

**Human and environmental factors explaining the structural and  
compositional variability in a Sub-tropical Dry Forest**

By

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## Abstract

The Guánica forest reserve is the most important conservation unit within the sub-tropical dry life zone of Puerto Rico. Its vegetation has largely recovered after diverse human and natural disturbances. This study examined the association of tree communities in the forest with human disturbances and topography. Sample sites were selected from a geographic information system database that included five land-cover temporal combinations and three topographic positions. A non-metric multidimensional scaling (NMS) ordination of species abundances indicated relationships with age of abandonment, distance to the sea, time to canopy closure and % of rock outcrop. Tree communities showed marked variation with respect to land-use history and classes of distance from the sea. Structural comparison among sub-sets of the data indicated that in flat terrain tree density and richness were greater on mature sites than on intensely harvested sites. At the same topographic position, mean tree height was greater on former agricultural sites than on intense stem harvested sites. On gentle slopes species richness was greater on former agricultural sites than on intense stem harvested sites. Mature forest on gentle slopes was taller than on hill ridges. No significant differences in basal area, species richness and tree diversity were detected among topographic positions. Former agricultural sites were characterized by novel tree communities dominated by a mix of native species and the exotic pioneer legume, *L. leucocephala*. Exotic species introduced to the reserve had failed to establish suggesting that the natural regeneration of native species is the most promising strategy to rehabilitate degraded areas.

## Resumen

La Reserva Forestal de Guánica es la unidad de conservación más importante en la zona de vida seca sub-tropical de Puerto Rico. Su vegetación se ha recuperado luego de diversos disturbios humanos y naturales. Este estudio examinó la asociación de las comunidades de árboles del bosque con los disturbios humanos y la topografía. Las parcelas fueron seleccionadas de una base de datos de información geográfica que incluyó cinco combinaciones temporales de cobertura del suelo y tres posiciones topográficas. Una ordenación "NMS" de la abundancia de especies indicó relaciones con edad desde el abandono, distancia del mar, tiempo desde el cierre del dosel y % de afloramiento de rocas. Las comunidades de árboles mostraron una variación marcada con respecto a la historia de uso de terreno y a clases de distancia al mar. Comparaciones estructurales a través de subdivisiones de los datos indican que en topografía llana la densidad y riqueza de árboles fueron mayores en sitios de vegetación madura que en sitios donde se taló intensivamente. En esta misma posición topográfica, la altura promedio de los árboles fue menor en los sitios talados intensivamente que en las fincas abandonadas. En pendientes suaves la riqueza de especies fue mayor en fincas abandonadas que en sitios donde se taló intensivamente. La vegetación madura en pendientes suaves fue ligeramente mas alta que en los topes de las colinas. No se detectaron diferencias significativas a través de posiciones topográficas en cuanto a área basal, riqueza y diversidad de especies. Las fincas abandonadas se caracterizaron por tener una comunidad de plantas nueva dominada por una mezcla de especies nativas y la leguminosa pionera naturalizada *L. leucocephala*. Las especies exóticas introducidas a la Reserva han fallado al establecerse sugiriendo que la regeneración natural de las especies nativas es la estrategia más prometedora para rehabilitar las áreas degradadas.

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## Introduction

Human have been actively altering Puerto Rico's natural vegetation for many centuries. By the 1940s, the conversion of the forest vegetation to either pasture or crop land reached nearly 94 % (Birdsey & Weaver, 1987). The change from an agrarian to an industrial economy in the middle of the 20th century encouraged people to abandon farms. Today secondary forests make up the majority of forest cover on the island (Helmer, 2004).

In the sub-tropical dry life zone, the forests were cleared almost completely (Murphy & Lugo, 1986). In this life zone, 23 % of the original forest has recovered from other land uses (Ramjohn, 2004). The main dry forest cover today represents young fragments within a pasture, crop, and urban matrix with nearly 4,000 ha of land remaining as old-growth vegetation (Murphy et al., 1995). The Guánica Forest Reserve is the largest area of mature dry vegetation on the island. This reserve has revegetated after diverse human and natural disturbances (Molina Colon & Lugo, 2006; Murphy et al., 1995).

Various studies have addressed forest recovery in the Guánica Forest Reserve. The vegetation of the Reserve had a relatively rapid recovery after forest cutting. The potential to recover to a relatively mature state quickly after clear cut makes it more resilient (Ewel, 1977). The Guánica forest has a relatively simple structure in terms of basal area and is low in height with regrowth caused mainly by coppicing. Ewel (1971) found in a 1 ha plot 13 years after clearcutting that 59% of the species were mature forest plants. Pioneer species accounted for 46% of stem density and 28% of vascular plant species. Molina Colón and Lugo (2006) found that former selective logging sites, which only had branches and stems removed without other

stand modification, were 66 percent more recovered than former agriculture and housing sites after 45 years of recovery.

Distinctiveness in tree species assemblages may vary with variations in soil depth, slope angle, and aspect as a function of soil water availability (Lugo et al., 1978). Although there is an important relationship between physical factors and structure and composition of the island dry forests, its contribution to forest recovery has been assessed superficially.

Vegetation studies in the Guánica forest have focused on mapping the main plant associations and a description of the association of the upland forest type (Lugo et al., 1978), characterization of the structure, biomass, and composition of particular sites within the forest (Murphy & Lugo, 1986), and assessment of the natural recovery after the cessation of different land uses (Molina & Lugo, 2006). The results of these studies are of important relevance, but they cannot be extrapolated to the whole forest domain because of their limited replication. Understanding of how the vegetation reflects the great environmental and land use heterogeneity is still lacking, although it is of great relevance to forest conservation and management.

## **Objectives**

The general objective of this study was to document the variability in forest structure and composition of the Guánica State Forest.

Specifically this study

1. describes forest structure and composition in the most abundant combinations of land-use and topographic position and
2. determines the environmental and land use factors that best correlate with the structural and compositional variability.

## Methods

### *Study area*

The Guánica Forest Reserve is located in SW Puerto Rico centered at approximately Latitude 17° 58' N and Longitude 65° 30' W (Figure 1). This forest lies within the Subtropical Dry Forest life zone (*sensu* Holdridge, 1967). The forest is composed of three separate portions which together total about 4,400 ha. It receives an average annual rainfall of 860 mm. The dry season is bimodal, experiencing a major drought from December to April and a minor dry period between June and August, representing one of the driest forest types in the tropics (Murphy & Lugo, 1990).

This study only deals with the largest portion of the forest (Figure 1). Elevation ranges in the study area from sea level to 228 meters. Parent materials are mostly limestone of Miocene to Oligocene age (Monroe, 1976, as cited in Lugo et al., 1978), with minor outcrops of basaltic and ultramafic materials of cretaceous origins, volcanic materials of tertiary origins, and sedimentary deposits of quaternary origins (Bawiec, 2001). Soils in the reserve have been classified into 12 series and series complexes (USDA-NRCS 2008). The four soil series covered in this study occupy almost 90 % of the reserve. The Pitahaya and La Cobana series consist of shallow, well drained, very slowly permeable soils on ridge tops, summits, and side slopes. The Seboruco series consists of moderately deep, well drained, slowly permeable soils on saddles. The Descalabrado series is derived from basic volcanic rock and consists of shallow, well drained, moderately permeable soils on side slopes and summits of hills. Two situations limit using soil type as an independent variable: (a) many of the characteristics related to soil moisture for each soil type are almost identical and (b) soil mapping was done at a very broad scale (Lugo, pers. com.).

Guánica Forest was designated a reserve in 1917; its boundaries were expanded in the 1930s (Van Bloem et al., 2003) and in the late 1990s (Canals Mora, pers. com.). In 1982 it was designated an International Biosphere Reserve by the UNESCO Man and the Biosphere Program. Before 1930, the forest had been disturbed in many ways over a long period of time (Murphy et al., 1995). Previous land uses recorded for the reserve were subsistence farming, tree plantations, logging, grazing by domestic animals, and selective logging for charcoal production and fence posts (Molina Colon & Lugo 2006). Thinning of small stems for fence posts was continued until the late 1970s (Canals Mora, pers. com.). Drovers of wild goats were all around the forest prior to 1930 (Wadsworth, 1990).

#### *Geographic database*

A geographical information system database was generated using landform and land-use history maps as variables for stratifying the study area. The Guánica forest land-use maps from 1936 and 1971 (Lugo et al., 1996) were used because they best portrayed the main land cover changes in the forest. A simplified landform map composed of four topographic classes (flat, ridge, gentle slope, upper slope; although the upper slope category was not further considered in this study due to its small extent) was combined with the 1936-71 land cover change map to generate sampling strata (Table 1). Preliminary results did not show clear compositional patterns related to land use history or topography. Therefore, I checked history of each site using the 1936, 1950-51, 1961, and 1971 aerial photographs from the Photogrammetry Service of the Highway Authority of Puerto Rico and reclassified the plots. The new site history classification was based on interpretations of the 1936, 1950-51, 1971 photos and followed the same designations used by Lugo et al. (1996) and FAO (1993). Five land-use history classes resulted from these three dates (Table 3).

With the entire series of aerial photographs (1936, 1950-51, 1961, and 1971), I estimated the age of each site as the difference between (a) the year of sampling and (b) the midpoint between the year of the last photograph showing a particular land-use (agriculture, intense selective logging, or weak selective logging) and the first photograph to show signs of abandonment (either shrubs, open or closed forest depending on the type of use). The time to canopy closure was another temporal variable estimated as the difference between (a) the year of sampling and (b) the midpoint between the year of the last photograph showing an open canopy and the first photograph showing a closed canopy. Both variables were used in the analyses to explore which reflected the best correlation.

#### *Vegetation sampling*

A total of 36 sample sites were selected randomly within the sampling strata using the random module in IDRISI Kilimanjaro GIS software (Eastman, 2003) (Table 1). Each sample unit was a circular plot with a 9.78 m radius (area = 300 m<sup>2</sup>; for trees with  $\geq 5$ cm in dbh) and three smaller circular subplots with a 2.5 m radius each (area per subplot = 20 m<sup>2</sup> for trees between 2.5cm and <5cm in dbh). Tree heights in the main plot were measured on the five trees with the largest dbh and on five randomly selected trees. In each sub-plot, heights were measured in three randomly selected individuals. Percent slope and aspect for each site were measured in the field. Percent of outcrop rock were estimated for each site. Nomenclature followed Liogier and Martorell (2000).

### *Analysis*

An indirect gradient analysis was conducted using the “slow-and-thorough” autopilot mode of non-metric multidimensional scaling (NMS) ordination in PC-ORD (McCune & Mefford 1999). The procedure used random starting configurations for 40 runs with real data and 50 runs with randomized data. The stability criterion for accepting a solution was 0.00001, 400 iterations. The ordination was performed on species’ importance values (i.e. the average of species relative basal area and species relative tree density) with Sorensen’s index as the distance measure. Species with fewer than three occurrences were removed from the ordination analysis to reduce the impact of infrequent species. One sample unit (an outlier) was removed from the analysis because its Sorensen distance was  $>2$  standard deviations away from the mean Sorensen distance of all sample units; however, no species turned out to be outliers by this criterion. Habitat variables were superimposed on the resulting ordination using a joint plot, based on the correlations of those variables with the axes of the ordination. Geophysical and historical variables included on the ordination are shown in Table 2.

Variables, and combinations of them, resulting in the most significant correlations with the ordination axes were used to group plots. These groups were further evaluated with Multi-Response Permutation Procedures (MRPP) to test the hypothesis of no compositional difference between groups. The A statistics from MRPP describes the effect size, the “chance-corrected within-group agreement.” When  $A = 0$ , the groups are no more or less different than expected by chance; when  $A = 1$ , all sample units are identical within each group.

An Indicator Species Analysis (Dufrene and Legendre 1997) was done to detect which species are significant indicators of the variables generating the groups of plots mentioned

above. The significance of each indicator value was tested at the 5 % level by a Monte Carlo test with 1000 permutations.

Analysis of variance was conducted in InfoStat (version 2006) to detect significant differences in structural characteristics between groups of sample units. Regression analyses were also done in Infostat to determine the best predictors of structural dependent variables: basal area, tree density, stem density, mean tree height, species richness and diversity. The data were transformed when Shapiro-Wilks test indicated non-normal distributions of the data or when the Levene test indicated heterogeneity of variances. When the transformations did not result in homogenous variances or normal distributions, Kruskal Wallis tests were used. Statistical significance was accepted at  $P < 0.05$ .



## Results

### *Species composition*

A total of 64 woody species with dbh  $\geq$  2.5 cm within 30 families were found in the study (Table 4). Of these species, seven were endemic, four were exotic and 13 were found in only one sample unit. The number of tree species per plot ranged between eight and 23 species with a mean of 15 species. *Pisonia albida* was the most frequently encountered tree, occurring in 86% of all the sample units. It was followed by *Pictetia aculeata* (80%), *Bursera simaruba* (77%), *Thouinia striata* var. *portorisensis* (66%), *Exostema caribaeum* (63%), *Gymnanthes lucida* (60%), *Tabebuia heterophylla* (60%), and *Coccoloba microstachya* (57%).

The best NMS solution was a three-dimensional solution (stress = 13.7, instability = 0.00001). The importance of land use history is shown by the separation of history classes in the ordination of plots. The first three axes explained 82.8% of the community variation (Figure 2). Groups CCC, OOO and ACC were clearly separated while groups OOC and OCC overlapped. Group CCC was most clearly separated from OOO and ACC along axis 3, which was most closely correlated with time since abandonment ( $r = -.56$ ), suggesting a successional axis; this axis explained 44% of the variation. The second most important axis (axis 1) explained 28% of the variation and was correlated with distance to the sea ( $r = .61$ ), time since canopy closure ( $r = .51$ ) and outcrop rock ( $r = .51$ ), suggesting an environmental and successional axes. Distance to the sea was correlated with time since canopy closure and elevation ( $r = 0.65$  and  $r = 0.70$  respectively). Percent of rock outcrop was correlated with elevation ( $r = -0.45$ ).

MRPP results indicated significant compositional differences among groups of plots classified according to the combination of land-use history x classes of distance from the sea, land-use history alone, classes of distance from the sea alone, and the combination of land-use history x landform (Table 5). Using landform alone as grouping variable did not produce significant MRPP results.

Only the ACC and OOO groups of the first partition of the Indicator Species Analysis resulted with significant indicator species (Figure 3). In sites with an ACC history *Amyris elemifera*, *Leucaena leucocephala*, *Capparis hastata* and *Bouyeria succulenta* had the highest indicator species values. *Pilocereus royenii* was the only significant indicator species in sites with OOO history. In the second partition only group CCC had sufficient numbers of plots per group for the evaluate species as indicator based on the categories of distance from the sea (near, intermediate, and far). Only the far category had significant indicator species at this partition: *Bucida buceras* and *Eugenia rhombea*. The other land-use history groups at the second partition did not divide into different groups and were not compared.

#### *Structural characteristics, species richness and diversity*

Due to non-normality of distributions or heteroscedasticity, analyses of variance on basal area, tree densities, and tree diversity ( $H'$ ) were conducted using Kruskal Wallis test. Stem density was transformed using the natural logarithm (Ln).

There were significant positive relationships between some forest characteristics and time since canopy closure (species richness,  $R^2 = 0.40$ ; tree height,  $R^2 = .32$ ) (Figure 4). Species richness and tree height increased an average of 12 species and 4.7 m over 64 years. Also distance from the sea had a significant effect on species richness and mean tree height ( $R^2 = 0.32$  and  $R^2 = .24$  respectively) (Figure 5). Species richness and mean tree height were

negatively related with % rock outcrop (species richness,  $R^2 = 0.19$ ; tree height,  $R^2 = .19$ ) (Figure 6).

On sites with CCC history, mean tree height on gentle slopes was 1.65 m higher than on ridges ( $F = 4.69$ ,  $p = 0.04$ ) (Figure 7). No significant differences in basal area ( $H = 14.37$ ,  $p = 0.21$ ), in tree density ( $H = 23$ ,  $p = 0.029$ ), species richness ( $F = 3.1$ ,  $p = 0.01$ ) and tree diversity ( $H'$ ) ( $H = 16.02$ ,  $p = 0.14$ ) were detected among topographic positions. Land-use history on sites with gentle topography had a great effect on species richness. Sites with OOO history had 6 species lower than sites with ACC history ( $F = 4.52$ ,  $p = 0.044$ ) (Figure 8). Land-use history in flat terrain sites had a considerable effect on tree density, species richness and tree height. Sites with CCC history had 7 and 5 more species than sites with OOO ( $F = 11.52$ ,  $p = 0.0025$ ) and OOC ( $F = 4.88$ ,  $p = 0.037$ ) histories respectively (Figure 9a). Moreover, CCC sites had the double of tree density than OOO ( $H = 9.16$ ,  $p = 0.0025$ ) and OOC ( $H = 4.31$ ,  $p = 0.038$ ) sites (Figure 9b). Mean tree height in OOO sites were 2.7 m lower than in CCC sites ( $F = 13.13$ ,  $p = 0.0014$ ) (Figure 10).

## Discussion

Consistent with Molina & Lugo (2006), distinct plant communities were found on sites with different land use histories. Moreover, plant communities could also be distinguished along an environmental gradient. These results are not surprising since the sampling at the present study included more environmental heterogeneity than earlier studies (Lugo et al., 1978; Murphy & Lugo, 1986; Molina Colon & Lugo, 2006).

### *Patterns of species composition*

Ordination and MRPP clearly distinguished CCC sites from OOO or ACC sites. This distinction reflects a gradient in disturbance intensity. As sites with an ACC history were deforested for agriculture and OOO sites were harvested for wood until 1971, the CCC group was closed since 1936 reflecting minimal logging. Furthermore, time since abandonment was the best correlated variable on the axis that separates them. Groups with OOC and OCC histories are more similar to OOO and CCC sites respectively, reflecting a gradient in logging intensity, but dissimilar to ACC sites where clear cut was done.

*Eugenia rhombea*, *Jacquinia berteroi*, *Zanthoxylum flavum*, *Bourreria virgata*, *Colubrina arborecens*, *Coccoloba diversifolia* and *Eugenia foetida*, all late successional species, were absent on OOO and OOC sites (*C. diversifolia* and *E. foetida* were scarce on OOC sites), but frequent on CCC sites. The eight most common species in the sample, five of them pioneer, were present on CCC, OOC and OOO sites. These patterns in species assemblies suggest that the canopy and understory of OOO sites were heavily affected and its soil conditions retard regeneration. Besides the logging history of OOO sites, they were the most affected by goat grazing before 1930s (Van Bloem, pers. com.).

In the ACC sites were present *Capparis hastata*, *Bourreria succulenta*, *Eugenia foetida*, *Erythroxylum rotundifolium*, *Guettarda elliptica* and six rare native species. These species were absent in the OOO sites. The 17 most common trees of the sample were present in the OOO sites, but absent in the ACC sites. Almost all native species in ACC sites, except *B. succulenta*, were non pioneer species; more than half the species present in OOO sites were pioneer. This may suggest that ACC sites are more suitable to the regeneration of those late successional species than the OOO sites. Furthermore, measurements of most non pioneer species present in OOO sites reflect high basal area or stem density suggesting that are remnant individuals.

Similar to Lugo et al. (1978)'s scrub forest, the OOO and OOC groups were characterized by *Pilosocereus royenii*, *Bucida buceras*, *Bursera simaruba*, *Exostema caribaea* and *Coccoloba microstachya*. In contrast to Lugo et al. (op. cit.), the Indicator Species Analysis found the cactus *Pilosocereus royenii* as the dominant species in the OOO group with *Pictetia aculeata* and *Pisonia albida* showing high importance values on both groups (OOO and OOC) (Table 6). Moreover, Lugo et al. (op. cit.) found as a dominant species *Reynosia uncinata*, an insignificant species in the present study. This difference may be a result of the few number of samples (1000 m<sup>2</sup> on 1 sample unit) they made in comparison with the widespread sampling of this study (2100 m<sup>2</sup> on 7 sample units).

Consistent with the deciduous forest described by Murphy and Lugo (1986), *Gymnanthes lucida*, *Pisonia albida*, *Exostema caribaeum* and *Pictetia aculeata* were abundant in the CCC and OCC groups. The abundance of *Bucida buceras* in the CCC group contradicts Murphy and Lugo (op. cit.) where this species was absent. The restricted small area (1500 m<sup>2</sup>) sampled by Murphy and Lugo (op. cit.) may explain this difference. The results on CCC and

OCC sites are based on a 5700 m<sup>2</sup> randomly selected sampling area widespread around the forest.

Among the seven indicator species of the ACC group, only *Leucaena leucocephala*, a naturalized self dispersed pioneer species and the native *Pithecellobium unguis-cati* were present in Molina Colon & Lugo (2006) agricultural sites at high important values. Likewise, *L. leucocephala* was the most important species of this type of land-use (Fig. 3). Agricultural activity has a particular effect on the habitat by the removal of natural vegetation and root systems and compaction of soils. After abandonment, the microflora and fauna of soils may be considerably altered depleting soils of much of their original nutrient potential and seed bank (Mueller-Dombois & Ellenberg, 1974). *L. leucocephala* is well suited to the highly disturbed conditions of the former agricultural sites because it fixes nitrogen and has high light demand for growth (Parrota, 2000).

The indicator native species found in the ACC group, with exception of *Pithecellobium unguis-cati* are bird dispersed species and were commonly used as fencepost or domestic use (torches) (Little & Wadsworth, 1964). This result reinforce the idea that the occurrence of remnants and/or fence rows trees in the former agricultural patches, typical in subsistence agriculture, may contribute to seed dispersal by providing perches for birds (Aide et al., 1996). Furthermore, the conditions to recovery of the agricultural sites may be more favorable in Guánica forest because of the relative small disturbance patches, nearby seed sources, and the scarcity of fires.

In MRPP analysis, distance to sea separates well the tree communities and was the best correlated variable with the second most important axis (1) in the ordination. A similar pattern was found for the spatial arrangement of the tree communities in the Bahaman's dry

forest (Smith & Vankat, 1992). It suggests that plants growing in the coastal hedge zone must be adapted to intensive salt spray, high wind velocity and shallow rocky soil. The intensity of these factors begins to decrease as they get further from the sea (Lugo, 1983). This pattern is reflected in the gradual change in abundance of particular species tolerant to the coastal conditions (e.g. *Pilosocereus royenii*).

#### *Patterns of species richness and diversity*

Time to canopy closure was the best predictor of species richness. This suggests that as the woody cover established, the forest accumulated species rapidly. As a result of the canopy closure, those sites are less exposed to the drying effects of the wind and sun allowing more adequate conditions for species development.

The rate of canopy closure may be influenced by environmental factors as well. For example, time to canopy closure, distance to the sea and elevation were all positively correlated between each other. Furthermore, percent of rock cover was negatively correlated with elevation. This may suggest that even if sites with high rocky cover (less soil) were abandoned at the same time as sites with more soil content, their canopies may close at different rates.

Also, distance to sea added to the explained variability in species richness. This pattern is not surprising since the strong correlation between distance to sea and time to canopy closure. As the distance to the sea decreases, the intensity of salt spray and the velocity of winds increase, affecting species establishment (Lugo, 1983). These results partially contradict Lugo et al. (1978) who did not find a close relationship between species richness and distance to the sea. This difference may be a result of the smaller diameter threshold used in this study (2.5 versus 5.0 cm).

The significant relationship found between species richness and percent rock outcrop supports the observations made by Lugo et al (1978). They suggested that the proximity of the limestone bedrock to the soil surface is a predictor of the number of species. According to Lugo et al. (op. cit), as soil characteristics vary, a wide diversity of habitats is generated supporting a high number of species.

Mature forest (CCC sites) had higher species richness than OOO and OOC sites. This result reflects differences in the intensity of logging and grazing of goats. Also, species richness was higher on ACC sites than on OOO sites. Molina & Lugo (2006) found lower species richness on former agricultural sites than on sites logged for charcoal production. Their logged sites were less exposed to environmental stressors (i.e. wind, poor developed soils and salt spray) than OOO sites. Moreover, sites with OOO history were located on poorly developed soils suggesting that recovery rates of these sites may be lower.

#### *Patterns of forest structure*

Topographic position had an effect on mean tree heights. Trees of CCC sites on gentle slopes were slightly taller than on ridges (Fig. 7). The relatively greater exposure to winds on ridges, shallower soils and soil moisture differences can contribute to this pattern. Limestone hills occur on the south coast as well as on the north coast, the Southern Limestone and the Karst Belt, respectively, sensu Lugo et al., (2001). Topographic positions on the hills of the Karst Belt show a clear pattern in terms of soil characteristics resulting from the rapid weathering of the substrate. In contrast, I observed an atypical pattern in the Guánica Forest where flat terrain has similar soil characteristics to ridges or slopes. With the exception of canyons and specific soil types of volcanic origin (not included in this study),



basal area, tree and stem density, and species richness and diversity were almost the same on all topographic positions.

Mature forest (CCC sites) had higher tree density and height than sites where logging was higher (OOO and OOC sites). The more exposed limestone with occasional solution holes and shallow soil pockets that characterize OOO and OOC sites may explain this pattern (Lugo et al., 1978). The higher frequency of soil pockets in CCC sites allows the accumulation of more individuals and an increment height. In contrast, Molina & Lugo (2006) did not find significant differences in tree density among land use types. However, their study was restricted to a portion of the forest not comparable with OOO or OOC sites.

The results show that time to canopy closure and distance to the sea are correlated with mean tree heights in the Guanica forest. It suggests that stands approximately 65 years-old approach the tree height of the oldest stands. Two reasons make reasonable the increase in tree height as it gets further away from the coastal zone. First, the least developed soils were located near the sea and soils conditions get better as stray from the coast. Second, the salt spray condition near the coast may produce necroses at terminal buds causing continues crown thinning (Schulze et al., 2002).

#### *Exotic species*

Only 6.2 % of the vegetation surveyed in this study was exotic species. The naturalized *L. leucocephala* was dominant in young intensively disturbed sites. Molina Colon & Lugo (2006) found a similar pattern in its agricultural sites. Likewise, the abundance of this species in Murphy & Lugo (1986) sample (mature forest) was scarce. This study shows that *L. leucocephala* can exist in disturbed sites but also in gaps of mature forest (Table 6). Among the exotic species found, only *L. leucocephala* was frequent throughout the area surveyed.

Although *Swietenia mahogani* and *Haematoxylon campechianum* were introduced in large quantities to the reserve (Wadsworth, 1990), they were found at low densities in this study. China (1990) found the presence of *S. mahogani* and *H. campechianum* on former plantations of those species but absent in mature forest. Molina Colon & Lugo (2006) found low abundance of *S. mahogani* mainly on former house sites and farmland. According to Marrero (1950), natural regeneration of native species was the most promising strategy to rehabilitate degraded areas in the reserve.

#### *Forest management*

A human-induced disturbance regime involve human activity that is responding to social and economic factors and its footprint influences the structural and compositional attributes of the ecosystem involved (Lugo, 2004). Tree community dynamics in Guánica forest have been affected both structurally (e.g. tree density) and compositionally by land use history. Former agricultural use has resulted in new conditions that give competitive advantage to some exotic species.

*L. leucocephala* replenishes the soil organic matter that is usually depleted after intense human use. However, native species (e.g. *Capparis hastata*, *Bourreria succulenta*, *Amyris elemifera*) can also invade post-agricultural landscapes along with *L. leucocephala*. Exotic species could be creating conditions that are not favorable to the typical vegetation of limited disturbed sites, but allow other native species to establish. After improving site conditions, a selective thinning of *L. leucocephala* accompanied with the reintroduction of native species may result in faster establishment of more “desirable” late-successional forest. However, unless removal of *L. leucocephala* is accompanied by the reintroduction of native species, further delay in the ecosystem recovery is likely to occur.

## Conclusions

The following are the most important findings of this study:

1. The variable that best correlated with the trees' structure and composition in the Guánica dry forest was the land-use history. Logged sites showed species assemblages that reflected an intensity gradient of this disturbance, and former agricultural sites were dissimilar to the logged sites.
2. Tree communities in the Guánica forest were distinguished along an environmental gradient determined mainly by the distance to the sea. Along with the distance to the sea, gradients of soil depth, salt spray intensity, and wind velocity also appear to be controlling species assemblages. The effect of these factors seems to decrease in intensity further from the seashore.
3. The vegetation of the Guánica forest did not vary in different topographic locations in terms of basal area, tree density, species richness and diversity. The differences in soil characteristics among topographic locations were not strong enough to suggest dissimilarities.
4. However, in mature sites trees on the gentle slopes were significantly taller than those on ridges. On the slopes, trees measured 6.9 m on average, and on the ridges the average height was 5.0 m.
5. Species richness was greater where the canopy had more time to develop. Apparently the most closed sites are less exposed to the drying effects of the wind and sun, allowing more adequate conditions for species development.
6. Former agricultural sites were characterized by novel tree communities dominated by native trees and the exotic pioneer legume, *L. leucocephala*. This exotic

- species could be creating conditions that are not favorable to the typical vegetation of limited disturbed sites, but allow other native species to establish.
7. The conditions for recovery in the agricultural sites may be favorable in the Guánica forest because of the relative small disturbance patches, nearby seed sources, and the scarcity of fires.
  8. Almost all the late-successional native species found in the former agricultural sites were absent in the intensively logged and poor developed soil sites. This suggests that the former agricultural sites are more suitable to the regeneration of those late successional species than the OOO sites.
  9. Although exotic species were introduced to the reserve in large quantities, they represent only 6.2 % of the species surveyed. This reinforces the idea that the natural regeneration of native species is the most promising strategy for rehabilitating degraded areas in the reserve.

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## Tables

Table 1. The combinations of land-cover classes based on Lugo et al. (1995) maps and landforms used to generate the sampling strata.

Landcover		landform	% of study area
1936	1971		
close	close	flat terrain	13.2
close	close	gentle slopes	18.5
close	close	ridges	6.4
open	close	flat terrain	19.6
open	close	gentle slopes	20.6
open	close	ridges	5.2
Area not studied			16.5



Table 2. Geophysical and historical variables included in the analysis.

<b>Variable</b>	<b>Description</b>
LU	Land-use history categories based on the combination of land use as interpreted from the 1936, 1950-51 and 1971 aerial photos.
Topo	Topographic positions: flat, ridge, or gentle slope.
LUxTopo	Combination of land use history categories and 3 topographic positions.
SeaD	Distance to the sea in meters.
DtSea	Categories of distance to the sea. 1 ranges from 0–1,478 m, 2 ranges from 1,479 to 2,956 m, and 3 ranges from 2,957 to 4,435 m.
LUxSeaD	Combination of land use history categories and categories of distance to the sea.
Elev	Elevation above mean sea level in meters
Rock	Categories of % outcrop limestone rocks based on visual estimates. 1 ranges from 0-20 %, 2 ranges from 21-40%, 3 ranges from 41-60 %, 4 ranges from 61-80 %, 5 ranges from 81-100%.
Age	Stand age in years.
TtCC	Time to canopy closure in years.
Slp%	Percent slope inclination.
SoilT	Soil type: Pitahaya limestone outcrop-Seboruco complex, La Cobana-Seboruco Limestone outcrop complex, Seboruco gravelly clay and Descalabrado clay loam.
Asp	Slope aspect in degrees.
Irad	Potential solar irradiation based on McCune 2002.

Table 3: Land-cover categories based on interpreting the actual 1936, 1950-51 and 1971 aerial photos at each sampling site.

<b>Landcover</b>			<b>Code</b>
<b>1936</b>	<b>1950/51</b>	<b>1971</b>	
agriculture	closed	closed	<b>ACC</b>
closed	closed	closed	<b>CCC</b>
open	closed	open	<b>OCC</b>
open	open	closed	<b>OOC</b>
open	open	open	<b>OOO</b>

Table 4. Tree species found in the study including their family and the status in Puerto Rico.

<b>Abr.</b>	<b>Genera</b>	<b>Species</b>	<b>Family</b>	<b>Status</b>
Eug xer	<i>Eugenia</i>	<i>xerophytica</i>	Myrtaceae	end
Gue kru	<i>Guettarda</i>	<i>krugii</i>	Rubiaceae	end
Lep qua	<i>Leptocereus</i>	<i>quadricostatus</i>	Cactaceae	end
Mac por	<i>Machaonia</i>	<i>portoricensis</i>	Rubiaceae	end
Rey gua	<i>Reynosia</i>	<i>guama</i>	Rhamnaceae	end
Ron ine	<i>Rondeletia</i>	<i>inermis</i>	Rubiaceae	end
Tho por	<i>Thouinia</i>	<i>portoricensis</i>	Sapindaceae	end
Dur ere	<i>Duranta</i>	<i>erecta</i>	Verbenaceae	exo
Hae cam	<i>Haematoxylon</i>	<i>campechianum</i>	Leguminosae	exo
Leu leu	<i>Leucaena</i>	<i>leucocephala</i>	Leguminosae	exo
Swi mah	<i>Swietenia</i>	<i>mahoganii</i>	Meliaceae	exo
Amy ele	<i>Amyris</i>	<i>Elemifera</i>	Rutaceae	n
Ant acu	<i>Antirhea</i>	<i>acutata</i>	Rubiaceae	n
Bou suc	<i>Bourreria</i>	<i>suculenta</i>	Boraginaceae	n
Bou vir	<i>Bourreria</i>	<i>virgata</i>	Boraginaceae	n
Buc buc	<i>Bucida</i>	<i>buceras</i>	Combretaceae	n
Bun gra	<i>Bunchosia</i>	<i>grandulosa</i>	Malpighiaceae	n
Bur sim	<i>Bursera</i>	<i>simaruba</i>	Burseraceae	n
Can wit	<i>Canella</i>	<i>winterana</i>	Canellaceae	n
Cap cyn	<i>Capparis</i>	<i>cynophallophora</i>	Capparaceae	n
Cap fle	<i>Capparis</i>	<i>flexuosa</i>	Capparaceae	n
Cap has	<i>Capparis</i>	<i>hastata</i>	Capparaceae	n
Cap ind	<i>Capparis</i>	<i>indica</i>	Capparaceae	n
Cit fru	<i>Citharexylum</i>	<i>fruticosum</i>	Verbenaceae	n
Clu ros	<i>Clusia</i>	<i>rosea</i>	Clusiaceae	n
Coc div	<i>Coccoloba</i>	<i>diversifolia</i>	Polygonaceae	n
Coc mic	<i>Coccoloba</i>	<i>microstachya</i>	Polygonaceae	n
Col arb	<i>Colubrina</i>	<i>arborescens</i>	Rhamnaceae	n
Col eli	<i>Colubrina</i>	<i>elliptica</i>	Rhamnaceae	n
Com dod	<i>Comocladia</i>	<i>dodonea</i>	Anacardiaceae	n
Cro fla	<i>Croton</i>	<i>flavens</i>	Euphorbiaceae	n
Cro rac	<i>Crossopetalum</i>	<i>rhacoma</i>	Celastraceae	n
Ela xyl	<i>Elaeodendron</i>	<i>xylocarpum</i>	Celastraceae	n
Eri fru	<i>Erithalis</i>	<i>fruticosa</i>	Rubiaceae	n
Ery aer	<i>Erythroxylum</i>	<i>areolatum</i>	Erythroxylaceae	n
Ery rot	<i>Erythroxylum</i>	<i>rotundifolium</i>	Erythroxylaceae	n
Eug foe	<i>Eugenia</i>	<i>foetida</i>	Myrtaceae	n
Eug rho	<i>Eugenia</i>	<i>rhombea</i>	Myrtaceae	n
Exo car	<i>Exostema</i>	<i>caribaeum</i>	Rubiaceae	n
Fic cit	<i>Ficus</i>	<i>citrifolia</i>	Moraceae	n
Flu aci	<i>Flueggea</i>	<i>acidoton</i>	Euphorbiaceae	n
For seg	<i>Forestiera</i>	<i>segregata</i>	Oleaceae	n
Gua off	<i>Guaiacum</i>	<i>officinale</i>	Zygophyllaceae	n
Gua san	<i>Guaiacum</i>	<i>sanctum</i>	Zygophyllaceae	n
Gue eli	<i>Guettarda</i>	<i>elliptica</i>	Rubiaceae	n
Gym luc	<i>Gymnanthes</i>	<i>lucida</i>	Euphorbiaceae	n
Hyp tri	<i>Hypelate</i>	<i>trifoliata</i>	Sapindaceae	n

Jac ber	<i>Jacquinia</i>	<i>berteroi</i>	Theophrastaceae	n
Jat her	<i>Jatropha</i>	<i>hernandiifolia</i>	Euphorbiaceae	n
Kru fer	<i>Krugiodendron</i>	<i>ferreum</i>	Rhamnaceae	n
Pic acu	<i>Pictetia</i>	<i>aculeata</i>	Leguminoceae	n
Pil roy	<i>Pilosocereus</i>	<i>royenii</i>	Cactaceae	n
Pis alb	<i>Pisonia</i>	<i>albida</i>	Nyctaginaceae	n
Pit ang	<i>Pithecellobium</i>	<i>unguis-cati</i>	Leguminoceae	n
Plu alb	<i>Plumeria</i>	<i>alba</i>	Apocynaceae	n
Ran acu	<i>Randia</i>	<i>aculeata</i>	Rubiaceae	n
Rey unc	<i>Reynosia</i>	<i>uncinata</i>	Rhamnaceae	n
Sav ses	<i>Savia</i>	<i>sessiliflora</i>	Euphorbiaceae	n
Sch sch	<i>Schoepfia</i>	<i>schreberi</i>	Olacaceae	n
Sid obo	<i>Sideroxylon</i>	<i>obovatum</i>	Sapotaceae	n
Sid sal	<i>Sideroxylon</i>	<i>salicifolium</i>	Sapotaceae	n
Tab het	<i>Tabebuia</i>	<i>heterophylla</i>	Bignoniaceae	n
Xim ame	<i>Ximena</i>	<i>americana</i>	Olacaceae	n
Zan fla	<i>Zanthoxylum</i>	<i>flavum</i>	Rutaceae	n

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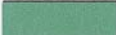
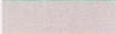







Status: N = native, X = exotic, E = endemic.

Table 5. MRPP results based on Sorencen distance;  $g$  = number of groups;  $A$  = chance corrected within-group agreement;  $p$  = probability of type I error for  $H_0$ : no differences between groups.

<b>Grouping variable</b>	<b>g</b>	<b>A</b>	<b>p</b>
Combination LU x Distance from sea	7	0.35	<0.001
Land Use history	5	0.27	<0.001
Distance from sea (m)	3	0.18	<0.001
Combination LU x Landform	10	0.24	0.001
Landform	3	0.02	0.260

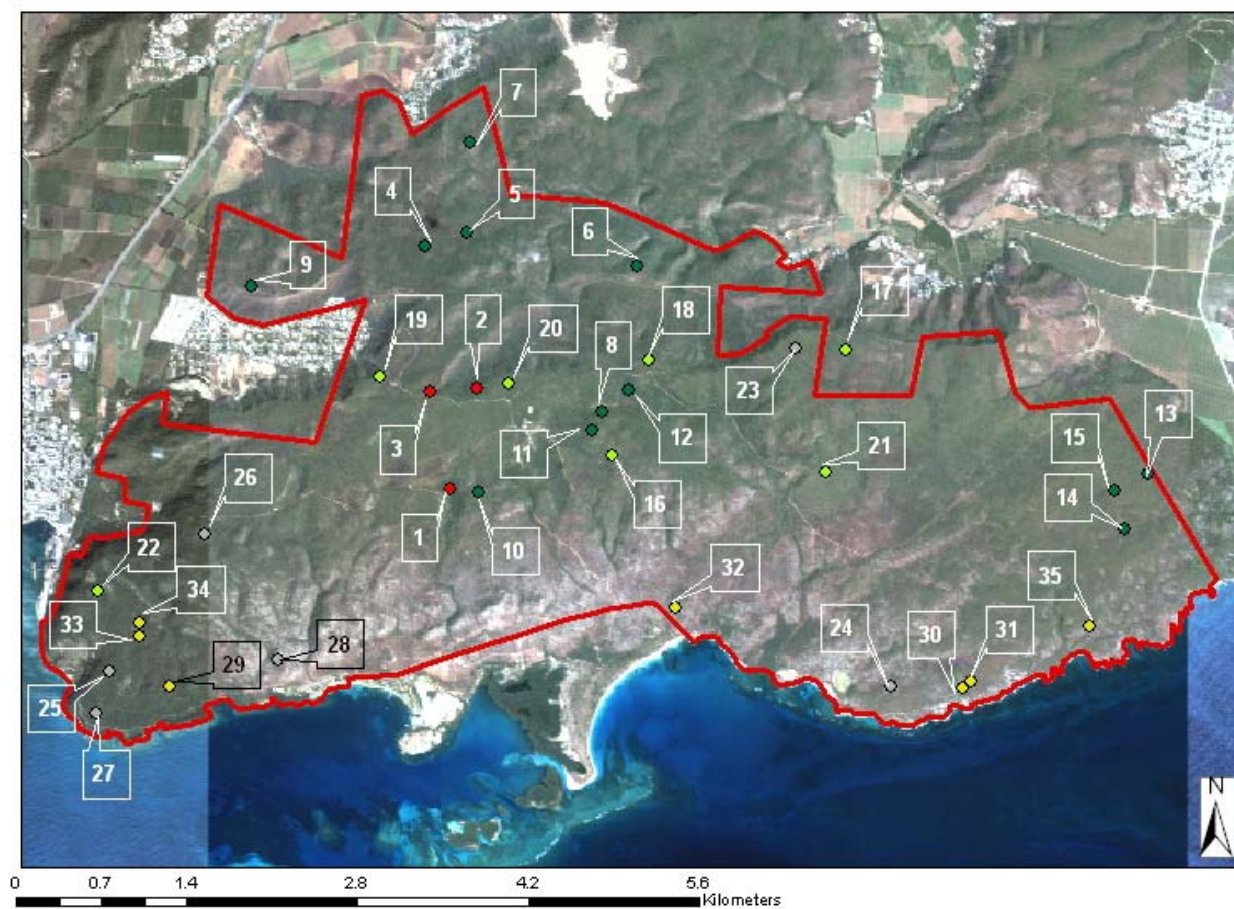


## Legend of Table 6

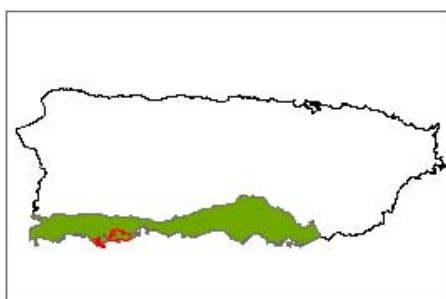
Leyenda	
	Agricultura
	Tala selectiva
	CCC
	OCC
	OOC
	OOO
	Lejos del mar
	Distancia intermedia al mar
	Cerca del mar

## Figures

## Study Area



## Legend










	Subtropical Dry Zone	Land Use History
	Guánica Forest Reserve	 ACC
		 CCC
		 OCC
		 OOC
		 OOO

Figure 1. Map of the study area with former land uses. Inset shows the location of the Guánica Dry Forest in southwestern Puerto Rico.

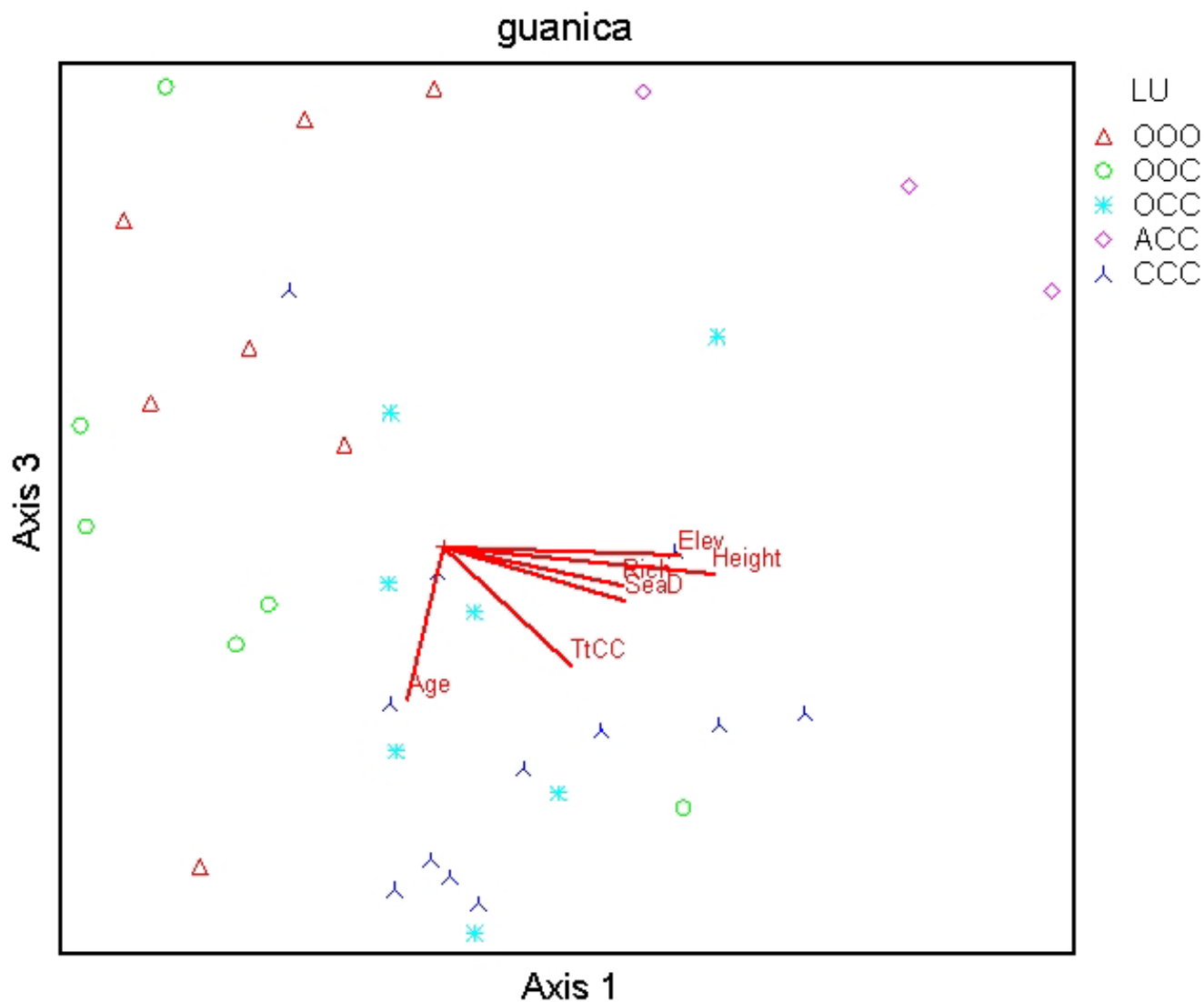


Figure 2. Non-metric multidimensional scaling ordination on axes 1 and 3. Variables correlated with ordination axes with  $r^2 \geq .30$  are shown in magenta; lines radiating from the center of the ordination show directions and relative strengths (lengths of lines) of the correlations.



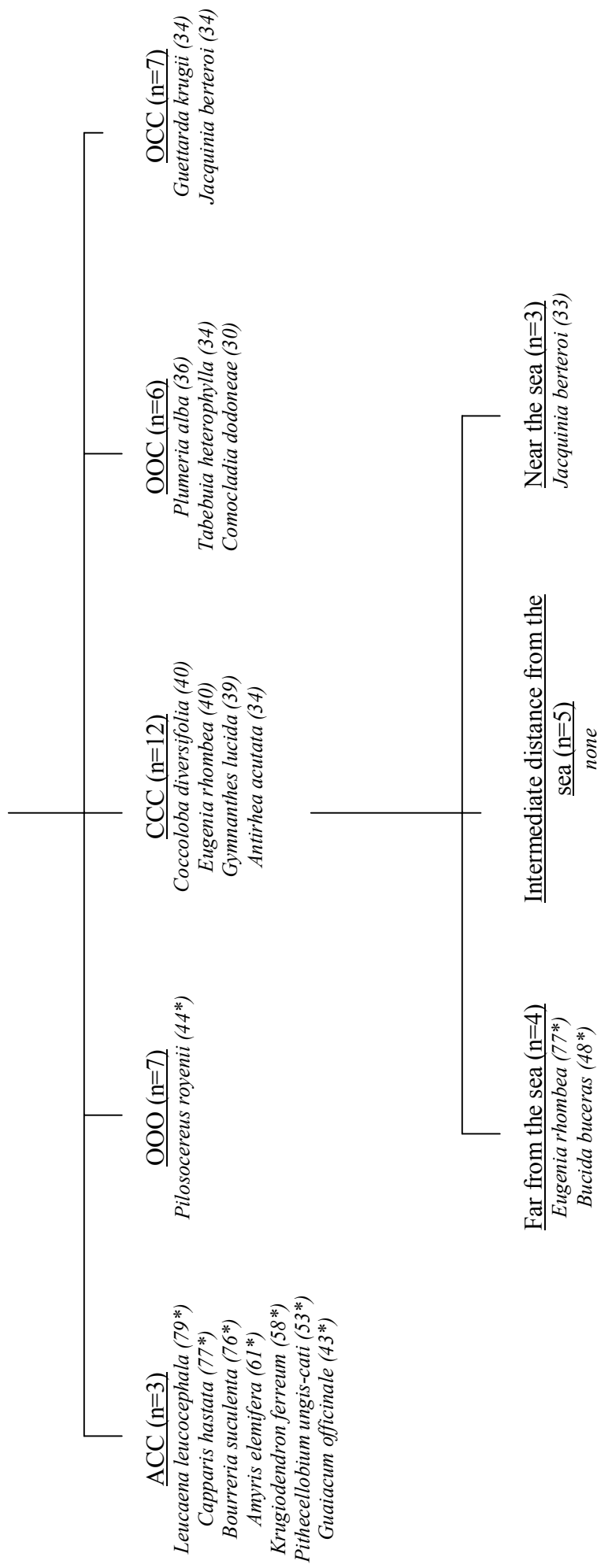
All Groups (n=35)

Figure 3. Species group arrangement from the Indicator Species analysis. Only species with an indicator value 30 are included. Values in parenthesis are the indicator species value at a partition. Indicator values with an asterisk indicate statistical significance at the 5 % level.

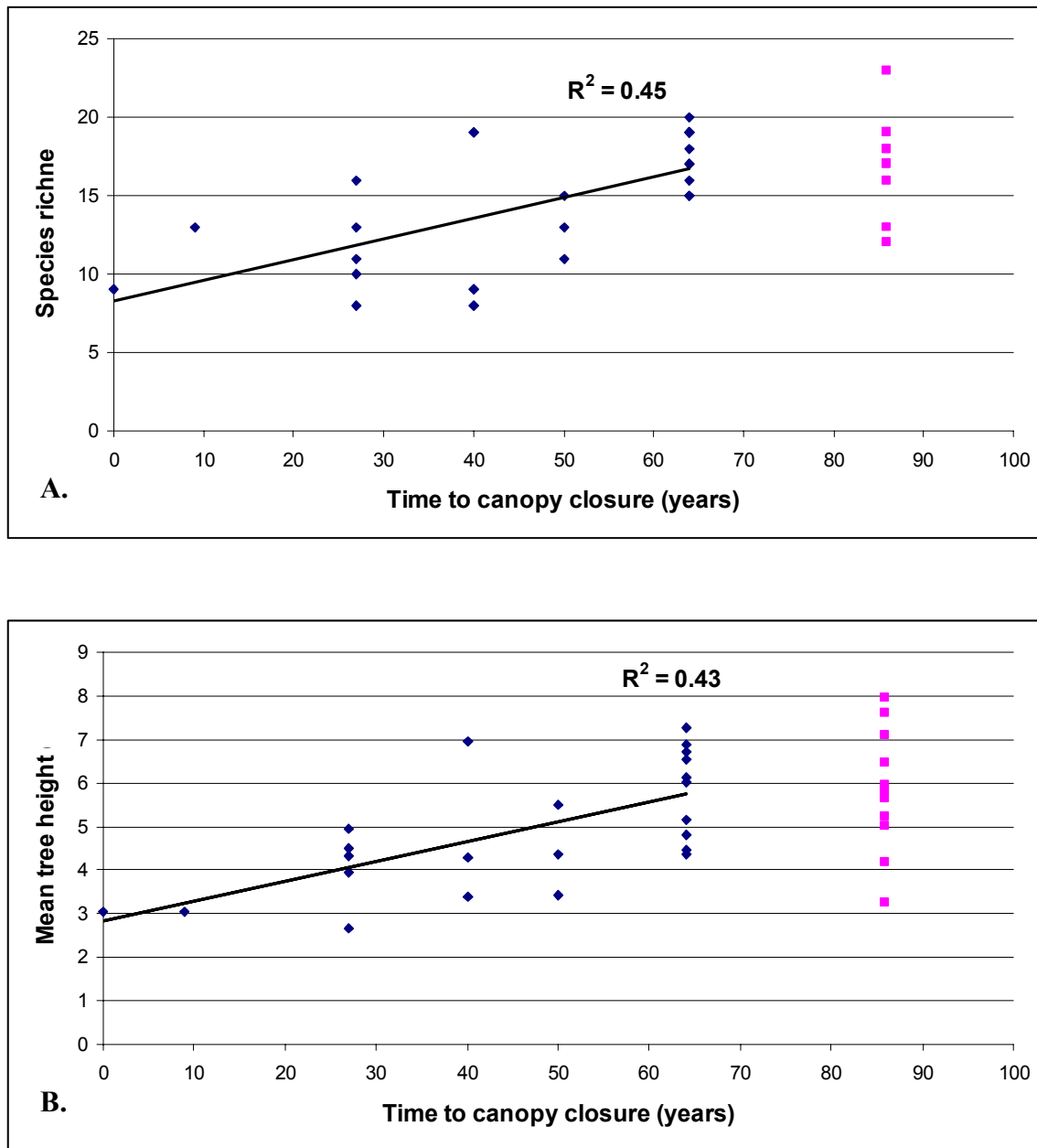


Figure 4. Relationships between species richness (a) and tree height (b) with time since canopy closure for the 35 sample units. Only data from sites <65 years old were used to calculate the regression lines.

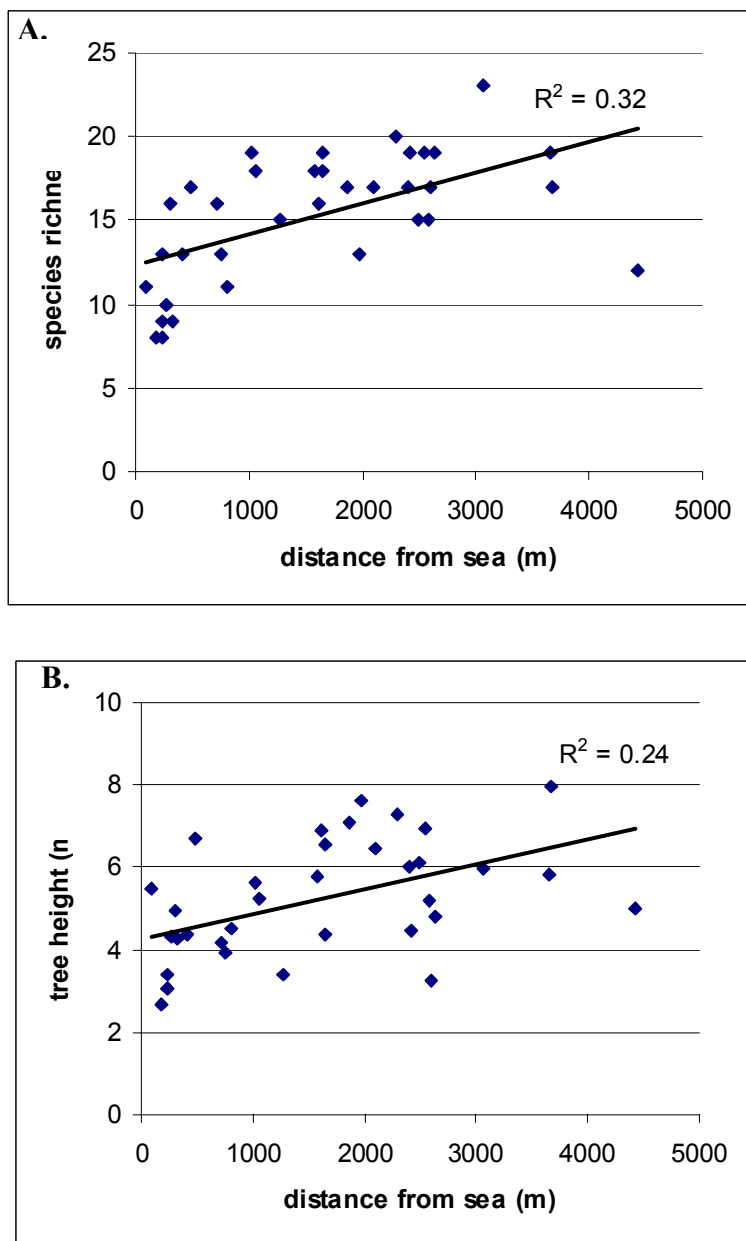


Figure 5. Relationships between species richness (a) and mean tree heights (b) with distance from the sea for the 35 sample units.

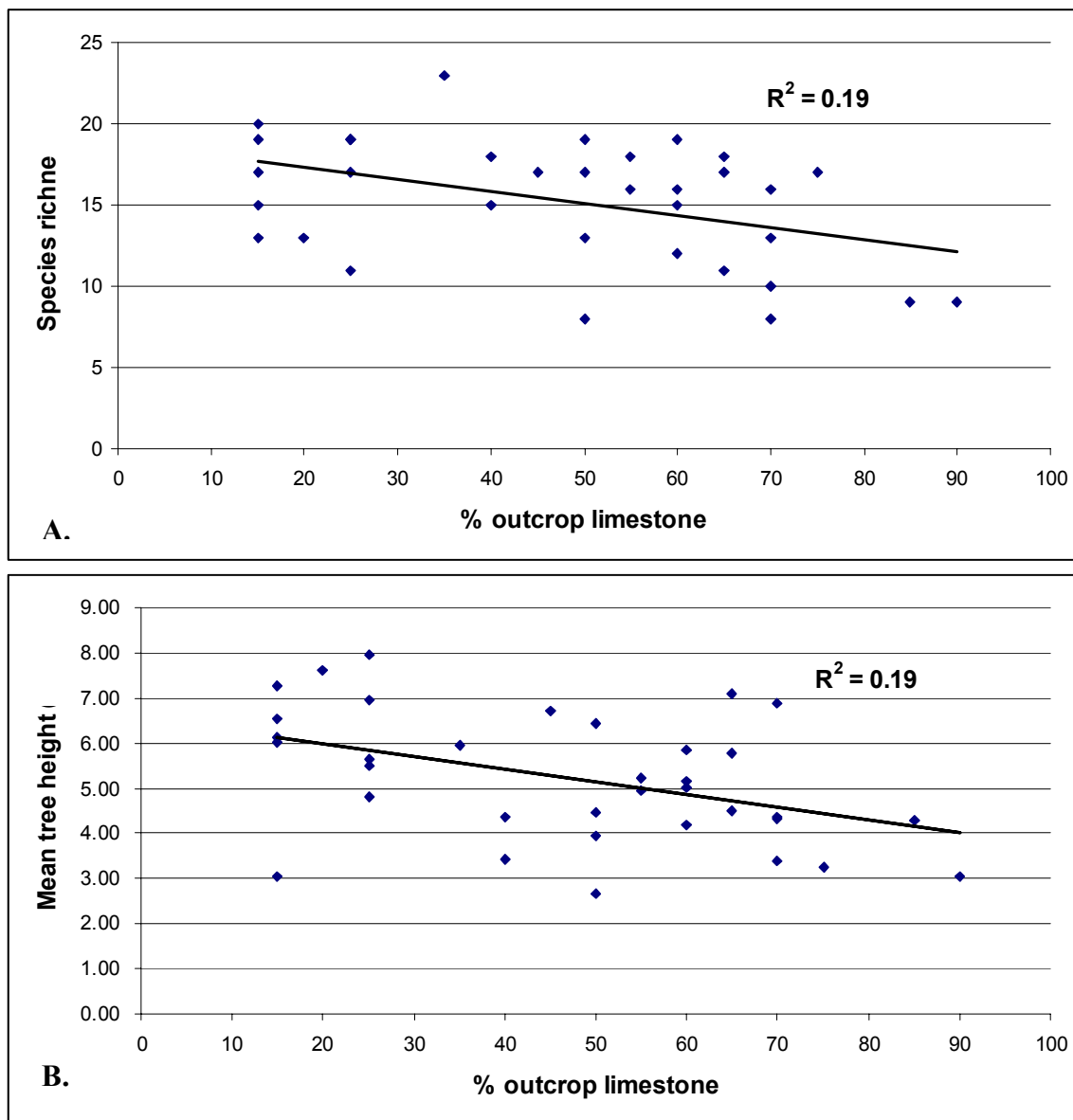


Figure 6. Relationships between species richness (a) and mean tree height (b) with % of outcrop limestone for the 35 sample units.

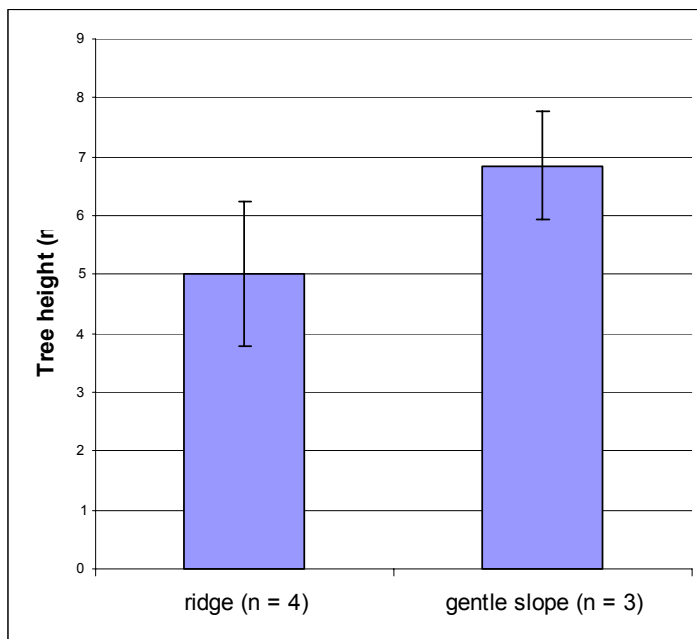


Figure 7. Comparison of mean tree heights between sites with gentle slopes and ridges within CCC history. Error bars denote standard deviation.

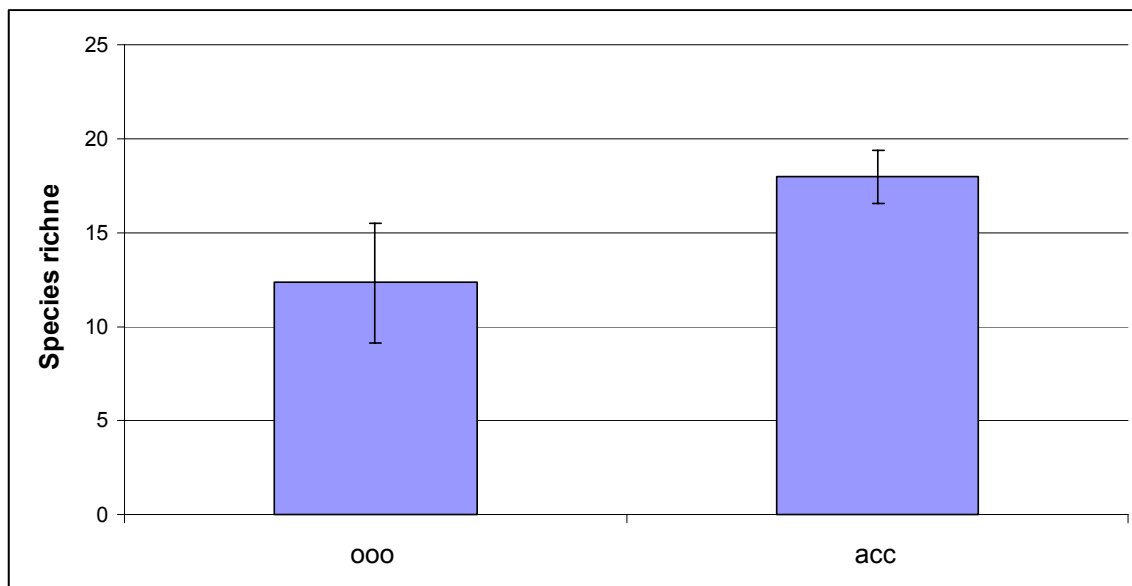


Figure 8. Comparison of species richness between OOO and ACC within gentle slopes. Error bars denote standard deviation.

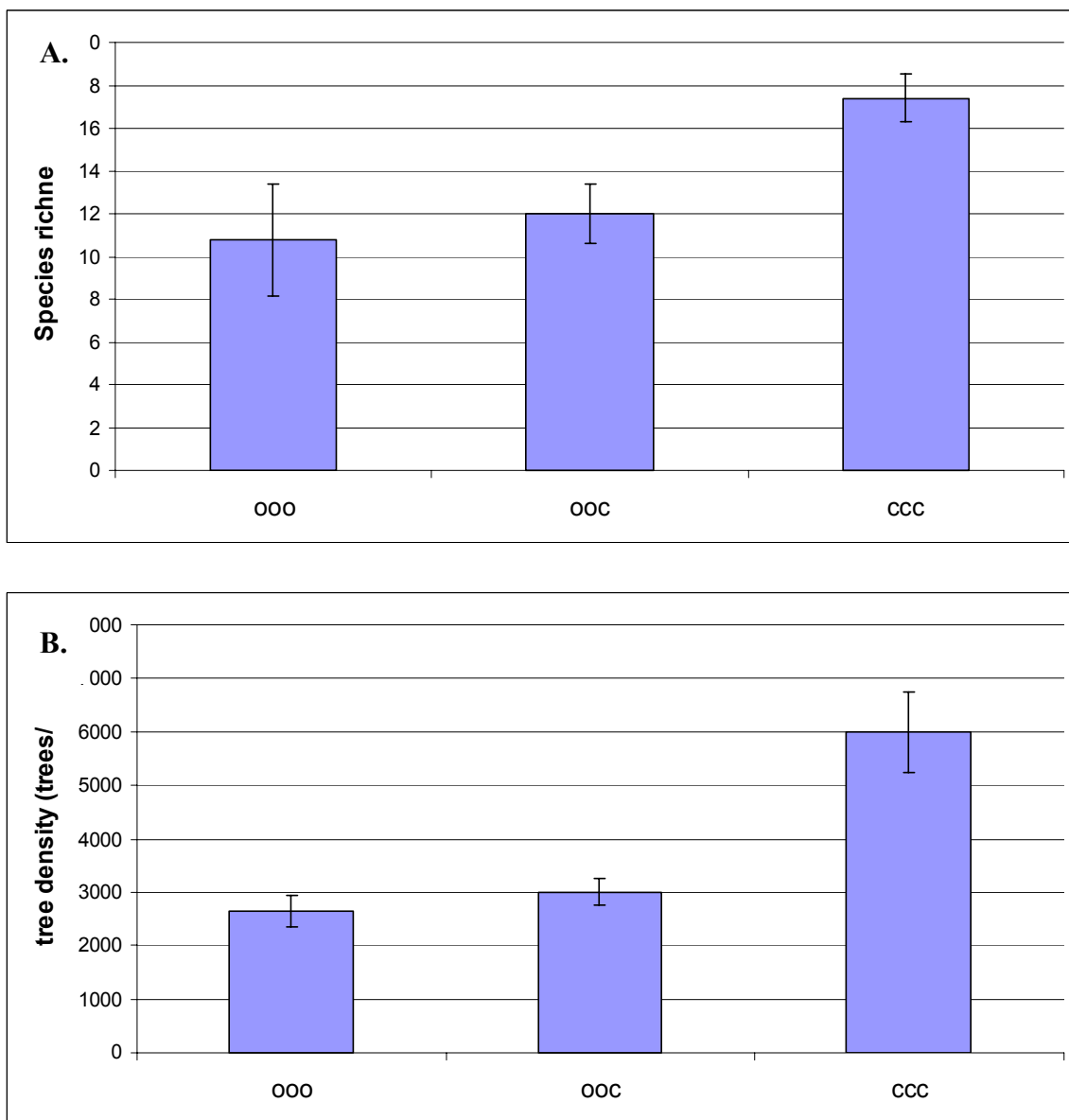


Figure 9. Comparison of species richness (a.) and tree density (b.) between CCC with OOO and OOC histories within flat terrain. Error bars denote standard deviation.

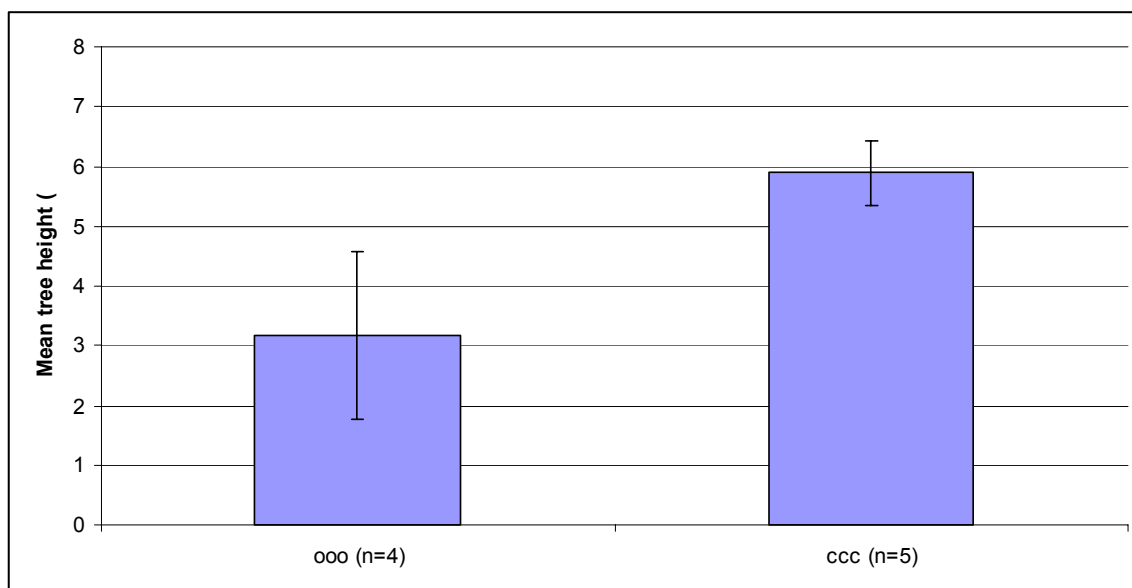


Figure 10. Comparison of tree height between OOO and CCC histories on flat terrain. Error bars denote standard deviation

Appendix 1. Description of the geophysical and historical variables for each simple unit. Species richness (Rich) and Shannon diversity index ( $H'$ ) were included as compositional variables.

Plot	LUXTopo	LU	Topo	DtSea	LuxSeaD	Elev	Rock	Age	TtCC	slp%	soilt	Asp	SeaD	Iradd	Rich	$H'$
1	10	acc	gen	2	6	206	1	64	64	30	Pit-Seb	55	1652	1.013	19	2.52
2	10	acc	gen	2	6	250	1	64	64	24	Coba-Seb	360	2400	0.877	17	2.22
3	9	acc	flat	2	6	240	1	64	64	11	Coba-Seb	65	2496	1.060	15	2.03
4	13	ccc	gen	3	9	157	3	86	86	22	Coba-Seb	183	3648	1.096	19	2.50
5	11	ccc	flat	3	9	143	2	86	86	10	Seb	110	3673	1.099	17	2.46
6	12	ccc	rid	3	9	193	2	86	86	13	Desc	51	3060	1.038	23	2.64
7	12	ccc	rid	3	9	143	3	86	86	13	Coba-Seb	193	4435	1.095	12	1.99
8	13	ccc	gen	2	8	160	3	86	86	16	Pit-Seb	344	1973	0.964	13	2.09
9	12	ccc	rid	2	8	137	4	86	86	12	Coba-Seb	317	2600	1.026	17	2.39
10	12	ccc	rid	2	8	139	4	86	86	9	Pit-Seb	170	1573	1.077	18	2.13
11	13	ccc	gen	2	8	224	4	86	86	25	Pit-Seb	285	1857	1.090	17	2.35
12	11	ccc	flat	2	8	190	3	86	86	9	Pit-Seb	155	2088	1.087	17	2.39
13	11	ccc	flat	1	7	24	4	86	86	24	Pit-Seb	229	1055	1.168	18	2.32
14	11	ccc	flat	1	7	114	3	86	86	15	Pit-Seb	341	722	0.974	16	2.35
15	11	ccc	flat	1	7	84	2	86	86	4	Pit-Seb	220	1028	1.064	19	2.57
16	8	occ	gen	2	5	218	4	79	64	40	Pit-Seb	250	1610	1.186	16	2.18
17	7	occ	rid	2	5	204	2	79	64	15	Coba-Seb	190	2634	1.097	19	2.62
18	7	occ	rid	2	5	243	1	79	64	10	Coba-Seb	159	2290	1.091	20	2.75
19	7	occ	rid	2	5	195	3	79	64	16	Coba-Seb	130	2581	1.134	15	2.43
20	7	occ	rid	2	5	200	3	79	64	18	Coba-Seb	137	2411	1.141	19	2.32
21	7	occ	rid	2	5	115	2	79	64	18	Coba-Seb	185	1641	1.095	18	2.29
22	8	occ	gen	1	4	120	3	79	64	39	Pit-Seb	95	476	1.150	17	2.43
23	5	occ	rid	2	3	196	2	79	40	18	Coba-Seb	182	2539	1.089	19	2.61
24	6	occ	gen	1	2	57	4	79	40	17	Pit-Seb	266	231	1.116	8	1.89
25	4	occ	flat	1	2	68	4	79	50	9	Pit-Seb	225	412	1.095	13	2.29
26	5	occ	rid	1	2	116	2	79	50	18	Coba-Seb	125	1266	1.143	15	2.41
27	4	occ	flat	1	2	7	2	79	50	5	Pit-Seb	205	83	1.068	11	1.93
28	5	occ	rid	1	2	48	5	79	40	29	Pit-Seb	235	321	1.183	9	1.65
29	3	ooo	gen	1	1	68	3	79	27	22	Pit-Seb	153	300	1.143	16	2.21
30	2	ooo	flat	1	1	88	1	79	9	1	Pit-Seb	190	231	1.043	13	2.20
31	2	ooo	flat	1	1	18	3	79	27	2	Pit-Seb	200	185	1.049	8	1.79
32	3	ooo	gen	1	1	84	4	79	27	24	Pit-Seb	225	262	1.166	10	1.38
33	2	ooo	flat	1	1	109	3	79	27	10	Pit-Seb	149	750	1.097	13	2.11



34	3	ooo	gen	1	1	108	4	79	27	34	Pit-Seb	180	802	1.084	11	2.15
35	2	ooo	flat	1	1	30	5	79	0	1	Pit-Seb	73	239	1.042	9	1.58

## Appendix 2. Kruskal Wallis results for basal area.

## Kruskal Wallis

Variable	Treatment	N	Mean	S.D.	
AB (m2/ha)	(2)OOO/flat	4	22.26	20.77	<b>H = 14.37</b> <b>p value = 0.213</b>
AB (m2/ha)	(3)OOO/slope	3	22.00	7.59	
AB (m2/ha)	(4)OOC/flat	2	20.06	5.37	
AB (m2/ha)	(5)OOC/ridge	3	16.60	1.36	
AB (m2/ha)	(6)OOC/slope	1	10.06	0.00	
AB (m2/ha)	(7)OCC/ridge	5	17.09	2.19	
AB (m2/ha)	(8)OCC/slope	2	25.38	6.54	
AB (m2/ha)	(9)ACC/flat	1	29.74	0.00	
AB (m2/ha)	(10)ACC/slope	2	15.64	5.50	
AB (m2/ha)	(11)CCC/flat	5	20.98	2.95	
AB (m2/ha)	(12)CCC/ridge	4	24.17	6.74	
AB (m2/ha)	(13)CCC/slope	3	15.78	2.06	

## Appendix 3. Kruskal Wallis results for tree density.

- Proving different topographic position within the same LU history.

Kruskal Wallis	H	P	
		23	0.019
Contrast	H	Var(c)	p
2 vs 3	1.80E-03	61	0.966
4 vs 5	1	87	0.3635
4 vs 6	1	157	0.4733
5 vs 6	2	140	0.1391
7 vs 8	4	73	0.0557
9 vs 10	6.40E-03	157	0.9365
11 vs 12	1	47	0.2882
11 vs 13	2	56	0.1757
12 vs 13	1.30E-01	61	0.7173

- Proving different LU histories within the same topographic position.

Kruskal Wallis	H	p	
	22.8	0.019	
Contraste	H	Var(c)	p
2 vs 4	0.11	78.74	0.7353
2 vs 9	2.2	131.23	0.1378
2 vs 11	9.16	47.24	0.0025
4 vs 9	1.24	157.48	0.2646
4 vs 11	4.31	73.49	0.0379
9 vs 11	0.11	125.98	0.7349
5 vs 7	1.26	55.99	0.2616
5 vs 12	0.07	61.24	0.7983
7 vs 12	0.87	47.24	0.3518
3 vs 6	0.29	139.98	0.5924
3 vs 8	0.11	87.49	0.7349
3 vs 10	3.57	87.49	0.0589
3 vs 13	1.53	69.99	0.2168

6 vs 8	0.57	157.48	0.449
6 vs 10	3.66	157.48	0.0558
6 vs 13	1.98	139.98	0.1589
8 vs 10	2.00	104.99	0.157
8 vs 13	0.59	87.49	0.4436
10 vs 13	0.61	87.49	0.433

Appendix 4. ANOVA results for the natural logarithm (Ln) of stem density.

F.V.	SC	gl	CM	F	p-valor
Model	1.41	11	0.13	1	0.4788
Treatment	1.41	11	0.13	1	0.4788
Error	2.97	23	0.13		
Total	4.39	34			

Appendix 5. Analyses of variance (ANOVA) for species richness.

F.V.	SC	gl	CM	F	p-valor
Model	291.29	11	26.48	3.1	0.0106
Treatment	291.29	11	26.48	3.1	0.0106
Error	196.25	23	8.53		
Total	487.54	34			

- Proving different topographic positions within the same LU history.

Treatment	F	p-valor
2 vs 3	0.5	0.485
4 vs 5	0.77	0.3906
4 vs 6	1.25	0.2751
5 vs 6	3.53	0.0732
7 vs 8	0.48	0.4936
9 vs 10	0.7	0.4103
11 vs 12	2.60E-03	0.9597
11 vs 13	0.25	0.6218
12 vs 13	0.27	0.606

- Proving different LU histories within the same topographic position.

Treatment	F	p-valor
2 vs 4	0.24	0.6259
2 vs 9	1.69	0.206
2 vs 11	11.52	0.0025
4 vs 9	0.7	0.4103
4 vs 11	4.88	0.0374
9 vs 11	0.56	0.4608
5 vs 7	3.29	0.083
5 vs 12	2.01	0.1692
7 vs 12	0.13	0.7242
3 vs 6	1.65	0.2117
3 vs 8	2.44	0.1318
3 vs 10	4.52	0.0445

3 vs 13	2.81	0.1071
6 vs 8	5.65	0.0262
6 vs 10	7.81	0.0103
6 vs 13	6.1	0.0213
8 vs 10	0.26	0.6125
8 vs 13	3.90E-03	0.9507
10 vs 13	0.39	0.5381

Appendix 6. Kruskal Wallis for Shannon diversity index.

Kruskal Wallis	H	p
	16.02	0.1406

Appendix 7. Analyses of variance (ANOVA) for mean tree heights.

F.V.	SC	gl	CM	F	p-valor
Model	40.12	11	3.65	2.94	0.0141
Treatment	40.12	11	3.65	2.94	0.0141
Error	28.56	23	1.24		
Total	68.68	34			

- Proving different topographic position within the same LU history.

Treatment	F	p-valor
2 vs 3	2.8	0.108
4 vs 5	1.60E-03	0.9687
4 vs 6	1.24	0.2767
5 vs 6	1.32	0.2618
7 vs 8	2.93	0.1006
9 vs 10	0.01	0.91
11 vs 12	1.39	0.2512
11 vs 13	1.4	0.2485
12 vs 13	4.69	0.0409

- Proving different LU histories within the same topographic position.

Treatment	F	p-valor
2 vs 4	3.28	0.0833
2 vs 9	5.59	0.0269
2 vs 11	13.13	0.0014
4 vs 9	0.77	0.3894
4 vs 11	1.06	0.3133
9 vs 11	0.04	0.8483
5 vs 7	0.17	0.6881
5 vs 12	0.02	0.8876
7 vs 12	0.08	0.7821
3 vs 6	0.86	0.362
3 vs 8	4.72	0.0404
3 vs 10	2.72	0.1127

3 vs 13	6.11	0.0213
6 vs 8	6.23	0.0202
6 vs 10	4.43	0.0463
6 vs 13	7.17	0.0134
8 vs 10	0.23	0.6375
8 vs 13	1.50E-03	0.9696
10 vs 13	0.32	0.5798

#### Appendix 8. Regression analysis for species richness.

- Distance to the sea

Variable	N	R <sup>2</sup>	R <sup>2</sup> Aj	ECMP
Riqueza	35	0.32	0.3	12.3

#### Coefficientes de regresión y estadísticos asociados

Coef	Est.	EE	LI(95%)	LS(95%)	T	p-valor	CpMallows
const	12.41	0.92	10.54	14.27	13.56	<0.0001	
Dist mar (m)	1.80E-03	4.70E-04	8.80E-04	2.80E-03	3.92	0.0004	15.97

#### Cuadro de Análisis de la Varianza (SC tipo III)

F.V.	SC	gl	CM	F	p-valor
Modelo	155.06	1	155.06	15.39	0.0004
Dist mar (m)	155.06	1	155.06	15.39	0.0004
Error	332.49	33	10.08		
Lack of Fit	319.99	32	10	0.8	0.7281
Error Puro	12.5	1	12.5		
Total	487.54	34			

- Time to canopy closure

Variable	N	R <sup>2</sup>	R <sup>2</sup> Aj	ECMP
Riqueza	23	0.45	0.43	10.29

#### Coefficientes de regresión y estadísticos asociados

Coef	Est.	EE	LI(95%)	LS(95%)	T	p-valor
const	8.28	1.58	4.98	11.57	5.22	<0.0001
Edad desde el cierre	0.13	0.03	0.07	0.2	4.16	0.0004

#### Cuadro de Análisis de la Varianza (SC tipo III)

F.V.	SC	gl	CM	F	p-valor
Modelo	152.37	1	152.37	17.31	0.0004
Edad desde el cierre	152.37	1	152.37	17.31	0.0004
Error	184.85	21	8.8		
Lack of Fit	37.15	4	9.29	1.07	0.4023
Error Puro	147.7	17	8.69		
Total	337.22	22			

- % of outcrop limestone

Variable	N	R <sup>2</sup>	R <sup>2</sup> Aj	ECMP
Richness	35	0.19	0.17	13.42

Coefficientes de regresión y estadísticos asociados

Coef	Est.	EE	LI(95%)	LS(95%)	T	p-valor
const	18.86	1.4	16.02	21.71	13.48	<0.0001
cober rock	-0.08	0.03	-0.13	-0.02	-2.79	0.0087

Cuadro de Análisis de la Varianza (SC tipo III)

F.V.	SC	gl	CM	F	p-valor
Model	93.11	1	93.11	7.79	0.0087
cober rock	93.11	1	93.11	7.79	0.0087
Error	394.43	33	11.95		
Lack of Fit	145.96	12	12.16	1.03	0.4601
Error Puro	248.47	21	11.83		
Total	487.54	34			

#### Appendix 9. Regression analysis for mean tree height

- Distance to the sea

Variable	N	R <sup>2</sup>	R <sup>2</sup> Aj	ECMP
Altura	35	0.24	0.21	1.81

Coefficientes de regresión y estadísticos asociados

Coef	Est.	EE	LI(95%)	LS(95%)	T	p-valor	CpMallows
const	4.28	0.36	3.54	5.02	11.79	<0.0001	
Dist mar (m)	6.00E-04	1.90E-04	2.20E-04	9.70E-04	3.21	0.0029	11.04

Cuadro de Análisis de la Varianza (SC tipo III)

F.V.	SC	gl	CM	F	p-valor
Modelo	16.35	1	16.35	10.31	0.0029
Dist mar (m)	16.35	1	16.35	10.31	0.0029
Error	52.33	33	1.59		
Lack of Fit	5.23E+01	32	1.63	24.79	0.1579
Error Puro	0.07	1	0.07		
Total	68.68	34			

- Time to canopy closure

Variable	N	R <sup>2</sup>	R <sup>2</sup> Aj	ECMP
Height	23	0.43	0.4	1.31

Coefficientes de regresión y estadísticos asociados

Coef	Est.	EE	LI(95%)	LS(95%)	T	p-valor
const	2.82	0.57	1.64	4.01	4.95	0.0001
Edad desde el cierre	0.05	0.01	0.02	0.07	3.97	0.0007

Cuadro de Análisis de la Varianza (SC tipo III)

F.V.	SC	gl	CM	F	p-valor
Modelo	17.93	1	17.93	15.73	0.0007
Edad desde el cierre	17.93	1	17.93	15.73	0.0007
Error	23.93	21	1.14		
Lack of Fit	1.75	4	0.44	0.34	0.85
Error Puro	22.18	17	1.3		
Total	41.86	22			

- % of outcrop limestone

Variable	N	R <sup>2</sup>	R <sup>2</sup> Aj	ECMP
Height	35	0.19	0.17	1.89

#### Coefficientes de regresión y estadísticos asociados

Coef	Est.	EE	LI(95%)	LS(95%)	T	p-valor
const	6.57	0.52	5.5	7.64	12.53	<0.0001
cober rock	-0.03	0.01	-0.05	-0.01	-2.82	0.008

#### Cuadro de Análisis de la Varianza (SC tipo III)

F.V.	SC	gl	CM	F	p-valor
Model	13.37	1	13.37	7.98	0.008
cober rock	13.37	1	13.37	7.98	0.008
Error	55.31	33	1.68		
Lack of Fit	19.06	12	1.59	0.92	0.5447
Error Puro	36.25	21	1.73		
Total	68.68	34			