

There was the same amount of similarity between canopy and saplings, and between canopy and seedlings in the two forest covers (Fig. 6), and none of the paired sites had higher similarity in this category (p>0.05).

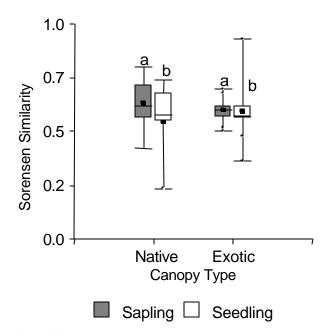


Figure 6. Comparison of the Sorensen similarity index between canopy and understory in the native and exotic canopy dominated areas. Letters show significant difference between each height level in the two forest covers.

In general there was low similarity in the presence and abundance of species between the understory of native and exotic dominated areas. Sorensen similarity index (Table 3) between the understory of native and exotic saplings at each paired site shows that the highest similarity in composition and abundance of species was 40% and it was found in pairs #1 and #2. The lowest similarity in species and abundance was only 2% and it was found the pair #9. The similarity in the seedling category was comparable to those obtained in the sapling category (40%) in two sites, #3 and #4. The other seven pairs of sites had much lower similarity in their seedlings than they had among saplings. The lowest similarity was of 1% and it was obtained in Tamarindo-Magueyes pair site (pair #5).

чру										
	Pair	Native Sites	Saplings	Seedlings	Exotic Sites					
	1	Peñuelas	0.40	0.06	Peñuelas					
	2	Tallaboa	0.40	0.05	Tallaboa					
	3	Main Plot	0.25	0.40	Granados					
	4	La Hoya	0.32	0.20	Baseball Park					
	5	Magueyes	0.35	0.01	Tamarindo					
	6	La Jungla	0.20	0.02	Golf Course					
	7	La Jungla II	0.29	0.02	La Jungla					
	8	Yauco N	0.39	0.02	Yauco					
	9	Cabo Rojo	0.02	0.01	Cabo Rojo					

Table 3 . Similarity index of sapling and seedling categories between each pair of native and exotic canopy dominated areas.

Of the overall number of species found in the study, 45 species were in the understory of both types of forest cover, 26 species were in the native sites but absent in the exotic sites and 8 species were present in exotic understory and absent in the understory of native dominated canopy areas (Table 4). Eight species of the total species found in the three levels were exotics. *Leucaena leucocephala* and *Prosopis juliflora* were the two most common. The other six species were found in the study with less abundance. In exotic areas *Meloccocus bijugatus, Swietenia macrophylla, Tamarindus indica* and *Pithecellobium dulce* were found in the same order of abundance and importance. *Carica papaya* and *Delonix regia* were the other exotics present with low importance values (less than 0.25). Although 53% of the species were native except for *Delonix regia* and *Carica papaya* that were found in only two native places and were probably planted long ago by humans. Of the other 24 native species, 23 of them are dispersed by birds, small vertebrates or autodispersed. Only *Tabebuia heterophylla* had wind dispersed seeds. Three of the species that were absent in native sites were exotics.

In the exotic- forest areas the canopy level was highly dominated (Fig. 6A) by the exotics *L. leucocephala* and *P. juliflora* with 22.2% and 12.8%, importance respectively. The third most important species was *Pithecellobium ungiscati* with an importance value of 6.67. The sapling category was dominated by the exotic *Leucaena leucocephala* with an importance value of 17.9, followed by the native pioneer species *Amyris elemifera*, *Croton humilis*, and *Eugenia foetida* with importance values of 6.13, 5.70 and 5.25 respectively. The other common exotic species, *P. juliflora*, was 8th in importance with 4.2. The seedling category was dominated by *L. leucocephala* with 29.9 and it was followed by native *A. elemifera* and *Eugenia monticola* with 10.8 and 10.5 respectively. The exotic *P. juliflora* occupied the 11th place in importance value with 1.78.

Importance Values		Native			Exotic	_
Species	Canopy	Sapling	Seedling	Canopy	Sapling	Seedling
Leucaena leucocephala	2.45	1.96	9.56	22.21	17.86	29.92
Amyris elemifera	3.90	2.72	14.80	2.00	6.13	10.87
Eugenia foetida	4.32	12.01	9.35	0.94	5.25	2.87
Croton humilis ^s	1.44	15.20	6.22	0.42	5.78	1.69
Pithecelobium ungiscatti	1.96	1.47	2.11	11.68	4.51	7.32
Thouinia portoricensis	9.88	3.64	4.58	4.05	2.28	3.89
Krugiodendrum ferreum	2.85	5.87	3.79	2.60	5.04	3.30
Prosopis juliflora	0.44			12.77	4.20	1.78
Gimnanthes lucida	5.48	6.67	5.82		0.73	0.32
Bursera simaruba	2.78	3.01	3.87	1.64	2.56	2.93
Exostema caribaeum	5.25	2.89	2.71	3.23	1.81	0.66
Bourreria succulenta	3.33	2.26	1.77	3.79	2.80	0.99
Eugenia rhombea	3.14	3.34	1.90	0.48	3.48	1.03
Shaefferia frutescens		1.97	3.63	1.00	1.91	3.10
Eugenia monticola		0.30		0.58		10.55
Guaicum officinale	0.54	0.32	1.01	3.85	3.98	1.65
Capparis flexuosa	0.83	0.44	1.47	2.83	4.32	1.38
Coccoloba microstachya	4.57	1.85	1.73	0.29	0.68	0.33
Crossopetalum rhacoma	2.15	3.25	1.72		0.94	0.68
Guaicum sanctum	1.07	1.17	0.27	2.08	1.66	1.61
Bucida buceras	2.75	0.96	0.96	1.77	0.51	0.64
Bumelia obovata	0.68	1.31	1.77	0.83	1.71	1.26
Pictetia acuelata	5.01	0.80	1.72			
Pisonia albida	4.51	1.32	1.09	0.35		
Coccoloba diversifolia	3.45	1.82	0.74	0.65	0.43	
Guettarda elliptica	2.40	1.12	2.30	0.35	0.69	
Randia acuelata	0.39	1.37	0.44	1.29	2.07	1.19
Colubrina arborescens	1.52	0.80	1.05	2.72	0.35	0.31
Comocladia dodonea	1.02	1.49	1.70	0.29	0.65	1.40
Capparis cynophallophora		0.15	0.21	1.89	2.33	1.83
Erythroxylum rotundifolium	1.86	0.30	1.36	0.58	1.02	0.64
Erythroxylum aerolatum	0.58	0.15	0.79	0.58	1.96	0.96
Capparis hastata	0.59	0.48		1.71	1.85	
Tabebuia heterophylla	3.08	0.67	0.62			
Guettarda krugii	1.86	1.77		0.58		
Erithalis fruticusum	1.47	0.80	1.93			
Pilosocereus royenii	0.39	0.54	0.74	2.17		
Reynosia uncinata	0.83	1.12	0.76	0.29	0.24	
Bourreria virgata	1.22	0.67	0.21	0.58	0.43	
Canella winterana	1.52	0.54	0.74			
Anthirea acutata*	1.08	0.71	0.94			
Citharexylum fruticosa		0.63			0.22	1.63
Lantana strigulosa ^s	0.19	1.31	0.25		0.65	
Trichilia hirta				0.35	0.75	1.15
Croton rigidus* ^s	0.64	2.26	0.71			
Securinega acidoton ^s	0.19	0.69		0.29	0.81	

Table 4. Importance values in percentages of all the species found in the study. Empty cells indicate the species was not present in that vegetation layer. Exotic species are in bold.

Meloccocus bijugatus	0.19	0.45	0.36		0.46	0.42
Eugenia biflora*	0.44	0.87	0.46			
Zanthoxylum monophyllum	0.39			0.65		0.64
Plumeria alba	0.39	0.30		0.29	0.24	0.31
Tamarindus indica ^a				1.29	0.22	
Lantana camara ^{as}				0.48	0.99	
Leptocereus quadricostatus	0.58	0.41		0.29		
Capparis indica ^a				0.29	0.54	0.39
Pithecelobium dulce ^a					1.17	
Eugenia lingustrina		0.59			0.56	
Chrysophyllum pauciflorum	0.49	0.23		0.35		
Colubrina elliptica	0.49	0.26	0.25			
Jacquinia arborescens*	0.98	0.80	0.48			
Swetenia macrophylla ^a				0.29	0.32	0.34
Cresentia linearifolia		0.17		0.87		
Acacia farnesiana				0.87	0.80	
Gyminda latifolia	0.19	0.15	0.23		0.22	
Rochefortia acanthaphora		0.30			0.46	
Zyziphus reticulata				0.29	0.43	
Zanthoxylum flavum [*]	0.39		0.25			
Conocarpus erectus*	0.24	0.34				
Randia portoricensis* ^s	0.19		0.23			
Erythroxylum brevipes	0.19				0.22	
Hypelate trifoliate*	0.24	0.15				
Cassine xylocarpa*		0.15	0.21			
Machaonia portoricensis				0.29		
Delonix regia*			0.21			
Coccoloba krugii*	0.19					
Eugenia xerophytica*	0.19					
Guettarda valenzuelana*	0.19					
Polygala cowellii*	0.19					
Reynosia guama*	0.19					
Carica papaya*		0.15				
Clusia rosea*		0.15				
Laguncularia racemosa*		0.15				
L. reticulata*		0.15				
Thrinax morrisii*		0.15				

* Present in native sites but absent in exotic sites.

^a Present in exotic sites but absent in native sites.

s Shrub species - maximum height < 3m.

In the native areas the canopy level was dominated by *T. portoricensis*, *G. lucida* and *E. caribaeum* with importance values of 9.88, 5.48 and 5.25 respectively. The sapling category was dominated by *C. humilis*, *E. foetida* and *G. lucida* with importance values of 15.2, 12.01, and 6.01, respectively. The highest exotic ranking, *L. leucocephala*, occupied the 14th place with importance value of 1.96. The seedling class was dominated by *A. elemifera* with 14.8, followed by the exotic *L. leucocephala* (9.56) and the native *E. foetida* (5.82).

As shown in Figure 6B the exotic areas had high dominance of one to three species. The canopy was highly dominated by three species, the exotics *L. leucocephala* and *P. juliflora*, and the native pioneer *P. ungisticati*. The sapling category was highly dominated only by the exotic *L. leucocephala* and the seedlings had three dominant species, *L. leucocephala*, *A. elemifera* and *E. monticola* (*E. monticola* was abundantly found only in the exotic site of Tallaboa). In contrast native sites show more evenness or equitable distribution of the individuals of each species in the three layers. The most abundant canopy species was *T. portoricensis*. In the sapling class four species were common (*C. humilis*, *E.foetida*, *G. lucida* and *K. ferreum*). In the seedling category, five species were common in all the sites (*A. elemifera*, *L. leucocephala*, *E. foetida* and *G. lucida*).

Effects of Exotic Canopy and Age since Abandonment in Sapling and Seedling Individuals

The presence of exotic individuals in the sapling category was less than 10% of the total sapling individuals in all the samples of native canopy areas (Fig. 7). Less than 50% of the total numbers of saplings were from exotic species in 92% of the transects from exotic-dominated canopies. By contrast the seedling category had more than 50% exotic individuals in 66% of the exotic-site samples. Native-canopy dominated areas had 11% of its samples with 50% or more exotic seedling individuals (fig. 7). The percentage of exotics in the canopy appeared to increase the percentage of exotic saplings in the understory (N=27, R²=0.3, p=0.002) of native-dominated sites. It was found that, in native sites, the percentage of exotic individuals in the sapling class ranged from 0%, with no presence of exotics in the canopy, to 12% with 9% of exotic canopy cover. When testing for the relationship between the percentage of exotics individuals in the understory (saplings and seedlings) and the age since abandonment, it was found that there was negative relationship in the two age classes (saplings: N=18, R²=0.71, p=0.0001; seedlings: N=18, R²=0.48, p=0.0014). Percentages of exotics ranged from 22 to 45% in 35-year-old sites to 0 to 9% in the > 77 year old sites (Fig. 8) for native-dominated forest.

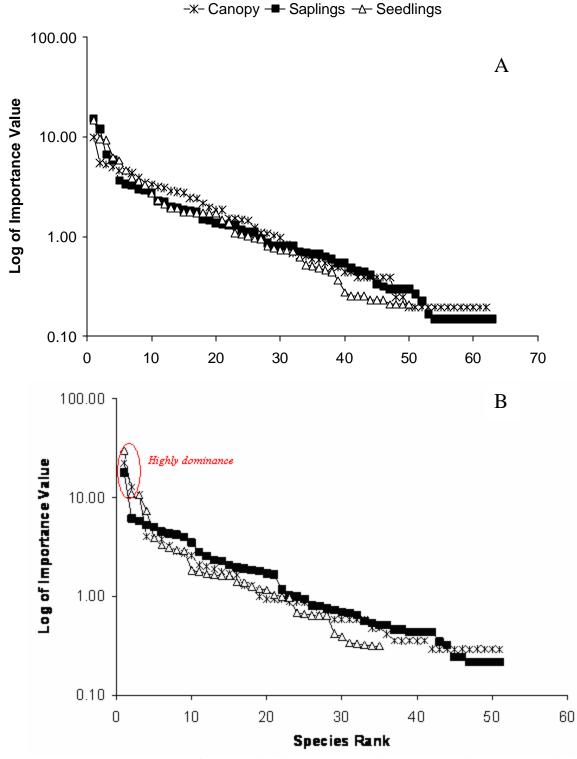


Figure 7. Importance values of all species in canopy, sapling and seedlings categories in the native (A) and exotic (B) canopy dominated areas. Y-axis is in log scale. Note different scales on x-axes.

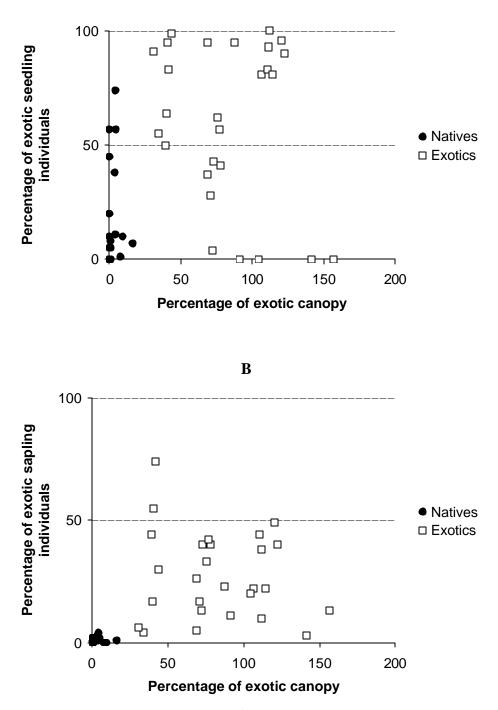


Figure 8. Relationship between the percentage of exotic canopy coverage and the percentages of native and exotic sapling (A) and seedling (B) individuals in each transect sampled (n=54). Dashed lines represent the 50% exotic individuals.

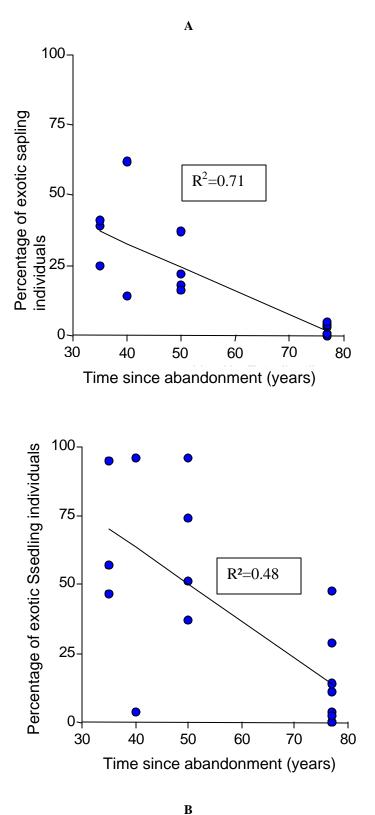


Figure 9. Relationship between age since abandonment and the percentage of exotic individuals in the sapling (A) (y=-0.85x+66.78) and seedling (B) (x=-1.35x+117.56) categories.

DISCUSSION

Few studies have focused on the study of understory species composition in dry forest, nevertheless these types of studies can reveal the regenerative capacity of secondary dry forest after the abandonment of agricultural lands. Although the species composition of understory is a good predictor of which species can develop and dominate future forest canopy layers, care should be taken in the interpretation of these results to generalize any pattern found in this study because of the variation of regeneration patterns across tropical dry forest and differences in growth and mortality among species.

-Patterns of Species Composition

Molina Colon and Lugo (2006) found low similarity for composition between native forest and old abandoned farm lands in their study of forest recovery in dry forest. Likewise, this study shows that exotic canopy dominated forest had 46 of the 75 species found in the understory of native forest cover. When the species (Table 4) present in each forest understory are compared, it is notable that the majority of the species that are absent in exotic forest were rare and had low ranking values in native forest. This suggest that areas that have canopies dominated by exotics facilitate the conditions for common native species to grow in the understory of those areas but the low similarity in presence and abundance found in the Sorensen index shows that succession is not in the same pattern as in native-dominated areas. The majority of the species found in these areas had seeds that are dispersed by birds (Table 5) and just very few of the winddispersed species were present in these sites. This suggests that these exotic trees such as L. *leucocephala* and *P. juliflora* served as perches for birds that at the same time transport seeds to those areas. Also the fact that rare species are absent from exotic areas suggest that: (1) the major dispersal agent of those species, which are mainly birds, had not been attracted to those areas if the rare species are dispersed by different bird species than the common tree species, (2) that the presence of mature trees (seed sources) are restricted to less-disturbed native forest areas far from exotic-dominated canopy areas, or (3) that reproductive capacities of those rare species are more limited than the other native species present in the exotic sites. The fact that one of the two native wind dispersed species, Tabebuia heterophylla, was not present in exotic forest suggests that these areas do not improve the conditions for the germination and establishment of this species. The last observation is based on the fact that this species was found as seed in areas

near exotic dominated forest, opening the opportunity for the movement of propagules into to

exotic forest understory.

Table 5. List of the native species found in the understory (sapling and seedling) of exotic sites and their main seed dispersal agents. Seed dispersal agents were assigned on the basis of the syndromes displayed by the fruits (Castilleja, 1991).

played by the fituits (Casting	
	Mainly Seed
Species	Dispersed Agent
Amyris elemifera	Bird
Bucida buceras	Unknown
Bumelia obovata	Bird
Burceras simaruba	Bird
Bourreria succulenta	Bird
Bourreria virgata	Bird
Colubrina arborescens	Unknown
Capparis cynophalophora	Bird
Coccoloba diversifolia	Bird
Comocladia dodonea	Bird
Capparis flexuosa	Bird
Cytharexylum fruticosum	Bird
Capparis hastata	Bird
Croton humilis	Auto
Capparis indica	Bird
Coccoloba microstachia	Bird
Crossopetalum rhacoma	Bird
Erytroxylum aerolatum	Bird
Erytroxylum brevipes	Bird
Exostema caribaeum	Wind
Eugenia foetida	Bird
Eugenia lingustrina	Bird
Eugenia monticola	Bird
Eugenia rhombea	Bird
Erytroxylum rotundifolium	Bird
Guettarda elliptica	Vertebrate
Gyminda latifolia	Bird
Gymnanthes lucida	Auto
Guaiacum officinale	Bird
Guaiacum sanctum	Bird
Krugiodendrum ferreum	Bird
Lantana camara	Bird
Lippia strigulosa	Bird
Plumeria alba	Wind
Rockelfoltia acanthaphora	Bird
Randia acuelata	Bird
Reynosia uncinata	Vertebrate
Securinega acidoton	Bird
Shaefferia frutescens	Bird
Thouinia portoricensis	Wind
Zanthoxylum monophyllum	Bird
Ziziphus reticulate	Bird

The species that were in common in the two forest covers were species that are recognized in other studies of Puerto Rican dry forest (Molina Colon and Lugo, 2006, Ramjohn, 2001, Castilleja, 1998, Murphy et al., 1995, Murphy and Lugo, 1986) as common species of mature dry forest. This study reflects that there were differences in the way those species were abundant in the two forest covers because they were not ranked in the same way. For example in exotic sites four species had I.V > 15%, in three levels, (Figure 6) which represents greater dominance by few species in exotic sites than in native sites where the species were distributed more evenly, similar to results from other studies (Molina Colon and Lugo, 2006, Ramjohn, 2001, Castilleja, 1998, Murphy et al., 1995, Murphy and Lugo, 1986). Of the eight species that were absent in native forest but present in exotic sites three of them were exotic remnants of past land use such as farms, tree plantations and yards (*T. indica* and *S. macrophylla*). Other ones such as *A. farnesiana* and *L. camara* are common species in the first stages of succession (Molina Colon and Lugo, 2006) which explains their exclusion from native forest. The other three species (List them) are native species whose presence is limited to particular areas in the south coast of Puerto Rico.

-Native Species Regeneration

Although in this study the quantity of solar radiation under the canopy was not measured, results suggested that tree crowns in exotic areas covered the same area that native crowns trees covered on its areas. Therefore, in terms of canopy coverage, exotic-dominated areas have some conditions that can support the growth of native shade-tolerant species. Although the higher values of richness and diversity in the understory of native canopies suggested that these areas created a variety of conditions to support a higher number of native species in the understory, exotic areas supported a considerable number of species (45 and 30 species in the sapling and seedling categories versus 60 and 45 in the native site) of which most have the capacity to emerge in the canopy in the future. In addition it was found that in the sapling class at the majority of the exotic sites >50% of the individuals were native species. Therefore, this suggests that native seeds are being brought to these areas by dispersal agents such as birds, mammals and abiotic agents because they were not present in the canopy layer or there were some trees present near the study sites. However, the seedling category had > 50% of the exotic individuals in 66% of the exotic sites sampled which supports what some authors have postulated, that one of the

reasons of the failure of *L. leucocephala* forest in increasing species richness is that seedling survivorship through the dry season is low under its fairly open deciduous canopy. This study also provides evidence of that pattern because it was found that exotic canopy dominated areas had low number of species in the seedling category.

-Invasion and Continuous Growth of Exotic Species

In studies of regeneration in moist forest of Puerto Rico (reported by Lugo, 2004) the presence of exotics in the understory diminished as the canopy closed because the exotics species, especially *Spathodea campanulata*, were shade intolerant. My results did not show any trend between the percentage of exotics in the canopy and percentage of exotics in the understory of exotics sites. However, in the seedling class the majority of the exotic sites had highest number of exotics individuals. Although my study did not measure regeneration directly I can use height class to predict the species that can grow from seedling stage to juveniles. In the case of the most dominant species, *L. leucocephala*, results suggested that it diminished in density in taller height classes. In native-dominated canopies the results showed that the presence of exotics in the understory but not present in the canopy reflect that exotics, such as *L. leucocephala*, can be spread by wind very easily for great distances and may be invading these forests, if the seedlings survive to maturity.

Some studies in moist and wet forest (Zimmerman et al., 1995, Aide et al., 1996 and Chinea, 2001) identified the age since abandonment from agricultural activities as one of the best predictors to determine the trend of some structural characteristics of secondary forest. My results showed a negative relationship between age since abandonment and the percentage of exotic individuals in understory. As the forest gets older the conditions for exotic species to establish in the understory gets less advantageous. The presence of exotics was higher in the seedlings reflecting that *L. leucocephala* had a wide range of dispersal and germination capacities. Some authors have suggested that dry forests exhibit conditions that may permit the introduction and persistence of exotic species. According to Murphy and Lugo (1986) the leaf area index of dry forests is much lower than in wetter forests resulting in a more open canopy. This increases the amount of sunlight reaching the forest floor that can help exotic pioneer species grow in native forests. The results suggest that exotics (i.e., *L. leucocephala*) had the opportunity to arrive and germinate in areas of natives as seedlings. The question will be if they can reach other height stages and become part of native forest. From this study I can predict that it can become part of the native forest where physical and environmental conditions permit it. Some of these conditions can be open canopies and gaps from dead trees.

-Patterns in Rare Species Across the Landscape

Some native species were found in specific sites in different parts across the study area. Rare species were established according to their environmental requirements and their presence could be a result of the fragmentation that occurred during the deforestation peak during the first half of the 20th century and the consequent establishment as part of natural regeneration in abandoned land areas. This pattern should contribute to the restriction of those species to some areas. Some examples could be the presence of *Guaicium sanctum* and *Eugenia monticola* in the sites of Peñuelas, *Randia portoricensis, Eugenia xerophytica* and *Zanthoxylum flavum* in the easternmost part of Guanica State Forest, *Polygala cowelii, Clusia rosea* and *Thrinax morisii* in an old forest sites in La Hoya, Guanica Forest and *Cassine xylocarpa* in the sites of La Jungla, western Guanica.

-Possible Effects of Land Use and time since Abandonment

Although this study was not designed to test for the effects of past land use or time since abandonment, these two variables could have a direct effect on the differences found between the understory of native- and exotic-dominated areas. The dominance of the exotic species in the canopy depends directly of the type of past land use in each area. For example, the sites in which the past land use was cattle production were dominated by *Prosopis juliflora*. This suggests that the cattle play an important role in the dissemination of *P. juliflora*. The other sites in which the past land use included activities such as farm lands, communities and sports fields were dominated by *Leucaena leucocephala*. I could not identify any pattern of the effects of each of the exotic species on understory richness and diversity (table 2), but certainly there could be differences in the environment that each species provides to the understory (e.g., quantity of light that reaches the understory, production and germination of its seeds, etc.). At the same time these differences could be important to each exotic species' own regeneration. In the understory of the areas dominated by *P. juliflora*, its saplings or seedlings were absent or were very few.

Otherwise in the understory of the areas dominated by *L. leucocephala* the presence of its own saplings and seedling were very high. Also there were no particular differences in the native species that were present beneath each exotic species. Species that were present in *L. leucocephala* understory were also present in the understory of *P. juliflora*. Apparently, the identity of the dominant exotic species had little influence on the native species composition in the understory. What was more important was that the canopy type was exotic, and that would be a result of previous land use and time since abandonment.

The exotics areas that were abandoned 35 years ago (more recently) contain species like *Acacia farnesiana* that are common in the first stages of succession in areas of intensive land use in dry forest (Ramjohn, 2001). The presence and abundance of this thorny vine decreases as time since abandonment increases. This suggests that time since abandonment could determine the presence of some specific pioneer species such as *A. farnesiana*.

-Management Implications

Often the role of exotic trees in the recovery of degraded ecosystems has been ignored, especially in tropical dry forests due to the dramatic changes that come from a long history of anthropogenic abuses. Although areas dominated by those species do not have the same structural characteristics, richness, and diversity as natural native forest, they protect against erosion and fires caused by humans and also may serve to rehabilitate ecosystem properties when natives are not capable of recolonizing immediately. Their high growth rate and productivity is likely to replenish environmental conditions that can improve the conditions for establishment of native flora. The removal of these exotic species could increase native flora regeneration by decreasing competition but at the same time could severely degrade ecosystem function and consequently, further delay in ecosystem recovery. Alternatively, if fast restoration is desired, planting native species and managing the exotics sapling individuals can be a silvicultural technique that can accelerate natural forest development in degraded dry forest areas.

CONCLUSIONS

 Canopy coverage did not show any significant difference between native and exotic sites. Tree crowns in exotic areas were covering the same area that native crowns were covering in their areas. Therefore exotic dominated areas provided conditions that can support the growth of native shade tolerant species and may eliminate some shade intolerant species.
 The seedling and sapling density between exotic and native areas were not significantly different, however, there were differences in the species identities between forest types. Therefore exotic sites can support the same amount of individuals that native sites have and, possibly, that can reach the canopy layer.

3) Results show that native-canopy dominated areas had significantly higher species richness, in the canopy level, than exotic canopy dominated areas.

4) The understory of native sites had significantly more species and higher species richness than the understory of exotic dominated areas. Although this result suggests that native canopies create a variety of conditions to support more species in the understory, exotic areas support a considerable number of species of which most of them have the capacity to emerge in the canopy in the future.

5) In the two forest types the sapling class had higher richness than the two other height classes. Two possible reasons were identified to explain that pattern: a) high rates of mortality had been documented in dry forests in seedlings because of limited soil surface moisture and drought conditions which reduces the opportunity to some species to survive in that stage and b) the seedling plot was smaller than the sapling class plot and the richness of that class was not adequately sampled. In terms of the canopy level, one possible explanation of finding fewer species than in the sapling class is because of the dispersion and arrival of seeds from species that were not found in the canopy layer but were present near the area of the transects. Consequently, those individuals were established and grew over time.

6) The level of the canopy and the seedlings were more diverse in native sites and showed more equity in these two levels. In contrast, exotic sites were highly dominated by the species *L*. *leucocephala*, which explained the low values of diversity in the exotic sites.

7) The lack of differences obtained in the diversity of the sapling class suggest more equity between the number of species present in this level and also less dominance of the species *L*. *leucocephala* in the exotic sites.

8) This study showed that the canopy and the understory of native and exotic sites had more than 50% of the species in common which suggests that the canopy highly influenced what arrived and grew in the understory of dry forest areas.

9) The low values of similarity when comparing the presence and abundance of the species in the understory of the two forest types suggests that species that were found in native sites were not present in exotic understory sites and vice versa.

10) Results did not show any trend between the percentage of exotics in the canopy and percentage of exotics in the understory of exotics sites. Nevertheless it was found that in the sapling class the majority of the exotics sites had 50% of the individuals dominated by native species. Therefore, this suggests that exotic-canopy dominated areas provide conditions that can support the growth of native shade-tolerant species, and further, native species are being imported to these areas by dispersal agents such as birds, mammals and abiotic agents.

11) The results show a negative relation between age since abandonment and the percentage of exotics in the understory which suggests that as forest gets older the conditions for exotic species to establish in the understory gets less advantageous r the conditions for native species improves. The presence of exotics was higher in the seedlings reflecting that *L. leucocephala* had a wide range of dispersal and germination capacities.

12) In general the results show that the areas that have canopies dominated by exotics facilitate the conditions for common native species to grow but not in the same way that native-dominated areas do. I can predict that native species will be reintroduced naturally to areas where exotic species dominate but it will take longer for native species trees to dominate as opposed to native forest areas.

RECOMMENDATIONS

Permanent studies at the study sites should be done to collect data of growth and survivorship of exotic and native species to better understand the patterns of regeneration of exotic species.
 Evaluation of the nitrogen fixation of *L. leucocephala* and *P. juliflora* should be made to

recognize the contribution of those legumes in the nutrient cycles of dry forest.

3) Quantify the sun light that reaches the understory of the exotic-dominated canopy to know how these areas support the germination and establishment of native tree species.

4) Design and evaluate reforestation projects where using the species already identified in this study that were in the understory of exotic areas.

5) Measure the seed rain under the canopy of exotic dominated areas and determine which are the main dispersal agents that bring them into those areas to apply management practices in restoration projects.

6) Evaluate the germination and growth of the wind dispersed *Tabebuia heterophylla* under exotic dominated canopies to determine the effect of exotic canopies on the regeneration of this species.

BIBLIOGRAPHY

- Aide, T. M., J. K. Zimmerman, J. B. Pascarella, L. Rivera, and H. Marcano-Vega. 2000. Forest regeneration in a chronosequence of tropical abandoned pastures: Implications for restoration ecology. Restoration Ecology 8:328-338.
- Aide, T. M., J. K. Zimmerman, M. Rosario, and H. Marcano. 1996. Forest recovery in abandoned cattle pastures along an elevational gradient in Northwestern Puerto Rico. Biotropica 28:537-548.
- Birdsey, R.A., and P.L. Weaver. 1987. Forest area trends in Puerto Rico. U.S. Forest Service Research Note SO-331. Southern Forest Experimental Station, New Orleans. Louisiana.
- Brower, J.E., J.H. Zar, C.N. Ende. Field and Laboratory Methods for General Ecology. Third Edition. Wm. C. Brown Publishers, Dubuque, IA.
- Castilleja, G. 1991. Seed germination and early establishment in a subtropical dry forest. Ph.D. Dissertation. Yale University. 209 pp.
- Chinea, J. D. 2001. Tropical forest succession on abandoned farms in the Humacao Municipality of eastern Puerto Rico. Forest Ecology and Management 167:195-207.
- D` Antonio C., L.A. Meyerson and J. Denslow. Exotic Species and Conservation. in Soule, M.E. and G.H. Orians 2001. Conservation Biology: Research Priorities for the Next Decade.
- Dietz, J.L. 1986. Economic history of Puerto Rico. Princeton University Press, Princeton, New Jersey.
- Ewel, J. J. y J. L Whitmore. 1973. The ecological life zones of Puerto Rico and the U.S Virgin Islands. Institute of Tropical Forestry Rio Piedras, Puerto Rico. Forest Service U.S. Department of Agriculture. ITF-18.
- Guariguata, M.R., and R. Ostertag. 2001 Neotropical secondary forest succession: changesin structural and functional characteristics. Forest Ecology and Management 148:185-206
- InfoStat (2005). *InfoStat versión 2005*. Grupo InfoStat, FCA, Universidad Nacional de Córdoba, Argentina.
- Janzen, D.H. 1986. Chihuanhuan Desert nopaleras: defaunated big mammal vegetation. Annual Review of Ecology and Systematics 17:595-636.
- Liogger, A.H and L.F. Martorell. 2000 Descriptive flora of Puerto Rico and Virgin Islands: a systematic synopsis. Second Edition Revised. Editorial de la Universidad de Puerto Rico, Rio Piedras, Puerto Rico.

- Little, E.L., R.O. Woodbury, F.H. Wadsworth, 1974. Trees of Puerto Rico and the Virgin Islands, Vol 2. Handbook 449, USDA, Washington, DC, 1025 pp.
- Little, E. L., F.H. Wadsworth, J. Marrero. 2001. Arboles comunes de Puerto Rico y las Isla Virgenes. Editorial de la Universidad de Puerto Rico, Rio Piedrras, P.R.
- Lugo, A. E. 1992. Comparison of Tropical Tree Plantations with Secondary Forests of Similar Age. Ecological Monographs 62:1-41.
- Lugo, A. E. 2004. The outcome of alien tree invasions in Puerto Rico. Frontiers in Ecology and the Environment **2**:265-273.
- Lugo, A. E., O. Ramos, S. Molina Colón, F. N. Scatena, and L. L. Vélez Rodríguez. 1996. A fifty-three year record of land use change in the Guanica Forest Biosphere Reserve and its vicinity. USDA Forest Service, International Institute of Tropical Forestry, Rio Piedras, PR.
- Lugo Camacho, J.L. 2005. The soil Climate Regimes of Puerto Rico-Reassessment and Implications. University of Puerto Rico, Mayaguez, PR
- Molina Colón, S. 2006. Recovery of a Subtropical Dry Forest After Abandonment of Different Land Uses. Biotropica 38 (3): 354-364.
- Molina Colón, S. 1998. Long-term recovery of a Caribbean dry forest after abandonment of different land uses in Guánica, Puerto Rico. PhD Dissertation. University of Puerto Rico, Rio Piedras.
- Murphy, P. G., and A. E. Lugo. 1986. Ecology of Tropical Dry Forest. Annual Review of Ecology and Systematics **17**:67-88.
- Murphy, P. G., A. E. Lugo, A.J. Murphy and D.C- Nepstad. 1995. The Dry Forests of Puerto Rico's South Coast. Springer-Verlag. New York, Inc. Ney York, USA.
- Parrota, J.A., 1987 *Albizia procera* Roxb.) Benth. Institute of Tropical Frestry, Southern Forest Experimental Station, USDA Forest Service SO-ITF-SM-6
- Parrotta, J.A. 1995. Influence of overstory composition on understory colonization by native species in plantations on a degraded tropical site. Journal of Vegetation Science 6: 627-636.
- Ramjohn, I. A. 2001. The role of disturbed Caribbean dry forest fragments in the survival of native plant biodiversity. PhD Dissertation. Michigan State University, East Lansing.

- Ray, G.J. 1993. The ecological restoration of a Caribbean dry forest in the island of St. John, U.S. Virgin Island. Ph.D. University of Wisconsin, Madison.
- Ray, G. J., and B. J. Brown. 1995. Restoring Caribbean Dry Forests Evaluation of Tree Propagation Techniques. Restoration Ecology 3:86-94.
- Roth, L.C. 1999. Anthropogenic change in a subtropical dry forest during a century og settlement in Jaiqui Picado, Santiago Province, Dominican republic. Journal of Biogeography 26: 739-759.
- Scarano, F. 2000. Puerto rico Cinco Siglos de Historia. McGraw Hill/Interamericana Editores, S.A. de C. V.
- USDA Natural Resources Conservation Service. San German Soil Survey update (unpulished data)
- Wadsworth, F.H. 1950. Notes on the climax of Puerto Rico and their destruction and consecvation prior to 1900. Caribb. Forester 11, 38-56.
- Weaver, P. L. y J. D. Chinea. 2003. Secondary subtropical dry forest at the La Tinaja tract of the Cartagena Lagoon national Wildlife Refuge, Puerto Rico. Caribbean Journal of Science. 39(3): 273-285.
- Zimmerman, J. K., T.M. Aide, M. Rosario, and L. Herrera. 1995. Effects of land management and a recent hurricane on forest structure and composition in the Luquillo Experimental Forest, Puerto Rico. For. Ecol. Manage. 77: 65–76.

APPENDICES

APPENDIX I. Aerial photo of pair #1: Peñuelas. Native site is inside private land, south of road #2 and the exotic site is near a cell phone tower system. Native site is illustrated by a blue dot and exotic site is illustrated by a red dot.



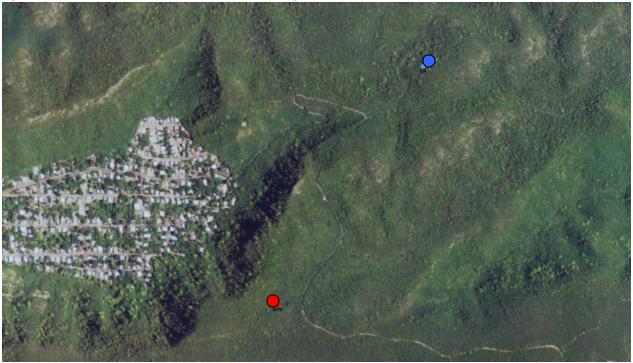
APPENDIX II. Aerial photo of pair #2: Tallaboa. Native site is located on a hill and exotic site in an alluvial valley. Native site is illustrated by a blue dot and exotic site is illustrated by a red dot.



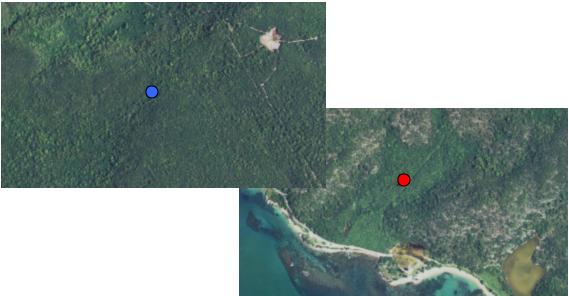
APPENDIX III. Aerial photo of pair #3. Guanica Forest. Native site is located in an old area of charcoal production and exotic site is on abandoned farm land. Native site is illustrated by a blue dot and exotic site is illustrated by a red dot.



APPENDIX IV. Aerial photo of pair #4. Guanica Forest. Native site is located in an old forest and exotic site is located at the site of an old baseball field. Native site is illustrated by a blue dot and exotic site is illustrated by a red dot.



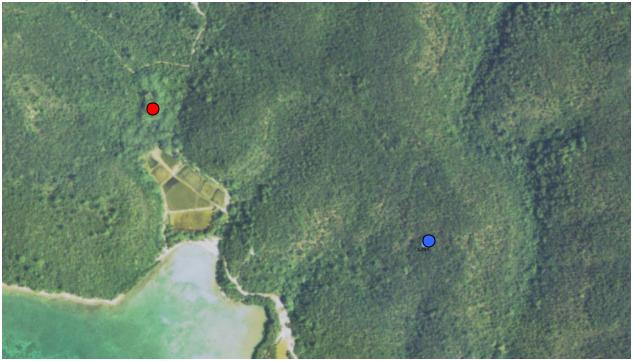
APPENDIX V. Aerial photo of pair #5. Guanica Forest. The native site (left photo) was located at the east part of Guanica Forest. The main human activity was charcoal production. The exotic site (right photo) was located near Playa Tamarindo and the area was a cattle farm. Native site is illustrated by a blue dot and exotic site is illustrated by a red dot.



APPENDIX VI. Aerial photo of pair #6. The native site was located in an area of charcoal production and the exotic was at the site of an old golf course. Native site is illustrated by a blue dot and an exotic site is illustrated by a red dot.



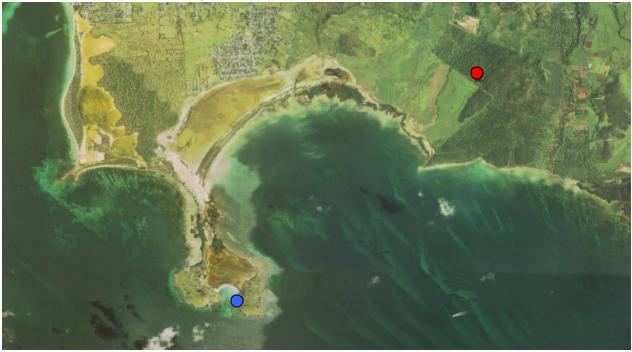
APPENDIX VII. Aerial photo of pair #7. Playa Santa, Guanica. Native site was inside an area of charcoal pits and the exotic site was located in an old cattle farm. Native site is illustrated by a blue dot and exotic site is illustrated by a red dot.



APPENDIX VIII. Aerial photo of pair #8. Yauco. The native site was located on a hill where charcoal production was a common practice and the exotic site was on an old tobacco farm. Native site is illustrated by a blue dot and exotic site is illustrated by a red dot.



APPENDIX IX. Aerial photo of pair #9. Cabo Rojo. Native site was located in an old uncut forest and the exotic site was on an old cattle farm. Native site is illustrated by a blue dot and exotic site is illustrated by a red dot.



APPENDIX X. Analysis of Variance (ANOVA) for block design for the percentage of canopy in native and exotic canopy coverage sites. Post-hoc comparisons between sites were done using a Tukey test.

Análisis de la varianza

Variable	Ν	R ²	R ²	Aj	CV
Can Cov	54	0.16	0	.00	26.73

Cuadro de	Análisis de	la Var	cianza (SC	tipo III)	
F.V.	SC	gl	CM	F	p-valor	
Modelo	13059.15	9	1451.02	0.96	0.4848	
Bloque	12161.55	8	1520.19	1.01	0.4452	
Trat	897.60	1	897.60	0.59	0.4449	
Error	66472.21	44	1510.73			
Total	79531.37	53				

Test:Tukey Alfa:=0.05 DMS:=73.27773

Error:	1510.7321 gl:	44			
Bloque	Medias	n			
CR-CR	116.78	б	A		
LJ2-GC	135.62	6	А		
M-T	135.70	6	А		
C-C	137.17	6	А		
MP-G	148.87	6	А		
LJ-LJ	150.90	6	А		
T-T	155.15	б	А		
LH-BP	157.18	б	А		
Y-Y	171.37	б	А		
MP-G LJ-LJ T-T LH-BP Y-Y	148.87 150.90 155.15 157.18 171.37	6 6 6 6	A A A A		,

Letras distintas indican diferencias significativas(p<= 0.05)

Test:Tukey Alfa:=0.05 DMS:=21.33346

Error:	1510.7321 gl:	44		
Trat	Medias	n		
Nativo	132.8	27	A	
Exotico	142.9	27	A	
-				

APPENDIX XI. Analysis of Variance (ANOVA) for block design for the logarithm of sapling density in native and exotic canopy coverage sites. Post-hoc comparisons between cover types and pairs were done using a Tukey test.

Análisis d	de la va	rian	za		
Varial	ole	N	R ²	R ² A	j CV
LOG10_Sap	l. Dens.	54	0.44	0.33	3 8.32
Cuadro de	Análisi	s de	la Vari	lanza	(SC tipo III)
F.V.	SC	gl	CM	F	p-valor
Modelo	3.51	9	0.39	3.87	0.0011
Bloque	3.43	8	0.43	4.25	0.0008
Trat	0.08	1	0.08	0.81	0.3741
Error	4.43	44	0.10		
Total	7.94	53			

Test:Tukey Alfa:=0.05 DMS:=0.59854

Error:	0.1008 gl: 44			
Bloque	Medias	n		
CR-CR	3.43	б	A	
LJ-LJ	3.54	6	А	
Y-Y	3.69	б	А	
T-T	3.72	б	A	
C-C	3.79	б	A	
LJ2-GC	3.88	б	A	
M-T	3.88	б	A	В
LH-BP	4.14	б		В
MP-G	4.27	6		В

Test:Tukey Alfa:=0.05 DMS:=0.17425

Error:	0.1008 gl: 4	44	
Trat	Medias	n	
Exotico	3.78	27	A
Nativo	3.85	27	A
Letras di	stintas indica	n diferencias	s significativas(p<= 0.05)

APPENDIX XII. Analysis of Variance (ANOVA) for block design for the logarithm of seedling density in native and exotic canopy coverage sites. Post-hoc comparisons between cover types and pairs were done using a Tukey test.

Seedling Density	r			
Variable	N	R ²	R² Aj	CV
LOG10_Seed. Dens	5. 54	0.25	0.10	105.98

Cuadro de	Análisis de	la Var	rianza (SC t	ipo III)	
F.V.	SC	gl	CM	F	p-valor	
Modelo	3.76	9	0.42	1.67	0.1265	
Bloque	3.75	8	0.47	1.87	0.0890	
Trat	3.6E-03	1	3.6E-03	0.01	0.9049	
Error	11.02	44	0.25			
Total	14.78	53				

Test:Tukey Alfa:=0.05 DMS:=0.94358

Error: 0.250	5 gl: 44		
Bloque	Medias	n	
LJ-LJ ·	-1.2E-03	6	A
M-T	0.20	6	A
CR-CR	0.27	6	A
T-T	0.45	б	A
LJ2-GC	0.52	б	A
MP-G	0.59	б	A
LH-BP	0.62	б	A
Y-Y	0.68	б	A
C-C	0.93	б	A
Letras distinta	s indican dif	erencias	significativas(p<= 0.05)

Test:Tukey Alfa:=0.05 DMS:=0.27471

Error:	0.2505	gl: 44	1		
Trat	Me	edias	n		
Nativo		0.46	27	A	
Exotico)	0.48	27	A	
Letras d	istintas	indican	diferencias	significativas(p<=	0.05)

APPENDIX XIII. Analysis of Variance (ANOVA) for block design for the number of species in the canopy level between native and exotic canopy coverage sites. Pos-hoc comparisons between cover types and pairs were done using a Tukey test.

Canopy Spe	ecies			
Variable	N	R ²	R² Aj	CV
Can. Sp.	54	0.69	0.63	24.91

Cuadro de	Análisis de	la Var	ianza (SC	tipo III)	l.
F.V.	SC	gl	CM	F	p-valor
Modelo	699.33	9	77.70	11.01	<0.0001
Bloque	213.33	8	26.67	3.78	0.0019
Trat	486.00	1	486.00	68.83	<0.0001
Error	310.67	44	7.06		
Total	1010.00	53			

Test:Tukey Alfa:=0.05 DMS:=5.00956

Error:	7.0606 gl: 44				
Bloque	Medias	n		_	
CR-CR	8.67	6	A	_	
C-C	9.00	6	A		
LJ-LJ	9.17	6	A		
T-T	9.17	6	A		
LJ2-GC	10.00	6	A		
M-T	10.17	6	A		
Y-Y	12.00	6	A		
LH-BP	13.33	6	A	В	
MP-G	14.50	6		В	
Letras d	istintas indican	diferencias	signifi	icativas(p<=	0.05)

Test:Tukey Alfa:=0.05 DMS:=1.45844

Error:	7.0606 gl: 44				
Trat	Medias	n			
Exotico	7.67	27	A		
Nativo	13.67	27		В	
		1/6		1.6.1	-

APPENDIX XIV. Analysis of Variance(ANOVA) for block design for the square root of the number of species in the sapling level between native and exotic canopy coverage sites. Post-hoc comparisons between cover types and pairs were done using a Tukey test.

Sapling Specie	s			
Variable	N	R 2	R² Aj	CV
RAIZ_Sap. Sp.	54	0.32	0.19	14.11

Cuadro d	de Análisi	s de	la Vari	lanza (SC tipo III)
F.V.	SC	gl	CM	F	p-valor
Modelo	5.62	9	0.62	2.34	0.0297
Bloque	2.95	8	0.37	1.38	0.2310
Trat	2.67	1	2.67	10.01	0.0028
Error	11.73	44	0.27		
Total	17.35	53			

Test:Tukey Alfa:=0.05 DMS:=0.97351

Error:	0.2666 gl: 44	1	
Bloque	Medias	n	
CR-CR	3.16	6	A
Y-Y	3.47	б	А
M-T	3.55	б	А
LJ-LJ	3.70	б	А
LJ2-GC	3.70	б	А
LH-BP	3.71	б	А
T-T	3.78	б	А
C-C	3.93	б	А
MP-G	3.97	б	A
Letras di	stintas indican	diferencias	<pre>significativas(p<= 0.05)</pre>

Test:Tukey Alfa:=0.05 DMS:=0.28342

Error: 0.	2666 gl: 44				
Trat	Medias	n			
Exotico	3.44	27	А		
Nativo	3.88	27		В	
	1	116		1.6.1	-

APPENDIX XV. Analysis of Variance (ANOVA) for block design for the number of species in the seedling level between native and exotic canopy coverage sites. Pos-hoc comparisons between cover types and pairs were done using a Tukey test.

Seedling Species

Variab	le	Ν	R 2	R² Aj	CV
Seed.	Sp.	54	0.54	0.45	37.13

Cuadro de Análisis de la Varianza (SC tipo III)

F.V.	SC	gl	CM	F	p-valor
Modelo	472.33	9	52.48	5.84	<0.0001
Bloque	240.04	8	30.00	3.34	0.0045
Trat	232.30	1	232.30	25.85	<0.0001
Error	395.37	44	8.99		
Total	867.70	53			

Test:Tukey Alfa:=0.05 DMS:=5.65137

Error:	8.9857 gl: 44			
Bloque	Medias	n		
M-T	4.33	6	А	
CR-CR	5.83	б	А	
MP-G	6.67	б	А	
Y-Y	7.00	6	А	
LJ-LJ	8.67	6	А	
LJ2-GC	9.00	6	А	В
T-T	10.00	6		В
C-C	10.17	6		В
LH-BP	11.00	6		B

Letras distintas indican diferencias significativas(p<= 0.05)

Test:Tukey Alfa:=0.05 DMS:=1.64529

Error:	8.9857 gl: 44	!				
Trat	Medias	n				
Exotico	6.00	27	A			
Nativo	10.15	27	I	3		
Totrad di	iatintoa indiaon	diformaina	aignific	at imag(n/-	0	

APPENDIX XVI. Analysis of Variance (ANOVA) for block design for the diversity in the canopy level between native and exotic canopy coverage sites. Pos-hoc comparisons between cover types and pairs were done using a Tukey test.

Canopy Diversity

Variable	Ν	R 2	R² Aj	CV
POT_H`Can	54	0.54	0.44	39.60

Cuadro de	Análisi	s de	la Vari	ianza (SC tipo III)
F.V.	SC	gl	CM	F	p-valor
Modelo	3.74	9	0.42	5.65	<0.0001
Bloque	1.36	8	0.17	2.32	0.0359
Trat	2.38	1	2.38	32.33	<0.0001
Error	3.23	44	0.07		
Total	6.98	53			

Test:Tukey Alfa:=0.05 DMS:=0.51119

Error:	0.0735 gl: 4	44		
Bloque	Medias	n		
C-C	0.38	б	A	-
T-T	0.53	б	A	
LJ-LJ	0.63	б	A	
CR-CR	0.64	б	A	
LJ2-GC	0.70	6	A	
LH-BP	0.72	6	A	
M-T	0.77	6	A	
Y-Y	0.86	6	A	
MP-G	0.94	6		В
Latrag d	istintas indica	n diferenc	ing gianifi	astivas(nr- 0

Letras distintas indican diferencias significativas(p<= 0.05)

Test:Tukey Alfa:=0.05 DMS:=0.14882

Error:	0.0735 gl: 44	ł			
Trat	Medias	n			
Exotico	0.47	27	А		
Nativo	0.89	27		В	
T / 7		1'C '			~

APPENDIX XVII. Analysis of Variance (ANOVA) for block design for the diversity in the canopy level between native and exotic canopy coverage sites. Pos-hoc comparisons between cover types and pairs were done using a Tukey test.

Sapling Di	versi	ty			
Variable	N	R ²	R 2	Aj	CV
H`Sap	54	0.22	0	.06	16.71

Cuadro de	Análisi	.s de	la Vari	ianza	(SC tipo III)
F.V.	SC	gl	CM	F	p-valor
Modelo	0.25	9	0.03	1.40	0.2155
Bloque	0.23	8	0.03	1.49	0.1898
Trat	0.01	1	0.01	0.75	0.3902
Error	0.86	44	0.02		
Total	1.10	53			

Test:Tukey Alfa:=0.05 DMS:=0.26310

Error:	0.0195 gl: 44	!	
Bloque	Medias	n	
LH-BP	0.74	6	A
Y-Y	0.75	б	А
MP-G	0.80	б	А
M-T	0.81	б	А
LJ2-GC	0.81	б	А
CR-CR	0.87	6	А
LJ-LJ	0.88	6	А
C-C	0.89	6	А
T-T	0.96	6	A
Letras di	stintas indican	diferencias	significativas(p<= 0.05)

Test:Tukey Alfa:=0.05 DMS:=0.07660

Error: 0.0	195 gl: 44	1	
Trat	Medias	n	_
Exotico	0.82	27	A
Nativo	0.85	27	A
Letras distin	tas indican	diferencias	significativas(p<= 0.05)

APPENDIX XVIII. Analysis of Variance (ANOVA) for block design for the diversity in the seedling level between native and exotic canopy coverage sites. Pos-hoc comparisons between cover types and pairs were done using a Tukey test.

Seedling Diversity

Variable	Ν	R 2	R² Aj	CV
H`Seed	54	0.56	0.47	41.81

Cuadro de	Análisi	s de	la Vari	anza	(SC tipo III)
F.V.	SC	gl	CM	F	p-valor
Modelo	2.83	9	0.31	6.32	2 <0.0001
Bloque	1.71	8	0.21	4.30	0.0007
Trat	1.12	1	1.12	22.51	<0.0001
Error	2.19	44	0.05		
Total	5.02	53			

Test:Tukey Alfa:=0.05 DMS:=0.42071

Error: C	0.0498 gl: 44				
Bloque	Medias	n			
Y-Y	0.31	6	A		
M-T	0.34	6	A		
C-C	0.37	6	A		
MP-G	0.41	6	A		
LJ2-GC	0.58	6	A		
LJ-LJ	0.61	6	A		
LH-BP	0.65	6	A		
CR-CR	0.68	6	A		
T-T	0.87	6		B	
Letras dis	stintas indican	diferencias	signifi		0.05)

Test:Tukey Alfa:=0.05 DMS:=0.12248

Error:	0.0498 g	gl: 44	1			
Trat	Med	lias	n		_	
Exotico	0).39	27	A	-	
Nativo	0	.68	27		В	
Letras di	stintas in	ndican	diferencias	signifi	.cativas(p<=	0.05)

APPENDIX XIX. List of species and importance values of Pair #1. Native Exotic								
Species	Canopy	Sapling	Seedling	Canopy	Sapling	Seedling		
Amyris elemifera	0.236	0.082	0.711	0.011	0.031	0.010		
Bucida buceras	0.021	0.004	••••		0.001	0.0.0		
Bumelia obovata	0.014	0.018	0.001					
Bursera simaruba	0.049	0.004	0.020	0.011	0.055	0.008		
Bourreria succulenta	0.014	0.011	0.001					
Coccoloba diversifolia	0.035	0.057	0.003					
Comocladia dodonea	0.007	0.004						
Capparis flexuosa	0.007	0.004	0.005		0.031			
Citharexylum fruticosum		0.004						
Capparis hastata		0.007						
Croton humilis		0.064	0.012		0.016			
Coccoloba microstachya	0.076	0.025	0.001		0.031			
Crossopetalum rhacoma		0.071			0.109			
Delonix regia			0.001		0.047			
Exostema caribaeum	0.021	0.004		0.034				
Eugenia foetida	0.021	0.121	0.010					
Eugenia lingustrina		0.004						
Eugenia monticola		0.004						
Eugenia rhombea	0.007	0.021						
Eugenia rotundifolia	0.014							
Guettarda elliptica	0.021		0.001					
Gymnanthes lucida	0.063	0.125	0.026					
Guaiacum officinale			0.002					
Guaiacum sanctum	0.014	0.014	0.002	0.148	0.016	0.008		
Jacquinia arborea			0.001					
Krugiodendrum ferreum	0.076	0.263	0.146	0.034	0.313	0.017		
Leucaena leucocephala	0.021	0.004	0.024	0.716	0.250	0.950		
Lippia strigulosa					0.016			
Meloccocus bijugatus	0.007	0.018	0.006					
Pictetia acuelata	0.042		0.002					
Pisonia albida	0.042	0.007						
Pithecelobium ungiscatti		0.011	0.001		0.016			
Rockefoltia acantaphora		0.004						
Randia acuelata					0.031			
Securinega acidoton	0.007	0.011						
Shaefferia frutescens		0.028	0.016	0.011	0.008	0.004		
Thouinia portoricensis	0.181	0.011	0.009	0.034	0.031	0.004		
Zanthoxylum flavum	0.007		0.002					

APPENDIX XIX.	List of species	and importance	values of Pair #1.
----------------------	-----------------	----------------	--------------------

		Native			Exotic	
Species	Canopy	Sapling	Seedling	Canopy	Sapling	Seedling
Amyris elemifera		0.025			0.019	
Bucida buceras	0.059	0.059	0.080	0.015	0.028	0.003
Bumelia obovata			0.027		0.019	
Bursera simaruba		0.034	0.004		0.019	
Bourreria succulenta	0.059	0.008	0.201		0.028	0.004
Bourreria virgata	0.024	0.008				
Colubrina arborescens	0.024			0.059		
Capparis cynophalophora				0.029	0.121	0.016
Comocladia dodonea	0.012	0.034	0.049			
Capparis flexuosa			0.018			
Citharexylun fruticosum					0.019	0.107
Capparis hastata					0.009	
Coccoloba microstachya		0.004				
Crossopetalum rhacoma		0.042	0.054		0.037	
Canella winterana			0.018			
Chrysophylum pauciflorum	0.047	0.021			0.037	
Eugenia biflora	0.012	0.055	0.018			
Exostema caribaeum	0.094	0.089	0.027	0.015	0.009	
Eugenia foetida	0.035	0.042	0.103		0.037	0.001
Eugenia monticola		0.004		0.029	0.084	0.782
Eugenia rhombea		0.017				
Erytroxylum rotundifolium			0.004			
Guettarda elliptica	0.012	0.004	0.045			
Guettarda krugii		0.004				
Krugiodendrum ferreum	0.059	0.148	0.067	0.132	0.112	0.017
Leucaena leucocephala	0.071	0.004	0.042	0.132	0.084	0.031
Pictetia acuelata	0.176					
Pisonia albida	0.035					
Poitea caribaea					0.028	
Prosopis juliflora	0.024			0.471	0.065	0.006
Rockefoltia acantaphora		0.093				
Randia acuelata		0.072		0.015	0.093	0.020
Randia portoricensis			0.009			
Shaefferia frutescens		0.021	0.027		0.075	0.008
Tabebuia heterophylla	0.012					
Thouinia portoricensis	0.247	0.208	0.205	0.029	0.047	0.001
Zanthoxylum martinicensis				0.044	0.028	0.003

APPENDIX XX. I	List of	species and	importance	values	of Pair #2
----------------	---------	-------------	------------	--------	------------

		Native			Exotic	
Species	Canopy	Sapling	Seedling	Canopy	Sapling	Seedling
Amyris elemifera	0.036	0.020	0.840	0.048	0.168	0.535
Bumelia obovata				0.048	0.025	0.002
Bursera simaruba	0.055	0.045	0.021	0.008	0.007	0.001
Bourreria succulenta	0.022	0.013		0.040	0.007	
Colubrina arborescens				0.063	0.008	
Coccoloba diversifolia	0.014	0.014			0.001	
Comocladia dodonea	0.014	0.014			0.001	0.001
Capparis flexuosa					0.004	
Citharexylum fruticosum		0.014			0.001	
Capparis hastata	0.044			0.024	0.003	
Croton humilis		0.250			0.007	
Coccoloba krugii	0.025					
Coccoloba microstachya	0.018	0.037				
Crossopetalum rhacoma	0.022	0.014				0.004
, Croton rigida		0.046				
Erytroxylum aerolatum						
Exostema caribaeum	0.078	0.014		0.040	0.004	0.003
Eugenia foetida					0.003	
Eugenia rhombea	0.032	0.113	0.034	0.024	0.134	0.022
Erytroxylum rotundifolium	0.036	0.058		0.032	0.081	0.027
Eugenia xerophytica				0.008		
Erithalis fruticosa	0.014					
Guettarda elliptica	0.036	0.048				
Guettarda krugii					0.017	
Gyminda latifolia	0.018	0.048				
Gimnanthes lucida					0.001	
Guaiacum officinale	0.186	0.114	0.105		0.007	
Guaiacum sanctum	0.022			0.111	0.030	0.006
Guettarda valenzuelana					0.008	0.001
Jacquinia arborea	0.014	0.028				
, Krugiodendrum ferreum	0.040					
Leucaena leucocephala	0.047			0.016	0.051	0.015
Lippia strigulosa				0.286	0.268	0.360
Meloccocus bijugatus		0.016				
Pictetia aculeate	0.044					
Plumeria alba		0.014				
Pisonia albida		0.013			0.003	0.001
Prosopis juliflora	0.014			0.016		
Pithecelobium ungiscatti				0.135	0.133	0.011
Randia acuelata	0.014			0.016	0.003	0.006
Reynosia guama		0.013				
Reynosia uncinata	0.014					
Swetenia mahogany	0.014	0.013		0.008		
Shaefferia frutescens						0.002
				0.004	0.004	
Tabebuia heterophylla				0.024	0.001	
Tabebuia heterophylla Tamarindus indica	0.047			0.024	0.001	

APPENDIX XXI. List of species and importance values of Pair #3

Thounia portoricensis		0.013			
Zanthoxylum					
monophyllum	0.048	0.019	0.048	0.020	0.004

		Native			Exotic	
Specie s	Canopy	Sapling	Seedling	Canopy	Sapling	Seedling
Amyris elemifera	0.039	0.015	0.349	0.009	0.041	0.025
Anthirea acutata		0.018				
Bucida buceras	0.055			0.009		
Bumelia obovata		0.015	0.005		0.017	0.005
Bursera simaruba	0.008	0.015		0.044	0.048	0.009
Bourreria succulenta		0.006		0.035	0.019	
Bourreria virgata		0.009	0.002			
Colubrina arborescens				0.009		
Coccoloba diversifolia	0.219	0.083	0.007	0.026	0.017	
Comocladia dodonea	0.008		0.005	0.009	0.017	0.045
Capparis flexuosa	0.008	0.003				
Croton humilis		0.064	0.017		0.248	0.122
Coccoloba microstachya		0.003		0.009		
crosoppetalum rhacoma	0.008	0.003				
Capparis flexuosa				0.009		
Clussia rosea		0.003				
Comocladia dodonea						
Cresentia linearifolia		0.006				
Erytroxylum aerolatum	0.008		0.046		0.036	0.002
Erytroxylum brevipes	0.008					
Exostema caribaeum	0.008	0.003		0.053	0.092	0.007
Eugenia foetida	0.070	0.349	0.210	0.009	0.087	0.020
Erithalis fruticosa	0.008	0.003	0.017			
Eugenia lingustrina		0.028				
Eugenia rhombea	0.125	0.070	0.036		0.036	
Erytroxylum rotundifolium	0.055	0.003	0.002		0.000	
Guettarda elliptica	0.016			0.018		
Guettarda krugii	0.008					
Gyminda latifolia	0.000	0.003	0.005			
Gymnanthes lucida	0.070	0.049	0.031			
Guaiacum officinale	0.070	0.003	0.002		0.017	
Guaiacum sanctum	0.008	0.058	0.002		5.017	
Krugiodendrum ferreum	0.000	0.092	0.041	0.018	0.044	
Leucaena leucocephala	0.023	0.032	0.041	0.404	0.138	0.743
Plumeria alba	0.077	0.003	0.110	0.707	0.100	0.140
Pisonia albida	0.070	0.000	0.005			
Poligala cowellii	0.070		0.000			
Pithecelobium ungiscatti	0.008	0.015	0.046	0.158	0.053	0.009
Prosopis juliflora	0.005	0.010	0.040	0.150	0.000	0.009
Rockefoltia acanthaphora	0.000	0.003				
Randia acuelata		0.003		0.009		
Reynosia uncinata		0.009	0.002	0.009		
-		0.009	0.002			
Securinega acidoton		0.000		0.000	0.024	
Swetenia mahogany		0.040	0.004	0.009	0.024	
Shaefferia fruticosum	0.046	0.012	0.024			
Tabebuia heterophylla Thouinia portoricensis	0.016 0.047	0.009	0.017	0.167	0.063	0.009

APPENDIX XXII. List of species and importance values of Pair #4.

		Native			Exotic	
Species	Canopy	Sapling	Seedling	Canopy	Sapling	Seedling
Amyris elemifera	0.059	0.060	0.355	0.016	0.074	
Acacia farnesiana				0.032		
Bucida buceras	0.025					
Bursera simaruba		0.009	0.105			
Bourreria succulenta		0.009			0.014	
Capparis cynophalophora					0.023	
Coccoloba diversifolia	0.034					
Comocladia dodonea	0.034	0.026				
Capparis flexuosa				0.048	0.023	0.005
Capparis hastata				0.081	0.060	
Croton humilis		0.103				
Coccoloba microstachya	0.042					
Crossopetalum rhacoma		0.052				
Erytroxylum aerolatum				0.016	0.074	
Erytroxylum brevipes					0.005	
Exostema caribaeum	0.017					
Eugenia foetida		0.069	0.008		0.014	0.005
Eugenia lingustrina					0.019	
Eugenia rhombea	0.025	0.078	0.040		0.042	
Erytroxylum rotundifolium				0.016	0.037	
Guettarda elliptica	0.008					
Guettarda krugii	0.085			0.032		
Gymnantes lucida	0.203	0.491			0.005	
Guaiacum officinale				0.065	0.204	0.005
Guaiacum sanctum				0.032	0.079	
Hypelate trifoliate	0.034	0.009				
Krugiodendrum ferreum		0.009			0.005	
Lippia strigulosa		0.009				
Leucaena leucocephala	0.025	0.009	0.484	0.339	0.213	0.967
Picetetia acuelata	0.127	0.009				
Pisonia albida	0.085	0.009				
Pithecelobium ungiscatti	0.025	0.009		0.032	0.009	0.009
Prosopis juliflora				0.258	0.014	
Randia acuelata					0.005	
Reynosia uncinata	0.008				0.009	
Shaefferia frutescens			0.008		0.079	0.009
Tabebuia heterophyla	0.051		0.000		0.070	0.000
Thounia portoricensis	0.076	0.009				
Zanthoxylum	0.070	0.000				
monophyllum	0.008					

APPENDIX XXIII List of species and importance values of Pair #5.

Native Exotic							
Species	Canopy	Sapling	Seedling	Canopy	Sapling	Seedling	
Acacia farnesiana	0.012		0.061				
Anthirea acutata				0.003		0.012	
Bucida buceras		0.011		0.003			
Bumelia obovata			0.038			0.035	
Bursera simaruba		0.032		0.024		0.008	
Bourreria succulenta	0.048	0.021	0.008	0.010	0.001		
Capparis cynophallophora			0.050				
Coccoloba diversifollia						0.004	
Comocladia dodonea			0.004	0.003		0.016	
Capparis flexuosa	0.012		0.092		0.015		
Capparis hastata			0.008				
Croton humilis			0.019	0.366	0.003	0.294	
Capparis indica			0.023		0.011		
Coccoloba microstachya		0.095		0.010		0.086	
Crossopetalum rhacoma		0.074		0.021	0.002	0.008	
Cordia rickseckeri		0.021					
Croton rigidus		0.021		0.069		0.012	
Canella winterana							
Cassine xylocarpa						0.004	
Erytroxylum areolatum			0.008				
Exostema caribaeum		0.074		0.021		0.024	
Eugenia foetida		0.021		0.169		0.173	
Eugenia lingustrina				0.003			
Eugenia rhombea		0.011		0.007			
Erytroxylum rotundifolium		0.074				0.016	
Eritalis fruticosa				0.010		0.024	
Exostema caribaeum			0.004				
Guettarda krugii		0.042		0.014			
Gyminda latifolia		0.011					
Gymnanthes lucida		0.011		0.017		0.110	
Guaiacum sanctum		0.011		0.003			
Jacquinia arborescens		0.032		0.010		0.016	
Lantana camara			0.011				
Laguncularia racemosa				0.003			
Leptocereus	0.010						
quadricostatus	0.012		0.000		0 570		
Leucaena leucocephala	0.143		0.383	0.004	0.576	0.040	
Lippia strigulosa	0.010			0.024		0.012	
Machaonia portoricensis	0.012	0.000		0.014		0.040	
Pictetia acuelata		0.063		0.014		0.016	
Plumeria alba Biognia albida		0.021		0.004		0.000	
Pisonia albida Pilosocorous rovonii	0.024	0.021		0.021		0.008	
Pilosocereus royenii		0.044	0 4 0 0	0.007	0.204	0.000	
Pithecelobium ungiscatti	0.357	0.011	0.188	0.007	0.384	0.020	
Prosopis juliflora	0.381		0.011		0.003		
Rockefoltia acanthaphora			0.011	0.047	0.004	0.004	
Randia acuelata		0.044	0.046	0.017	0.004	0.004	
Randia portoricensis	l	0.011					

APPENDIX XIV. List of species and importance values of Pair #6.

Reynosia uncinata		0.017	
Securinega acidoton	0.027		
Shaefferia frutescens	0.008		0.004
Tabebuia heterophylla	0.053	0.014	
Thounia portoricensis	0.263	0.021	0.078

APPENDIX, XV. List	or species	Native	por tunce		Exotic	
Species	Canopy	Sapling	Seedling	Canopy	Sapling	Seedling
Anthirea acutata	0.050	0.004	0.018	Callopy	oapinig	occumy
Bumelia obovata	0.050	0.004	0.018			
Bursera simaruba	0.010	0.031	0.010			
	0.010	0.001			0.054	
Bourreria succulenta	0.059	0.008			0.054	
Bourreria virgata Colubrina arborescens	0.010	0.004			0.022	
Capparis	0.010	0.004				
cynophalophora			0.004	0.087	0.097	0.224
Colubrina elliptica	0.020	0.027	0.013			
Conocarpus erectus		0.015				
Capparis flexuosa			0.009	0.043	0.172	
Croton humilis		0.510	0.352			
Coccoloba microstachya	0.040		0.026			
Crossopetalum rhacoma	0.020	0.004	0.004			
Croton rigida		0.077	0.053			
Canella winterana	0.010					
Erytroxylum aerolatum	0.010	0.004				
Exostema caribaeum	0.178	0.061	0.013			
Eugenia foetida	0.030	0.077	0.053		0.011	
Eugenia rhombea		0.004	0.004			
Erytroxylum	0.000		0.000		0.044	0.004
rotundifolium	0.069		0.022		0.011	0.034
Guettarda krugii	0.020	0.011				
Gimnanthes lucida	0.010	0.015	0.053			
Guaiacum officinale	0.020			0.072	0.032	0.069
Guaiacum sanctum	0.030	0.011			0.022	0.052
Jacquinia arborea		0.004				
Krugiodendrum ferreum						0.034
Leptocereus	0.020	0.031				
quadricostatus	0.020	0.031			0 1 1 0	
Lantana camara		0.000	0 1 5 0	0.014	0.140	0 5 4 7
Leucaena leucocephala		0.008	0.150	0.014	0.151	0.517
Lippia strigulosa	0 000	0.023	0.000			
Pictetia acuelata	0.030	0.004	0.066			
Pisonia albida	0.059		0.013	0.047	0.047	0.000
Pithecelobium dulce				0.217	0.247	0.069
Prosopis pallida	0 000	0.045	0.000	0.507	0.011	
Pilosecereus royenii	0.030	0.015	0.009	0.058		
Pithecelobium ungiscatti	0.020	0 00 i	0.040			
Randia acuelata	0.000	0.004	0.013			
Reynosia uncinata	0.030	0.004	0.035		0 000	
Securinega acidoton		0.004	0.010		0.022	
Shaefferia frutescens		0.011	0.018		0.011	
Tabebuia heterophylla	0.040					
Thounia portoricensis	0.188	0.019	0.040			

APPENDIX. XV. List of species and importance values of Pair #7.

		Native			Exotic	
Species	Canopy	Sapling	Seedling	Canopy	Sapling	Seedling
Amyris elemifera	0.008	0.003		0.011	0.019	
Anthirea acutata	0.038	0.022	0.009			
Bucida buceras	0.061					
Bumelia obovata	0.008					
Bursera simaruba	0.015	0.017	0.031	0.011	0.009	0.00
Bourreria succulenta	0.031	0.006		0.100	0.074	0.00
Bourreria virgata				0.011		
Colubrina arborescens	0.008	0.006		0.078	0.009	0.00
Capparis cynophalophora					0.019	
Coccoloba diversifolia	0.046					
Comocladia dodonea		0.003	0.004			0.00
Capparis flexuosa	0.015		0.009		0.009	0.00
Cytharexylum fruticosum	0.015	0.008				
Capparis hastata		0.003				
Croton humilis		0.228	0.094	0.033	0.130	
Coccoloba microstachya	0.015	0.003				
Carica papaya		0.003				
Crossopetalum rhacoma	0.008					
Cannela winterana	0.015					
Cassine xylocarpa		0.003				
Eugenia biflora	0.015	0.014				
Eugenia caribaeum	0.023	0.019	0.009	0.011		0.00
Eugenia foetida	0.137	0.418	0.411			
Eugenia lingustrina					0.028	
Eugenia rhombea	0.038	0.017	0.004			
Guettarda krugii	0.076	0.011	0.013			
Gymnanthes lucida	0.023	0.019	0.040			
Krugiodendrum ferreum	0.038	0.053	0.018		0.037	
Leucaena leucocephala	0.015	0.058	0.326	0.500	0.620	0.96
Lippia strigulosa		0.011			0.028	
Pictetia acuelata	0.015		0.009			
Plumeria alba				0.011		
Pisonia albida	0.084	0.011				
Pithecelobium ungiscati	0.023	0.008	0.004	0.089	0.009	0.01
Prosopis juliflora				0.067		
Shaefferia frutescens		0.028	0.018	0.011		0.01
Tabebuia heterophylla				0.056		
Tamarindus indica					0.009	
Thouinia portoricensis	0.214	0.017				
Zanthoxylym monophylum	0.008					

APPENDIX XXVI List of species and importance values of Pair #8.

APPENDIX XXVII. List of species and importance values of Pair #9.							
	_	Native			Exotic		
Species	Canopy	Sapling	Seedling	Canopy	Sapling	Seedling	
Amyris elemifera						0.071	
Bucida buceras				0.119	0.056		
Bursera simaruba					0.022	0.055	
Bourreria succulenta	0.123	0.139					
Bourreria virgata	0.099	0.038					
Colubrina arborescens	0.111	0.063	0.169				
Capparis							
cynophalophora					0.022		
Coccoloba diversifolia	0.012						
Caparis flexuosa					0.033		
Capparis hastata				0.015	0.022		
Croton humilis		0.241					
Capparis indica				0.015			
Coccoloba microstachya	0.247	0.152	0.054			0.016	
Crossopetalum rhacoma	0.049	0.139	0.092				
Canella winterana	0.148	0.101	0.031				
Exostema caribaea			0.162				
Eugenia foetida					0.022		
Erythalis fruticosa	0.099	0.051	0.246				
Eugenia rombea					0.067	0.011	
Guettarda elliptica	0.012		0.100				
Gymnanthes lucida						0.011	
Guaiacum officinale		0.025	0.062	0.015	0.033		
Krugiodendrum ferreum					0.100		
Leucaena leucocephala				0.418	0.378	0.473	
Meloccocus bijugatus					0.022	0.077	
Prosopis juliflora				0.209	0.033		
Pithecelobium ungiscatti				0.060	0.056	0.077	
Randia acuelata				0.030	0.022		
Tabebuia heterophylla	0.099	0.051	0.085				
Trichilia hirta				0.030	0.078	0.159	
Thouinia portoricensis				0.030	0.011	0.049	
Ziziphus reticulate				0.015	0.022		

APPENDIX XXVII. Li	st of s	pecies and	importance	values of	of Pair #9.
---------------------------	---------	------------	------------	-----------	-------------