

THE SAPOTACEAE OF A LOWLAND RAINFOREST:
DIVERSITY AND DISTRIBUTION IN THE LOS AMIGOS
WATERSHED, MADRE DE DIOS, PERU

by

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INTRODUCTION

Tropical moist forests cover about six percent of the Earth's total surface with 60% of this area, about 5.5 million km², represented by the Amazon rainforest of South America (Jepma 1995). Amazonian forests account for about 10% of the world's terrestrial primary productivity and 10% of carbon stores in these ecosystems (Melillo 1993), with an estimated 1.1×10^{11} metric tons of carbon stored in its biomass (Tian *et al.* 2000). Amazonia also contains the planet's most diverse populations of birds, butterflies, reptiles, amphibians, mammals, and tree species (Gentry 1988b).

The neotropical flora is more diverse than any other in the world, being comprised of more than 100,000 plant species, in comparison to 45,000 species that are known to exist in African-Malagasy forests, and about 42,000 species that occur in Indo-Asian forests (Prance 1994). Western Amazonia has been found to contain the most species rich forests with Gentry (1988b) and Valencia *et al.* (1994) recording 283 and 307 species among trees with diameters ≥ 10 cm in one-hectare forest plots. This richness has been considered a result of the Andes Mountains of western South America creating relatively higher rainfall and soil nutrient levels in the western Amazon (Gentry 1988a); however, a similar one-hectare (ha) forest plot in central Amazonia with poor nutrient soils and reduced rainfall was found to have 285 species by Oliveira and Mori (1998). This result of nearly equal species diversity being found in the absence of higher rainfall and soil nutrients shows that there is still much to explain about the underlying mechanisms driving the patterns of high species richness in the world's most biodiverse ecosystem.

Amazonia currently faces several threats stemming from natural resource exploitation including deforestation, gold mining, oil exploration, cattle ranching, and slash and burn agriculture (Jepma 1995). The global ecological and economic importance of this rainforest coupled with the current degradation of its pristine ecosystems clearly signals the necessity for scientific research that contributes to conservation planning and decision-making. Clearly, assessments of the botanical and ecological diversity at multiple spatial scales in the Amazon are important for conservation programs. Although several large scale monographic studies have been completed and are currently underway, our knowledge of the great biodiversity found in the tropical forests of the Amazon is still largely insufficient. An example is the Flora Neotropica series of plant family monographs which has an estimated completion time of 300-400 years at its current rate of publication. Despite the work and intensity involved, these monographs are quickly outdated as more collections are made and newly described species are found in these diverse forests (Gentry 1992). Tropical botany and ecology form an important foundation for much of the conservation planning and policy in areas like the Amazon, but many more botanical studies are needed, especially with a more local approach that combines long-term floristic and quantitative ecological studies, as recommended by Phillips and Raven (1997).

The Sapotaceae is a family of large, often emergent, tropical trees that have been found to be a significant presence in wet or moist lowland tropical forests worldwide with an estimated 800 species in 65 genera. Detailing just the neotropical Sapotaceae, Volume 52 of the Flora Neotropica series was completed by the renowned expert of this family T. D. Pennington who described 396 species in 11 genera including 71 new species and 5

new subspecies as a result of its publication (Pennington 1990). The Sapotaceae are highly diverse, abundant, often represent locally dominant species, and have been found to be one of the ten most important plant families at representative forest plots in the lowland forests of the Amazon, Africa, and Asia (Condit *et al.* 2002, Gentry 1988a, Oliviera and Mori 1998, Prance 1994, Terborgh and Anderson 1998, Ter Steege *et al.* 2000). The high diversity, abundance, and widespread distribution of the Sapotaceae make it an ideal family to be used as a biological model to investigate diversity, evolution, distribution, and conservation at multiple spatial scales in the Amazonian region.

Throughout its range, this family is economically important, being utilized for its hard wood, sweet and edible fruit, seed oil such as the popularized shea butter, and latex that serves as medicine and the natural source of chewing gum (or “chicle”). The fruits produced by these trees are also eaten by a variety of local fauna including monkeys and birds, giving this family a vital ecological importance when also considering its vast distribution, abundance, and physical size.

Despite its importance, the Sapotaceae are currently limited by a poorly understood taxonomy that has eluded concise definition by botanists for over 100 years. In the neotropics, the largest genus *Pouteria* contains almost 200 species grouped into eight sections, and is considered a “wastebasket” genus by taxonomists, collecting species not clearly defined by other genera. These problems arise because species can often be clearly delineated; however, few characters are available for differentiation at the generic level, with no neotropical Sapotaceae genera having a clear, defining

characteristic shared by all species (Pennington 1991). Further study and collection of this family will be necessary to more accurately define its complex taxonomy.

The global ecological importance and need for conservation of this family is what led me to produce this summary of the diversity and distribution of the Sapotaceae within a pristine sample of lowland moist forest habitat in southeastern Peru (Spichiger 1996). Literature review has shown few studies primarily deal with the Sapotaceae, and that none of these studies have been carried out in Peru, an established biodiversity hotspot (Gentry 1988a). According to T. D. Pennington (1990), of the few studies that have been completed, some of the more valuable for understanding diversity of this family have been completed for regions in the Guyana Highlands (Aubreville 1965), Guatemala (Standley 1967), and Panama (Blackwell 1968). Therefore, I present an approach that combines local botanical and ecological studies to inventory the Sapotaceae species found in the Los Amigos River watershed of Peru to investigate and quantify its species diversity and distribution.

METHODS

Study Location

The department of Madre de Dios in southeastern Peru lies in the western Amazon basin near the base of the Andean foothills. In the central portion of this state, the Los Amigos River watershed approximates the pristine lowland moist forest once found throughout most of upper Amazonian South America. Its location is marked in Figure 1, it consists of 1.6 million ha (3.95 million acres), and offers the opportunity to study rain forest as it was before the disruptive encroachment of modern human civilization. Although the region of Madre de Dios is becoming more heavily influenced

by logging, gold-mining, and colonization, this watershed is still in a relatively pristine state as evidenced by its local population of ten primate species (Voss and Emmons 1996).

The Los Amigos conservation area is a private 150,000 ha conservation concession established in 2002 by the Peruvian government in conjunction with the Amazon



Figure 1. Map of Study Location in Peru.

Asociación para la Conservación de la Cuenca Amazonica (ACCA), who manage the conservation area and its active research site, the Los Amigos Biological Station (CICRA). The conservation area protects pristine ecosystems including palm swamps and wetlands, expansive floodplain forests and upland terra firme forests between 250-320 meters in altitude. The area receives most of its estimated 2000 mm of annual rainfall in a wet season typically lasting from November until May (Pitman *et al.* 1999), and is located between 12°49' and 12°59' S latitude and 70°07' and 70°17' W longitude (Janovec *et al.* 2006).

Five study locations were utilized throughout the Los Amigos conservation area with most of the compiled data from the CICRA and adjacent CM1 study locations. Each location was classified by habitat type of alta for upland terra firme forest or baja for lowland floodplain forest. The CM2, Rio Amiguillos, and Refugio 2 study locations were respectively located 19 km, 21 km, and 44 km northwest of CICRA and were less

intensely sampled. As a result, CICRA becomes the most important sample location for upland or alta forests, while CM1 becomes the most important location for baja or floodplain forest sampling as illustrated in Figure 2. With sampling in three separate locales along its length and to examine individual differences, the CM1 baja habitat was considered to be three separate subgroups named: north, center, and south. A summary of all study locations can be seen as Table 1.

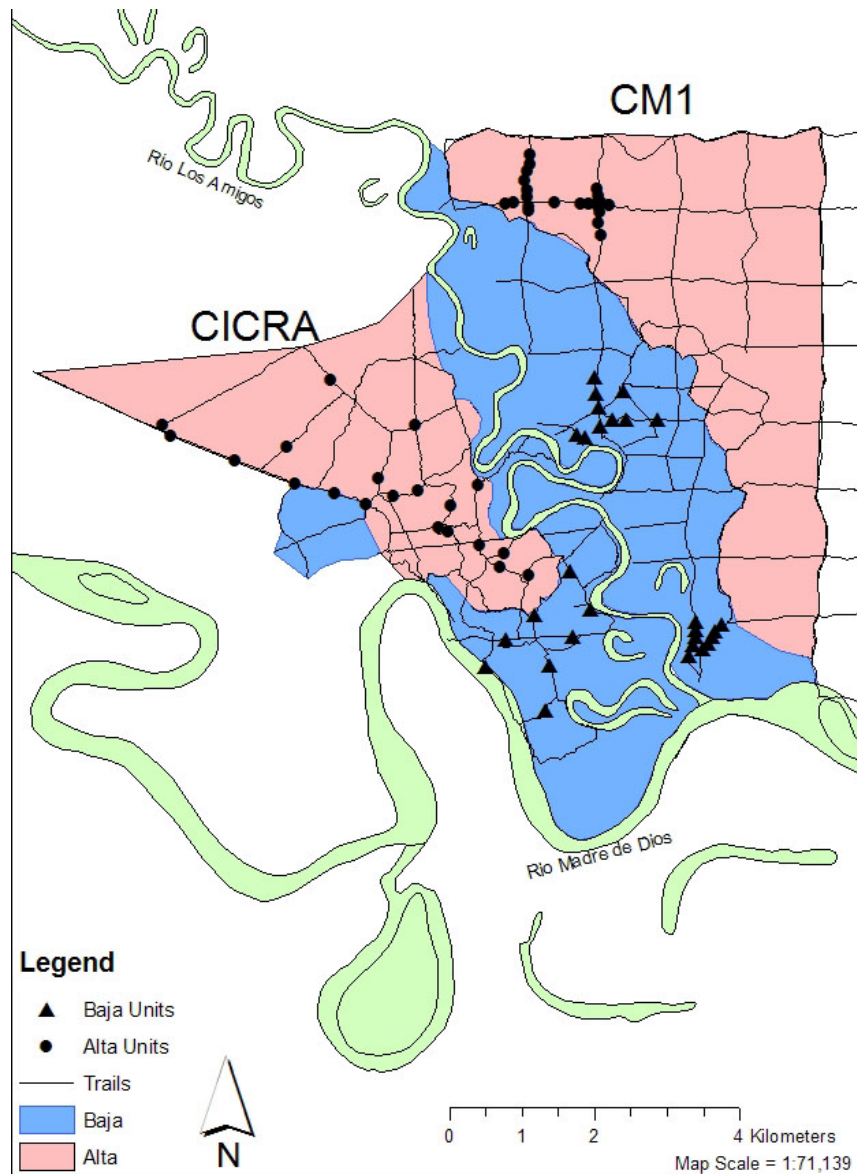


Figure 2. Unit and Habitat Locations at CICRA and CM1.

Table 1. Summary of Habitats and Study Locations.

Study Site	CICRA	CICRA	CM1	CM1 - North	CM1 - South	CM2	Refugio 2	Rio Amiguillos
Habitat	Alta	Baja	Alta	Baja	Baja	Baja	Baja	Baja
Area Sampled (km²)	4.57	1.13	0.49	0.48	0.10	-----	-----	-----
Number Transects	210	90	220	100	100	34	30	9
Number Individuals	345	88	367	118	94	46	16	13
Latitude (South)	12.551	12.570	12.515	12.540	12.571	12.455	12.231	12.436
Longitude (West)	70.110	70.089	70.087	70.081	70.069	70.255	70.338	70.271

* = Using ArcGIS 9.2, calculated as the smallest polygon to contain all sample units within each habitat.

Field Data

The data presented are a direct result of the studies associated with the Andes to Amazon Biodiversity Program (AABP) of the Botanical Research Institute of Texas (BRIT). From 2003 until 2007, AABP field teams collected one of the largest ecological datasets in the history of the Andes-Amazon region of South America.

The sampling tool utilized across the landscape of the Los Amigos watershed was the Gentry 0.1-ha transect method. Data from 750 transects were obtained as groups of ten, termed units, to simplify quantitative analysis and to achieve a standard total area of 0.1-ha per unit. An additional 43 transects not organized into complete units also yielded data for the analysis.

The Gentry method begins by collecting metadata of a starting location with GPS and a cardinal heading with a compass, measuring a 50 meter line in that direction, and collecting data on every tree within one meter of the line. A single transect encompasses a 2 m x 50 m area of 100 meters². Ten individual transects grouped together as a unit will contain 10 m x 100 m totaling an area of 1000 meters² or 0.1-ha. The data obtained for each tree were: morphospecies code, height in meters, and diameter breast height (dbh) in centimeters. The dbh was measured at approximately 1.3 meters from ground level, and only trees with a dbh \geq 2.5 cm were included. This method is easily repeated, adaptable to any terrain type, and efficient affording the inclusion of smaller diameter trees than traditional 1-ha forest plots while accounting for almost the same number of species and stems (Phillips and Raven 1997). The main limitation being its temporary status compared to permanent 1.0-ha forest plots where trees are identified, mapped, and

routinely studied at intervals to determine important ecological factors like tree growth and mortality rates.

To direct the focus of this study to the Sapotaceae, the data for this family were separated from the other species in the AABP botanical dataset. A total of 1087 Sapotaceae trees were sampled with 1012 individuals from the CICRA and CM1 locations. Only 13, 16, and 46 Sapotaceae individuals were sampled from Refugio 2, Rio Amiguillos, and CM2 locations forcing their exclusion from most quantitative analyses due to these low sample sizes that would greatly under represent the diversity found at each locale.

Each sampled tree was initially identified by a morphospecies code before it could be identified. A leaf from each unique morphospecies collected was clearly labeled with its morphospecies code, and kept as a comparative leaf guide in the field to establish a consistent record of identification and prevent the description of the same morphospecies twice. Only voucher specimens were collected of each new morphospecies for herbarium reference. This method delineates morphologically distinct species allowing for species richness estimates in the absence of absolute taxonomic identifications, but may introduce bias towards overstating richness levels as multiple morphospecies may represent a single, highly polymorphic species of Sapotaceae. It may also occur that genetically distinct taxa may occur as undistinguishable morphospecies. However, those biases can be reduced with further botanical study. Through careful examination at the field herbarium of CICRA, the resources of the BRIT herbarium in Texas, and the expertise of T. D. Pennington, many species have been identified including several new to the floras of Peru or Madre de Dios. The morphospecies serve their vital function of

providing an initial grouping of species complexes. The initial 134 morphospecies were revised into 86 morphospecies used in the quantitative analyses. These are summarized with their local abundances in all study locations by Appendix A.

All field data and images collected by the AABP team were uploaded into a web-based ecological data management system known as Atrium[®] (<http://atrium.andesamazon.org>). This integrative database brings ecology, botany, meteorology, geology, hydrology, and GIS mapping technologies together through an ordinary internet connection to allow researchers worldwide access to its wealth of data. A database of high resolution photography allows for continued revision of plant taxonomy by experts and researchers worldwide. This integration and communication between scientists is essential for them to be properly informed with an ever progressing scientific knowledge base, and to help with decisions of proper conservation.

Data Analysis

Three software packages were used in the analysis including: ESRI's ArcGIS 9.2, the Statistical Analysis System 9.0 package (Der and Everitt 2001), and EstimateS 8.0 (Colwell 2006). GIS data and shapefiles of the study area including local trail systems and waterways were available through AABP's online database Atrium[®].

Two graphing techniques were performed as a part of the diversity analysis to investigate the completeness of sampling and species abundances in each habitat. Species rarefaction curves were calculated for each habitat of the CICRA and CM1 locations using the Chao 1 estimator in EstimateS 8.0. The Chao 1 estimator use the number of rare species in the data to estimate the number of rare species that may have been missed in the sampling. Chao 1 defines rareness based on the abundance of species,

and those that are represented by a total of fewer than three individuals. As suggested by Gotelli and Colwell (2001), individual based rarefaction curves were used to avoid potential misleading results from comparing raw species numbers between transects without accounting for their individual differences in stem density.

Species abundance curves for all habitats of CICRA and CM1 were used to graphically compare species diversities, abundances, and dominance. In each habitat, the relative proportion of abundance for all species present were computed, sorted in descending order, and ranked from most to least abundant in each habitat. This abundance data from all habitats was then graphed as suggested by Magurran (1988) to create a rank abundance plot, also known as a species abundance curve.

A Venn diagram was used to compare the species compositions between alta and baja habitats for the CICRA and CM1 locations, and the species shared between habitats. Expected random distributions of species between habitats were based on the relative sampling area, and significance of the difference between the expected and observed data was tested with a G-test procedure that is less insensitive to bias from small sample sizes.

Similarity indices or coefficients are one of the most commonly used tools to analyze spatial distributions. The software package EstimateS 8.0 was used to calculate the similarity coefficients among the study locations, and among all the units found at the CICRA and CM1 locations. The Jaccard Classic and Chao-Jaccard Raw Abundance Based indices were both employed for comparative analysis.

The Jaccard Classic coefficient is a non-parametric index that uses raw data, is based on the incidence of all species, and measures the dissimilarity between sample sets. The Chao-Jaccard Raw Abundance Based coefficient is also a non-parametric index that

uses the relative abundances of species to estimate the probability that two randomly chosen individuals both belong to species shared by both samples, but not necessarily the same shared species. A correction factor in the denominator of its equation serves to “uncorrect” this index for unseen species in the dataset as a way to protect the analysis from undersampling the species diversity (Colwell 2006). It will yield higher results because it includes species undetected by other coefficients like the Jaccard Classic.

The equation for the Jaccard Classic index calculation is: $J_c = W / (U+V+W)$. Where U = the number of species in sample 1, V = the number of species in sample 2, and W = the number of species in both samples. The equation for the Chao-Jaccard Raw Abundance Based index is similar to that of the Jaccard Classic: $J_{abd} = W / (U+V-W)$ except that U = the sum of the relative abundances of species in sample 1 that also occur in sample 2, V = the sum of the relative abundances of species in sample 2 that also occur in sample 1, and $W = U + V$. As the values from either coefficient increase, the two samples are considered to be increasingly similar (Colwell 2006).

Finally, beta-diversity occurs between habitats and was plotted graphically using the calculated similarities between units within each location and habitat. Beta-diversity and similarity hold an inverse relationship, so as the similarity between unit's increases, the beta-diversity decreases and vice versa. Each habitat is represented by a box plot showing the median similarity bounded by its interquartile range, and complemented by the maximum and minimum similarity value to give a complete account of the variation among habitats.

RESULTS

PART 1 - DIVERSITY

Floristics and Taxonomy

The Sapotaceae is characterized by a complex and highly disputed taxonomy. Before the updated monograph of this family was published in 1990 by T. D. Pennington, the only comprehensive account was described in Martius's "Flora Brasiliensis" in 1863 (Pennington 1990). No one genera among the neotropical Sapotaceae is defined by a single character, so several characters are grouped into different combinations to delineate genera with the resulting taxonomy weighted to the character set of primary value.

Pennington (1990) illustrated the problem this creates by referencing the last two major revisions of the neotropical Sapotaceae by Aubréville (1964) and Baehni (1965). Based primarily on fruit and seed type Baehni recognized 63 genera, while based on the complicated floral characters Aubréville found 123 genera, with the single encompassing genus *Pouteria* described in 1990 by Pennington equating to over 40 distinct genera in the Aubréville classification system. These profound differences in professional opinions have impeded classification of additional collections as authors do not know where to place additional species, and has created a massive list of synonyms for both genera and species as they are moved, combined, or change names only increasing the level of difficulty ascribed to dealing with Sapotaceae taxonomy. The current monograph (Pennington 1990) organized only 11 neotropical genera to describe the variation, relationships, and important field characters among this family. By comparison, Aubréville cited 23 genera in his treatment of the Sapotaceae for the Guyana highlands

alone (Pennington 1990). By distinguishing fewer and broader genera Pennington has created a more organized, integrated, user-friendly, and natural method of classification for the neotropical Sapotaceae.

The following results present an overview of the genera and species encountered at Los Amigos with an emphasis on persistent and obvious field characters as suggested by Pennington (1990) and Gentry (1993). Many Sapotaceae species are still known only by a type specimen, others still have their fruit and/or flower types unknown, and additional species indicate a wide morphological variability that has yet to be firmly established. Combined with the overwhelming majority of Los Amigos collections lacking flowers and/or fruits due to their difficult access high in the canopy layer, and because of the importance of this family to scientists such as primatologists, entomologists, and ornithologists who have a less technical understanding of botany but a need to relate their results to Sapotaceae biodiversity, this simplified vegetative survey emphasizing obvious characters for field recognition is perhaps more immediately useful than an intensely technical treatment.

Gentry (1993) showed that petiole, leaf, and venation types can be used to clearly distinguish the Sapotaceae genera. Based upon study results and a combination of the generic descriptions provided by Pennington (1990) and Gentry (1993), a primarily vegetative revised key for the neotropical Sapotaceae genera is presented; followed by an overview of the Sapotaceae characteristics and comparison to other similar families in the field, descriptions of genera, and species identified from this study with each supplemented by discussion and available field photography.

Key to the Genera of Neotropical Sapotaceae

1. Large, caducous stipules present
 2. Large, coriaceous leaves with short intersecondaries, parallel tertiaries oblique to secondaries, yellow latex, and pedicellate flowers 1. *Chromolucuma*
 2. Large, coriaceous leaves with closely parallel tertiaries perpendicular to secondaries, and sessile flowers 2. *Ecclinusa*
1. Large, caducous stipules absent
 3. Petiole base notably enlarged giving a “pop bottle” shape
 4. Leaves alternate and distichously arranged
 5. Small leaves with strong brochidodromous secondary venation on underside of leaf, and drying a pinkish color 3. *Sarcaulus*
 4. Leaves spirally arranged
 6. Trees of inundated or swamp forest with leaves being thin, extremely coriaceous, and minutely punctuate on underside of leaf 4. *Elaeohuma*
 6. Leaves small to large, veins variable but never striate, with tertiaries usually perpendicular to midvein, and having ellipsoid seeds with broad scars that lack endosperm 5. *Pouteria*
 3. Petiole base not notably enlarged
 4. Leaves alternate and distichously arranged
 7. Small, thin leaves with long apex, finely striate venation that dries a black color, and strong marginal vein 6. *Diploön*
 7. Small to medium sized, mainly elliptic leaves with finely striate venation, and ellipsoid seeds with endosperm 7. *Micropholis*
 7. Leaves clustered at branch apices, usually with evenly parallel tertiaries to midvein often appearing striate, rarely spirally arranged, often sericeous below, and usually having laterally compressed seeds with copious endosperm 8. *Chrysophyllum*
 4. Leaves spirally arranged
 8. Small, shrubby dry forest trees with spine tipped branches 9. *Sideroxylon*
 8. Canopy and emergent trees with leaves clustered at branch apices, venation striate and brochidodromous with submarginal vein usually present, finely striate tertiaries, and infrequently with small stipules present 10. *Manilkara*
 4. Leaves whorled or oppositely arranged
 9. Leaves with short petioles, midrib and secondaries sunken on upper leaf surface, and tertiaries usually parallel but perpendicular to midvein and oblique to secondaries 11. *Pradosia*

Figure 3. Dichotomous Key to Genera of Neotropical Sapotaceae.

All Sapotaceae leaves are simple with entire margins, a milky latex present in the trunk, twigs, petioles, and fruit with one *Pouteria* species and the genera *Chromolucuma* having yellow latex, and bark that is commonly reddish or grayish brown with deep to shallow fissures or scaling in strips along a typically straight trunk that is slightly fluted or with buttresses at its base.

Trends in the similarity of flowers and fruit can be seen across all genera of neotropical Sapotaceae. Sapotaceae flowers have radial symmetry or are actinomorphic, small, usually greenish or whitish but being red in *Pradosia*, and usually present in groups called fascicles along axils or branches with the petals and sepals of each flower fusing into a tube that may continue into a pedicel or have direct, sessile attachment. Flower shape is open or rotate in *Manilkara*, *Diploön*, *Elaeoluma*, and *Pradosia*, while the flowers of all other genera typically have urceolate or urn-shaped flowers (Gentry 1993).

Sapotaceae fruits are always indehiscent meaning they do not open at maturity, are often large, regularly fleshy and edible, commonly found on short pedicels but also with sessile attachment, and frequently eaten by a number of local animal species. When available, the characteristic seeds have a shiny or dull, dark brown testa of various textures with a light brown scar of various sizes located along one side of the seed. This yields two overall seed types with the first represented by *Chrysophyllum*, *Sarcaulus*, *Manilkara*, a few white sand *Pouteria*, and exemplified by having seed endosperm present, a narrow, adaxial to basally located scar, and thin, foliaceous cotyledons; while the second type lacks endosperm, has a broad adaxial scar, and thick, fleshy cotyledons as seen by the other genera of Sapotaceae including *Pouteria*. These are usually referred to as simply the *Chrysophyllum* and *Pouteria* seed types (Gentry 1993).

The prominent family Moraceae boasts copious milky latex that quickly flows from a trunk slash, but Sapotaceae latex usually presents as individual droplets and may only be present in petioles during a strong dry season. Discrimination between the two families is also capable because Moraceae typically has smooth bark and a distinctive

cone shaped stipule that covers the terminal bud, while the terminal bud of Sapotaceae typically has a dense indumentum of reddish, golden, or whitish hairs.

Lauraceae and Myristicaceae both can have similar bark but are distinguished by having a red, watery exudate; while Apocynaceae often has milky latex but also oppositely arranged leaves rarely found in Sapotaceae; whereas Clusiaceae has finely striate venation like some Sapotaceae genera but yellow latex, a combination never found in Sapotaceae. Another distinguishing feature compared to these families is the standard presence of malphigiaceous hairs in Sapotaceae characterized by having two branches with one arm much longer than the other, and are often appressed against the lower leaf surface, twigs, and petioles of some species (Pennington 1990).

Four of the eleven genera recognized by Pennington, including *Diploön*, *Elaeoluma*, *Sideroxylon*, and *Pradosia*, were not sampled within the study location. *Diploön* is the only monotypic genus of the neotropical Sapotaceae, but was not found in any transects of this study despite an apparent widespread distribution in Amazonia. Easily recognized in the herbarium by small and narrow leaves with a caudate apex and finely striate venation that dries a distinct black color, a lack of collections from this genus can confidently be attributed to not sampling it within the study area.

Elaeoluma is represented by four species in the neotropics and generally found in the Guyana Shield, with only *Elaeoluma glabrescens* potentially occurring in the study area but restricted to igapó or black-water inundated forest. This species, and hence genera, was not found in the study area like *Manilkara inundata*, another species previously collected in Madre de Dios and considered restricted to igapó forests. The

lack of truly inundated forest habitat in the study area suggests this result to be logical and is supported by the additional absence of another igapó restricted species.

Sideroxylon has a widespread range throughout the dry forests and savannahs in both Americas represented by 50 species. It is unique to have spine tipped branches amongst other adaptations for its arid habitat, and clearly was not collected in the sample area of this study.

Pradosia has 23 species in the neotropics, with *P. atrovioleae* being distributed across Amazonia, but no collections of this genus were made in this study. It is possible specimens were grouped with the large genus *Pouteria* and will be found accordingly with further study, but improbable because this genus is unique to have opposite or whorled leaf arrangements. This obvious vegetative character indicates incorrectly placed collections would be few in number if they exist, making this genus a relatively minute component of the local Sapotaceae.

Of the seven genera that were collected, *Chromolucuma* was by far the most surprising with the only previous collections of its two species occurring in Venezuela, central Amazonian Brazil, and Magdalena valley of the Colombian chocó. Thus, this genus and its inclusive species are new additions to the flora of Peru. This genus features very large, usually coriaceous leaves spirally arranged with eucamptodromous venation, stipules 2-4 cm long, a distinct red-orange calyx below flowers, and unique yellow latex (Pennington 1990).

The other Sapotaceae genus bearing stipules is *Ecclinusa*, represented by 11 neotropical species generally of the Guyana Shield occurring in savannah, lowland rainforest, and cloud forest near Oxapampa, Peru to 1300 m altitude (Pennington 1990).

This genus is distinguished from *Chromolucuma* by having smaller leaves and stipules, sessile compared to pedicellate flowers, an absence of intersecondary veins, and its closely parallel tertiary veins oblique to the secondaries; however, both genera share a *Pouteria* type seed and the “pop bottle” shaped petiole with a swollen base.

The 30 neotropical *Manilkara* species are almost always emergent or canopy trees recognized by their reddish bark with deep vertical fissures in mature trees. Small, spirally arranged leaves are usually clustered near shoot apices with brochidodromous venation, and closely parallel intersecondary and tertiary veins giving a striate appearance. *Manilkara* have petioles without noticeably enlarged bases; rarely have small stipules present, and a *Chrysophyllum* type seed with basal scar. This genus is the natural source of chewing gum or chicle (*Manilkara chicle*) and contains one of the densest woods in the Amazon known locally in Peru as quinilla (Pennington 1990).

Sarcaulus is represented by 6 species of lowland forest trees in the neotropics, and is closely related to *Pouteria* as it shares its seed type and standard “pop bottle” shaped petiole. The two are easily separated with *Sarcaulus* having small, narrow leaves usually arranged alternate and distichously, few brochidodromous secondary veins, and prominent reticulate tertiary venation on the underside of the leaf which distinctively dries a pinkish color.

Micropholis is exclusively found in the neotropics representing 38 species occurring primarily in non-flooded upland forest. This genus was split by Pennington (1990) into two sections based upon stamen position and flower size, with all species collected in this study belonging to the major *Micropholis* section. This entire genus has finely striate venation resulting from the secondary, intersecondary, and tertiary veins

closely paralleling one another. Striate venation combined with the usually elliptic leaves arranged alternate and distichously, a petiole lacking a noticeably enlarged base, and a *Chrysophyllum* seed type is characteristic of *Micropholis*.

Chrysophyllum is considered the second most important genus of this family, includes 43 species in the neotropics, and has been grouped into five sections by Pennington (1990) based on leaf, seed, and flower characters. This genus is often confused with *Pouteria* but differs by seed, petiole, leaf arrangement, and venation types. *Chrysophyllum* species of Sections 3, 4, and 5 have spirally arranged leaves like *Pouteria* but the *Chrysophyllum* type seed; while species of *Chrysophyllum* Sections 1 and 2 have the *Pouteria* seed type but also an alternate and distichous leaf arrangement, a combination never found in any *Pouteria* species. Also, *Chrysophyllum* species lack the petiole with a swollen-base typified by *Pouteria*, and often have tertiary veins closely parallel, obtuse to secondaries, and descending from the margin. By comparison, *Pouteria* species can sometimes have tertiary veins perpendicular to the midvein and may have intersecondary veins, both of which are usually absent among *Chrysophyllum* species. All neotropical Sapotaceae genera except *Chrysophyllum* can be easily distinguished from *Pouteria* in the field and herbarium, likely under representing this genus in the study results due to the incomplete identification of its collections amongst *Pouteria*. This result also suggests that all other collections should be accurately sorted to at least the generic level.

Pouteria is the highly polymorphic, primary genus with 188 of the 396 total neotropical species of Sapotaceae circumscribed by Pennington (1990) into eight different sections based on seed and flower characters. With further collection and

notation of intraspecific variability, all eight sections could potentially warrant distinct generic status in the future. All species have spirally arranged leaves, as well as the “pop bottle” petiole typical of *Pouteria*. The six species within the third Section *Oligotheca* are the exception among this entire genus by having the *Chrysophyllum* type seed (Pennington 1990). Classification in this genus is primarily divided upon floral characters, so identifying the mostly sterile collections became significantly difficult when comparing vegetative characters of almost 200 possible species. Many species of *Pouteria* were identified in this study, but most remained as their original morphospecies name assigned during the collection process.

Brako and Zarucchi (1993) described 10 genera with 84 species and 19 subspecies of Sapotaceae in a catalogue of Peru’s flora. According to the recent monograph of Pennington (1990), six genera with 20 species and 7 subspecies had currently been collected in Madre de Dios. The results of this study identified 19 species and 7 subspecies in common with those described by Brako and Zarucchi, while 10 species and 4 subspecies identified in common with the current monograph by Pennington. Both floras are expanded by the study results with four newly described species to Peru and ten newly described species to Madre de Dios.

The majority of collections resulted from the extensive Gentry 0.1-ha transect network across the study area, but additional sampling was made by the AABP botany team and author, with the latter making duplicate original collections but without the standardized AABP voucher specimen. Collections from outside the transect network were only used for botanical information and did not contribute to quantitative analyses. Following are detailed descriptions of identified Sapotaceae species with updated species

information referenced from the current monograph of Pennington (1990), and presenting original discussion of species habit, range, field characters, and photography.

***Chromolucuma* Ducke**

Type Species: *Chromolucuma rubiflora* Ducke

1. *Chromolucuma rubiflora* Ducke

AABP Voucher: PM 3063

Distribution: Southern Venezuela, central Amazonian Brazil, Magdalena Valley of Colombia, and southeastern Peru along riversides in periodically flooded forest.

Field Characters: Tree to 30 m high, 40 cm in diameter, small buttresses, and cream colored slash with scant yellow latex.

Vegetative Characters:

Stipules: 2-4 cm long, lanceolate and tapering at the apex, glabrous, and striate.

Leaves: Clustered, spiral, chartaceous, 23-45 cm long, oblanceolate, a narrowly cuneate leaf base, and glabrous.

Venation: Eucamptodromous, 17-40 secondary pairs curved and parallel, intersecondaries short or absent, and numerous tertiaries oblique to secondaries.

Petiole: 4-8 cm long, channeled, and glabrous.

Discussion: One collection of this species was made in the CICRA baja habitat along the Rio Los Amigos, and is a new record to the floras of Madre de Dios and Peru. This species differs from *C. baehniana* in its glabrous leaves with a narrowly cuneate base, and glabrous stipules.



Figure 4. Leaves and Stipules of *Chromolucuma rubiflora*.

2. *Chromolucuma baehniana* Monachino

AABP Voucher: PM 2649

Distribution: The Guianas and northern Amazonian Brazil in dry evergreen forest over white sand; southeastern Peru and Magdalena Valley of Colombia along riversides in periodically flooded forest.

Field Characters: Tree to 30 m high, 70 cm in diameter, buttresses up to 9 m high, scaling, reddish bark, and cream colored slash with scant yellow or white latex.

Vegetative Characters:

Stipules: 1-2 cm long, narrowly oblong, and puberulous with reddish hairs.

Leaves: Clustered, spiral, coriaceous, 11-42 cm long, broadly oblanceolate, an acute to rounded leaf base, and glabrous above but sericeous below with golden to reddish hairs.

Venation: Eucamptodromous, 13-26 secondary pairs parallel and rarely curved, intersecondaries absent, tertiaries oblique to secondaries, and quaternary reticulum clear below.

Petiole: 1.5-7 cm long, strongly channeled, and appressed puberulous to glabrous.

Discussion: Ten collections were made from both alta and baja forests of CICRA and CM1, and is a new record to the floras of Madre de Dios and Peru. The lower leaf surface and stipules of this species are sericeous to having few reddish, persistent hairs, and an acute to rounded leaf base. The fruit of this species is unknown, but could be later described due to the referenced tree locations from this study.



Figure 5. Leaves, Leaf Underside, and Stipules of *Chromolucuma baehniana*.

Ecclinusa Martius

Type Species: *Ecclinusa ramiflora* Martius

3. *Ecclinusa lanceolata* (Martius & Eichler) Pierre

AABP Voucher: PM 2612

Distribution: Brazil and the Guianas in seasonal evergreen forests that are never or periodically flooded; reported in wet montane forests up to 1300 m altitude in Peru, Colombia, and Panama, but also in the non-flooded upland and floodplain forests in southeastern Peru.

Field Characters: Tree to 35 m high, 50 cm in diameter, lacking buttresses, with strongly dappled, dark brown bark, and cream to orange slash with abundant sticky white latex.

Vegetative Characters:

Stipules: 1-2 cm long, often striate, and appressed puberulous to glabrous.

Leaves: Clustered, spiral, thinly coriaceous, 16-42 cm long, oblanceolate, glabrous, and both leaf apex and base usually attenuate.

Venation: Eucamptodromous, 20-33 secondary pairs parallel and slightly curved, intersecondaries absent, and numerous parallel tertiaries oblique to secondaries.

Petiole: 2-4 cm long, channeled, and appressed pubescent.

Discussion: The morphological variation of this species is not fully understood, and is previously known from seasonal evergreen forest over white sand and wet montane forest. Of 1087 trees sampled, this species represented 215 individuals with the next most abundant Sapotaceae species having only 40 individuals. Primarily found in alta forests, the only study location without this species is Refugio 2 with this likely due to its small sample size. Despite this abundance, this species is a new collection to the flora of Madre de Dios.



Figure 6. Trunk Slash, Stipules, and Leaves of *Ecclinusa lanceolata*.

Manilkara Adanson

Type Species: *Manilkara kauki* (Linnaeus) Dubard

4. *Manilkara bidentata* subsp. *surinamensis*

AABP Voucher: PM 2549

Distribution: West Indies, Panama, and northern South America; occurring in periodically and non-flooded forests of Amazonia, semi-evergreen forests in the Caribbean, and dry campina forest over white sand in parts of Brazil.

Field Characters: Shrub-like in dry forest, but in rainforest a large tree of 40 m or more in height, often buttressed, with deeply fissured grey-brown bark, and a pink to deep red slash with copious sticky white latex.

Vegetative Characters:

Stipules: Absent in subspecies *surinamensis*, but 2-5 mm long in subspecies *bidentata* if present.

Leaves: Clustered, spiral, chartaceous, 7-21 cm long with an average of 12.2 cm, oblong to oblanceolate, leaf apex typically rounded, and glabrous.

Venation: Brochidodromous, 12-25 secondary pairs parallel and curved, marginal vein present, and quaternary venation coarsely areolate obscuring the tertiaries.

Petiole: Less than 2.5 cm long, not channeled, and glabrous.

Discussion: 18 collections were made from both alta and baja habitats of CICRA and CM1 with the majority from baja forests. Previously only known from northern Peru, this subspecies is a new record for Madre de Dios. This subspecies is distinct from subsp. *brasiliensis* by having more oblanceolate leaves with a rounded apex, a lack of small stipules, and occurring in a variety of habitats from upland to permanently flooded forests.



Figure 7. Habit of *Manilkara bidentata*.

Sarcaulus Radlkofer

Type Species: *Sarcaulus macrophyllus* (Martius) Radlkofer

5. *Sarcaulus brasiliensis* (A. de Candolle) Eyma subsp. *gracilis* Pennington

AABP Voucher: JJ 3624

Distribution: Wet lowland rain forest of Amazonian Peru between 180-500 m.

Field Characters: Tree to 8 m high, and 14 cm in diameter with white latex.

Vegetative Characters:

Leaves: Spaced, alternate and distichous to spiral, chartaceous, usually less than 9 cm long, elliptic or oblong-elliptic, apex acuminate to caudate, base attenuate to obtuse or rounded, and glabrous.

Venation: Eucamptodromous or brochidodromous, 8-12 secondary pairs convergent and curved, short to long intersecondaries, marginal vein present, and tertiaries a lax reticulum.

Petiole: 0.2-1.5 cm long, slightly channeled, and becoming glabrous.

6. *Sarcaulus vestitus* (Baehni) Pennington

AABP Voucher: PM 2562

Distribution: Western Amazonian Brazil in periodically flooded forest, and southeastern Peru in non-flooded upland and floodplain forest.

Field Characters: Tree to 30 m high, 50 cm diameter, with fissured and scaling grey-brown bark, and an orange slash with abundant white latex.

Vegetative Characters:

Leaves: Spaced, alternate and distichous, chartaceous, 8-15 cm long, elliptic or oblong, apex acuminate and base attenuate, and glabrous above with appressed puberulous whitish indumentum below being lost with age.

Venation: Eucamptodromous or brochidodromous in upper half, 9-13 secondary pairs curved and slightly convergent, intersecondaries absent or short, and tertiaries a lax reticulum.

Petiole: 7-8 mm long, slightly channeled, and becoming glabrous.

Discussion: This species was collected from both alta and baja habitats, and nearly a third of all Sapotaceae collections at the CM2 location. This species is a new record for the flora of Peru and Madre de Dios, extending its known range west from Acre, Brazil.



Figure 8. Trunk Slash and Leaves of *Sarcaulus vestitus*.

***Micropholis* (Grisebach) Pierre**

Section 1. *Micropholis* (Grisebach) Pierre

Type Species: *Micropholis rugosa* (Swartz) Pierre

7. *Micropholis egensis* (A. de Candolle) Pierre

AABP Voucher: PM 2703

Distribution: Panama and northern Amazonian extending south into Ecuador, Peru, Brazil; occurring primarily in permanently and periodically flooded forest or rarely in non-flooded forest to 500 m altitude.

Field Characters: Tree to 40 m high, 60 cm in diameter, larger trees with small buttresses, smooth to finely fissured bark grey to reddish-brown in color, and with pink to orange slash with sticky white latex.

Vegetative Characters:

Leaves: Spaced, alternate and distichous or rarely partially spiral, thinly coriaceous, 7-20 cm long, elliptic or oblong-elliptic, apex acuminate or attenuate, base attenuate or cuneate, and glabrous.

Venation: Brochidodromous or craspedodromous, strong marginal and submarginal veins, midrib flat or raised above, and ascending secondaries indistinguishable from intersecondaries and tertiaries making leaf finely striate.

Petiole: 0.3-1.5 cm long, channeled, and glabrous.

8. *Micropholis guyanensis* (A. de Candolle) Pierre

AABP Voucher: JJ 2381

Distribution: Costa Rica and Panama, West Indies, Amazonia west to Ecuador, south to Bolivia, and east to coastal Brazil; occurring in non-flooded lowland forest below 200 m altitude.

Field Characters: Tree to 35 m high, 100 cm in diameter, larger trees with steep buttresses, reddish-brown bark being smooth or with fine fissures, a pink to orange slash exuding sticky white latex, and obvious tan to bronze undersides of leaves.

Vegetative Characters:

Leaves: Spaced, alternate and distichous or rarely spiral, coriaceous, 4-20 cm long, elliptic to oblong or oblanceolate, apex cuspidate to attenuate, base attenuate to obtuse, and glabrous above but sericeous indumentum of reddish hairs below turning a golden color with age.

Venation: Brochidodromous, rarely with marginal vein but secondaries join near margin to create a submarginal vein, midrib typically sunken above, 15-30 secondary pairs parallel and slightly curved, intersecondaries extend to margin, and higher order venation areolate.

Petiole: 0.4-3 cm long, channeled, and puberulous with hairs golden to reddish.

9. *Micropholis madeirensis* (Baehni) Aubréville

AABP Voucher: AB 772

Distribution: Central and western Amazonian Brazil and adjacent eastern Peru in lowland rainforest.

Field Characters: Tree to 30 m high with white latex.

Vegetative Characters:

Leaves: Spaced, alternate and distichous, thinly coriaceous, 10-16 cm long, elliptic or oblanceolate, apex cuspidate to attenuate, base obtuse to rounded, and glabrous above but tomentose indumentum of reddish hairs persisting along midrib and veins below.

Venation: Brochidodromous, 40-50 secondary pairs parallel and slightly curved, marginal vein present, midrib flat or raised above, intersecondaries extend to margin and parallel with tertiaries, and appearing finely striate.

Petiole: 0.8-1.5 cm long, channeled, and stiff tomentose of dark reddish hairs.

Discussion: This species has previously been found in northern Peru and adjacent Brazil, but is a new record to the flora of Madre de Dios. Only collected from the alta and baja habitats of the CM1 study location up to 300 m altitude. Figure 9 illustrates the close venation of this species and that typifies the genus *Micropholis*.



Figure 9. Leaf Close-up of *Micropholis madeirensis*.

10. *Micropholis porphyrocarpa* (Baehni) Monachino

AABP Voucher: PM 2610

Distribution: The Guianas, Amazonian Brazil, and Peru in non-flooded upland forests to 500 m altitude.

Field Characters: Tree to 35 m high, 60 cm in diameter, with dark to orange-brown bark scaling in small thin pieces, and an orange to cream slash with white sticky latex.

Vegetative Characters:

Leaves: Spaced, alternate and distichous or rarely spiral, coriaceous, 6-15 cm long, narrow elliptic or oblanceolate, apex acuminate to rounded, base acute to attenuate, and glabrous above but densely sericeous below with golden hairs persisting or lost with age.

Venation: Craspedodromous, strong marginal vein, midrib sunken above, and ascending secondaries indistinguishable from intersecondaries and tertiaries making leaf finely striate.

Petiole: 0.5-1 cm long, channeled, and tomentose of orange-reddish hairs.

Discussion: This species is a new record to the flora of Madre de Dios and extends its range west from Acre, Brazil. Collections were primarily made from alta habitats, but also baja forests. This species is distinct from close relatives because of its densely golden, sericeous leaf undersides and terminal branches.



Figure 10. Trunk Slash, Terminal Branch, and Leaves of *Micropholis porphyrocarpa*.

11. *Micropholis trunciflora* Ducke

AABP Voucher: AB 428

Distribution: Central and western Amazonian Brazil and adjacent Peru in upland, non-flooded forest.

Field Characters: Tree to 20 m high, 12 cm in diameter and with small amount of white latex from trunk slash.

Vegetative Characters:

Leaves: Spaced, alternate and distichous, thinly coriaceous, 8-22 cm long, oblong to elliptic, apex attenuate or cuspidate, base attenuate or acute, and glabrous or with sparse hairs along midrib below.

Venation: Brochidodromous or craspedodromous, strong marginal vein and usually submarginal vein present, midrib sunken above, and secondaries nearly perpendicular to midrib and indistinguishable from intersecondaries or tertiaries making leaf finely striate.

Petiole: 0.5-1 cm long, channeled, and tomentose to glabrous.

Discussion: This species is a new record to the flora of Madre de Dios extending its distribution south and west from Loreto, Peru and Acre, Brazil. It is distinct from close relative *Micropholis egensis* by having secondary veins nearly perpendicular to the midrib which is sunken on the upper leaf surface.

12. *Micropholis venulosa* (Martius & Eichler) Pierre

AABP Voucher: AB 517

Distribution: Panama, the Guianas, Amazonian east to coastal Brazil and west to Ecuador; occurring in permanently, periodically, and non-flooded forests, but also dry cerrado and dwarf campina forests in Brazil, and wet montane forest to 900 m altitude in Venezuela.

Field Characters: Tree up to 70 m high, 100 cm in diameter or larger, steep buttresses up to 3 m high, with grey-brown bark having fine fissures or scaling, and with a reddish-brown slash with copious milky latex.

Vegetative Characters:

Leaves: Spaced, alternate and distichous or rarely spiral, chartaceous to thinly coriaceous, 4-9 cm long, lanceolate or rarely oblong, apex caudate or attenuate, base attenuate to rounded, and glabrous.

Venation: Brochidodromous or craspedodromous, strong marginal vein and submarginal vein present, midrib flat or raised above, and secondaries indistinguishable from intersecondaries or tertiaries making leaf finely striate.

Petiole: 1.5-5 mm long, channeled, and pubescent to glabrous.

Discussion: This species is noted as especially widespread and common throughout the neotropics. Only three collections, all from CM1 baja, resulted from this study; however, its wide distribution and high variation in morphology suggests unidentified *Micropholis* morphospecies may be this species. Its sweet, edible fruit is safe for human consumption and reportedly dispersed by birds.

Chrysophyllum Linnaeus

Section 1. *Chrysophyllum* Linnaeus

Type Species: *Chrysophyllum cainito* Linnaeus

13. *Chrysophyllum acreanum* A. C. Smith

AABP Voucher: Non-Voucher (AW 17)

Distribution: Western Amazonian Brazil and adjacent southeastern Peru in periodically and non-flooded forest.

Field Characters: Tree to 25 m high, gray-brown scaling and fissured bark, and cream slash with little white latex.

Vegetative Characters:

Leaves: Spaced, alternate and distichous, coriaceous, 5-11 cm long, lanceolate to narrowly oblong, apex attenuate, base rounded, and glabrous or with few residual hairs along midrib on both leaf surfaces.

Venation: Brochidodromous, midrib sunken above, 9-15 secondary pairs parallel and straight, tertiaries descending from margin parallel to secondaries, and quaternaries finely reticulate.

Petiole: 2-4 mm long, not channeled, and glabrous or with few light brown hairs.

Discussion: This species is a new record to the flora of Peru extending its distribution west from its only known location in adjacent Acre, Brazil. The fruit of this species is previously unknown, but the collection made by the author in the alta forest of CM1 had immature fruits and flowers as seen by Figure 11.



Figure 11. Trunk Slash, Immature Fruit, and Leaves of *Chrysophyllum acreanum*.

14. *Chrysophyllum argenteum* Jacquin subsp. *auratum* (Miquel) Pennington
AABP Voucher: AB 966

Distribution: Northern Amazonia including Brazil and west to Ecuador; occurring in lowland rainforest, seasonal semi-evergreen forest, montane and cloud forest, and rarely in permanently flooded forest but frequently along riverbanks.

Field Characters: Tree to 35 m high, 65 cm in diameter, small rounded buttresses, smooth grayish bark scaling and fissuring with age, and a pink to reddish slash with plentiful sticky white latex.

Vegetative Characters:

Leaves: Spaced, alternate and distichous, coriaceous, 8-18 cm long, broadly oblong to elliptic or rarely oblanceolate, apex attenuate, base attenuate to obtuse, and glabrous above but sericeous below with golden hairs.

Venation: Eucamptodromous or brochidodromous, midrib sunken above, 8-16 secondary pairs parallel and curved, intersecondaries short to long, tertiaries descending from margin parallel to secondaries or creating a lax reticulum.

Petiole: 0.3-2 cm long, channeled, and sericeous to glabrous with golden hairs.

Discussion: This species is a new record to the flora of Madre de Dios extending its distribution south and west. Subspecies *auratum* of *Chrysophyllum argenteum* has the widest ecological range of all four subspecies, and was collected from both alta and baja habitats. It is characterized by the lower leaf surface being densely sericeous with whitish hairs and curved secondary veins.



Figure 12. Leaves of *Chrysophyllum argenteum* subsp. *auratum*.

Section 4. *Priourella* (Pierre) Pennington

Type Species: *Chrysophyllum cuneifolium* (Rudge) A. de Candolle

15. *Chrysophyllum amazonicum* Pennington

AABP Voucher: Non-Voucher (AW 14)

Distribution: Amazonian Brazil, eastern Peru and Colombia, and southern Venezuela in non-flooded forest to 800 m altitude.

Field Characters: Tree to 35 m high, 50 cm in diameter, without buttresses, smooth to scaling gray or red-brown bark, and orange to reddish slash with abundant white latex.

Vegetative Characters:

Leaves: Loosely clustered near shoot apex, spiral, thinly coriaceous, 9-18 cm long, oblanceolate, apex rounded or shortly cuspidate, base attenuate to acute, and glabrous or with few residual hairs along midrib below.

Venation: Eucamptodromous, midrib raised above, 10-13 secondary pairs being curved and slightly convergent or parallel, intersecondaries absent, and numerous parallel tertiaries oblique to secondaries.

Petiole: 1-2.2 cm long, not channeled, and glabrous.

Discussion: This species is a new record to the flora of Madre de Dios extending its distribution south and west.



Figure 13. Trunk Slash and Leaves of *Chrysophyllum amazonicum*.

Section 5. *Aneuchrysophyllum* Engler

Type Species: *Chrysophyllum imperiale* (Linden ex Koch) Bentham & J. D. Hooker

16. *Chrysophyllum pomiferum* (Eyma) Pennington

AABP Voucher: Non-Voucher (AW 32)

Distribution: Venezuela, Colombia, the Guianas, Amazonian Brazil, and Peru; occurring primarily in mixed lowland rainforest but also in cloud forest of 600-700 m altitude.

Field Characters: Tree to 40 m high, 90 cm in diameter, with scaling or fissuring gray to red-brown bark, and yellow to orange slash with milky white latex.

Vegetative Characters:

Leaves: : Spaced or loosely clustered near shoot apex, spiral, chartaceous to coriaceous, 5-14 cm long, usually broadly oblanceolate, apex obtuse to rounded, base broadly to narrowly attenuate, and glabrous.

Venation: Brochidodromous or rarely eucamptodromous, midrib flat or raised above, 7-10 secondary pairs curved and convergent or parallel, intersecondaries short to long, and tertiaries a lax reticulum.

Petiole: 3-7 mm long, not channeled, and glabrous.



Figure 14. Trunk Slash and Leaf Surfaces of *Chrysophyllum pomiferum*.

17. *Chrysophyllum venezuelanense* (Pierre) Pennington

AABP Voucher: AB 527

Distribution: Mexico, Central America, and western South America south to Bolivia, with possible records from Amazonian Brazil; occurring in wet lowland rainforest, seasonal evergreen forest, as well as montane and cloud forests to 1200 m altitude.

Field Characters: Tree to 40 m high, 60 cm in diameter, rarely with small buttresses, with smooth or finely fissured gray-brown bark, and dark yellow slash exuding a small amount of thin white latex.

Vegetative Characters:

Leaves: Spaced or loosely clustered near shoot apex, spiral, usually chartaceous, 9-25 cm long, oblanceolate to elliptic, apex broadly attenuate to rounded, base acute to attenuate, and glabrous.

Venation: Eucamptodromous, midrib flat above, 8-12 secondary pairs curved and slightly convergent or parallel, intersecondaries short or absent, and tertiaries usually horizontal but also rarely a lax reticulum.

Petiole: 0.5-4 cm long, often channeled, appressed puberulous becoming glabrous.

Pouteria Aublet

Section 1. *Franchetella* (Pierre) Eyma

Type Species: *Pouteria guianensis* Aublet

18. *Pouteria bangii* (Rusby) Pennington

AABP Voucher: PM 1203

Distribution: Amazonian South America, extending south to Brazil and Bolivia, west to Peru and Ecuador, and north to Colombia and Venezuela; occurring primarily in non-flooded rain forest to 1200 m altitude.

Field Characters: Tree to 30 m high, 40 cm in diameter, gray to whitish-gray vertically cracked bark, and pink slash with abundant white latex.

Vegetative Characters:

Leaves: Spaced, spiral, coriaceous, 9-21 cm long, elliptic to lanceolate, apex acuminate or attenuate, base acute to attenuate, and glabrous above but appressed puberulous below with golden hairs being lost with age.

Venation: Eucamptodromous, marginal vein often present, midrib raised above, 7-14 secondary pairs curved and parallel or slightly convergent, intersecondaries short or absent, and tertiaries horizontal or reticulate.

Petiole: 1-2 cm long, not channeled, and appressed puberulous to glabrous.

19. *Pouteria bilocularis* (Winkler) Baehni

AABP Voucher: JJ 2144

Distribution: Northern and western Amazonia south to Bolivia and Brazil; occurring in lowland rainforest or rarely in periodically flooded forest to 1200 m altitude.

Field Characters: Tree to 35 m high, 40 cm in diameter, buttresses to 2 m high, and cream slash with white latex.

Vegetative Characters:

Leaves: Spaced, spiral, coriaceous, 6-15 cm long, elliptic to oblanceolate, apex acute or attenuate, base narrowly attenuate, and glabrous but lower surface often minutely punctate.

Venation: Eucamptodromous, marginal vein present, midrib raised above, 7-11 secondary pairs curved and convergent, intersecondaries moderate to long, and tertiaries parallel to secondaries or reticulate.

Petiole: 0.5-2 cm long, slightly channeled, and glabrous.

20. *Pouteria durlandii* (Standley) Baehni

AABP Voucher: JJ 2619

Distribution: Atlantic drainage of Mexico and Central America, northern South America to southeast Brazil, Amazonian Peru and Bolivia; occurring primarily in wet lowland rainforest but also evergreen and semi-deciduous forest in Central America, Venezuela, and Brazil.

Field Characters: Tree to 25 m high, 65 cm in diameter, gray to reddish-brown bark scaling in thin strips, and pink slash with copious white latex.

Vegetative Characters:

Leaves: Spaced or loosely clustered near shoot apex, spiral, coriaceous, 8-30 cm long, elliptic or oblanceolate, apex acuminate or attenuate, base narrowly attenuate, and glabrous or with few appressed hairs below.

Venation: Eucamptodromous or rarely brochidodromous in upper half, marginal vein often present, midrib flat or raised above, 7-20 secondary pairs slightly curved and usually convergent, intersecondaries short or absent, and tertiaries creating a fine reticulum visible on both surfaces.

Petiole: 0.5-2 cm long, not channeled, and sparsely pubescent or glabrous.

Discussion: Collections of this species have not been keyed to its two subspecies, but neither has been collected in Madre de Dios making this a new record to its flora.

21. *Pouteria reticulata* (Engler) Eyma

AABP Voucher: JJ 2552

Distribution: Mexico, Central America, South America to Peru, Bolivia, and coastal Brazil; occurring commonly in seasonal semi-deciduous forest, wet lowland rainforest, montane forest to 1500 m altitude, and rarely periodically flooded forest.

Field Characters: Tree to 40 m high, 50 cm in diameter, buttresses to 2 m high, brown to pale gray bark scaling in long pieces, and slash cream to reddish or orange with white latex.

Vegetative Characters:

Leaves: Spaced, spiral, coriaceous, 5-22 cm long, oblanceolate to elliptic, apex acuminate or attenuate, base acute to attenuate, and glabrous above but appressed puberulous below with golden hairs lost with age.

Venation: Eucamptodromous or brochidodromous, marginal vein usually present, midrib flat or raised above, 8-16 secondary pairs curved and slightly convergent, intersecondaries usually present but variable in length, and tertiaries reticulate.

Petiole: 0.5-1.5 cm long, not or slightly channeled, and subglabrous.

Discussion: Collections of this species have not been keyed to its two subspecies, but neither has been collected in Madre de Dios making this a new record to its flora. Additionally, subspecies *surinamensis* has not been reported from Peru, so its identification would yield another Sapotaceae species to the flora of Peru.

22. *Pouteria vernicosa* Pennington

AABP Voucher: PM 2690

Distribution: Peruvian and western Amazonian Brazil in mixed lowland, non-flooded forest.

Field Characters: Tree to 35 m high, 50 cm in diameter, and white latex.

Vegetative Characters:

Leaves: Spaced, spiral, coriaceous with upper surface glossy, 7-13 cm long, oblanceolate, apex narrowly attenuate, base rounded, and glabrous.

Venation: Eucamptodromous, marginal vein present, midrib raised above, 9-12 secondary pairs curved and parallel or slightly convergent, intersecondaries short to long, and tertiaries few or absent being reticulate.

Petiole: 1-2 cm long, not channeled, and glabrous.

Discussion: This species is a new record for the flora of Madre de Dios extending its range west from Brazil and south from Huánuco, Peru. Collected mainly from alta habitats, this species is unique by having small, lanceolate, coriaceous leaves with a rounded base, and a shiny upper leaf surface compared to *Pouteria* species with similar floral characteristics.

Section 4. *Rivicoa* (A. de Candolle) Baehni

Type Species: *Pouteria lucuma* (Ruiz & Pavón) Kuntze

23. *Pouteria macrophylla* (Lamarck) Eyma

AABP Voucher: JJ 3532

Distribution: The Guianas, coastal and Amazonian Brazil, and adjacent Amazonian Peru and Bolivia; occurring primarily in lowland, non-flooded forest, but also in drier semi-deciduous, cerrado-type, and transitional dwarf campina forests in Brazil.

Field Characters: Tree to 30 m high, 35 cm in diameter, with small buttresses, finely fissured dark brown bark, and cream slash with copious white latex.

Vegetative Characters:

Leaves: Spaced or loosely clustered near shoot apex, spiral, chartaceous to thinly coriaceous, 7-21 cm long, oblanceolate or rarely elliptic, apex broadly cuspidate to attenuate, base narrowly attenuate, and subglabrous above but lower surface slightly glaucous and sparsely puberulous.

Venation: Eucamptodromous, thin marginal vein present, midrib flat or raised above, 12-18 secondary pairs parallel and straight or slightly curved, intersecondaries absent, tertiaries oblique but often obscure, and reticulate quaternaries visible on upper surface.

Petiole: 0.9-2 cm long, not channeled, and appressed puberulous.

Section 6. *Pouteria*

Type Species: *Pouteria congestifolia*

24. *Pouteria torta* (Martius) Radlkofer subsp. *glabra* Pennington

AABP Voucher: JJ 3545

Distribution: Colombia, the Guianas, and western South America through Amazonian Brazil to Bolivia; occurring in periodically and non-flooded rainforest, and lower montane forest to 1000 m altitude.

Field Characters: Tree to 32 m high, 50 cm in diameter, larger trees with buttresses to 4 m high, brown to grayish-white bark scaling or with shallow fissures, and pale brown slash with scant white latex.

Vegetative Characters:

Leaves: Clustered near shoot apex, spiral, coriaceous, 20-45 cm long, oblanceolate with tapering base, apex broadly cuspidate to attenuate, base narrowly attenuate, and glabrous.

Venation: Eucamptodromous, marginal vein present, 17-39 secondary pairs curved and parallel or slightly convergent, intersecondaries short or absent, tertiaries oblique to secondaries, and quaternaries finely reticulate.

Petiole: 0.5-6 cm long, not channeled, and glabrous.

25. *Pouteria torta* (Martius) Radlkofer subsp. *torta*

AABP Voucher: Non-Voucher (AW 12)

Distribution: Central and coastal Brazil in dry cerrado, savannah, and campina forest, but also non-flooded, lowland rainforest in southeastern Peru.

Field Characters: Shrub to small tree to 20 m high, 75 cm in diameter, deeply fissured gray-brown bark, and cream slash with plentiful white latex.

Vegetative Characters:

Leaves: Clustered near shoot apex, spiral, chartaceous, 7-15 cm long, oblanceolate with tapering base, apex rounded or emarginate, base narrowly attenuate, with persistent hairs along midrib above, and a dense indumentum of crisped, reddish hairs below.

Venation: Eucamptodromous, marginal vein present, 13-18 secondary pairs curved and parallel, intersecondaries short or absent, and higher order venation a lax reticulum with tertiaries and quaternaries indistinguishable.

Petiole: 0.5-6 cm long, slightly channeled, and with crisped tomentose reddish hairs.

Discussion: This subspecies has one collection in Madre de Dios prior to this study, but is otherwise exclusive to the dry cerrado and campina forests of eastern Brazil where it occurs as a small, twisted tree. Collecting this species confirms its presence in lowland forests of southeastern Peru; however the cause of this peculiar species distribution is unknown leading to speculation of human interference or insufficient botanical collection.



Figure 15. Trunk Slash, Bark, and Leaves of *Pouteria torta* subsp. *torta*.

26. *Pouteria torta* (Martius) Radlkofer subsp. *tuberculata* (Sleumer)

Pennington

AABP Voucher: Non-Voucher (AW 15)

Distribution: Atlantic drainage of Mexico and Central America, Ecuador, Peru and adjacent Amazonian Brazil; occurring primarily in lowland rainforest but also seasonal evergreen forest and lower montane forest to 700 m altitude.

Field Characters: Tree to 35 m high, 60 cm in diameter, rarely with small buttresses, dark brown bark scaling in thin strips or slightly fissured, and cream slash with white latex.

Vegetative Characters:

Leaves: Clustered near shoot apex, spiral, coriaceous, 15-45 cm long, oblanceolate with tapering base, apex attenuate to broadly cuspidate, base narrowly attenuate, and glabrous above but lower surface with dense indumentum of stiff reddish hairs.

Venation: Eucamptodromous, marginal vein present, 17-37 secondary pairs curved and parallel, intersecondaries short or absent, tertiaries oblique to secondaries, and quaternaries a fine reticulum.

Petiole: 0.5-6 cm long, strongly channeled, and with indumentum of stiff, reddish hairs.



Figure 16. Trunk Slash, Petioles, and Leaves of *Pouteria torta* subsp. *tuberculata*.

Species Richness

Species rarefaction curves were employed first to investigate whether the sampling effort was sufficient to adequately determine species richness for each location. A rarefaction curve that reaches a plateau with little or no slope signifies that the area was adequately sampled with few additional species being likely to be found as more individuals are sampled. Species

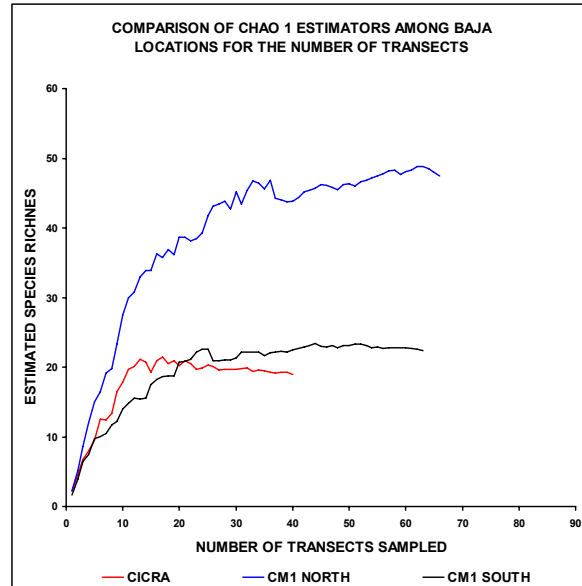


Figure 17. Estimated Species Richness For Baja Habitats.

accumulation will occur at a faster rate in a spatially random distribution (Chazdon *et al.* 1998). A summary of the estimated species richness and corresponding 95% confidence intervals for the locations and habitats of CICRA and CM1 can be found in Table 2.

Figure 17 shows the calculated individual based rarefaction curves using the Chao 1 estimator for baja habitats; while Figure 18 represents the alta habitats.

Table 2. Species Richness of CICRA and CM1 From the Chao 1 Procedure.

Habitat	Observed	Estimated	Number of	95% Confidence Interval	
	No. Species	No. Species		Individuals	Low
CICRA Alta	42	41	345	40.11	48.97
CM1 Alta	42	51	367	44.37	73.66
CICRA Baja	24	19	67	18.11	26.97
CM1 Baja - North	37	48	118	40.11	72.49
CM1 Baja - South	21	22	94	21.19	31.56

The sample size of CICRA baja was reduced for this analysis to 67 individuals as two units were dropped from the analysis due to occurring in an area of baja separated by alta from the other baja locations.

CICRA alta appears (Figure 18) to have been adequately sampled by 345 individuals found in 210 transects (Table 1). The small confidence interval also suggests that the richness of this habitat has been accounted for. The CM1 alta habitat is smaller in area, but appears to be more diverse with an estimated 10 more species. The CM1 alta rarefaction curve in Figure 18 continues to rise

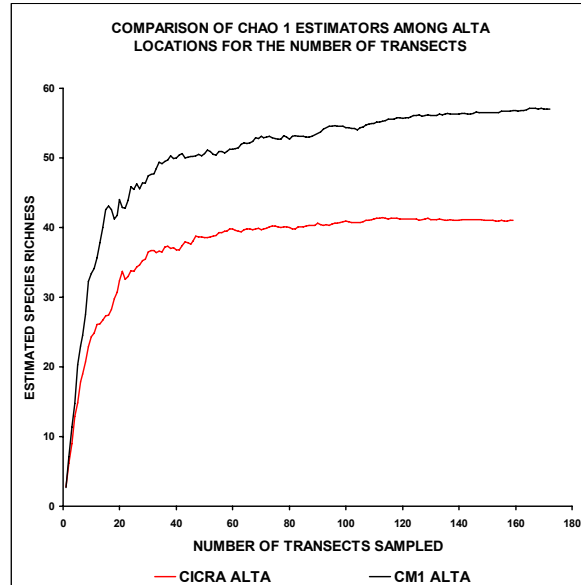


Figure 18. Estimated Species Richness For Alta Habitats.

slightly after a sample of 267 individuals in 210 transects (Table 1) which suggests an incomplete sampling of the Sapotaceae diversity in this habitat, and is supported by its large confidence interval of 44 to 74 for the estimated species total for the habitat. Curves for both habitats accumulated quickly to between 30 and 40 species only 60 individuals had been sampled which suggests a random spatial distribution of the data.

Of the baja locations, CICRA had the smallest sample size of 67 individuals in 90 transects but appeared to be adequately estimated with low richness. The neighboring southern subgroup of CM1 had a similar sample size and small confidence interval suggesting these two forest locations are similar in species richness. Both also had rapid increases in estimated richness with increasing sample size. The rarefaction curve of the northern subgroup of CM1 baja seen in Figure 17 shows increasing richness values through rising slope and large confidence interval despite having 118 individuals sampled in 100 transects (Table 1). These results suggest that the sampling effort did not

sufficiently account for all species present. Nevertheless, this subgroup is most diverse of the baja habitats as seen in Figure 18 and Table 3. With similar species richness estimated in adjacent and even different habitats, the rarefaction results show that more than broad generalities in habitat type are involved in determining the species richness across the study landscape.

Species abundance curves or rank abundance plots distinctly show the patterns of species richness, dominance, abundance, and rarity at each location in each habitat of CICRA and CM1 in Figure 19. A main advantage of this method is that relative abundance data is still easily visualized in the presence of relatively few species, as opposed to a histogram comparison where the same data would be hard to interpret (Magurran 2004). A logarithmic scale is utilized on the y-axis to account for especially abundant species, and species are represented as relative proportional abundances or their proportion of the total abundance in each habitat. Ranked from most to least abundant, the width of each curve illustrates the amount of species richness. A steep curve shows the influence of dominant species, while a curve with a shallow slope represents high species evenness in the habitat.

Alta habitats have curves showing the influence of one or more relatively abundant Sapotaceae species with *Ecclinusa lanceolata* dominating both as seen by their upper most data points in Figure 19. The baja habitats are characterized by curves indicating a mixture of more evenly abundant Sapotaceae species. High species richness can be seen in the continual accumulation of width by a curve, showing alta habitats to be more diverse, and the northern subgroup of CM1 baja to be the most species rich among the baja habitats. These two most species rich habitats can be seen to have many species

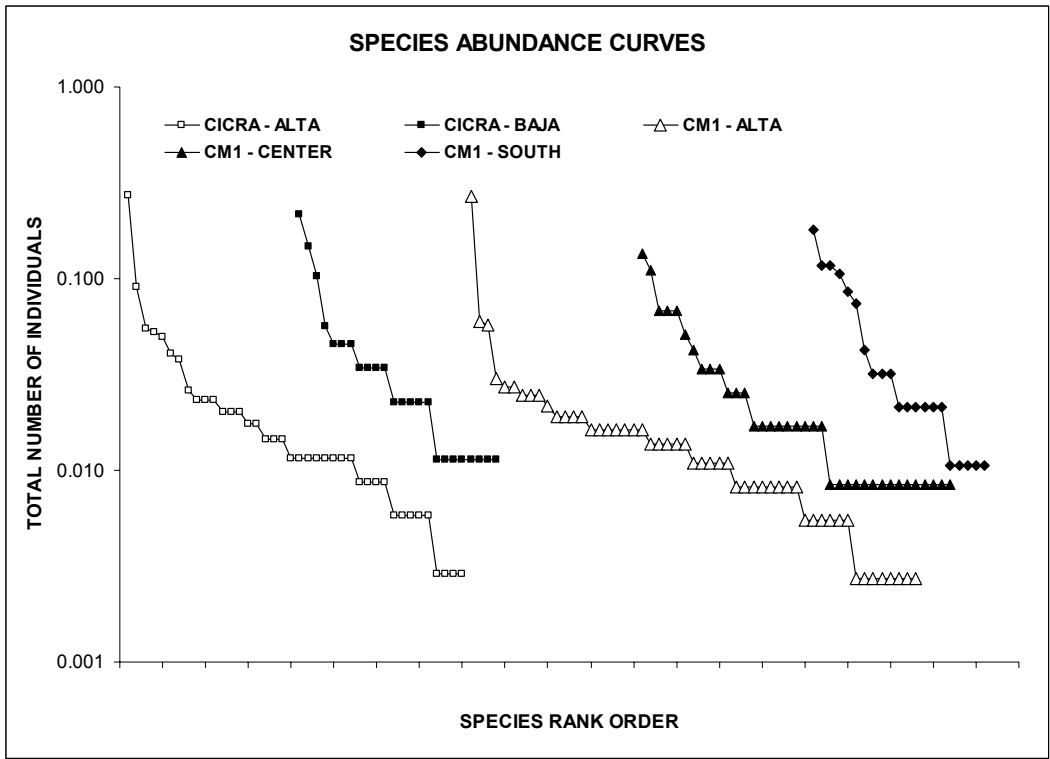


Figure 19. Species Abundance Curves for CICRA and CM1.

of low relative abundances, and supports previous rarefaction results that the Sapotaceae richness is incompletely estimated at these two locations. Results from these analyses of CICRA and CM1 demonstrate most habitats have been well if not completely assessed for their biodiversity, and combined with results of the botanical survey, Sapotaceae has been shown to be a diverse and prominent family in forests across the local landscape.

PART 2 – DISTRIBUTION

Forest Structure and Composition

A comparison of Sapotaceae diversity to other important tree families from all AABP transect data shows it to be the fourth most dominant family in terms of stems, and the third most species rich across the forests of the study landscape with habitat structures summarized in Table 3. The study forests were found to be dominated by Fabaceae with 1626 stems sampled, followed by Myristicaceae with 1228 stems, and Moraceae having 1094 stems, only seven more than Sapotaceae. Fabaceae was also found to be the most species rich with 161 species, followed by Lauraceae with 101 species, the Sapotaceae with a total of 95 species and five subspecies, and followed by Moraceae with 59 species. This shows the study results to closely follow the previously determined habit of Sapotaceae including high species diversity, and having a prominent presence in lowland Amazonian rainforests. The almost dominant distribution and high species diversity of the Sapotaceae indicates successful adaptation to the different habitat conditions found in the study area.

Table 3. Sapotaceae Structure at CICRA and CM1 Habitats.

Study Site	CICRA	CICRA	CM1	CM1 -	CM1 -
Habitat	Alta	Baja	Alta	North	South
Number Individuals	345	67	367	Baja	Baja
Total Basal Area (m²)	15.20	3.66	15.00	1.59	1.70
Maximum Height (m)	51.0	37.0	45.0	29.0	34.0
Maximum DBH (cm)	82.0	110.0	105.0	40.0	64.5
Average DBH (cm)	16.754	14.771	15.354	9.310	8.931

The number of shared species is a standard measure of similarity between two communities as it is a function of each species recorded (Chao 2000); however, this can

also inform about species distinct to communities and was visualized through a Venn diagram analysis. The botanical study identified 86 Sapotaceae morphospecies were collected in transects; however, only 70 had the required sample size ($n \geq 2$) for the analysis. Results in Figure 20 show a comparison of species composition between alta and baja habitats of CICRA and CM1.

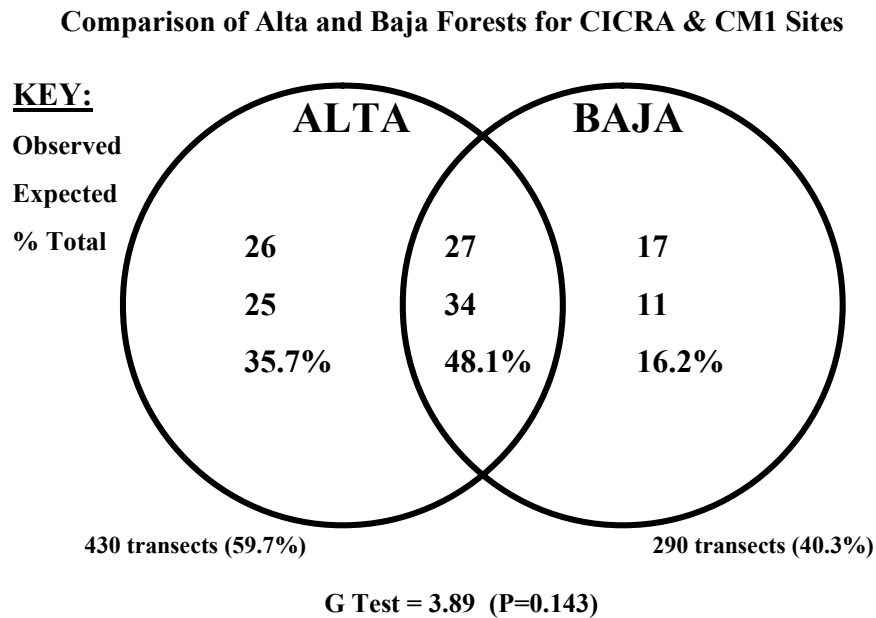


Figure 20. Venn Diagram Composition Analysis of CICRA and CM1 Habitats.

The observed number of species and that expected for random distributions among habitats listed as the top and middle numbers in Figure 20, and a G-test indicates no significant difference ($P=0.143$) between observed and expected numbers of species with more species than expected being found in baja habitats and fewer species than expected being found in both habitats.

Figure 20 shows most Sapotaceae species have specialized to exist in only one habitat type, with more species exclusive to alta habitats supporting their higher richness

compared to baja habitats. Specialization in the baja habitats may be relatively higher as seen by the greater number of unique species than expected despite the less intense sampling representing 40.3% of the total. These results show the local Sapotaceae populations to be highly adapted to a variety of habitat conditions as one of the most abundant and diverse families across the study landscape.

Forest Similarities

Final analyses compared species similarity between study locations and sample units of CICRA and CM1, with the other three study sites lacking an insufficient sample for comparison. Table 4 presents similarity results of the two indices computed, the Jaccard Classic and Chao–Jaccard Raw Abundance Based, as mean values representing all unit data from habitats within CICRA and CM1.

Table 4. Results of Two Similarity Coefficients Between CICRA and CM1 Habitats.

	CICRA Baja	CM1 Alta	CM1 Baja North	CM1 Baja South
Jaccard Classic				
CICRA Alta	0.255	0.640	0.453	0.318
CICRA Baja		0.222	0.224	0.135
CM1 Alta			0.521	0.277
CM1 Baja - N				0.208
Chao - Jaccard Abundance Based				
CICRA Alta	0.397	0.793	0.521	0.493
CICRA Baja		0.397	0.336	0.196
CM1 Alta			0.648	0.592
CM1 Baja - N				0.225

Table 4 shows a comparison of alta habitats to have an calculated similarity of 0.640 for Jaccard Classic and 0.793 for the Chao–Jaccard index. Baja habitats are found

to be less similar with results ranging from 0.224 to 0.135 for Jaccard Classic and 0.397 to 0.196 for Chao-Jaccard indices.

The baja habitats of CICRA and southern CM1 have previously had similar trends in analyses as seen by Figures 17 and 19; however, similarity results are low between these habitats with estimated values of 0.135 and 0.196 for the two computed indices. Interestingly, the baja habitats of CM1 are found to be more similar to both alta habitats than CICRA baja, with the northern subgroup of CM1 baja calculated to be almost as similar to CM1 alta as is the other alta habitat of CICRA.

Similarity results were further analyzed by comparing beta-diversity of the habitats at CICRA and CM1. Each unit contains species data from ten transects, so a comparison of similarity between species present in the units of each habitat allows for beta-diversity, that

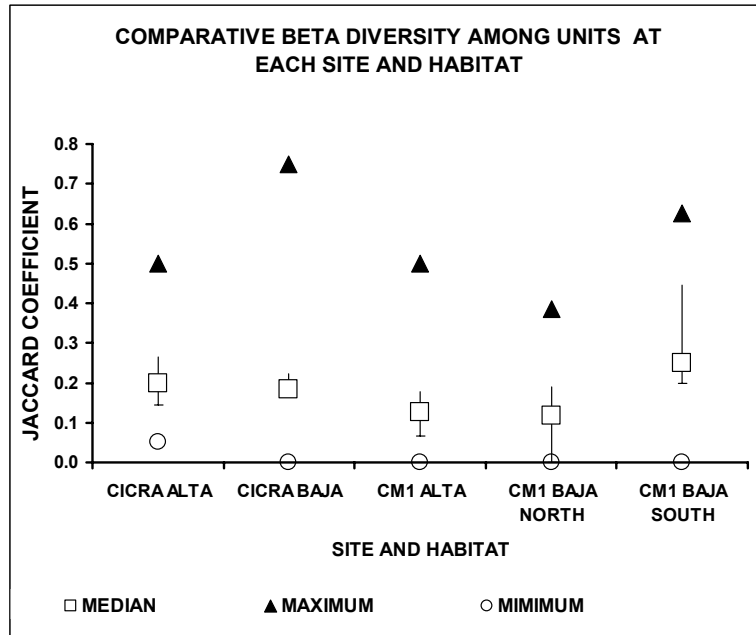


Figure 21. Beta-diversity Among Units of CICRA and CM1 Sites Using the Jaccard Classic Index.

occurring between habitats, to be quantified by the median result of calculated similarity indices. Beta-diversity and similarity hold an inverse relationship, so as similarity increases, the variation between samples, or beta-diversity, in these areas would decrease. This measure symbolizes species turnover or the rate of change in species diversity

between communities or habitats, and is an important ecological parameter in conservation planning to help select reserves that preserve the maximum number of species (Magurran 2004). The interquartile range about the median and the maximum and minimum results were added to each graph to completely explore all variability between habitats as seen by Figure 21 for the Jaccard Classic index.

Figure 21 illustrates all study habitats to have median similarity values near 0.2, with CM1 alta and the northern subgroup of CM1 baja having the least similar results indicating these to have the highest levels of within habitat beta-diversity. With the highest within habitat similarity, the southern subgroup of CM1 baja is shown to have the least beta-diversity and largest interquartile range. Four of the five habitats have at least one unit combination lacking a single common species as seen by the minima of Figure 21, so the true variation between these groups is shown by the maximum similarity values showing the lowest levels of betadiversity in each habitat. Most importantly, the results seen in Figure 21 show an overall low proportion of similarity between the units of each study habitat indicating a high degree of beta-diversity.

DISCUSSION

The floristic analysis of the local Sapotaceae delineated 86 morphospecies and combined with other unique collections found a total of 95 species and 5 subspecies distributed in different compositions throughout the habitats of the study landscape. Illustrating its great importance to local forests, when compared to transect data of other tree families the Sapotaceae was found to be the third most species rich and fourth most abundant considering all stems with $\text{dbh} \geq 2.5$ cm across the study landscape. Condit *et al.* (2002) found Sapotaceae to be the third most common family in both Peruvian and Ecuadorian plots behind the families Lauraceae and Moraceae. Miliken (1998) studied a terra firme forest plot in central Brazil finding 34 plant families, and calculated the Sapotaceae to be the third most important family behind Fabaceae and Lecythidaceae. Another study from Madre de Dios similarly found the Sapotaceae to be one of the two most abundant and diverse families behind Fabaceae (Spichiger 1996).

In comparison to the forests of baja habitats, the terra firme forests of alta habitats are found to be richer in Sapotaceae species, with species abundances more evenly distributed despite a heavy influence of the dominant species *Ecclinusa lanceolata*, and with species compositions having a higher degree of similarity. These differences may be partially explained by the more intensive sampling effort in the alta habitats which contain 59.7% of the sample transects. As the most species rich baja habitat, the northern subgroup of CM1 may have comparable species richness to alta habitats with further sampling as its total estimated richness was not completely accounted for in this study (Figure 17). This overall greater diversity in alta forests is supported by many publications including Gentry (1988b), Pitman *et al.* (1999), Pitman *et al.* (2001)

Despite differences in species richness, Figure 19 shows two distinct trends in the species abundances of alta and baja habitats. The high degree of relative abundance shows some species, especially *Ecclinusa lanceolata* in alta forests, to be much better suited to the local habitats. Baja habitats are indicated to have Sapotaceae communities with numerous well-suited, competing and coexisting species of moderate to low relative abundances. Although rarely inundated at these locations, the baja habitats collect plentiful runoff from the upper terraces, and potentially confront species with additional stressors in comparison to alta habitats, further restricting their richness, similarity, and abundances as seen by Table 4 and Figures 17, 18, 19, and 20.

The high degree of similarity in alta habitats is expected with previous analyses showing similar trends, and such high values can mainly be attributed to the exceptional relative abundance of *Ecclinusa lanceolata* in both these habitats. The greater estimated similarities of the alta habitats could also be due to less variation in local controlling factors such as hydrology.

As was found by Terborgh and Anderson (1998), baja habitats were found more similar to adjacent alta forests than adjacent baja forests. This could reflect the amount of seeds delivered to baja habitats from the upper terrace of alta forests, and result from limited dispersal methods or germination capability among the Sapotaceae of baja habitats. The comparison between adjacent baja habitats of CICRA and southern CM1 shows similar estimated species richness (Figure 17) structured differently into dissimilar compositions (Table 5). This could be the product of a similar disturbance, like a flood, that set a common successional event in motion ultimately yielding two final communities composed of different but ecologically similar species.

CONCLUSIONS

The results of this study have confirmed the Sapotaceae to be one of four most diverse and abundant families across the study landscape, and the Gentry 0.1-ha transect method to be a sufficient sampling technique in lowland Amazonian forests. Most importantly, the Sapotaceae flora of Peru has been expanded with the description of four new species, and ten additional species are reported for Madre de Dios. About a quarter of the total richness of 95 species and 5 subspecies found in the study landscape were found in common with the last revision of the flora of Peru by Brako and Zarucchi (1993) which listed only 84 Sapotaceae species in all of Peru leading to the conclusion that many additional species collected in this study could be described with further study and identification. Results of quantitative analyses show the family to be locally beta-diverse with most morphospecies existing in only one main habitat types, but specify the highest Sapotaceae abundance, similarity, and diversity in alta habitats.

The results lead to some important questions about the forests in the Los Amigos watershed. First, what mechanisms drive similarity and beta-diversity in local Sapotaceae populations and what is the result on their ecological success? Secondly, what may explain species distributions that have been greatly extended from other countries or regions? Thirdly, what characteristics or factors lead to the dominant success of *Ecclinusa lanceolata* across the study landscape? Finally, what factors are primarily responsible for driving local species diversities and distributions across this study landscape?

These questions could be answered with further study and collection of this family in the Los Amigos watershed, especially the CM1 study location, and beyond

throughout Amazonia. Much additional work is needed to resolve the complex taxonomy of this group, and virtually no neotropical Sapotaceae species have known pollination mechanisms. Most importantly, this widespread, diverse, and abundant family could be a conservation tool used as a predictive model to investigate a number of ecological parameters like abundance, dominance, diversity, and distribution in the Amazon or tropical lowland forests worldwide.

APPENDIX A. Morphospecies Abundance at All Study Locations.

Species Identity or Morphospecies Code	CICRA - Alta	CICRA - Baja	CM1 - Alta	CM1 - Baja	CM2	Refugio 2	Rio Amiguillos	Total Number	Botanical Voucher*
<i>Chromolucuma baehiana</i> Monachino	3		6	1				10	PM2649
<i>Chromolucuma rubiflora</i> Ducke		1						1	PM3063
<i>Chrysophyllum argenteum</i> Jacquin, Enum subsp. <i>auratum</i> (Miquel) Pennington	2		2	1				5	AB966
<i>Chrysophyllum</i> sp.1				1				1	AB831
<i>Chrysophyllum</i> sp.2		2						2	PM3019
<i>Ecclinusa lanceolata</i> (Martius & Eichler) Pierre	94	13	99		8		1	215	PM2612
<i>Ecclinusa</i> sp.1	5		6					11	JJ3592
<i>Manilkara bidentata</i> (A. de Candolle) Chevalier subsp. <i>surinamensis</i> (Miquel) Pennington	2	1	3	11			1	18	PM2549
<i>Micropholis egensis</i> (A. de Candolle) Pierre		9		4	1			14	PM2703
<i>Micropholis madeirensis</i> (Baehni) Aubreville			6					6	AB772
<i>Micropholis porphyrocarpa</i> (Baehni) Monachino	7		3	2	3	1		16	PM2610
<i>Micropholis</i> sp.1	1		6	5			1	13	AB236
<i>Micropholis</i> sp.2				1				1	AB327
<i>Micropholis</i> sp.3			4	1				5	AB399
<i>Micropholis</i> sp.4			1					1	AB854
<i>Micropholis</i> sp.5	18		2					20	JJ3612
<i>Micropholis</i> sp.6						3		3	PM3223
<i>Micropholis</i> sp.7						1		1	PM3248

APPENDIX A CONTINUED

<i>Micropholis</i> sp.8	7	1	10					18	PM2608
<i>Micropholis</i> sp.9	4		5					9	PM2632
<i>Micropholis venulosa</i> (Martius & Eichler)			1	2				3	AB517
<i>Pouteria bilocularis</i> (Winkler) Baehni				5				5	JJ2144
<i>Pouteria durlandii</i> (Standley) Baehni			3	3	1			7	JJ2619
<i>Pouteria macrophylla</i> (Lamarck) Eyma	2		9	1				12	JJ3532
<i>Pouteria</i> sp.1	1	4	7	14	1			27	AB1021
<i>Pouteria</i> sp.2	4	19	5	12				40	AB1061
<i>Pouteria</i> sp.3		2		4				6	AB1210
<i>Pouteria</i> sp.4				1				1	AB170
<i>Pouteria</i> sp.5	5		6	3				14	AB194
<i>Pouteria</i> sp.6				4				4	AB201
<i>Pouteria</i> sp.7			5	1				6	AB224
<i>Pouteria</i> sp.8				1				1	AB243
<i>Pouteria</i> sp.9				3				3	AB279
<i>Pouteria</i> sp.10				18				18	AB290
<i>Pouteria</i> sp.11				3				3	AB401
<i>Pouteria</i> sp.12				13				13	AB430
<i>Pouteria</i> sp.13		3	1	3				7	AB481
<i>Pouteria</i> sp.14				1				1	AB565
<i>Pouteria</i> sp.15	1				1			2	AB62
<i>Pouteria</i> sp.16			4					4	AB630
<i>Pouteria</i> sp.17			4	2				6	AB827
<i>Pouteria</i> sp.18			4	15				19	AB860

APPENDIX A CONTINUED

Pouteria sp.19			1					1	AB973
Pouteria sp.20	17	1	4	6	3	1	3	35	JJ2439
Pouteria sp.21		2						2	JJ2735
Pouteria sp.22	8		22		1	1		32	JJ3562
Pouteria sp.23	6		9		2	1		18	JJ3573
Pouteria sp.24	5		3		1			9	JJ3591
Pouteria sp.25	4							4	JJ3624
Pouteria sp.26	3		10	8				21	JJ3666
Pouteria sp.27	4	4	11	21				40	PC110
Pouteria sp.28	13		7			1		21	PM628
Pouteria sp.29				1				1	PM1236
Pouteria sp.30				1				1	PM1729
Pouteria sp.31	4		4		2			10	PM1929
Pouteria sp.32					1			1	PM1966
Pouteria sp.33			3	18	2			23	PM1984
Pouteria sp.34	14		21		1	1		37	PM2562
Pouteria sp.35	31	3						34	PM2596
Pouteria sp.36	9		8					17	PM2612
Pouteria sp.37	3		3		2	2		10	PM2650
Pouteria sp.38	8		2					10	PM2690
Pouteria sp.39		2						2	PM2733
Pouteria sp.40		1						1	PM2867
Pouteria sp.41		3						3	PM2941
Pouteria sp.42		4						4	PM2947
Pouteria sp.43		3		2				5	PM2952
Pouteria sp.44	3	1	4					8	PM2984

APPENDIX A CONTINUED

Pouteria sp.45	1	5	2	11				19	PM3005
Pouteria sp.46	4							4	PM3102
Pouteria sp.47		1	1					2	PM3123
Pouteria sp.48	4		10					14	PM3624
Pouteria sp.49	2	1	7			1		11	PM929
Pouteria sp.50			6					6	AB662
Pouteria sp.51			1					1	AB668
Pouteria sp.52			3					3	AB700
Pouteria sp.53			2					2	NONE
Pouteria sp.54	2		2					4	PM2610
Pouteria sp.55	4		3					7	PM2732
Pouteria sp.56				1				1	AB203
Pouteria sp.57				1				1	NONE
Pouteria sp.58				2				2	AB348
Pouteria sp.59				2				2	AB476
<i>Pouteria torta</i> (Martius) Radlkofer subsp. <i>glabra</i> Pennington	8	2	3		2			15	JJ3545
<i>Pouteria vernicosa</i> Pennington	19		7			1	5	32	PM2690
<i>Sarcaulus brasiliensis</i> (A. de Candolle) Eyma subsp. <i>gracilis</i> Pennington	7		5	2	1			15	JJ3624
<i>Sarcaulus vestita</i> (Baehni) Pennington	6		1		13	2	2	24	PM2562
Total Individuals:	345	88	367	212	46	16	13	1087	

* Listed voucher collectors are Angel Belarezo (AB), Pedro Centeno (PC), John Janovec (JJ), and Piher Maceda (PM)

* Herbarium sheets deposited at BRIT, La Molina (MOL) Herbarium in Peru, and are online at <http://atrium.andesamazon.org>

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ABSTRACT

THE SAPOTACEAE OF A LOWLAND RAINFOREST: DIVERSITY AND DISTRIBUTION IN THE LOS AMIGOS WATERSHED, MADRE DE DIOS, PERU

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The Sapotaceae is a highly diverse and abundant family of large tropical trees that have a significant ecological importance in lowland tropical forests worldwide. The goal of this study is to inventory Sapotaceae species of the Los Amigos River watershed, and investigate local variations of species diversity and distribution. 1087 individual trees sampled in 75 0.1-hectare Gentry transect units across upland and floodplain forests show this family of trees to be the third most species rich and fourth most abundant across the study landscape. A total of 95 species and five subspecies of Sapotaceae are reported with four new species described for the flora of Peru and ten new to Madre de Dios. Statistical and similarity analyses conclude higher levels of diversity and abundance for the Sapotaceae communities of upland or 'terra firme' forests.