Forest Recovery on Abandoned Farms of the Añasco River Watershed of Western Puerto Rico

By

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Abstract

Species composition and forest structure were described for abandoned farmlands in the Añasco River Watershed. Prior to abandonment, coffee was cultivated on the slopes surrounding the valley while sugar cane and coconut palms were cultivated in the valley. Plots were randomly chosen from an age class map produced from aerial images taken in 1936, 1963, 1994, 2001 and vegetation data collected in 1978. Vegetation was sampled in 500 m^2 circular plots, individuals with diameter at breast height (dbh) greater than 2.5 cm were measured and identified. Structural characteristics were calculated from the data collected in the field. Communities on abandoned coffee plantations and palm plantation were clearly identified, but not for abandoned sugar plantations. There were a total of sixty-nine species identified and six unknown species. Results from the ordination technique determined that age since abandonment was the highest correlated variable to species composition. No significant differences were determined in structural characteristics between plot of the same age on the valley and on the mountains, except for tree density. Species composition at the abandoned coffee plantations resembles the composition of species at the Luquillo Experimental Forest and Central Cordillera Forest of Puerto Rico. Forest structure for some plots on the Añasco River Watershed reached levels comparable to that of mature forests after 80 years of vegetation succession.

Resumen

La composición de especie y la estructura del bosque fueron descritas para las fincas abandonadas en la cuenca de drenaje del Río Añasco. Se cultivaba café en las laderas que rodean el valle, mientras en el valle se cultivaba cana de azúcar y palma de coco. Las parcelas fueron escogidas al azar de mapas de clase de edades producido con ayuda de imágenes aéreas de 1936, 1963, 1994, 2001 y datos de vegetación de 1978. Se muestreo la vegetación in parcelas circulares de 500 m^2, los individuos con 2.5 cm o mas de diámetro a altura del pecho fueron medidos e identificados. Se calcularon las características estructurales de los datos tomados en el campo. Se pudieron identificar comunidades en fincas abandonadas de café y palma, pero no para fincas abandonadas de caña. Se identificaron un total de sesenta y nueve especies y hubo seis desconocidos. Los resultados de la técnica de ordenación determinaron que tiempo de abandono fue la variable más altamente correlacionada a la composición de especie. No se detectaron diferencias significativas en características estructurales entre parcelas de la misma edad en el valle y las montañas. La composición de especie de las fincas abandonadas de café se semeja a la composición de especie del Bosque Experimental de Luquillo y de la Cordillera Central de Puerto Rico. La estructura del bosque para algunas parcelas en la cuenca del Río de Añasco llegó a niveles comparables con bosque maduro bajo 80 años de sucesión.

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- Thanks

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1 INTRODUCTION

Tropical deforestation for agriculture continues to be a major contributor to the worldwide loss of biodiversity (Reitsma *et al*. 2002). Northern Latin America loses 1 to 4 % of forest cover per year due to various forms of agriculture (Reitsma *et al*. 2002). Brazil has the highest deforestation rate in the world, according to some estimates; deforestation rates may be as high as 1.5×10^6 to 2.0×10^6 ha/yr (D.L Skole *et al* 1994). The Atlantic rain forest of Brazil covered more than 1,000,000 km^2 when the Portuguese colonists settled in the 16th century. Since then it has been reduced to 7.5% of its original size; only 10% of the remaining forest is primary vegetation (Le Breton, 2000). Deforestation mainly occurs to develop pastures, cultivate coffee, obtain fuel wood and prepare for urban development. Deforested land with short-term agricultural use, subsequent abandonment due to declining yields and poor management have resulted in extensive areas of secondary tropical forests (Brown and Lugo, 1990). Puerto Rico, as well as other tropical nations, was a victim of this massive deforestation. The Añasco Valley in western Puerto Rico was used to cultivate sugar cane and graze cattle. The surrounding mountains that border the northern and eastern portions of the valley were mainly used to cultivate coffee and citrus fruits.

In the late 1940s as the political status on the island was changing; so were the island's economic policies. The governments of the United States and Puerto Rico implemented the Law of Industrial Incentives of 1947 (Operation Bootstrap), a rapid industrialization program that shifted the economy from agriculture to light industry (textile production) (Deitz 1986, Grau *et al*. 2003). This economic strategy created jobs and induced economic growth. Hence, the rural population was forced to move to urban areas to work in manufacturing plants. This population shift and resulting farm abandonment resulted in the development of secondary forests through the natural regeneration process (Marcano-Vega *et al*. 2002).

These secondary forests play an essential role in forest ecosystem restoration and rehabilitation. They foster native and introduced plant species in their understory that will form mature ecosystems. Secondary forests prevent soil erosion. They improve soil and water quality, help conserve nutrients, moisture, soil organic matter and genetic diversity (Brown and Lugo, 1990). The services provided by secondary forests justify research, possible management and conservation. The forests of the Añasco Valley are some of the few lowland forests left in Puerto Rico.

Most studies on secondary forest dynamics have been conducted in the eastern and central portions of Puerto Rico. Secondary forest succession in the Añasco River Watershed presents an excellent opportunity to study forest regeneration post sugar cane, palm and coffee cultivation on the west coast of Puerto Rico. In this study I describe and compare species composition of the forests that have regenerated on abandoned farms in the Añasco River Watershed. Structural characteristics were calculated to assess regeneration of secondary forest on these abandoned farms.

My hypothesis stated that species composition and structural characteristics would differ among plots of the same age class and treated by different agricultural practices. Another prediction stated that age since abandonment would be the most influential factor determining species composition. If we understand the process of secondary succession on abandoned agricultural land, we may be able to accelerate their transition to mature forest (Aide *et al*., 1996)

2 LITERATURE REVIEW

2.1 Agriculture in Western Puerto Rico

Human activity has modified the vegetation of Puerto Rico for centuries. At one point, natural vegetation was almost completely removed (Wadsworth 1950). Aide *et al*. (1996) described the coastal valleys of Puerto Rico as being dominated by the cultivation of sugar cane while the mountainous areas were cultivated by coffee and tobacco in the late 19th century and early 20th century. By 1899, 55% of the island was converted to pasture (Grau *et al*. 2003). Agriculture was Puerto Rico's primary economic activity for the first four and a half centuries of its colonization. In 1934 agriculture represented 45% of the Gross National Product, while manufacturing only represented 7% (Grau *et al*. 2003).

The Añasco River Watershed and the Uroyoán Mountains were major agricultural sites in western Puerto Rico. The primary crops produced were sugar cane, coffee and citrus fruits. Other crops were grown for family consumption. Some portions of land in each location were used to graze cattle, and to extract wood for charcoal production. Agricultural production in this area declined following the implementation of the 1947 Law of Industrial Incentives (Operation Bootstrap). The number of farms in the municipality of Añasco dropped from 858 in 1940 to 303 farms in 1998 (Census Bureau, United States Department of Agriculture, Census of Agriculture 1950, 1998). Consequently, the agricultural sector lost its lead role in economic activity. Following the trend in the municipality of Añasco, sugar cane production in the municipality of Luquillo also declined from 28 percent of total agricultural production in 1936 to 0 percent in 1988 (Thomlinson *et al*., 1996). Thomlinson *et al.* (1996) calculated a dramatic increase in dense forest from 15 percent in 1936 to 54 percent in 1988. Coffee cultivation in the Luquillo Mountains declined due to hurricanes that caused extensive property damage and led many residents to leave the area in 1899, 1928, 1931, and 1932 (Zimmermann *et al*. 1995). The abandonment of agricultural practices and population displacement from rural areas to urban areas resulted in secondary forest succession.

Secondary forests regenerate largely through natural processes following major human and/or natural disturbances. The area of forested land, mostly secondary growth, in Puerto Rico has increased during the last half of the 20th century. In 1931 an estimated 81,000 ha were covered by forest (Birdsey and Weaver 1987). Helmer *et al*. (2002) reported that in 1992 an estimated 364,000 ha were covered by some type of forest. This increase in forested land is due in part by farmland abandonment since the late 1940s. Franco *et al*. (1997) estimated that 23,365 ha of the 143,993 ha of timberland available in Puerto Rico were located in abandoned coffee plantations.

2.2 Secondary Succession

Uhl *et al*. (1980) described successional patterns associated with slash and burn agriculture in the Upper Rio Negro on the Amazon Basin. They observed that sixteen months after abandonment the total density of non-woody plants had declined and woody plants dominated the study site with the tallest individuals 3-4 m in height. The first stage of forest succession in the lowland moist and wet neotropics is dominated by grasses, shrubs and forbs, which are eventually shaded out by short-lived and light demanding "pioneer" species (Guariguata and Ostertag 2001). After this period the canopy is dominated by long-lived, taller, light demanding tree species, which are eventually replaced by shade tolerant species. The speed of secondary succession depends on *in situ* environmental conditions.

Research has suggested that factors like low seed dispersal, seed predation, grass competition and lack of soil nutrients are barriers to forest regeneration (Uhl *et al*. 1988; Aide and Cavalier 1994). Uhl *et al*. (1988) stated that intensity of land use greatly influenced succession. Secondary forest composition was simpler in more intensely used pastures. Lightly used pastures returned to forest quickly. Uhl *et al*. (1988) reported an eight year old site with a 13 m high closed canopy. Heavily used pasture sites had few hardwoods and were mainly dominated by grasses. Guevara *et al*. (1986) observed that trees remaining in abandoned pastures provided favorable conditions for secondary forest trees to become established. Lightly used pastures with remnant trees may have the highest probability of regenerating into secondary forests.

2.3 Puerto Rico's Secondary Forests

The majority of the secondary forests in Puerto Rico developed on abandoned farms. These secondary forests are characterized by fast growth (Guariguata and Ostertag 2001). The coastal valleys of the island are mainly forested by fast growing pioneers and shrubs. They provide conditions suitable for the recolonization of mycorrhizae following agricultural use (Brown and Lugo 1990). They have short life cycles adapted to the cycle of human land use. Secondary species produce many seeds that can be widely dispersed. Seeds remain viable in the soil for long periods of time and can germinate on impoverished land, suggesting low nutrient requirements (Brown and Lugo 1990). Secondary forests play an important role as the precursors that prepare the stage for the development of mature forests.

Crow (1980) in his studies of forest dynamics identified two distinctive phases of structure at his study site noticeable in a period of 30 years. The first phase was characterized by an increase in the number of stems, basal area and stand biomass. In the second phase a reduced rate in basal area, total number of stems and species was observed, but biomass increased. Aide *et al.* (2000) observed similar results in their study of forest recovery in abandoned pastures. Basal area, stem density, biomass and the number of species increased rapidly in the first 25 years after abandonment. After forty years of recovery these structural characteristics leveled out or decreased, with the exception of biomass, which continued to increase.

Vegetation structure is affected by age since abandonment. During the first seven years after pasture abandonment Aide *et al.* (1995) observed virtually no woody vegetation, but during the following 10-15 years stem density increased rapidly. Marcano-Vega *et al.* (2002) concluded that there was a positive relationship between age since abandonment and basal area in abandoned shade coffee and abandoned pastures.

Other factors affect vegetation structure and species composition. Fernandes and Sandford (1995) stated that dissimilar edaphic factors produced by different agricultural practices had an observable effect on structural characteristics and species composition. They observed that abandoned cacao plantations had a higher basal area and stem density than abandoned pastures, but pastures had higher species richness than abandoned cacao plots.

Clark *et al.* (1998) showed that tree species composition of abandoned farmlands in Costa Rica varied by sites according to soil type. Land use history and its intensity determine species composition and structural characteristics of secondary forests.

Aide *et al.* (1996) described forest recovery along an elevation gradient; they determined that elevation did not affect the structural characteristics of vegetation, but did affect species composition. They concluded that the best predictor of forest recovery was not elevation but age since abandonment. However, in another study conducted in the karst region of Puerto Rico, Rivera and Aide (1998) stated that elevation changes were the best predictors of forest recovery, followed by age since abandonment. Secondary forests that regenerate on abandoned farmlands are affected by a varied set of anthropogenic and environmental factors.

3 MATERIALS AND METHODS

3.1 Study Site

The Añasco River is the longest river in western Puerto Rico. It is born in the Central Cordillera and drains west to the bay of Mayagüez. The Añasco Valley is located between the municipalities of Mayagüez and Añasco at roughly 18° 13’ 48’’N to 18° 19’ 0’’ N latitude and 66° 58’ 0’’ W to 67° 12’ 42’’ W longitude. The valley is bordered to the north by the La Cadena Mountains, to the southeast by the Uroyoán Mountains, and to the west by the bay of Mayagüez.

Annual precipitation for this area varies from 1650 mm to 1780 mm (National Weather Service Forecast Office Website, 2006). According to the Holdridge life zone system, the potential natural vegetation in the valley and adjacent mountain ranges is classified as subtropical moist forest (Ewel and Whitmore, 1988). The composition of the original forests is unknown, since they were cleared by the 1800’s, but surveys of relict sites suggest that *Manilkara bidentata*, *Calophyllum calaba*, *Byrsonima spicata*, and *Tabebuia heterophylla* were important species (Wadsworth, 1950).

The valley has rich alluvial soils, while the mountains surrounding the valley are dominated by volcanic soils. Forest removal was mainly done for agricultural practices and urban development. The main crops produced were sugar cane, citrus fruits, coffee and farinaceous crops (Bureau of Census, 1950). At the present time there is no sugar cane production and other agricultural practices have diminished considerably (Bureau of Census, 1990).

.3.2 Mapping Forest Cover

Sampling was done in secondary forests of abandoned farmlands located in the Añasco River Watershed. Forest cover was mapped for aerial images taken in 1936, 1963, 1994, 2001 and land cover data collected in 1977. Aerial photographs from 1936 and 1963 were acquired from the Photogrammetry Service of the Highway Authority of Puerto Rico. Aerial photographs from 1994 and Ikonos images from 2001 were provided by the Ecogeography Laboratory of the Biology Department at UPR-Mayagüez. Forest stands visible in the 1994 and 2001 images were digitized using Arc Map 8.0. Land cover data collected in 1977 were integrated to the digitized data and a forest age map was created with Idrisi 32. The 1936 and 1963 aerial photographs were manually processed and analyzed to verify forest cover on those two dates, respectively. The aerial images were also used to specify the perimeter of the study area and assess land use history.

3.3 Determining Forest Age and Land Use History

Site age was determined by calculating the difference of years between the date of the last photograph with agricultural activity to and the date of the first photographs with evidence of shrubs and small trees. The oldest forest sites were areas with forest cover seen in the 1936 aerial photograph. Land use history was assessed by photo interpretation and interviews with area residents and farm owners.

3.4 Sampling Design

Plot sites were selected in a stratified random design. Plots were distributed from sea level to a maximum elevation of 125 m (the maximum elevation of the south facing slopes of the La Cadena Mountains). Study site was divided into two major habitat areas, mountains and valley. The valley sites were located from sea level up to 25 m above sea level. Mountains plots were located at elevations greater than 25 m and up to 125 m above sea level. Plots were classified as abandoned sugarcane, palm and coffee plantations. Sampled sites were located in the field with USGS topographic maps, a GPS unit, compass and 50 meter tape.

Vegetation on site was sampled using a circular plot, with a 12.6 m radius (i.e., 500 m^2). Woody stems 2.5 cm or greater in diameter at breast height were counted, tagged, and identified. Floral and vegetative material from unknown trees was collected, when possible, for identification. Nomenclature of the identified individuals follows Liogier and Martorell (2000). Slope inclination was measured for all sample plots. Structural characteristics [basal area, stem density, Shannon-Weiner diversity index (H') and species richness] were calculated from data obtained at the plots. Importance values were calculated for each species from the individuals' basal area and density. This importance value was used in the ordination analysis for species composition.

3.5 Analysis

To detect significant differences in structural characteristics between plots sampled in the valley and on the mountains a Wilcoxon Rank Sum test (Mann-Whitney U-test) was performed with Info Stat Statistical Software (www.infostat.com.ar). This test assumes that independent random samples were taken from two populations with identical distribution, but that these populations can be shifted away from each other. A 5% ($\alpha = 0.05$) level of significance was used to run the test. Due to the unbalanced nature of the data, a non-parametric test was employed to detect significant differences between the age classes of different sampled areas. Plots of the same age class were compared.

To analyze species composition at the plots indirect gradient analysis was performed using non-metric multidimensional scaling ordination. Species considered for the analysis were those that were surveyed in two or more plots. Trees species occurring in one plot were not included in the analysis. The ordination was conducted using Sørensen distance on the entire dataset. Forty runs were performed using a random starting point with real data and 50 runs were performed with randomized data. The instability criterion for accepting the solutions was 0.000010 with a maximum of 400 iterations (McCune and Medford 1999).

Species that only occurred in one plot were removed from the species/plot matrix prior to the analysis. The environmental variables considered in this study (in order to assess their effect on vegetation patterns at the abandoned farms) were: elevation, time since abandonment, slope, aspect, and land use type (coffee, palm or sugar cane plantation). Using a flexible beta linkage with Sørensen distance and beta = -0.25, communities were classified according to land use history with in the data set.

Indicator species analysis was performed to characterize species composition according to previous land use. The analysis was performed with the importance values for identified species for each land use. The indicator value (IndVal method) proposed by Dufrêne and Legendre (1997) combines relative abundance and relative frequency. Each IndVal is the product of two indices:

$$IndVal_{ij} = A_{ij} \times B_{ij} \times 100$$

$$A_{ij} = \#\text{ of trees}_{ij} / \#\text{ trees}_{i}$$

$$B_{ij} = \#\text{ of sites}_{ij} / \#\text{ of sites}_{j}$$

where A_{ij} (a measure of specificity) is the mean abundance of species I at the group *j* sites compared to all groups in the study, and B_{ij} (measure of fidelity) is the relative frequency of occurrence of species I at group *j* sites. Statistical significance of indicator values was assessed using a Monte Carlo test with a 5 % significance level ($p \leq 0.05$) and 1000 randomized permutations. Species with IndVal values higher than 50% were accepted for analysis.

4 RESULTS

4.1 Forest Structural Characteristics

A wider range of stand age categories was obtained in the valley than on the mountains. Natural secondary forests on mountains were not distinguishable from coffee plantations on aerial photographs. Nine plots were sampled on the mountains; one plot was 35 years old; one 42 years old and seven were at least 84 years old (figure 2). Eight of mountain plots were classified as abandoned coffee plantations according to interviews with farm owners, area residents and old remnant coffee plants. According to a farm owner interviewed, plot M01, was an abandoned pasture.

Ten plots were sampled on the valley, which were classified abandoned coffee, sugarcane or palm plantations. Plots V02, V03, V11 and V16 were classified as abandoned coffee according to interviews with farm owners. Remnant palms and aerial images permitted plots V05, V09 and V10 to be classified as abandoned palm plantations. The remaining valley plots were classified as abandoned sugarcane plantation (V06, V07, and V08) according to the aerial images. The only statistically comparable age classes were the 84 year old class. The lack of younger age classes on the mountains limited our analysis to the oldest age class.

A Wilcoxon Rank Sum Test (Mann-Whitney U-test) was administered with the dataset from the oldest age class, 84-year old, to determine differences in structural characteristics. No significant differences between basal area ($T = 22$, $P = 0.2667$), diversity ($T = 11$, $p = 0.2667$) or species richness ($T = 14$, $P = 0.6833$) were detected among plots of same age class. A significant difference was determined for tree density (T = 7, P = 0.0333) between plots of same age class. A positive relationship could not be established between the structural characteristics (basal area, species richness, diversity (H'), and stem density) of abandoned sugar and palm plantations and age since abandonment.

4.2 Species Composition

A total of 1571 individual trees were surveyed within the 9500 m^2 total sampled area, sixty-nine species were identified in the study site and 6 species could not be identified due to a lack of reproductive material. Three unidentified species were found on the mountains and three were found in the valley. A total of fifty-two species were identified on the mountains and forty-two species were identified in the valley. Of the fifty-two species found in the mountain region, thirty-four were native, fourteen were exotics and four could not be identified. Plots sampled in the valley differed in species composition from plots on the mountains, but had a similar ratio of native to exotic species. In the valley forty-three tree species were identified, twenty-seven were native, fifteen exotic and one was unknown.

Syzygium jambos had the highest absolute density on the mountains followed by *Guarea guidonia* and *Inga laurina*. *Albizia procera* had the maximum absolute density value of all the identified species in the valley followed by *Psidium guajava*, and *Spathodea campanulata.* Tables 2 and 3 illustrate top ten species with the highest importance values at the abandoned coffee plantations on the mountains and in the valley. Twenty three species (Appendix II) were identified in both major habitats of the study area, nineteen were native and four were exotics. *Albizia procera* had the highest stem density value of al identified trees species on the valley and *Syzygium jambos* had the highest stem density on the mountains.

4.2.1 Ordination Results

Differences in species composition were reflected by the results of the ordination technique. The best Non Metric Multidimensional Scaling (NMS) solution was a 3-dimensional solution and 147 iterations were performed with the data set (stress = 10.9 and instability = 0.00001). Land use history was the anthropogenic variable most often separating plots. Abandoned coffee plantation plots were clustered together and separated from the other plots (abandoned sugar and palm plantations) (figure 3). This cluster of plots also contained some plots that were sampled in the valley (plots V11, V02 and V03). The other two smaller groups correspond to plots on abandoned palm plantations (V05, V09 and V10) and the plots on abandoned sugar plantations (M01, V07 and V08). There is a marked effect of past land use type and environmental variables illustrated by the ordination graph.

Age since abandonment, slope and elevation had the most influence on species composition, specifically in abandoned coffee plantations. According to the Pearson and Kendall correlation index, age since abandonment was the most correlated to ordination axis 1 ($r^2 = 0.345$). The second ordination axis was most correlated to slope ($r^2 = 0.249$), followed closely by elevation ($r^2 =.0.217$). The third ordination axis was most correlated to age since abandonment, but to a low degree ($r^2 = 0.124$). The ordination biplot in figure 4 illustrates the correlation of the variables to the plots. The NMS analysis reveals that environmental variables, such as age since abandonment and slope, have a marked effect on species composition. Elevation and aspect did not have a considerable effect on species composition.

There is a definite association between species composition and previous land use. The ordination graph illustrates a cluster of species that coincide with plots on abandoned coffee plantations (figure 5). The other two land uses (sugar and palm plantation) are associated with fewer species, than the abandoned coffee plantations. Indicator species analysis (Dufrêne and Legendre 1997) identified species representative of abandoned coffee plantations. These top indicators included *Guarea guidonia* (IndVal = 94.4), *Inga laurina* (IndVal = 86.9), *Ocotea leucoxylon* (IndVal = 79.8), *Zanthoxylum martinicense* (IndVal = 63.6), and *Spathodea campanulata* (IndVal = 62.2).

Abandoned palm plantation top indicator species included *Cocos nucifera* (IndVal = 100.0), *Calophyllum calaba* (IndVal = 100.0), *Terminalia catappa* (IndVal = 98.0), *Annona glabra* and *Coccoloba uvifera* (IndVal = 66.7). *Annona glabra* and *Coccoloba uvifera* are coastal plain tree species natives to Puerto Rico. Indicator species analysis did not determine indicator species for plots on abandoned sugar plantations. *Albizia procera* (IndVal = 45.9, $p = 0.083$) was the only individual closest to the 50% cut off point. These plots sampled in the valley were not associated with specific community of plants. A cluster analysis reinforced the results obtained from ordination by grouping the plots associated with the valley community and the plots associated to the slope community. Appendix III illustrates the graph resulting from the cluster analysis.

4.2.2 Uncommon species on the Añasco River Watershed

Twenty eight tree species were not considered in the Non Metric Multidimensional Scaling because they did not meet the criteria for analysis. Excluded species included uncommon native species on the Añasco River Watershed like *Tetrazygia elaeagnoides* and *Myrcia citrifolia* that occurred on the mountains. *Sabal casuarium*, a native palm, was identified in the valley. *Byrsonima spicata*, a species considered part of the original vegetation of lowland forests in Puerto Rico (Wadsworth 1950) was identified in the study area. These uncommon species are important components of plant diversity of the Añasco River Watershed.

5 Discussion

Centuries of land-use change has resulted in extensive areas of agricultural and pasture lands, plantations and degraded forest that have greatly altered the species composition of many landscapes (Ojima *et al.* 1994). Since Puerto Rico was colonized, its land was deforested and used for agriculture. The Añasco Valley located in western Puerto Rico was subjected to commercial agricultural practices for over three hundred fifty years. The best land for agricultural production was cleared and the original species composition of these lowland forests was lost. Wetland forest areas in the Añasco Valley that were not cleared may contain elements of what we can consider the original vegetation. From aerial photographs of 1936 it can be determined that these forest patches are of the oldest stands in the Añasco River Watershed. The mountains surrounding the Añasco Valley also contain some of the oldest forest of the watershed. These fragmented forested areas are limited to abandoned farmland on the valley and mountains, divided by urbanized areas and active farms.

The mountains that were used to cultivate coffee contain a defined and mature secondary forest community, in contrast to the undefined communities associated with the valley. The actual species composition observed in the study is a direct result of human manipulation of the vegetation and age since abandonment. The communities are composed of fast growing exotics and dispersed native species. The native species outnumber the exotics, but the exotics are more abundant. For example, *Syzygium jambos* and *Albizia procera* (two exotic tree species), had the highest densities on the mountains and in the valley, respectively. Anthropogenic and environmental factors have had a marked effect on the recovery of these forest communities.

The pattern of forest recovery in the Añasco River Watershed is similar to the case of Luquillo, in eastern Puerto Rico, reported by Thomlinson *et al*. (1996). They reported a constant decrease in sugar cane production from 1936 and an increase in forested area surrounding the Caribbean National Forest. Recent increase of urbanization projects on abandoned farmlands is reclaiming part of the regenerated secondary forests in Añasco (personal observation).

5.1 Forest recovery

Age since abandonment had a marked effect on species composition and secondary forest structure on abandoned coffee farms in the Añasco River Watershed. It is considered the best predictor of forest recovery in the study site. The sites sampled in the valley were subjected to two different land use practices, sugar and palm plantation. Forest recovery on the Añasco Valley is slow and erratic compared to recovery following other human and natural disturbances (Crow 1980, Uhl 1988, Brown and Lugo 1990). The sites on the mountains were cultivated with coffee.

Forest recovery for the Añasco River Watershed is dependent on site specific conditions. Three 15-year-old valley sites presented three very different values in basal area, density and species richness. For example, values for total basal area for three 15 years old plots varied from 6.38 to 20.3 to 42.1 (m^2ha^{-1}) (Appendix I); this may be due to land use intensity. It can be inferred that plots with lower values were used more intensely (higher use of mechanization and fire to clear land). Older sites that were sampled in the valley showed the same erratic pattern. Results obtained in this study differ from those obtained by Aide *et al*. (1995) and Aide *et al*. (1996), in which a positive relationship between age since abandonment and land use was established. Results obtained in this study concur with Rivera *et al*. (2000) in which the lack of a chronosequence did not allow for speculation on succesional trajectories among land uses. Results of this study represent a snapshot in time showing how the various uses of land by humans affect the structure and composition of forest recovery.

Land use history has affected forest regeneration at abandoned coffee plantations in the Añasco River Watershed. Forests on abandoned farms on the mountains surrounding the Añasco Valley on average have higher stem density, species richness and species diversity, but lower basal area. Results obtained from comparing the oldest sites in both major habitats, in which no significant differences where determined in three of four structural characteristics. This is evidence that given enough time, at least eighty years of recovery, the study area will attain structural values similar to those of an old growth mature forest. Zimmerman *et al.* (1995), Rivera and Aide (1998) and Pascarella *et al.* (2000) describe the convergence of forest structural characteristics for different types of land use. They have sated that after more than sixty years of growth the structural characteristics of secondary forests resemble those of old growth forests in Puerto Rico. They also pointed out that species composition after sixty years of recovery was very different from that of old growth forests. This suggests that forest recovery in the Añasco River Watershed is certain, but it will take centuries to obtain species composition similar to that found in old growth forests.

Species composition of secondary forests on the older abandoned coffee plantations of the Añasco River Watershed is similar to that of older abandoned coffee plantations of the Cordillera Central of Puerto Rico described by Marcano-Vega *et al.* (2002). *Guarea guidonia*, *Ocotea leucoxylon* and *Casearia sylvestris* were common species identified on both study areas

5.2 Species Composition of the Añasco River Watershed

Forests that regenerated in the Añasco River Watershed are represented by native and exotic species. Similar species composition was observed in studies by Aide *et al.* (1995); Aide *et al*. (1996); Chinea (2002); and Zimmermann *et al*. (2000). Most of the species specified by Marcano-Vega *et al*. (2002) at low elevations in different age classes are observed at the abandoned coffee plantations of the Añasco River Watershed. Abandoned coffee plantations in the Añasco Valley are dominated by *Syzygium jambos,* a shade tolerant, animal dispersed, invasive exotic tree that has the capacity to resprout and reproduce vegetatively. This tree does not produce numerous individuals but does produce numerous stems per individual, one reason why it obtained a value for high density. Aide *et al*. (2000) observed that *Syzygium jambos* is dispersing through old growth forests of the Luquillo Experimental Forest, so its spatial distribution is not limited to secondary forests, as it can invade different types of habitat.

Syzygium jambos was rare in the valley plots, in contrast to observations by Aide *et al.* (1995) that lowland sites were dominated by *Mangifera indica* and *S. jambos*. In this study individuals of *M. indica* were few in the mountains and the valley. They recorded high basal area values and density due to their large diameter at breast height (the largest dbh in this study was obtained from a *M. indica*). These *Mangifera indica* individuals identified in the study area are relicts that predate abandonment, planted and protected by farmers. These two species are not considered indicators in either of the two major habitat areas of the Añasco River Watershed.

The ordination technique conducted with the full data set suggested that land use history and age since abandonment had the strongest effect on species composition of plots associated with abandoned coffee plantations. The oldest sites in the Añasco River Watershed had the highest species richness and diversity values. The main species clustered by non-metric multidimensional scaling were *Syzygium jambos*, *Guarea guidonia*, *Ocotea leucoxylon*, *Zanthoxylum martinicense*, *Inga laurina*. Indicator species analysis corroborated the results obtained from the ordination technique, pointing out the abovementioned species as top indicators, with the exception of *S. jambos*. *Guarea guidonia* is a common, shade tolerant trees specie in old forest sites (Aide *et al.* 1996, Aide *et al.* 2000, Rivera *et al*. 2000) and covers an important niche in secondary forest recovery, because it can establish itself in different types of habitat with different past land use types.

Species composition on mountains surrounding the Añasco Valley is similar to that seen at abandoned coffee plantations of the Luquillo Experimental Forest and abandoned coffee plantations of the karst region of northern Puerto Rico, which are dominated by *G. guidonia* (Zimmermann *et al*. 1995, Rivera and Aide 1998). In contrast to Zimmermann *et al*. 1995 and Rivera and Aide (1998), who determined that *Inga vera* and *Inga laurina* were not abundant because they were harvested for charcoal production. These two species of *Inga* were as common in plots in the valley as they were on the hills, indicating that these trees were only used in the study area as shade trees and not as a direct source of income.

Ordination results suggest that species composition on abandoned farmlands in the Añasco Valley is simple and undefined. It differs from the composition of species on the mountains. Results obtained from the indicator species analysis performed on the dataset demonstrated that four exotic species were top indicators, while four of the top five indicators on the mountains were native species. Species composition and secondary succession in the Añasco Valley are similar to that described by Aide *et al.* 1996 in their study of abandoned pastures in northeastern Puerto Rico, where pioneers like *Albizia procera*, *Casearia sylvestris, Miconia prasina* and *Psidium guajava* are replaced by *Terminalia catappa*, *Calophyllum calaba*, *Andira inermis*, *and Guarea guidonia.*

Two outlying plots (V06 and V16) surrounding the large cluster of plots were more similar in species composition to the mountain community than to the valley community. One plot sampled on the mountains was grouped with the abandoned sugar cane plantation plots. This can be attributed to the proximity of this plot to the valley and current environmental conditions that resemble those of the valley.

5.3 Seed Dispersal

Forest regeneration may occur by four pathways: (1) advance regeneration (seedlings); (2) sprouts; (3) seed bank; (4) seed dispersal (Aide *et al.* 1995). Given that our sites were used at least for one growing season for as long as 40-50 years and the seed bank, seedlings and sprouts would have been wiped out after two or three years of continuous use, the only viable pathway of forest regeneration is seed dispersal. Seed dispersal encounters a series of barriers including a lack of perching sites for dispersing birds and bat, harsh environmental conditions, competition with other established herbaceous plants and distance from the seed source.

Seed dispersal in the Añasco valley is mainly carried out by wind. *Spathodea campanulata*, *Albizia procera* and *Leucaena leucocephala*, are all introduced, wind dispersed tree species were found in the Añasco Valley. These three individuals are common pioneer species of this watershed. They condition soil, prevents erosion, reconstitute microbial flora and develop favorable environment for arthropods and other soil invertebrates. *Tabebuia heterophylla*, a common wind dispersed native tree specie in pastures of eastern Puerto Rico (Zimmermann *et al* 2000), was rarely identified (only in plot V05) on the Añasco valley. This could be due to the harsh conditions for seed germination (seeds not reaching the ground), predation of seed or distance between the seed source and the valley. The harsh soil conditions on the valley are due the high intensity of land use of the valley site. The pattern of wind dispersal is not clear; but we can presume that wind dispersed individuals follow the general wind direction, NNE. This would indicate that seeds travel from the adjacent forest in an east to west trajectory, from the mountains to the valley below.

Animal dispersed trees species are less common in the valley, but no less important. Two of the top indicator species of the abandoned palm plantations of the valley, *Terminalia catappa* and *Calophyllum calaba*, are animal dispersed. Animals are dispersing seeds from the valley area to the mountains and vice versa. Animal dispersed species are more common on the abandoned coffee plantations than in abandoned sugarcane and palm plantations. Abandoned coffee plantations present positive conditions for forest regeneration. The vegetation cover of these abandoned coffee plantations provides a more hospitable environment for seed to germinate. Lower intensity of use of coffee plantations resulted in better soil quality, than soil quality of other more intense land uses. Plant recruitment is higher in the abandoned coffee because of more perching sites than in abandoned pastures, sugarcane or palm plantation. A more dense vegetations cover provides animal dispersers more protection from predators, than in open and exposed areas of abandoned sugarcane and palm plantations.

5.4 Secondary Forest Management

Future management and conservation of these secondary forests is necessary. As the demand to use land for commercial and urban development increases it is important to reserve ecologically sensitive and important areas. Birdsey and Weaver (1986) concluded that abandoned coffee plantations offered many opportunities if managed adequately, including timber harvesting, plantation forestry and a variety of agroforestry alternatives. In *Mata Atlantica,* terra firme forest of Brazil, LeBreton (2000) describe the effectiveness of some agroforestry techniques. LeBreton (2000) stated that intercropping (which reduces soil impoverishment and improves crop diversity), direct seeding, and native species management has been successful in sustainable farms in Brazil. He is also experimenting with the use of leguminous plants to maintain adequate soil properties to allow forest regeneration and high agricultural productivity. Awareness of the importance of natural resources, as in the case of secondary forests, has to be created among the public. The Añasco River Watershed presents the perfect situation for the management and conservation of natural resources in harmony with the current social and economical growth of Puerto Rico. To restore the original species composition in the study area may be difficult, due to lack of vegetation data pre-Columbian times and a lack of knowledge of Taino agricultural practices in the area. However, a functional ecosystem can be restored to be managed adequately for different purposes.

6 Conclusions

1. The secondary forest on abandoned coffee plantations Añasco River Watershed have similar in species composition as those described by Marcano-Vega *et al*. (2002).
2. Secondary forests of the Añasco River Watershed have a high conservation values. They contain valuable timber tree species like *Guarea guidonia* and *Calophyllum calaba*. They offer opportunities for agroforestry projects and ecotourism opportunities.
3. Secondary forests of the Añasco River Watershed help improve ecosystem condition. For example, they control soil erosion, which helps water quality and promote the reestablishment of native flora and fauna.

7 Recommendations

1. Federal, state and local natural resource management agencies, with collaboration of the communities of Añasco and Mayagüez municipalities and the scientific community of the University of Puerto Rico-Mayagüez should create an extensive management plan for the Añasco River Watershed.
2. State and local agencies and University of Puerto Rico-Mayagüez should promote ecotourism activities and agroforetry research.

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Table 1. Summary of mean values for structural characteristics and standard error calculated from data obtained from the oldest plots (84 years) on major land use areas. The structural characterisitics calculated were: basal area (BA), density (DENS), Shannon-Weiner Index (H') and species richness (RICH)

Area	BA ($m^{-2}ha^{-1}$)	DENS (tree ha^{-1})	H'	RICH
Mountains	**33.7 ±4.31**	**2077.1 ± 165.9**	**2.14 ± O.13**	**16.3 ± 1.86**
Valley	**48.5 ±9.10**	**1280 ± 197.3**	**1.84 ± 0.28**	**13.7 ± 4.33**

Table 2. Mean density (DENS) basal area (BA) of top ten species with highest importance value on the mountain plots. Density is expressed in number of trees per hectare (#/ha). Basal area is expressed in square meter per hectare ($m^{-2}ha^{-1}$)

SPECIES	**DENS (#/ha)**	**BA (m^{-2} ha^{-1})**
Syzygium jambos	**1660**	**18.6**
Inga laurina	**1560**	**44.9**
Guarea guidonia	**1240**	**16.6**
Ocotea luecoxylon	**540**	**7.85**
Spathodea campanulata	**480**	**8.74**
Hymenaea courbaril	**280**	**14.4**
Cecropia schreberiana	**220**	**26.8**
Mangifera indica	**200**	**81.8**
Casearia sylvestris	**180**	**2.6**
Andira inermis	**140**	**7.55**

Table 3. Mean density (DENS) basal area (BA) of top ten species with highest importance value on the valley plots. Density is expressed in number of trees per hectare (#/ha). Basal area is expressed in square meter per hectare ($m^{-2}ha^{-1}$)

SPECIES	**DENS (no./ha)**	**BA (m^{-2} ha^{-1})**
Albizia procera	**2500**	**23.6**
Calophyllum calaba	**1060**	**10.2**
Faramea occidentalis	**880**	**1.47**
Guarea guidonia	**780**	**16.2**
Inga vera	**600**	**9.62**
Terminalia catappa	**420**	**10.7**
Psidium guajava	**380**	**6.3**
Spathodea campanulata	**380**	**58**
Cocos nucifera	**220**	**11.7**
Mangifera indica	**40**	**40.3**

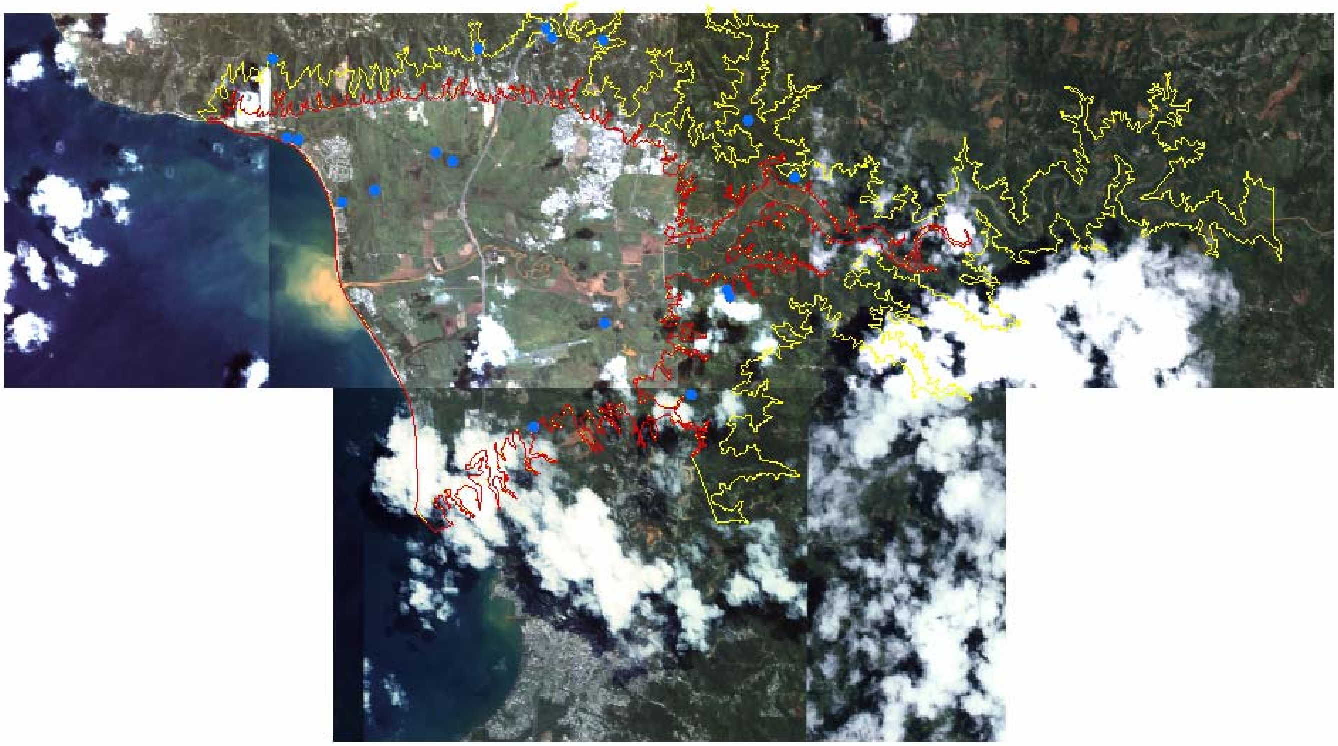


Figure 1. Aerial image of Añasco River Watershed marked with red contour lines that represent elevation from sea level to 25 m above sea level. The space between the outer yellow contour line and red contour line represents elevations from 25 m up to 125 m. The blue hexagons indicate the location of the sampled plots

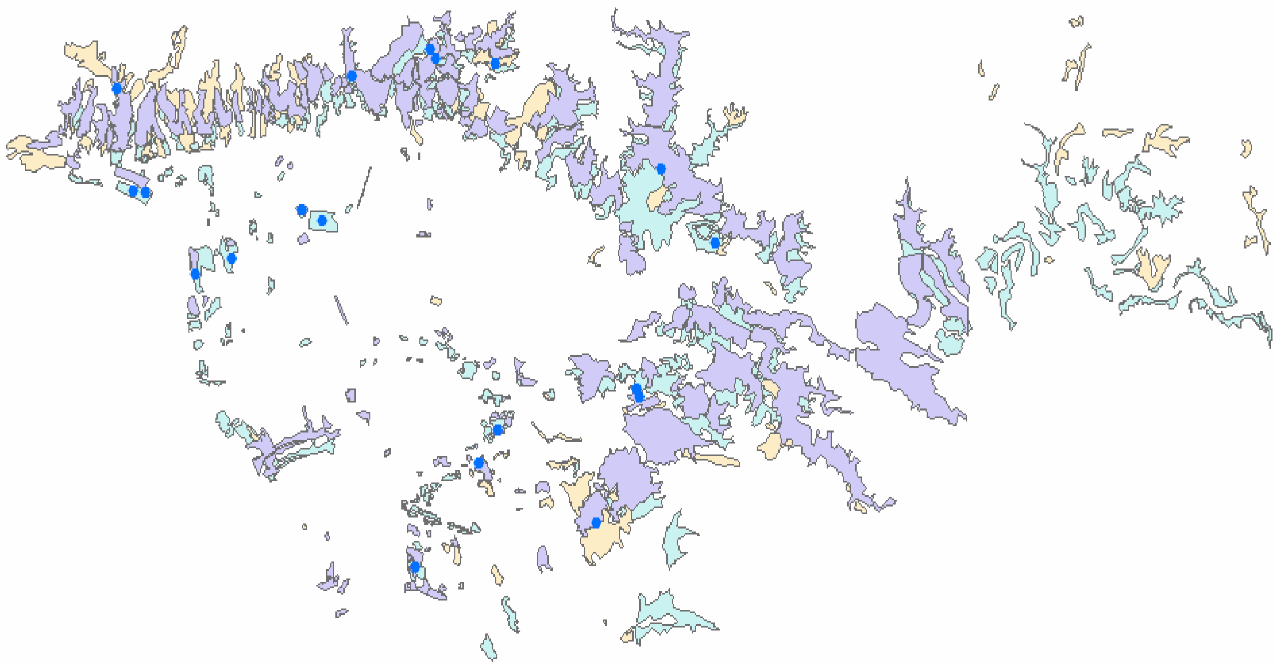


Figure 2. Forest age map of the Añasco River Watershed of western Puerto Rico with red hexagons the represent plot site location. The light green polygon represents oldest plots (84-year-old). The pink polygons represent intermediate age plots (28-42 year old) and the light blue polygons represent the youngest age class (15 year old plots)

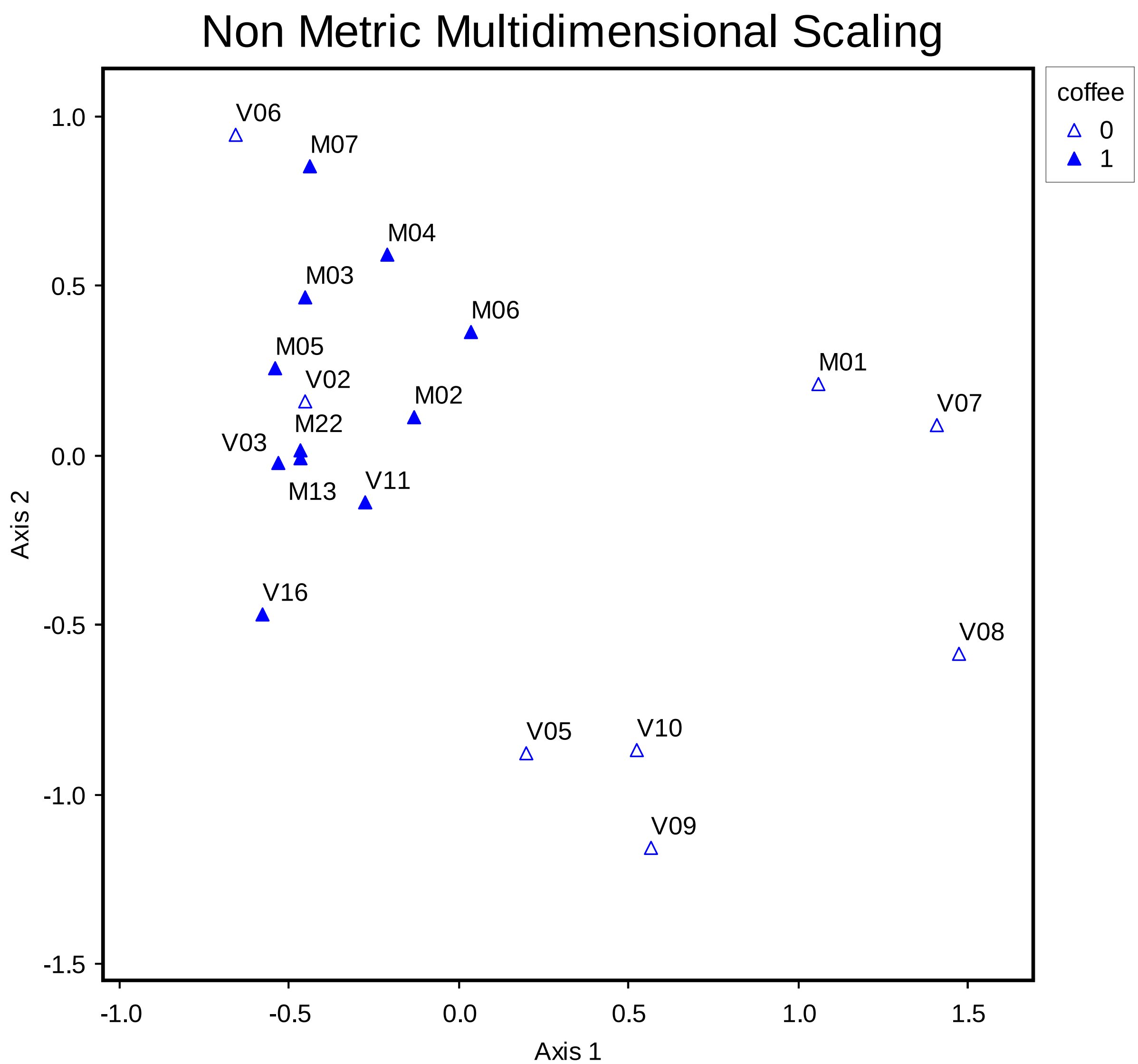


Figure 3. Non Metric Multidimensional Scaling ordination of species composition. The graph for the full dataset illustrates the separation of plots sampled on the valley and mountainss. Solid blue triangles represent the plots classified as abandoned coffee plantations. Open triangles represent plots classified as abandoned sugarcane or palm plantations. Plots are identified by habitat area and number. "M" represents mountain plots and "V" represents valley plots. Plots M22, M13 and V03 are layered on top of each other in the abandoned coffee cluster.

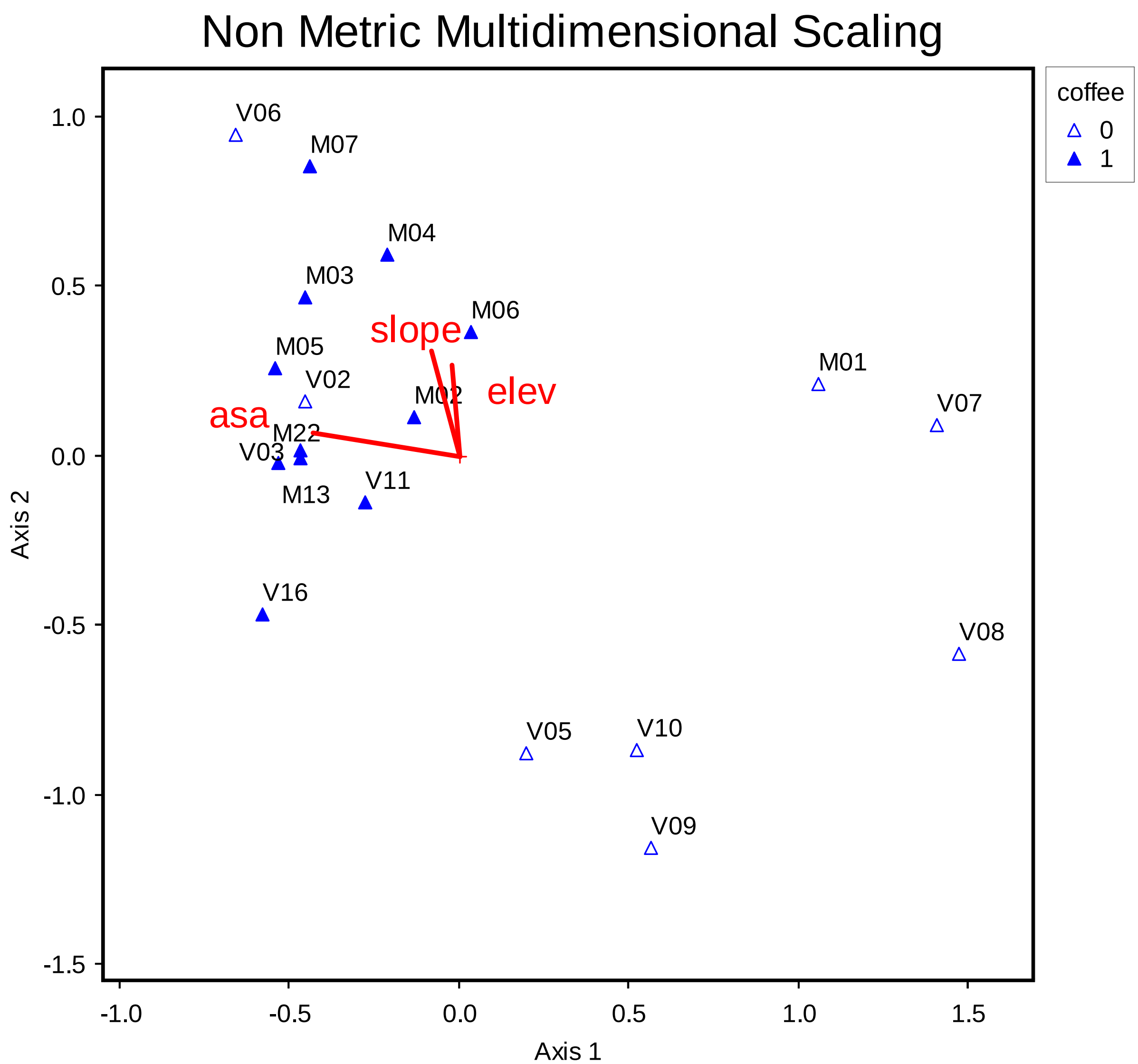


Figure 4. Non Metric Multidimensional Scaling ordination of species composition. The biplot, the same graph as figure 2, illustrates the relationship between the environmental variables and the sampled plots. Open triangles represent plots classified as abandoned sugarcane or palm plantation. Age since abandonment is represented by "asa" and elevation by "elev". Solid blue triangles represent the plots sampled on the mountains of abandoned coffee plantations. Open triangles represent plots sampled in the valley of sugar or palm plantations.

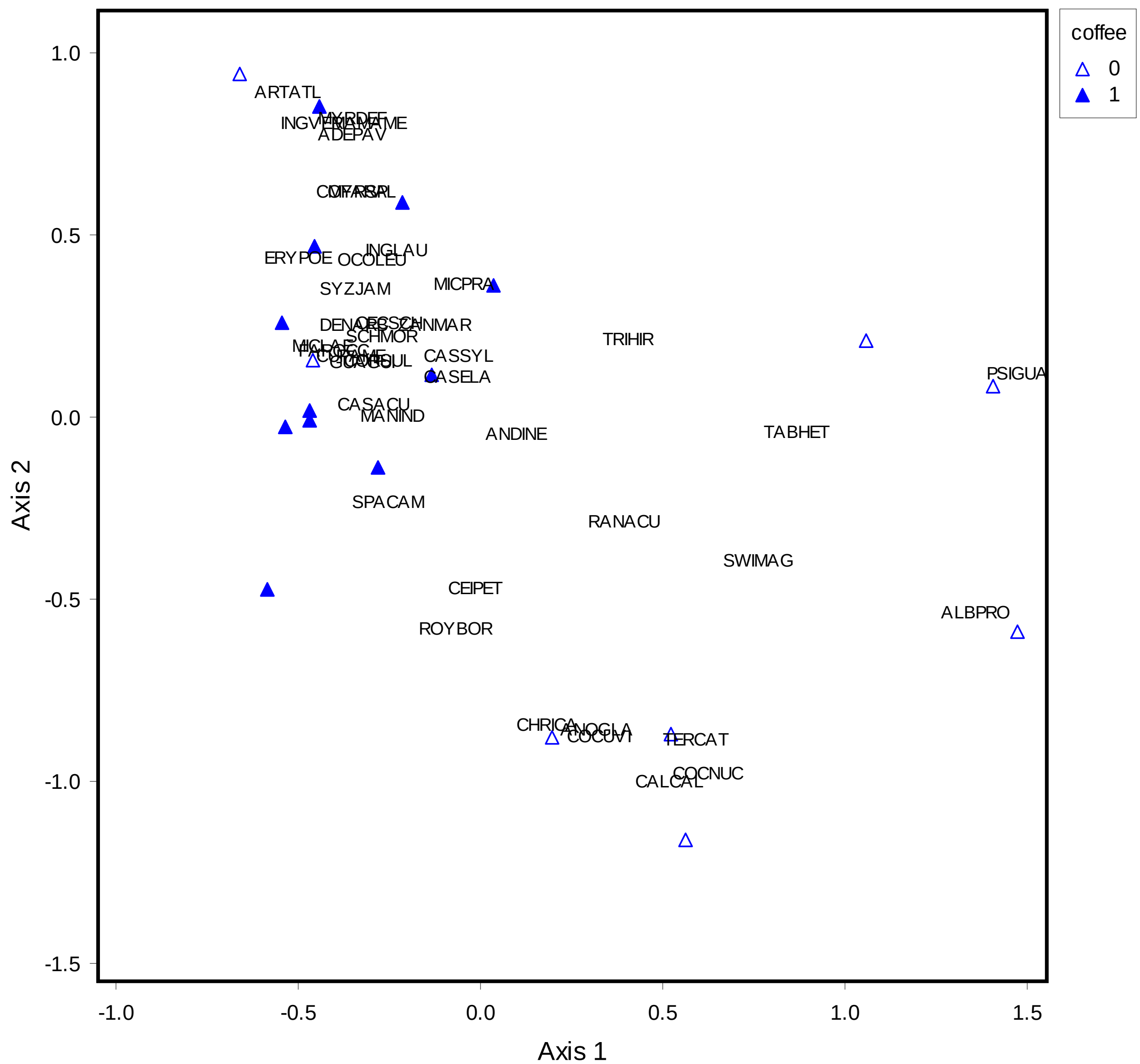


Figure 5. Graph (same ordination as figures 2 and 3) illustrates species associated with the different land use types. All the species are identified by a six letter species code (see Appendix I). Open triangles represent plots classified abandoned sugarcane or palm plantation. Solid triangles represent plots classified as abandoned coffee. The following species were grouped together on the top left corner: *Inga vera* (INGVER), *Adenanthera pavonina* (ADEPAV), *Mammea americana* (MAMAME), *Myrcia deflexa* (MYRDEF), *Coffea arabica* (COFARA) and *Myrcia splendens* (MYRSPL), *Dendropanax arboreus* (DENARB), *Zanthoxylum martinicense* (ZANMAR), *Miconia laevigata* (MICLAE), *Casearia sylvestris* (CASSYL), *Guarea guidonia* (GUAGUI), *Faramea occidentalis* (FAROCC) and *Schefflera morotononi* (SCHMOR).

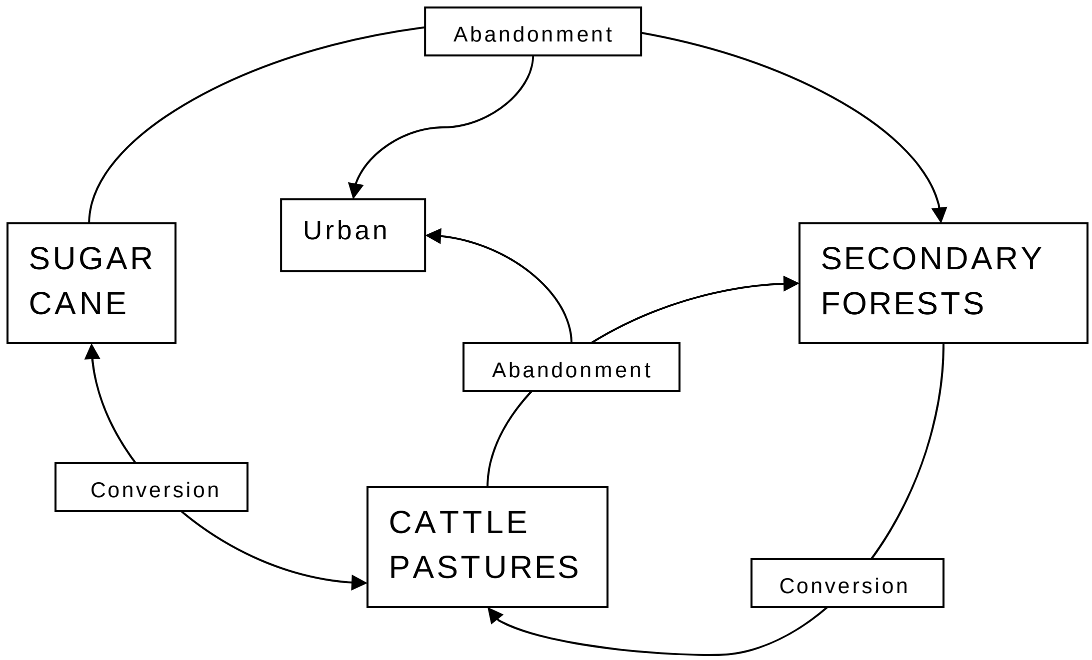


Figure 6. Flow chart of possible land use changes in the Añasco Valley

Appendix I

Structural characteristics calculated from of forest plots in the Añasco River Watershed. The age since abandonment is represented by "AGE", basal area by "BA", tree density by "DENS", diversity (Shannon-Weiner Index) by "H'" and species richness by "RICHNESS". Mean and standard error is calculated for all

PLOT	AGE (years)	BA (m2ha-1)	DENS (trees/ha)	H'	Richness (# of spp./area)
Mountains					
M06	**35**	**20**	**2300**	**2.3**	**19**
M01	**42**	**21.4**	**1380**	**1.8**	**13**
M07	**84**	**20.5**	**1960**	**2**	**13**
M03	**84**	**22.1**	**1800**	**2.3**	**15**
M05	**84**	**30.1**	**1340**	**2.3**	**14**
M04	**84**	**34.5**	**2240**	**2.1**	**15**
M13	**84**	**35.7**	**2500**	**2.5**	**25**
M02	**84**	**38.2**	**2640**	**2.3**	**21**
M22	**84**	**54.5**	**2060**	**1.4**	**11**
Mean	**n/a**	**30.8 ±3.8**	**2024.4 ±152.1**	**2.1 ± 0.1**	**16.2 ±1.5**
Valley					
V07	**15**	**6.4**	**440**	**0.3**	**3**
V08	**15**	**20.3**	**1180**	**0.1**	**2**
V02	**15**	**42.1**	**1440**	**2**	**11**
V10	**28**	**11.7**	**600**	**1.7**	**7**
V05	**28**	**37.3**	**2040**	**2.6**	**21**
V09	**42**	**26.9**	**1920**	**1.6**	**10**
V16	**42**	**65.2**	**1770**	**1.3**	**12**
V06	**84**	**33.7**	**920**	**1.3**	**6**
V03	**84**	**46.7**	**1320**	**2.2**	**21**
V11	**84**	**65.1**	**1600**	**2.1**	**14**
Mean	**n/a**	**35.5 ±6.4**	**1323 ±171.5**	**1.5 ±0.2**	**10.7 ±2.0**

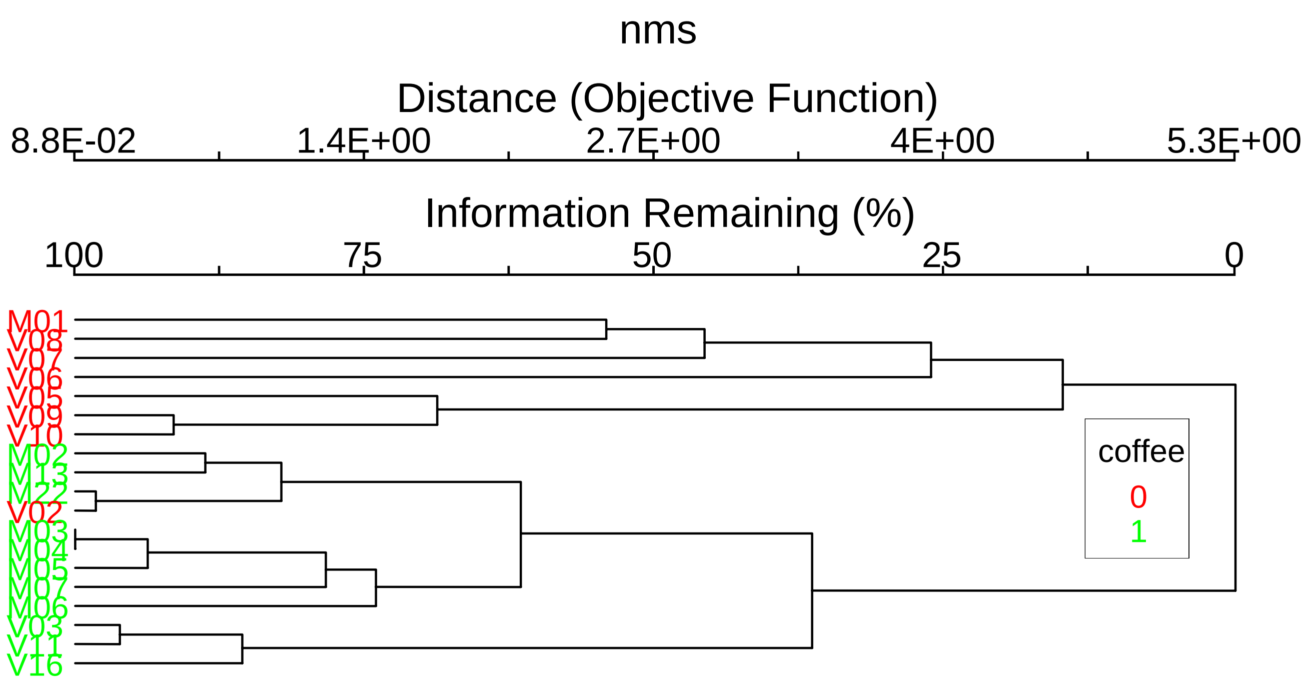
Appendix II

List of tree species shared by both major habitat a (mountains and valley) of study area. Species origin is depicted in the second column, “N” for native species and “I “for introduced species.

Specie	N/E
Roystonea borinquena	**N**
Faramea occidentalis	**N**
Inga vera	**N**
Inga laurina	**N**
Casearia sylvestris	**N**
Randia aculeate	**N**
Cupania americana	**N**
Zanthoxylum martinicense	**N**
Casearia aculeate	**N**
Cordia sulcata	**N**
Tabebuia heterophylla	**N**
Trichillia hirta	**N**
Cecropia schreberiana	**N**
Dendropanax arboreus	**N**
Ceiba pentandra	**N**
Miconia prasina	**N**
Myrcia splendens	**N**
Ocotea leucoxylon	**N**
Spathodea campanulata	**I**
Mangifera indica	**I**
Syzygium jambos	**I**
Albizia procera	**I**

Appendix III

Cluster dendrogram illustrating the plot clusters. Plot identification numbers colored green are associated with the vegetation community of abandoned coffee plantations. Plot identification numbers colored red are associated with the species composition described for the sugar or cattle pasture palm plantations.



Appendix IV

List of tree species identified and surveyed in the study area. The second column specifies the origin of the species, "N" for native and "I" for introduced. Species code is composed of the first three letters of the generic and specific name of each individual identified. The origin of unknowns is labeled as "n/a" and the family as "N/A", meaning not available. Nomenclature followed as listed by Liogier and Martorell (2000)

Species	N/I	Species code	FAMILY
Adenanthera pavonina	I	ADEPAV	Leguminosae
Albizia procera	I	ALBPRO	Leguminosae
Andira inermis	N	ANDINE	Leguminosae
Annona glabra	N	ANOGLA	Annonaceae
Artocarpus altilis	I	ATRATL	Moraceae
Bursera simaruba	N	BURSIM	Burseraceae
Byrsonima spicata	N	BYRSPI	Malpighiaceae
Calophyllum calaba	N	CALCAL	Guttiferae
Casearia aculeate	N	CASACU	Flacourtiaceae
Casearia sylvestris	N	CASSYL	Flacourtiaceae
Cassia siamea	I	CASSIA	Leguminosae
Castilla elastica	I	CASELA	Moraceae
Cecropia schreberiana	N	CECSCH	Moraceae
Ceiba pentandra	N	CEIPET	Bombacaceae
Chrysobalanus icaco	N	CHRICA	Chrysobalanaceae
Chrysophyllum argenteum	N	CHRARG	Sapotaceae
Chrysophyllum cainito	N	CHRCAI	Sapotaceae
Citharexylum spinosum	N	CITSPI	Verbenaceae
Citrus sinensis	I	CITSIN	Rutaceae
Coccoloba uvifera	N	COCUVI	Polygonaceae
Cocos nucifera	I	COCNUC	Palmae
Coffea arabica	I	COFARA	Rubiaceae
Comocladia glabra	N	COFARA	Anacardiaceae
Cordia sulcata	N	CORSUL	Boraginaceae
Cupania americana	N	CUPAME	Sapindaceae
Dendropanax arboreus	N	DENARB	Araliaceae
DESC-A	n/a	DA	N/A

Desc-1E05	**n/a**	**D1E05**	**N/A**
Desc-1E06	**n/a**	**D1E06**	**N/A**
Desc-1E04	**n/a**	**D1E04**	**N/A**
Desc-1I02	**n/a**	**D1I02**	**N/A**
Desc-1I11	**n/a**	**D1I11**	**N/A**
Erythrina poeppigiana	**I**	**ERYPOE**	**Leguminosae**
Eugenia monticola	**N**	**EUGMON**	**Myrtaceae**
Faramea occidentalis	**N**	**FAROCC**	**Rubiaceae**
Ficus citrifolia	**N**	**FICCIT**	**Moraceae**
Genipa Americana	**N**	**GENAME**	**Rubiaceae**
Guarea guidonia	**N**	**GUAGUI**	**Meliaceae**
Hymenaea courbaril	**N**	**HYMCOU**	**Leguminosae**
Inga laurina	**N**	**INGLAU**	**Leguminosae**
Inga vera	**N**	**INGVER**	**Leguminosae**
Leucaena leucocephala	**I**	**LEULEU**	**Leguminosae**
Mammea Americana	**N**	**MAMAME**	**Guttiferae**
Mangifera indica	**I**	**MANIND**	**Anacardiacecae**
Miconia laevigata	**N**	**MICLAE**	**Melastomataceae**
Miconia prasina	**N**	**MICPRA**	**Melastomataceae**
Morinda citrifolia	**I**	**MORCIT**	**Rubiaceae**
Myrcia citrifolia	**N**	**MYRCIT**	**Myrtaceae**
Myrcia deflexa	**N**	**MYRDEF**	**Myrtaceae**
Myrcia splendens	**N**	**MYRSPL**	**Myrtaceae**
Ocotea leucoxylon	**N**	**OCOLEU**	**Lauraceae**
Pisonia fragrans	**N**	**PISFRA**	**Nyctaginaceae**
Pouteria multiflora	**N**	**POUMUL**	**Sapotaceae**
Psidium guajava	**N**	**PSIGUA**	**Myrtaceae**
Randia aculeate	**N**	**RANACU**	**Rubiaceae**
Rauvolfia nitida	**N**	**RAUNIT**	**Apocynaceae**
Roystonea borinquena	**N**	**ROYBOR**	**Palmae**
Sabal causiarum	**N**	**SABCAU**	**Palmae**
Schefflera morototoni	**N**	**SCHMOR**	**Araliaceae**
Spathodea campanulata	**I**	**SPACAM**	**Bignoniaceae**
Sterculia apeltata	**I**	**STEAPE**	**Sterculiaceae**
Swietenia mahagoni	**N**	**SWIMAG**	**Meliaceae**
Syzygium jambos	**I**	**SYZJAM**	**Myrtaceae**
Tabebuia heterophylla	**I**	**TABHET**	**Bignoniaceae**
Tamarindus indica	**I**	**TAMIND**	**Leguminosae**
Terminala catappa	**I**	**TERCAT**	**Combretaceae**
Tetrazygia elaeagnoides	**N**	**TETELA**	**Melastomataceae**
Trichillia hirta	**N**	**TRIHIR**	**Meliaceae**
Zanthoxylum martinicense	**N**	**ZANMAR**	**Rutaceae**

Appendix V

List of geographic coordinates for sampled plots in study area. Plots are identified by habitat areas, “M” for mountain and “V” for valley. The coordinates were projected on maps and GPS units using Universal Transverse Mercator (UTM) and North American Datum of 1927.

PLOT	EASTING	NORTHING
M01	690112	2025139
M02	694240	2025396
M03	695718	2025656
M04	696758	2025603
M05	699684	2024072
M06	700644	2022974
M07	698617	2018705
M13	699313	2020752
M22	695614	2025812
V02	692179	2022617
V03	699358	2020617
V05	690649	2023575
V06	696867	2020079
V07	693743	2023203
V08	693398	2023358
V09	690419	2023599
V10	691546	2022373
V11	695449	2018012
V16	696535	2019620

Appendix VI

Table of environmental and anthropogenic variables used for the Non Metric Multidimensional Scaling. Elevation (elev) is expressed in meters above sea level; age since abandonment (asa) in years; aspect and slope were measured in degrees. Plots were classified according to their land use, "1" means classification as the column specifies and "0" means not classified as column specifies.

PLOT	elev	asa	aspect	slope	coffee	sugar	palm	pasture
M01	105	42	220	21	0	0	0	1
M02	95	84	231	24	1	0	0	0
M03	80	84	228	18	1	0	0	0
M04	75	84	245	22	1	0	0	0
M05	65	84	195	16	1	0	0	0
M06	90	35	252	25	1	0	0	0
M07	30	84	247	14	1	0	0	0
M13	40	84	271	21	1	0	0	0
M22	80	84	227	20	1	0	0	0
V02	2	28	256	2	1	0	0	0
V03	1	84	270	3	1	0	0	0
V05	2	42	271	5	0	0	1	0
V06	8	15	267	3	0	1	0	0
V07	2	15	258	1	0	1	0	0
V08	2	15	270	2	0	1	0	0
V09	2	42	225	1	0	0	1	0
V10	2	42	248	1	0	0	1	0
V11	30	84	260	10	1	0	0	0
V16	6	42	270	2	1	0	0	0

Appendix VII

Table of importance values (calculated from basal area and tree density) for species identified in mountain plots. The first column labeled "Species" informs the species code for each individual identified. The rest of the columns are labeled as mountain plots.

Species	M01	MO2	M03	M04	M05	M06	M07	M13	M22
ADEPAV	-------	-------	-------	--------	-------	-------	7.07	1.07	------
ALBPRO	8.20	-------	-------	--------	-------	------	-------	-------	------
ANDINE	1.51	4.26	3.35	4.59	4.97	8.69	-------	-------	0.50
ATRATL	-------	0.44	5.43	--------	-------	-------	-------	-------	-------
BURSIM	13.12	------	-------	--------	-------	-------	-------	-------	-------
BYRSPI	-------	------	-------	--------	-------	-------	-------	1.25	-------
CASACU	-------	------	-------	0.54	-------	0.48	-------	-------	-------
CASELA	-------	14.64	-------	--------	-------	-------	-------	-------	-------
CASSIA	-------	-------	-------	--------	-------	1.03	-------	-------	-------
CASSYL	3.62	15.53	-------	12.95	-------	1.41	-------	0.48	2.02
CECSCH	-------	1.75	1.57	16.17	18.32	--------	-------	11.98	-------
CEIPET	-------	-------	-------	--------	-------	-------	---------	0.84	-------
CHRARG	-------	-------	-------	--------	-------	-------	-------	1.00	-------
CITFRU	-------	2.37	-------	--------	-------	-------	-------	-------	-------
CITSIN	-------	1.81	-------	--------	-------	-------	-------	-------	-------
COFARA	-------	-------	3.64	--------	-------	-------	1.65	-------	-------
COMGL	-------	-------	-------	--------	-------	--------	0.54	-------	-------
CORSUL	-------	0.93	-------	--------	-------	1.44	0.79	0.43	2.68
CUPAME	-------	0.93	3.55	0.53	-------	0.49	-------	-------	-------
DA	-------	0.42	-------	--------	-------	-------	-------	-------	-------
D1E04	-------	-------	-------	0.78	-------	--------	-------	-------	-------
D1E05	-------	-------	-------	--------	9.46	-------	-------	-------	-------
D1E06	-------	-------	-------	--------	-------	13.42	-------	-------	-------
DENARB	-------	0.42	3.26	1.96	2.52	--------	-------	4.47	0.59
ERYPOE	-------	-------	-------	--------	-------	-------	-------	-------	-------
EUGMON	4.37	-------	-------	--------	-------	-------	-------	-------	-------
FAROCC	-------	-------	-------	--------	16.46	0.52	2.40	3.08	-------
GENAME	-------	-------	-------	0.57	-------	-------	-------	--------	-------
GUAGUI	-------	7.15	23.8	5.87	2.26	4.21	1.30	11.95	8.66
HYMCOU	43.88	-------	-------	--------	-------	------	0.00	------	-------
INGLAU	-------	10.06	19.05	29.12	4.58	26.81	31.77	13.56	2.05
INGVER	-------	4.30	6.10	5.03	0.88	1.61	-------	-------	1.88
MAMAME	--------	0.42	-------	----------	--------	--------	3.44	--------	-------
MANIND	-------	28.22	0.60	--------	---------	--------	-------	20.52	46.45

MICLAE	-------	-------	-------	--------	0.87	--------	-------	0.50	-------
MICPRA	1.74	0.46	-------	-------	0.95	1.99	2.73	2.40	-------
MYRCIT	-------	-------	-------	-------	-------	--------	------	1.95	-------
MYRDEF	-------	-------	-------	-------	-------	--------	5.25	0.44	-------
MYRSPL	-------	-------	3.07	2.77		0.00	8.73	1.46	1.02
OCOLEU	-------	2.31	10.23	11.40	14.58	1.98	9.96	1.60	------
PISFRA	-------	-------	-------	-------	-------	0.57	-------	-------	-------
PSIGUA	-------	-------	-------	-------	-------	--------	-------	0.94	-------
RANACU	0.75	-------	-------	-------	-------	--------	-------	-------	-------
RAUNIT	-------	-------	-------	-------	-------	--------	-------	------	-------
ROYBOR	-------	------	-------	-------	-------	--------	-------	0.59	-------
SCHMOR	-------	------	0.59	-------	-------	2.23	-------	1.75	-------
SPACAM	-------	0.46	3.41	-------	5.97	10.94	-------	10.83	-------
SWIMAG	1.45	------	-------	-------	-------	--------	-------	-------	-------
SYZJAM	-------	-------	12.35	7.18	14.21	0.47	24.39	0.42	32.64
TABHET	8.43	------	-------	-------	-------	--------	-------	0.46	-------
TAMIND	0.99	------	-------	-------	-------	--------	-------	--------	-------
TETELA	2.70	------	-------	-------	-------	--------	-------	--------	-------
TRIHIR	9.24	1.69	-------	-------	-------	10.12	-------	--------	-------
ZANMAR	-------	1.45	-------	0.54	3.97	11.60	-------	6.04	1.51

Appendix VIII

Importance values (calculated from relative basal area and relative tree density) for species identified in valley plots. The first column labeled “Species” informs the species code for each individual identified. The rest of the columns are labeled as valley plots.

Species	V02	V03	V05	V06	V07	V08	V09	V10	V11	V16
ADEPAV	-----------	-------	-------	-------	-------	-------	-------	-------	----------	-------
ALBPRO	-----------	-------	-------	-------	4.92	97.87	-------	26.49	----------	-------
ANDINE	4.13	3.90	4.69	-------	2.45	-------	7.47	1.75	1.93	
ANOGLA	-----------	-------	9.98	-------	-------	-------	0.57	-------	----------	-------
ATRATL	-----------	-------	-------	29.26	-------	-------	-------	-------	---------	-------
CALCAL	-----------	-------	22.89	-------	-------	-------	35.43	4.52	----------	-------
CASACU	0.76	-------	-------	-------	-------	-------	-------	-------	----------	1.29
CASELA	-----------	-------	-------	-------	-------	-------	-------	-------	2.64	-------
CASSYL	2.27	-------	1.03	-------	-------	-------	-------	-------	4.59	5.91
CECSCH	-----------	-------	-------	-------	-------	-------	-------	3.30	1.37	-------
CEIPET	-----------	-------	1.11	-------	-------	-------	-------	------	----------	-------
CHRCAI	-----------	-------	0.70	-------	-------	-------	-------	------	----------	-------
CHRICA	-----------	-------	-------	-------	-------	-------	1.19	------	----------	0.81
COCNUC	-----------	-------	2.36	-------	-------	-------	26.84	24.34	----------	-------
COCUVI	-----------	-------	5.47	-------	-------	-------	0.67	------	----------	-------
CORSUL	0.73	3.06	-------	-------	-------	-------	-------	------	0.71	-------
CUPAME	-----------	6.16	-------	-------	-------	-------	-------	------	----------	0.91
DENARB	4.28	0.90	-------	-------	-------	-------	-------	------	----------	-------
DSC-2I02	-----------	1.79	-------	-------	-------	-------	-------	------	----------	-------
DSC-2I11	-----------	-------	-------	-------	-------	-------	-------	------	0.66	
ERYPOE	-----------	16.61	-------	15.42	-------	-------	-------	-------	----------	1.43
FAROCC	18.28	15.15	-------	-------	-------	-------	-------	------	----------	1.19
FICCIT	-----------	-------	5.16	-------	-------	-------	-------	------	----------	-------
GUAGUI	3.90	17.54	-------	1.38	-------	-------	-------	------	20.26	9.99
INGLAU	10.52	4.16	-------	5.93	-------	-------	-------	------	7.63	1.04
INGVER	-----------	-------	-------	46.89	-------	-------	-------	------	----------	-------
LEULEU	-----------	-------	4.91	-------	-------	-------	-------	------	----------	-------
MANIND	26.81	-------	12.77	-------	-------	-------	-------	------	11.36	-------
MICPRA	-----------	0.77	-------	-------	-------	-------	-------	-------	----------	-------
MORCIT	-----------	-------	-------	-------	-------	-------	9.11	------	----------	-------
MYRSPL	-----------	0.84	-------	-------	-------	-------	-------	-------	----------	-------
OCOLEU	-----------	2.45	-------	1.11	-------	-------	-------	------	6.56	-------
POUMUL	-----------	-------	-------	-------	-------	-------	-------	------	3.35	-------
PSIGUA	-----------	-------	-------	0.00	92.63	-------	-------	------	----------	------

RANACU	**-----------**	**-------**	**0.56**	**-------**	**-------**	**-------**	**-------**	**-------**	**----------**	**0.59**
RAUNIT	**-----------**	**-------**	**0.70**	**-------**	**-------**	**-------**	**-------**	**------**	**----------**	**-------**
ROYBOR	**-----------**	**2.17**	**9.68**	**-------**	**-------**	**-------**	**-------**	**-------**	**----------**	**6.20**
SABCAU	**-----------**	**-------**	**4.87**	**-------**	**-------**	**-------**	**-------**	**-------**	**----------**	**-------**
SCHMOR	**7.65**	**-------**	**-------**	**-------**	**-------**	**-------**	**-------**	**-------**	**----------**	**-------**
SPACAM	**-----------**	**22.58**	**1.99**	**-------**	**-------**	**-------**	**-------**	**17.17**	**33.61**	**67.57**
STEAPE	**-----------**	**-------**	**1.22**	**-------**	**-------**	**-------**	**-------**	**-------**	**----------**	**------**
SWIMAG	**-----------**	**------**	**1.08**	**-------**	**-------**	**-------**	**0.61**	**-------**	**----------**	**------**
SYZJAM	**20.67**	**1.93**	**0.53**	**-------**	**-------**	**-------**	**0.57**	**-------**	**1.95**	**------**
TABHET	**-----------**	**-------**	**3.04**	**-------**	**-------**	**-------**	**-------**	**-------**	**----------**	**------**
TERCAT	**-----------**	**-------**	**5.26**	**-------**	**-------**	**2.11**	**17.55**	**22.43**	**2.73**	**------**
TRIHIR	**-----------**	**-------**	**-------**	**-------**	**-------**	**-------**	**-------**	**-------**	**----------**	**3.08**
ZANMAR	**-----------**	**-------**	**-------**	**-------**	**-------**	**-------**	**-------**	**-------**	**0.66**	**-------**