

DIVERSITY AND DISTRIBUTION OF THE
MYRISTICACEAE FAMILY OF PLANTS IN TERRA FIRME
AND SEASONALLY FLOODED FORESTS IN MADRE DE
DIOS, PERU

by

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1 Introduction

The greater botanical diversity of tropical areas, compared to that of northern latitudes has long been a subject in the scientific literature, and there have been various studies attempting to uncover the processes generating these patterns. Plant diversity in the tropics can reach to more than 300 species per hectare (Gentry, 1988) and the mechanisms underlying this diversity have been the subject of numerous scientific studies. Hypotheses explaining this diversity have ranged from disturbance phenomena, refugia history, habitat heterogeneity, niche exploitation, dispersal and specific effects of environmental parameters such as light and water availability, and soil fertility (Salo et al, 1986; Colinvaux, and de Oliveira, 2001; Gentry, 1982; John et al, 2007; Thomas et al, 2006; de Oliveira et al, 1999). It has been suggested that understanding the spatial structure and the species composition of these forests will elucidate those processes promoting this diversity (Tuomisto et al, 2003).

Classification of tropical forests has often involved a primary division based on landforms into upland terra firme forests and inundated forests (Prance, 1979; Tuomisto, 1993) with less emphasis on floristic homogeneity within these habitats. The high diversity in these areas has been an obstacle to making finer scale dissections of this primary topographic division. Although the ecological differences between them have been recognized (Harms et al, 2001; Pitman et al, 1999; Cornejo et al, 2006; Condit et al, 2000; Wittman et al 2006), controversies remain concerning the distribution of species across and within these habitats (Terborgh and Andresen, 1998). Due to the high species richness, it may be that it is sufficient to use the most common and dominant species to

further classify inundated and non-inundated habitats, rather than identifying all the species of a habitat,

In the Peruvian Amazon, further subdivisions of tropical forests into the two groups of terra firme forests (hereafter, TFF) and seasonally flooded forests (hereafter, SFF) have been achieved in recent years. Division have been made of more easily delimited subtypes, such as the palm swamps dominated by *Mauritia flexuosa* (Arecaceae) or bamboo forest dominated by *Guadua* (Poaceae) species; however, more detailed floristic comparisons of TFF and SFF or subdivisions of TFF and SFF are lacking. It is our intent to: 1) assess the diversity and abundance of the Myristicaceae species as potential indicators of habitat types in the Peruvian Amazon of the department of Madre de Dios, 2) asses how well species assemblages are maintained between the two major habitat types, and 3) evaluate the spatial distribution of these species in order to identify potential subdivisions within habitat types as suggested by non-random distributions of species within those habitats.

Existing data on Myristicaceae distribution based largely on georeferenced botanical collections are insufficient for our purposes as they indicate presence, but not necessarily absence. Nor do these data reflect abundance or local patterns of dispersion. Various researchers have commented on this fact (Tobler et al, 2007) and acknowledged that botanical collection data must be partnered with small scale analyses of ecological pattern through quantitative plot and transect work.

Some studies have attempted to synthesize plot and transect based floristic information (Phillips and Miller, 2002; Terborgh and Andresen, 1998) leading to particularly interesting observations on the floristics of different habitat types. Terborgh

and Andresen (1998) found that the floras of dissimilar habitats classification in close proximity were more similar to one another than to the floras of similar habitat classifications. These results and others (Gentry 1982; 1988) suggest that topographic and climatic classifications of habitats may be insufficient to delineate flora assemblages.

Climate (Holdridge, 1979), vegetation structure, soil type, drainage, topography, potential usage, and floristic assemblages have been used in tropical America to differentiate vegetation types (Kalliola et al, 1993; Tuomisto and Ruokolainen, 1994; Tuomisto et al, 1996; Tuomisto et al, 1993; Phillips et al, 2003; Harms et al, 2001; Clark et al, 1999). Of these, floristic assemblages have been the least refined to delineate habitat types, and have been inconsistently used. The attempt to emulate the classification systems of northern latitudes based on dominant plant species or assemblages has been complicated by the much greater diversity. However, application of this approach with selected plant taxa has proven useful. Researchers have attempted to use indicator species within taxonomic categories to identify habitat types along combinations of edaphic and topographic gradients, such as John et al (2007), Yamada et al (2007), Salovaara et al (2004), and Tuomisto et al (2003). Tuomisto et al (2003) utilized species of Pteridophytes and Melastomataceae to classify floristic patterns along a 43-km transect in Peru, and found them to be correlated with edaphic and topographic factors. Although the study involved two taxa, approximately 130 Pteridophytes and 91 species of Melastomataceae, this is more manageable. This subset of the flora was found to identify patterns evident in the abiotic features of the area. Personal observations of the high density of Myristicaceae species in the Peruvian Amazon prompted the hypothesis that perhaps this family can be used for a similar analysis of TFF and SFF.

The Myristicaceae often place within the top 10 most important families particularly in terms of species abundance (Gentry, 1988; 1982) and are present throughout TFF and SFF of the Los Amigos Conservation Concession in Madre de Dios, Peru. Our questions center on two key observations, the first, that Myristicaceae species are extremely abundant in the area and thus appropriate subjects for statistical tests. Secondly, the hypothesis that the spatial patterns exhibited by species in this family can be correlated with topographically defined habitats. In order to accomplish this, we sampled the diversity and abundance of Myristicaceae species along transects incorporating approximately 30 hectares in the SFF and TFF habitats at the Los Amigos Biological Station and Conservation Concession. It is not an entirely new concept to utilize the Myristicaceae to study and quantify habitat types; Kalliola et al (1993) described an inundated forest based on the dominance of three genera, *Ficus* (Moraceae), *Symphonia* (Clusiaceae), and *Virola* (Myristicaceae). Topographical units are the primary way by which habitats are defined, but this does not take into account differences across similar habitat types (as explored in Terborgh and Andresen, 1998, among others).

We suggest that by mapping the distribution of Myristicaceae species, it may be possible to identify species assemblages that distinguish among habitat types and provide a basis for more refined classifications that reduce the ambiguity with which within-habitat heterogeneity is addressed. We do not intend to identify processes from these data, but rather to document patterns that suggest processes that may be identified by experimental studies. The resulting database of georeferenced trees will provide a baseline source of data for future studies in the region, as well as a source for

comparative studies. With these data, we can begin to form a description of pattern and thus direct studies to achieve a grasp of process.

There are two particular factors which will be used to define species occurrence patterns, and these are abundance and spatial dispersal. Abundance will be defined as density measured on transects and will be considered for different size classes of individuals. Dispersal will be defined as form of distribution of individuals along the transect. This form may be: 1) indistinguishable from a random distribution; 2) indicative of distinct patches of local abundance termed clumps; or 3) a pattern, termed uniform, where individuals are consistently separated by distances greater than expected from random occurrences. Initial ideas and theories on plant distribution predicted that tropical trees were thinly and evenly dispersed in space, resulting in a uniform pattern of distribution (Hubbell, 1979). However, this has been challenged by the idea that natural populations exhibit a tendency towards clumped distribution rather than any other pattern (Armesto et al, 1986; Condit et al, 2000). It was our purpose to investigate whether or not the Myristicaceae adhered to this pattern. Clumped distributions could be due to dispersal limitation, patchy distribution of niches, such as soil type, natural or anthropogenic disturbances, or other explanations. Uniform distributions are much more rare (Armesto et al, 1986; Condit et al 2000) and perhaps suggest a competition among plants. Fine et al (2004) showed that herbivory and edaphic factors contributed to the distribution of some plants in the Burseraceae of the northern Peruvian Amazon. It is possible that density-dependent seedling and seed mortality due to herbivory is promoting a uniform distribution of plants. Random or uniform distributions may indicate a lack of floristic pattern. Clumped distributions, although they may result from

dispersal or disturbance processes, suggest the possibility of factors or processes that produce distinct floristic subtypes or habitats. These clumped distributions may be subsequently analyzed to measure the spatial extent of the clumping and the degree to which it involves segregation of Myristicaceae species.

2 Myristicaceae Description

The Myristicaceae are a pantropical flowering plant family comprised of approximately 500 species and 21 genera (Sauquet & Le Thomas, 2003) that have significant ecological and ethnobotanical importance in wetland tropical forests. In the Neotropics, this family is comprised of approximately 300 species in five genera. This family represents a wide diversity of geographic distributions in the neotropics, ranging from widespread, to disjunct between Central and South America, to regionally distributed or locally endemic (although endemism is relatively low). Members of the Myristicaceae have been recorded to occur from lowland elevations up to premontane forests at about 1800 m a.m.s.l (pers. obs. from specimen data). Floristic and ecological studies reveal the Myristicaceae to rank among the top ten most diverse and important tree families in lowland tropical forests (Gentry, 1982;1988; Paschal and Pelissier, 1996; Pousen et al., 1996; Ribeiro et al., 1994; Spichiger et al, 1996). Due to their importance in lowland tropical forests worldwide, the Myristicaceae are an ideal family for studying the diversity, evolution, and biogeography of tropical tree species. Their occurrence across all major habitats in the Neotropics and their patterns of abundance and endemism make them ideal candidates for studies regarding spatial distribution, habitat partitioning and maintenance of biodiversity.

The neotropical species of the Myristicaceae are generally canopy to sub-canopy trees that can grow to 40 m tall, but some species are small trees of understory. The trunks are cylindrical, branching existing only in the upper half (or third), and are occasionally buttressed or displaying stilt roots. The bark of the Myristicaceae is often helpful in distinguishing between species, especially color, hardness, texture, smell and

the extent of fissuring. When the bark is slashed, Myristicaceae species exude a resin that can vary in color, from red to pink to transparent, which is indicative of genus, and to some extent, the species. Rather uniquely, the entire family adheres to a single architectural model (Massart model; Halle et al., 1978) that is characterized by an orthotropic main stem, which experiences rhythmic growth and branching, resulting in a tiered branching pattern (Figure 1). This consistent and rigid architectural model makes the identification of the Myristicaceae in the field a much easier task, even from a distance.

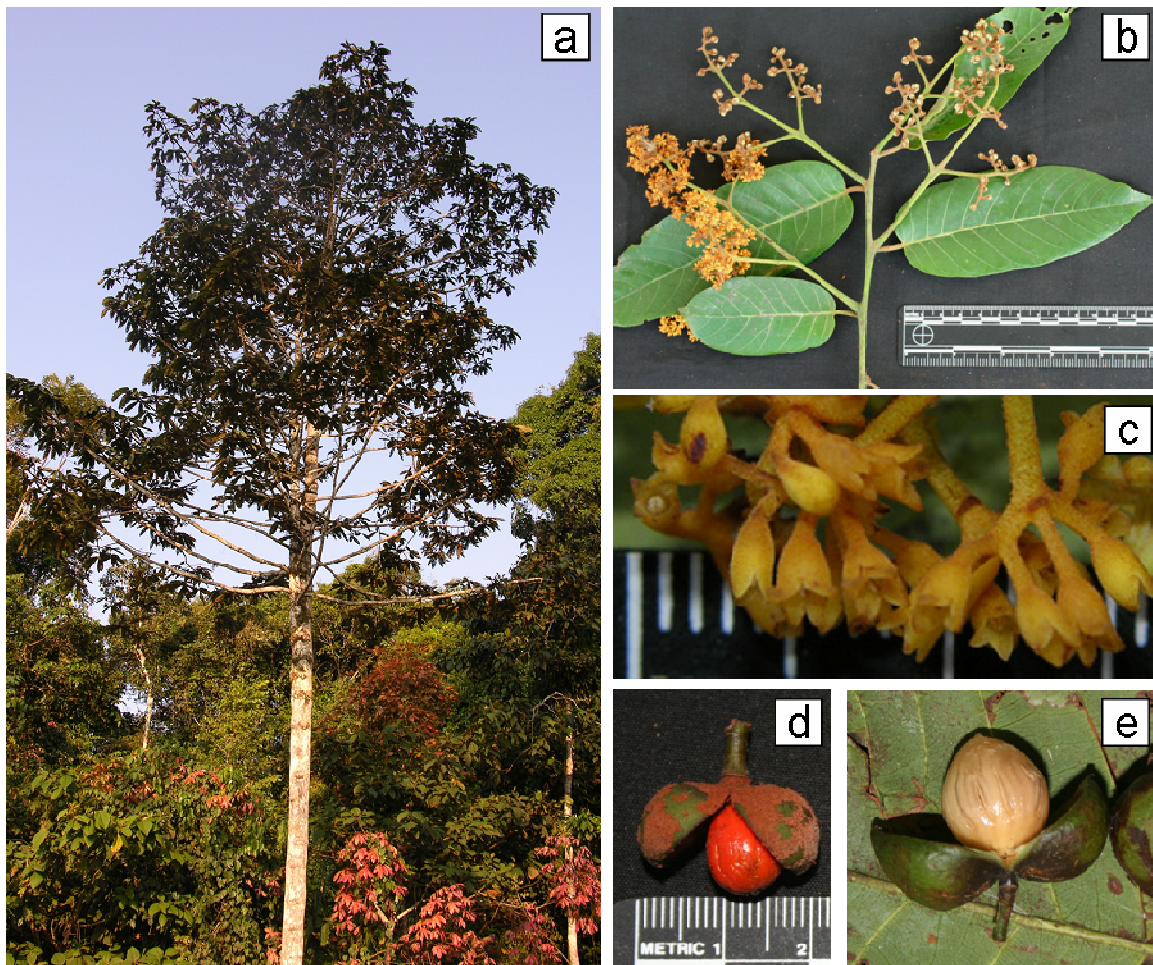


Figure 1. Morphological characteristics of the Neotropical Myristicaceae. **a.** The architectural model conserved by the species at the Los Amigos Biological Station, as observed in *V. flexuosa*. **b.** Examples of the leaves and male flowers of *V. sp 1*, **c.** Close-up view of the flowers of *V. sebifera*, **d.** the bright orange aril of *V. sebifera*, **e.** the translucent white aril of *Otoba* species.

The leaves of the Myristicaceae are simple, alternate, generally petiolate and pinnately veined. Adaxial lamina surfaces are glabrous (e.g. *Otoba* species) or pubescent (e.g. many *Virola* species), while abaxial surfaces are glabrous, pubescent, or occasionally glaucous (e.g. *Virola surinamensis*). Some leaf characteristics delineate genera, such as the two-branched hairs in *Otoba*, or the stellate hairs in *Virola*. Most species are evergreen, with the notable exception of some *Virola* species (i.e. *Virola multinervia*) (pers. comm., J. P. Janovec).

The majority of species in the Neotropics are dioecious, with morphologically similar sexes. The only genus in which this is not the case, *Iryanthera*, contains monoecious species (Smith, 1937), where male and female flowers have been recorded but not thoroughly investigated. Myristicaceae flowers are inconspicuous and generally held high in the canopy (except in *Iryanthera* species). Male plants have more flowers than female plants, but the latter produce slightly larger flowers. The external form of the male and female flowers is similar and comprises a white-yellow-green color with a single perianth whorl of three to four tepals that are fused to varying degrees. Female flowers produce a single large seed whose fruit consists of a two halves that dehisce to expose a waxy lipid-rich aril that varies from red to white in neotropical species. It has been recorded that seeds are dispersed by various agents, including birds (Holbrook, 2006) and primates (Russo, 2003). Male flowers consist of fused stamens with 2-60 anthers that are free or fused to varying degrees; they have been noted to be of greater significance in the delineation of species (Sauquet, 2003; Smith, 1937; Mera, 2004; de Wilde, 1990). It is suspected that beetle pollination may be particularly important in the

family (Armstrong, 1986) owing in part to light flower color, small form, fragrance and nectaries that are non-existent or poorly defined.

Most previous systematic studies of the Myristicaceae have involved an emphasis on species identifications, and the delineation of species complexes in genera and subgenera (Rodrigues 1980; Sinclair, 1958; 1961; Smith and Wodehouse, 1937; Warburg, 1897). The primary obstacles to early studies were the paucity of plant collections from which to identify and sort species; this is no longer the problem. Intensive plant collection in more recent years has increased the specimen base. However, there is only a single genus that is represented by a modern taxonomic treatment, *Virola* (Rodrigues, 1980), and that is incomplete as it only considers those species that occur within the political boundaries of Brazil. A second genus, *Compsonaura*, is also being treated but has yet to be published (pers. comm., J. P. Janovec). The other three genera in the Neotropics, *Iryanthera*, *Otoba*, and *Osteophloem* still need to be addressed through monographic work. Thorough treatments across all areas of distribution are required throughout the family, and may perhaps be begun through a synthesis of small-scale studies.

Other investigations into the Myristicaceae have included morphological and structural characteristics, such as wood, leaf, and floral anatomy, and floral, pollen, and inflorescence morphology (Armstrong, 1986; Braga, 1992; Garrat, 1933; Metcalfe, 1987; Morawetz, 1986; Siddiqui et al, 1976; Walker and Walker, 1979; de Wilde, 1991; and Wilson and Maculans, 1967). Also, few studies have directly addressed the dispersal of Myristicaceae fruit (Holbrook, 2006; Russo, 2003), and more often, information published about dispersal is a result of primatologists or ornithologists (Russo, 2005;

Holbrook, 2006) studying overall diet. The ethnobotanical importance of the Myristicaceae was surveyed by Schultes and Rafauff (1990). The most important species economically, the Asiatic species *Myristica fragrans*, is widely cultivated as the source of nutmeg and mace. In the neotropics, numerous species are valued as sources of food, medicine, hallucinogens, and timber (Gottlieb, 1979; Prance, 1970; Schultes and Raffaf, 1990; Phillips and Gentry, 1993a, 1993b).

3 Study Area

3.1 Location and background

Peru is located on the Pacific coast of tropical South America, comprising an area of approximately 1.2 million square kilometers bordered by Ecuador and Colombia to the north, Chile to the south and Bolivia and Brazil to the east (Figure 2). There are three distinct terrains identified, the *Costa* (western coastal plane), the *Sierra* (the high elevation Andean habitats), and the *Selva* (eastern lowlands). This study is focused on the *Selva*, an area within the watershed of the Amazon basin where some of the highest plant diversity per area has been recorded.



Figure 2. Map of Peru with three distinct terrains identified, *Costa*, *Sierra* and *Selva*.

This study was carried out at the Los Amigos Biological Station and Conservation Concession of the Amazon Conservation Association (ACCA, in Peru) which is located in the *selva* region of southeastern Peru. The 145, 918 hectare conservation concession is found in the lower Los Amigos River watershed (Figure 3), in the department of Madre de Dios, across the provinces of Tambopata and Manu. The closest established settlement to the Los Amigos Biological Station and Conservation Concession is Boca Amigos, which is approximately 3 km east (downriver) on the Madre de Dios River.

Fieldwork was conducted at two primary sites, and one secondary site used for descriptive purposes only. All locations were chosen for comparison and for proximity to the Los Amigos Biological Station. The two primary sites for which statistical analyses was employed are (1) the Los Amigos Biological Station, also known as the Training and Research Center of the Los Amigos River (hereafter, CICRA --*Centro de Investigación y Capacitación del río Amigos*) and (2) Monitoring Center 1 (Hereafter, CM1 --*Centro de Monitoreo 1*). The CICRA station is located at approximately 12°34'S 70°05'W, four kilometers west of the CM1 station at approximately 12°34'S 70°04'W and separated by the Los Amigos River. The third station is Monitoring Center 2 (Hereafter, CM2 --*Centro de Monitoreo 2*) and is located at 12°26'S 70°15'W, approximately 21 km from the other two study sites. Each of these locations provides the infrastructure and support for investigations being conducted throughout the conservation area.

Prior to the establishment of the conservation concession, the site had an interesting history of rubber tappers from the early 1900s to the mid-1900s; Pitman (2006) notes that although rubber tappers were quite probably tapping trees in the region, there is a noticeable absence of scarred trees at the CICRA. Moreover, *Hevea brasiliensis*

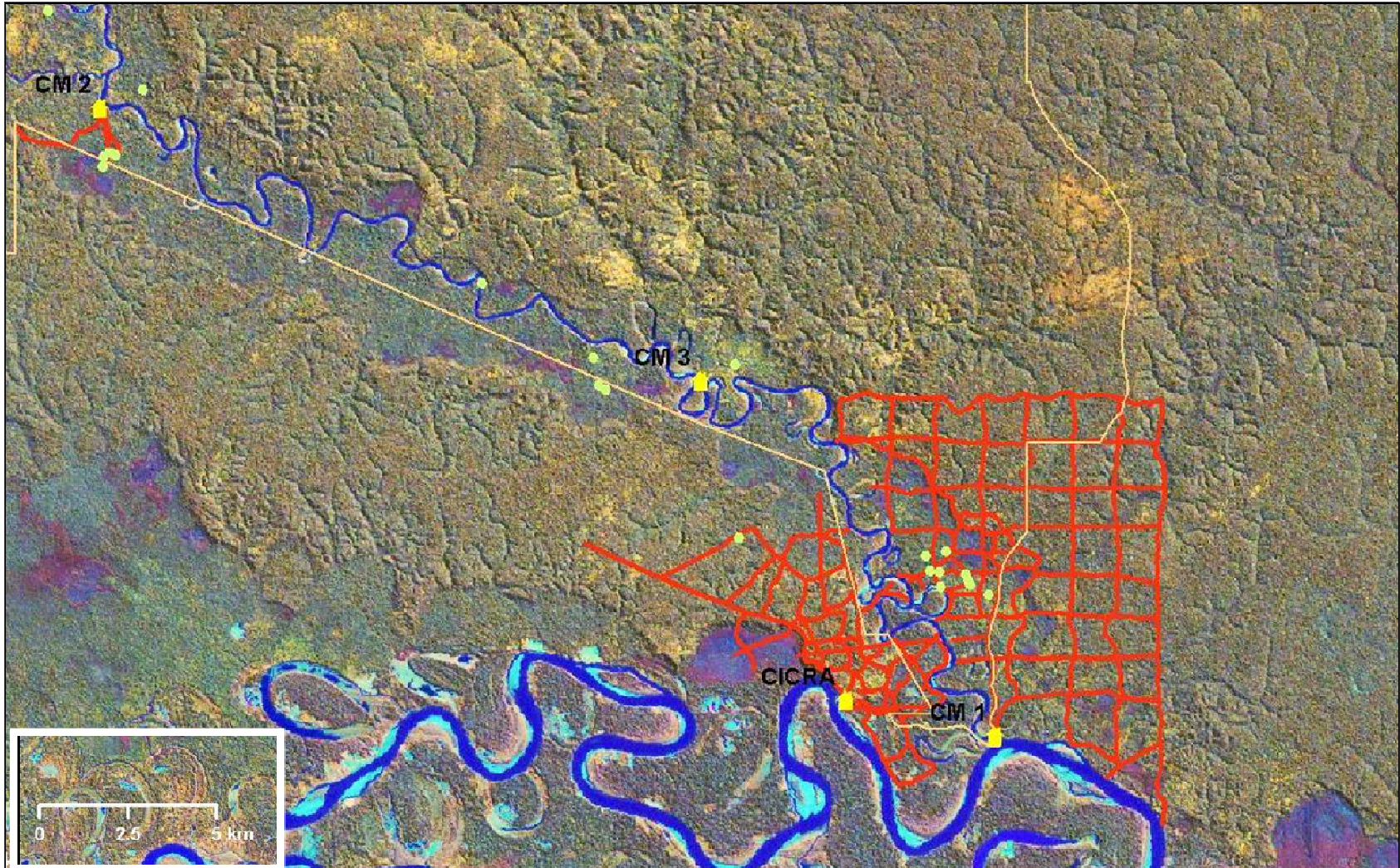


Figure 3. A map of the Lower Los Amigos watershed. Layered in front of an IKONOS image is the placement of the biological stations, the associated trail systems, and the two important rivers, the Los Amigos River and the Madre de Dios River.

(Euphorbiaceae), the prized rubber tree, is rare to absent in the Los Amigos watershed, replaced by its sister species, *Hevea guianensis*. In the late 1900s in the years between 1982-1999 (Pitman, 2006) the biological station was occupied by a mining camp, used as a base of operations entering further into the region, with as many as 120 men stationed there in the 1980s. Supporting this many men, it is certain that the area was fished and hunted, and utilized for survival. The lack of a strong presence in the 1990s allowed for some recovery, and the Los Amigos River watershed now harbors relatively healthy and rebounding animal and plant population (Pitman, 2006), even in spite of more recent illegal logging activities in the years preceding the purchase of the Los Amigos Biological Station and the implementation of the conservation concession in 2001.

3.2 Climate

According to the Holdridge classification of climatic zones, this area is listed as a tropical moist forest (Holdridge, 1985). Annual rainfall totals between 2700-3000 mm per year (year range: 2000-2006), varying from approximately 450 mm in one month in the wet season (October-May) to 30 mm in one month in the dry season (June-September) (Figure 4). River levels of the Los Amigos and the Madre de Dios Rivers, generally experience highs in January-February, and lows in July-September (Figure 5), with the largest recorded difference in these levels at 9.47 meters (Atrium: Biodiversity Information System, 2007). Although significant areas of the trail system at the Los Amigos Biological Station are impassable during the rainy season, no work has yet been done to relate the river level with flooding depths of the floodplain and swamp forests (Pitman, 2006).

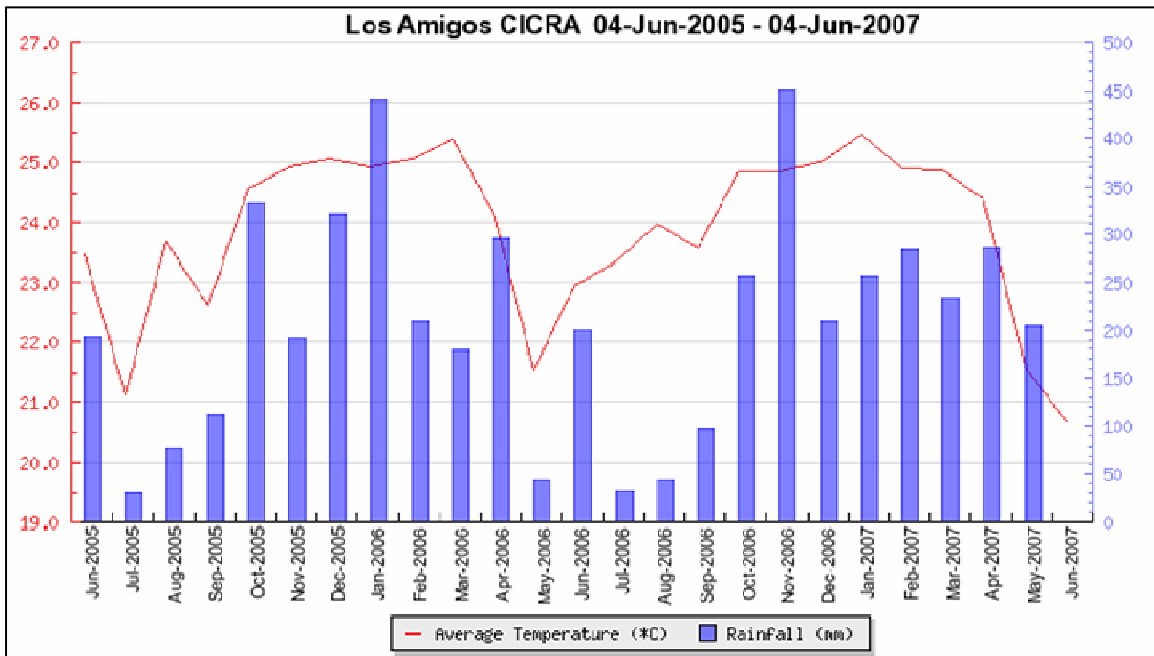


Figure 4. Rainfall and temperature recorded from the Los Amigos Biological Station. Obtained through Atrium(Atrium: Biodiversity Information System, 2007).

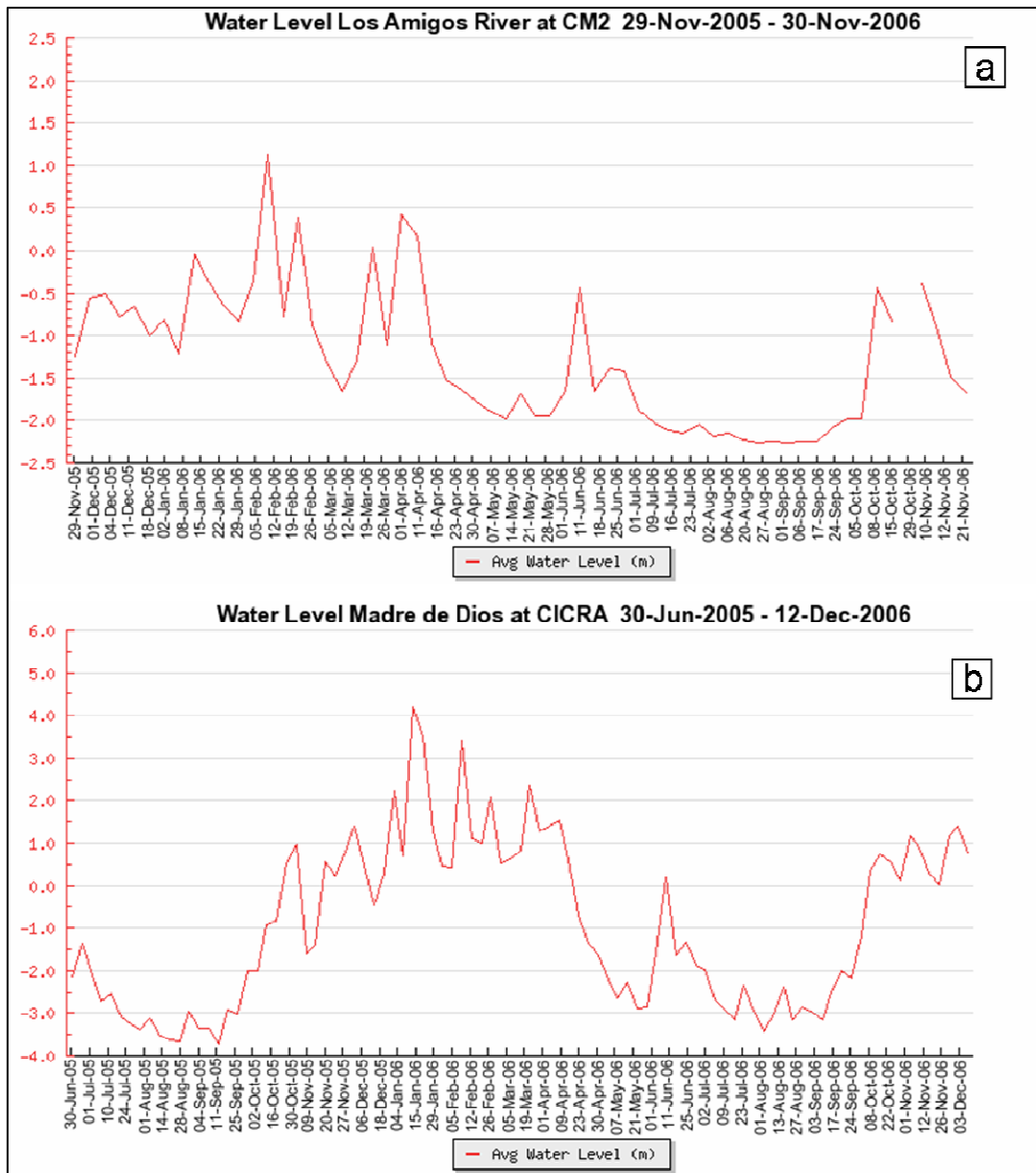


Figure 5. Water levels of the Los Amigos River and the Madre de Dios River, as measured from the Los Amigos Biological Station, from 2005-2006. Obtained through Atrium (Atrium: Biodiversity Information System, 2007).

3.3 Topography

The conservation concession is located on the Madre de Dios Formation, described by Antoine et al. (2003) as a series of alluvial and lacustrine deposits, partially as a result of an inner sea that existed in the upper Miocene. Tidal deposits were apparently important factors in the development of the terraces at Los Amigos, with the upland terraces dating at less than 200,000 years (Antoine et al, 2003). The youngest deposits are found along the floodplain, carried down from the Andean foothills, and include also the gold granules that are the object of local mining operations.

The Los Amigos River is a mixed water (Kalliola, 1993), lower gradient river that meanders across a broad floodplain of these multiple aged terraces (visible from satellite images; Atrium: Biodiversity Information System, 2007) moving silt and sand and producing many oxbow lakes along its 353 km length. The elevation varies only slightly between the three sites, with CICRA at an elevation of approximately 268 m a.m.s.l., CM1 at an elevation of approximately 238 m a.m.s.l., and CM2 at an elevation of approximately 259 m a.m.s.l. In spite of this small variation between sites, within each site there is a significant demarcation of terra firme upper terraces and the floodplain habitats. These topographical features differ in their elevation, their soil characteristics (Tuomisto and Ruokolainen, 1994), their moisture regime (Prance, 1979) and the assemblages and characteristics of their vegetation (Terborgh and Andresen, 1998; Balslev et al, 1987; Wittman et al, 2006; de Oliveira and Daly, 1999; Comita et al, 2007).

Vegetation types in this region are designated primarily by topographic position, and thus, flooding/non-flooding characteristics. Floodplain forests across the study sites

are lower elevation forests and are defined as such utilizing Prance's (1979) designation of inundated forest types. Seasonally flooded forests (SFF), comprise one of the major habitat types (Foster, 2001) at Los Amigos and are those forests in which periods of inundation are experienced as a result of flash flooding from extensive rains and occasional overflow of the river. These forests have finer soil structure and are not well drained and are depositional in nature (Figure 6).

In contrast to these, we have the more coarsely grained upland soils of the terra firme forests (TFF) that are very well drained and are never under any period of inundation (Figure 6). These terra firme forests are erosional in nature, thus heavily leached, and are noted to be sandier, less fertile and more acidic soils than those of the floodplain (Mazer, 1997). In general, TFF reportedly exhibit higher species richness (Gentry, 1988; Phillips, 2003; Prance, 1979; Kalliola, 1993; Salo et al, 1986; Harms et al, 2001; ter Steege et al, 2000) than SFF.

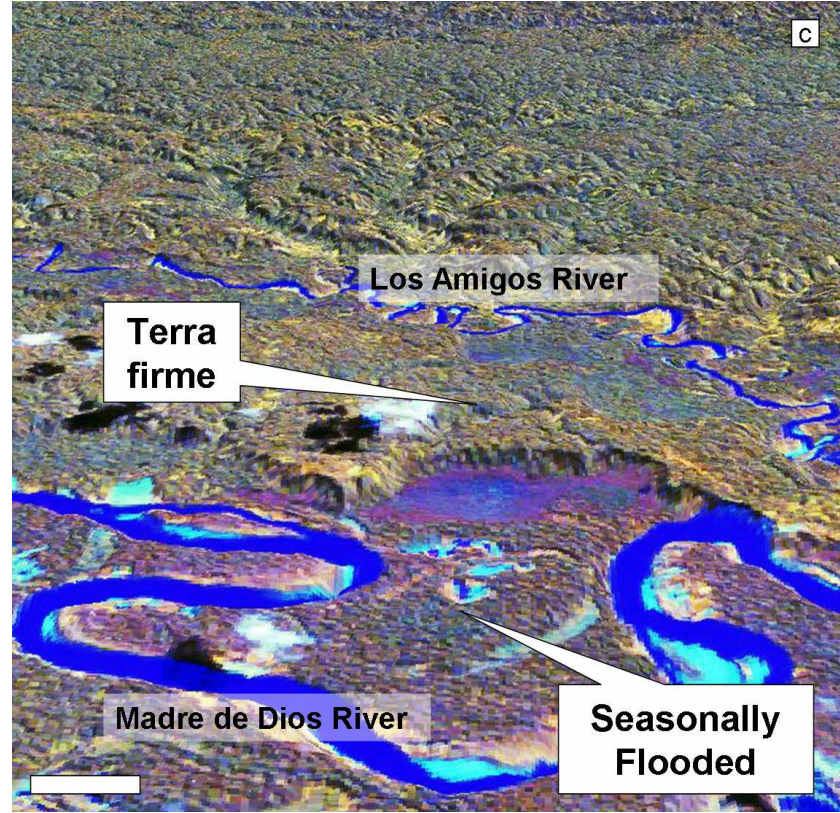


Figure 6. Seasonally Flooded and Terra Firme Forests of the Los Amigos Conservation Concession. **a.** seasonally flooded forests, **b.** terra firme forests, **c.** 3-D map displaying the elevation gradients between the habitats, to the immediate west of the Los Amigos Biological Station.

3.4 Vegetation

Utilizing the vegetation classification system proposed by Encarnación (1985), we can differentiate three forest habitats that are well delimited in the study area. These three are (1) the *aguajal* – these are swamp areas that are dominated by the aguaje palm (*Mauritia flexuosa*), located in low lying forests along rivers with soils that are inundated throughout the year; (2) Floodplain forests (corresponding to our SFF) –these are those forests that are at low-lying elevations, adjacent to the rivers, experiencing seasonal inundation and characterized by occasional emergent trees and a diversity of epiphytes; and (3) Upper terrace forests (corresponding to our TFF)– these are those forests far from rivers that never experience periods of inundation, that are characterized by the presence of emergent trees, and fewer epiphytes. Vegetation maps were created by Mendoza (2001), and the distribution of the two habitat types, SFF and TFF, along with other major habitats, can be seen across the Los Amigos Conservation Concession (Figure 7).

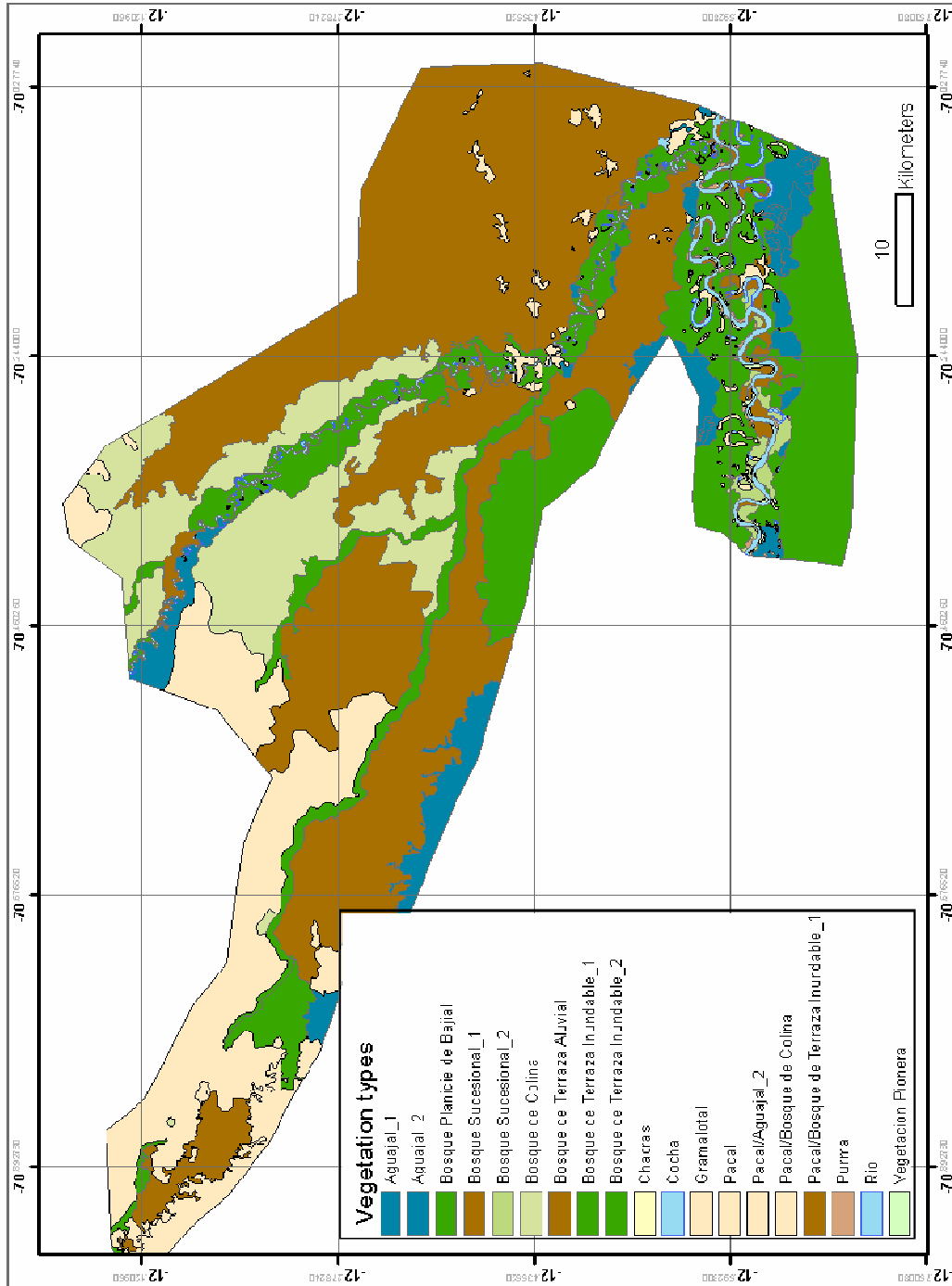


Figure 7. Vegetation map of the Los Amigos Conservation Concession as adapted from Mendoza (2001).

4 Materials and Methods

4.1 Research Design

Due to the difficulties in traveling in these forests, the necessity for data sets that were sufficiently large to carry out the intended analysis, and the potential for future re-sampling, this study was restricted to the previously existing trail system at the two primary study sites. As a result of this methodology, a larger number of transects were sampled across the study area in the allotted time frame, a total of about 3 weeks. Transects extended 10 meters into the forest on either side of the trail, and were from 1380 to 2523 m in length. (Figure 8a). Figure 9 (transect map layered above an vegetation map) shows the distribution of the transects for the two sites. Transects were installed in two forest types that are the most dominant in the study area. Efforts were made to allow some distance between sampled areas.

Six transects were installed at CICRA and two were installed at CM1. At CICRA there were four transects positioned in Terra Firme Forest (TFF) and two transects positioned in Seasonally Flooded Forest (SFF), all within a distance of approximately 3.7 km of the biological station. At CM1 there was a single transect placed in each habitat, both located within 7.1 km of the station. The two CM1 sites were located directly across the Los Amigos River from the biological station and the nearest distance between transects on either side of the river was approximately 1.8 km.

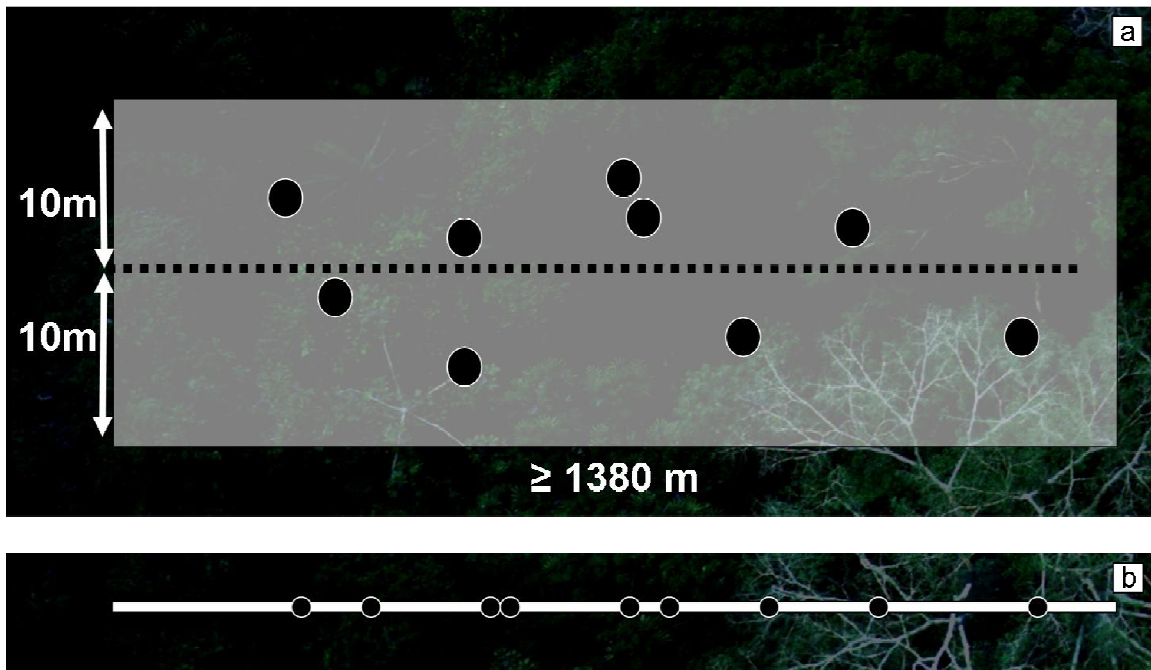


Figure 8. Transect design. **a.** Area transect design with imaginary stems identified by black dots, **b.** scaled transect design, modified to one-dimensional points (black dots) along a line.

4.2 Field Measurements

All individuals of the Myristicaceae family (height ≥ 0.5 m) encountered along each transect were identified in the field to species, based on expert assessment (pers. comm., J. P. Janovec), relevant identification keys (Rodrigues, 1980; Smith, 1937; Gentry and Rodriguez, 1993), and personal familiarity with the family through previous herbarium studies at the Botanical Research Institute of Texas (BRIT) and herbarium and field studies in Costa Rica and Peru. The geographical position of each tree was recorded using Global Positioning System (GPS) devices, including the Garmin GPS 76 and Garmin GPS 76c (Garmin International Inc. 1200 East 151st Street, Olathe, KS 66062-3426), with accuracy levels < 15 m (<http://www8.garmin.com/aboutGPS/waas.html>).

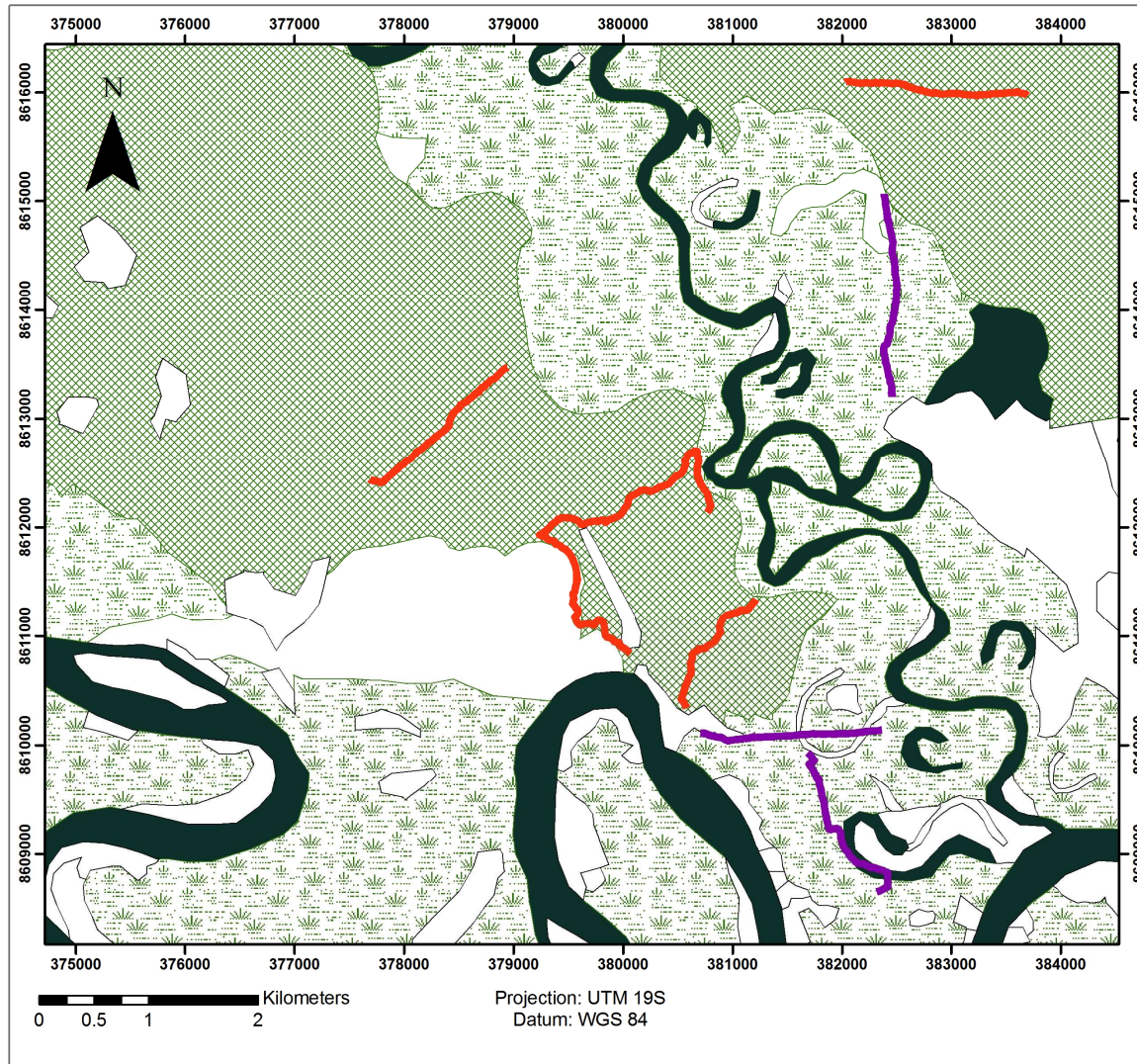


Figure 9. Map of installed transects at the Los Amigos Biological Station and at CM1. Red lines denote transects installed in TFF, and purple lines denote transects installed in SFF. Cross-hatch patterns denote the TFF habitats, while swamp patterns denote SFF habitats; those polygons without pattern denote other habitats that are of no significance in this study.

All trees were measured for their diameter at breast height (DBH; measured at ~1.3 m from base of tree) using a Forestry Suppliers metric fabric diameter tape (or for smaller individuals, calipers were found to be more efficient). Tree height was determined through consensus estimation by the field team. This method of estimating tree height was independently tested and found never to exceed a 1 m error, and was employed for the sake of timeliness and to avoid problems estimating height in a dense canopy. Phenological status was recorded for each individual, including fruiting, flowering and/or defoliation. In the case of flowering and fruiting, the abundance of reproductive material was ranked on a scale from 0-5, with zero for absence of reproductive material, up to 5 for maximum amounts of reproductive material (Cornejo and Janovec, unpublished, 2003).

Taxonomic notes were taken on a large number of individuals across developmental stages for each species, including hardness, texture and colour of trunk and bark, presence of buttresses, and any other important observations. The production of a field guide was accomplished as a result of these field observations that complemented the mapping protocol. Photographs of leaves, trunks, reproductive material and habitats of juvenile and adult trees were taken for each species (Appendix 1). Numerous voucher collections were made of juvenile and adults for each species identified in the study (Figure 10; Appendix 1). Material was pressed and dried according to conventional botanical preservation methods, with a propane fueled plant drier and a wooden plant press. All collections were deposited at the CICRA herbarium, with duplicates sent to the

San Marcos Herbarium (USM) in Lima, Peru, and to the Botanical Research Institute of Texas (Texas, U.S.A.).



Figure 10. Process of data collection and herbarium process. **a.** Swiss climbing irons were used to collect voucher specimens in fruit that were high in the canopy, **b.** collection of biometric data, such as DBH (diameter at breast height), **c.** voucher herbarium specimen of *V. surinamensis*, **d.** identification of Myristicaceae species in the field, **e.** pressing and drying of collected voucher specimens.

4.3 Data Processing

All field data were transcribed from “Rite-in-the-Rain” notebooks (<http://www.riteintherain.com>) to Microsoft Office Excel 2003, organized in spreadsheets, and then prepared for statistical analyses. The following paragraphs outline the procedure that was followed to prepare the data for analysis.

After direct transcription into Microsoft Excel data were partitioned into size classes, of juveniles and adults. This partitioning of data was based on height of an individual, $\geq 0.5\text{m}$ and $< 7\text{m}$ (juvenile) and $< 7\text{m}$ (adults). This division at 7m in height is admittedly rather arbitrary; however the reasons for its use are based on observing the frequency histograms of height for each species. When observing the frequency histograms for height, it was noted that for all species, flowering and fruiting was more prevalent in size classes above 7 m. Although in some species, such as *I. juruensis*, fruiting and/or flowering did begin at lesser heights, the prevalence of this phenological status greatly increased after 7 m height. Original data were maintained and division into size classes was completed using a division of 7 m in height. Analysis was carried out on the definition of adults and juveniles based on 7 m height.

After appropriate parsing out and partitioning into size classes, the data were imported into ArcMap (ArcGIS release version 9.1). Data were imported under the UTM 19S projection using the WGS 84 datum. In addition to the tree data, a vegetation layer created by Mendoza (2001) was imported (Figure 7). Individual trees were assigned to a habitat based on their presence within the borders of a vegetation habitat identified in Mendoza (2001). This new field then designated the presence of the individual in either SFF or TFF; this designation was compared with notes taken in the field with regards to habitat and was found to be consistent.

The next geographic layer imported was that of the trail system at Los Amigos (viewable in Figure 3), which was the backbone for the transects which we sampled. This layer was clipped so the resulting layer depicted only the length of the transects which were surveyed. Utilizing a development script that was obtained from ESRI/Oracle

Developer Miles Hitchen, through an ESRI User Forum thread (2007), each stem was assigned a distance along the line that was the transect. This was stored as a new field in the tree data layer. The resulting tree data file contains the field measurements, along with the added data for each stem that includes the pertinent size class, habitat, and distance along a line (in meters), and then is ready for analysis. The assumptions made during these processes are discussed in the following sections specific to the statistical tests that were run.

4.2 Statistical Analysis

4.2.1 G-Test for habitat associations

It is not sufficient to be able to state that there exists a difference or a deviation in the data from what is expected, but it must be quantified using a statistical test that provides a probability of obtaining the data given that a null hypothesis is true (Quinn and Keough, 2002). With the aid of Microsoft Excel and SPSS for Windows (, we were able to construct statistical tests for our various hypotheses. To test for habitat associations we used the G-test (Sokal and Rohlf, 1969; Gotelli and Ellison, 2004) which is a likelihood ration test that the number of individuals sampled within a habitat is proportional to the area sampled. Expressed as null and alternative hypotheses, these statements are:

Ho: The number of individuals observed in each habitat is proportional to the area sampled.

Ha: The number of individuals observed in each habitat differs from that expected from the proportions of area sampled.

The G-test is similar to the chi-square test but it is less affected by small sample numbers. The computed G value is compared to a chi square distribution with the degrees of freedom equal to the number of habitats, less one, and large G, which have probabilities ≤ 0.05 , indicate that the number of individuals in habitats differ from that expected from the proportion of area sampled. A positive association is indicated for the habitat where the individuals occur more frequently than expected. Sokal and Rohlf (1969) recommend that the G-test be employed consistently in place of the chi-square test.

Using the G-Test, we were able to evaluate the abundance of species of Myristicaceae across the two habitats surveyed, and across two developmental stages, juveniles and adults. This analysis allowed us to evaluate the distribution of these species across the two habitats in order to test for habitat associations. The G-test was utilized in various studies to compare abundance and density of organisms across sample and habitat sites, and is increasingly being used throughout the literature, and particularly in the ecological literature (Peterson, 2000; Mayfield and Daily, 2005; West et al, 1996; Nabe-Nielsen, 2001; Borgmann and Rooney, 1999).

For each species for which we had sufficient numbers, we carried out the G-test on two developmental stages, juveniles and adults. This segregation of tree frequencies was made in acknowledgement of the expectation that natural clumping of juveniles around adult trees should occur. It was expected that true (if present) associations with habitat would be revealed at the adult stage, where species were definitively established and approaching (or having reached) reproductive maturity.

We were unable to carry out the G-test on three species (*V. divergens*, *V. lorentensis*, and *V. mollissima*) due to insufficient total number of individuals sampled. We were also unable to carry out this test as outlined on two species, *V. sp. 1* and *V. surinamensis*, as these occurred in large numbers, but only in a single habitat. For these latter two species, simple probability calculations were used to determine habitat association.

4.3.1 Distance of individuals along transects

To determine whether individuals were distributed randomly, clumped, or uniformly along transects we (1) assumed that the width of the transect, which was 10 m to either side, was negligible compared to its length (≥ 1380 m) and (2) used an ArcMap script (Hitchen, 2007) to associate each individual's GPS location to a distance along the transect. This transformed locations to linear distances (Figure 8b). For an event, such as the occurrence of a tree, that has a small probability of occurring in a linear dimension such as time or distance, the frequency distribution of the number of events, within l units of time or distance follows a Poisson distribution and the time or distance between events follows an exponential distribution with a mean length between events of l/p (Johnson and Kotz, 1994). To test if the distributions were random, we (1) estimated p as the number of trees per length of the transect in meters and (2) compared the frequency distribution of length between trees to test for an exponential distribution with a mean of l/p using Lilliefors test for the exponential distribution (Lilliefors, 1969). This test has the null and alternative hypotheses of:

Ho: The data follow an exponential distribution.

Ha: The data do not follow an exponential distribution.

Where Lilliefors test indicated a statistically significant departure from the exponential distribution, observed means less than expected indicate clumping whereas observed means greater than expected indicate uniform distributions (Figure 11).

Lilliefors test was implemented in SPSS.

This is a preliminary evaluation to test spatial distributions of these species, and future analyses will involve subjecting the data to other forms of analysis that estimate the spatial scales of departures from random distributions, such as three-term local quadrat variance (Dale, 1999) and multi-species patterns in departures from random distribution such as three-term local quadrat covariance (Dale, 1999).

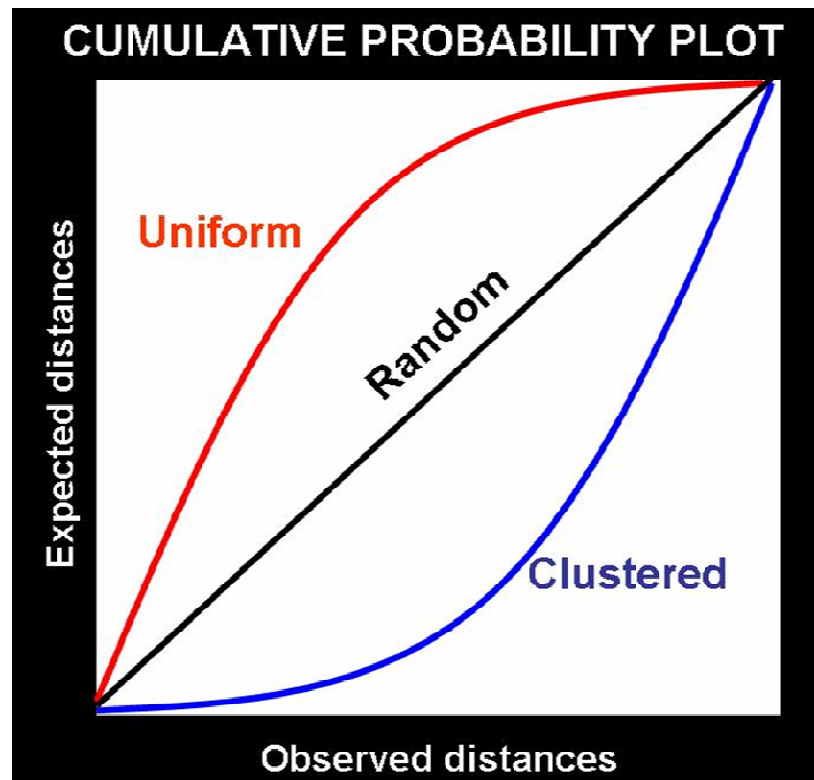


Figure 11. Cumulative probability plot displaying the three patterns of spatial distribution that were encountered on the transects.

5 Results

5.1 Species presence and abundance

A total of 15 species (3 genera) of Myristicaceae were encountered through the mapping of transects, general collection of the flora at the conservation concession biological stations over a five year period (2002-2007), and exploratory expeditions into the concession. A list of these species is compiled in Appendix 1. We encountered three species of *Iryanthera*: *I. juruensis*, *I. laevis*, and a morphospecies we labeled *I. 'grandis'*; two species of *Otoba*: *O. glyxicarpa* and *O. parvifolia*; and 10 species of *Virola*: *V. calophylla*, *V. divergens*, *V. elongata*, *V. flexuosa*, *V. lorentensis*, *V. mollissima*, *V. multinervia*, *V. sebifera*, *V. surinamensis* and one morphospecies, *V. sp. 1*.

A total of 9026 individual stems greater than or equal to 0.5m in height belonging to the Myristicaceae were mapped and subsequently analyzed (See Appendix 2). Of the 15 species known to occur in the study area, only 14 species were observed to occur on the transects; *I. 'grandis'* was only known from sites explored during an expedition far up the Los Amigos River, approximately 45 kilometers away from the CICRA station (during January, 2007).

A total of 8000 stems were mapped around the CICRA station, whereas only 1026 stems were mapped on the east side of the Los Amigos River, at CM1. This resulted in a density of 372 stems per hectare on the CICRA side, and 142 stems per hectare on the CM1 side (Table 1). The reasons for this are primarily due to the fact that two species which are rather abundant at the CICRA station, *V. sp.1* and *V. surinamensis*, are not present on the CM1 side.

The most abundant species across both mapping sites was *V. surinamensis*, followed by *O. parvifolia*, then *I. juruensis* (Table 1). At CICRA, the most abundant species followed this pattern. However at CM1 the most abundant species was *I. juruensis*, followed by *I. laevis*, then *V. calophylla*. According to Pitman et al. (2001), common species are defined as individuals that occur at ≥ 1 individuals per ha (at DBH ≥ 10 cm). Using these criteria we can identify only six species as abundant across the two sample sites (Table 2).

Species	CICRA		CM1		Total	
	No.	%	No.	%	No.	%
<i>Iryanthera juruensis</i>	815	10.2	436	42.5	1251	13.9
<i>Iryanthera laevis</i>	392	4.9	217	21.2	609	6.7
<i>Otoba glyxicarpa</i>	39	0.5	3	0.3	42	0.5
<i>Otoba parvifolia</i>	2210	27.6	2	0.2	2212	24.5
<i>Virola calophylla</i>	628	7.9	179	17.4	807	8.9
<i>Virola divergens</i>	0	0.0	1	0.1	1	0.0
<i>Virola elongata</i>	206	2.6	61	5.9	267	3.0
<i>Virola flexuosa</i>	39	0.5	18	1.8	57	0.6
<i>Virola lorentensis</i>	0	0.0	2	0.2	2	0.0
<i>Virola mollissima</i>	0	0.0	1	0.1	1	0.0
<i>Virola multinervia</i>	76	1.0	5	0.5	81	0.9
<i>Virola sebifera</i>	678	8.5	101	9.8	779	8.6
<i>Virola sp.1</i>	554	6.9	0	0.0	554	6.1
<i>Virola surinamensis</i>	2363	29.5	0	0.0	2363	26.2
TOTAL	8000		1026		9026	
Stems/ha	372		142		314	

Table 1. Number of stems and density (per hectare) of each Myristicaceae species encountered at CICRA and CM1, and the total number and density for the entire site.

Species	No.	No./ha	Abundance Status
<i>I. juruensis</i>	86	3.0	Abundant
<i>I. laevis</i>	110	3.8	Abundant
<i>O. glyxicarpa</i>	17	0.6	Rare
<i>O. parvifolia</i>	188	6.6	Abundant
<i>V. calophylla</i>	79	2.8	Abundant
<i>V. elongata</i>	22	0.8	Rare
<i>V. flexuosa</i>	7	0.2	Rare
<i>V. mollissima</i>	1	0.0	Rare
<i>V. multinervia</i>	8	0.3	Rare
<i>V. sebifera</i>	72	2.5	Abundant
<i>V. sp.1*</i>	27	2.5	Abundant
<i>V. surinamensis*</i>	70	6.6	Abundant

Table 2. Myristicaceae species stem number and density (per hectare) of individuals larger than 10 cm DBH (diameter at breast height), and their consequent abundance status. *Species that occurred in a single habitat; their abundance status was assessed only for the habitat in which they occurred.

Species were unevenly distributed across the transects sampled (Table 3), as the transect with the highest number of species per transect was T-A-Cch, at 3.2 species per hectare (See Appendix 3 for transect code and trail data). In spite of this fact, transect T-A-Cch did not contain the highest density of adult/large trees (Table 4). The transect with the least number of species was T-A-Plt, which perhaps is due to the amount of disturbance it may have been subjected to over the course of the site's history; this transect was also in the lower half when ranking the transects in order from highest density of adult/large trees.

Site	Transect	Habitat	Area (ha)	<i>I. juruensis</i>	<i>I. laevis</i>	<i>O. glyxicarpa</i>	<i>O. parvifolia</i>	<i>V. calophylla</i>	<i>V. divergens</i>	<i>V. elongata</i>	<i>V. flexuosa</i>	<i>V. lorentensis</i>	<i>V. mollissima</i>	<i>V. multinervia</i>	<i>V. sebifera</i>	<i>V. sp. 1</i>	<i>V. surinamensis</i>	Total no. of species	No. of species /ha
CICRA	T-A-Cst	TFF	5.05															8	1.6
CICRA	T-A-Lza	TFF	3.40															8	2.4
CICRA	T-A-Plt	TFF	3.50															6	1.7
CICRA	T-A-Prm	TFF	2.76															7	2.5
CICRA	T-A-Cch	SFF	3.40															11	3.2
CICRA	T-A-Lnd	SFF	3.40															9	2.6
CM1	T-B-Klo	TFF	3.40															10	2.9
CM1	T-B-ccc	SFF	3.84															10	2.6
CM2	2 trails	Both	6.46															12	1.9

Table 3. Myristicaceae species presence on surveyed transects, with indication of the habitat in which a transect was installed and the area surveyed. Totals for number of species and number of species per hectare are included for each transect.

Site	Transect	Trails	Area	Height \geq 7m	DBH \geq 10
CICRA	T-A-Cch	Trocha Cocha Lobo (0-1400 m) Trocha Playa (0-300 m)	3.4	227	136
CICRA	T-A-Lnd	Trocha Lindero (0-1900 m)	3.4	334	181
CICRA	T-A-Cst	Trocha Castanal (0-1875 m) Trocha Segundo Mirador (1700-1600 m)	5.0	321	139
CICRA	T-A-Lza	Trocha Luiza (0-1598 m) Trocha Huangana (1675-1577 m)	3.4	160	56
CICRA	T-A-Plt	Trocha Plataforma (0-1750 m)	3.5	139	50
CICRA	T-A-Prm	Trocha Primer Mirador (0-1380 m)	2.8	81	28
CM1	T-B-ccc	Trocha "C" (355-2275 m)	3.8	61	35
CM1	T-B-Klo	Trocha Kilo (1575-3275m)	3.4	245	60

Table 4. Installed transects and respective trail length surveyed, with number of individuals of Myristicaceae species \geq 7 m in height and individuals \geq 10 cm DBH (diameter at breast height).

No single transect retained all 14 species (Table 3), the maximum number of species on any transect was 11, and the minimum was 6 (these were observed on transect T-A-Cch and T-A-Plt, respectively). There were only 11 species recorded for CICRA, and 12 recorded for CM1. There were nine species common across both sides of the river, they were: *I. juruensis*, *I. laevis*, *O. glyxicarpa*, *O. parvifolia*, *V. calophylla*, *V. elongata*, *V. flexuosa*, *V. multinervia*, and *V. sebifera*. The species that were unique to CICRA were *V. sp. 1* and *V. surinamensis*; those unique to CM1 were *V. divergens*, *V. lorentensis*, and *V. mollissima*. Those species unique to CM1 were only observed at a

maximum of 2 individuals. Of those species observed uniquely at CICRA, the minimum number of individuals observed was 554.

The species occurring across all the transects were *I. juruensis*, *I. laevis* *V. calophylla*, *V. multinervia* and *V. sebifera*; this was followed by *V. elongata* and *V. flexuosa* that were observed on all but one transect. Those species occurring on fewer than three transects were *V. divergens*, *V. elongata*, *V. lorentensis*, *V. mollissima*, *V. sp. 1* and *V. surinamensis*.

For most species, the height range for individuals at the CICRA site exceeded those for the same species at CM1 (Table 5). The only exception to this was *V. flexuosa*, which has similar height ranges on either side of the river. The largest two trees across the study site were *O. parvifolia* and *V. surinamensis* at maximum recorded heights of 35m and 36m, respectively. These two were the largest trees at CICRA, however since *V. surinamensis* did not occur at CM1, and *O. parvifolia* only had a single juvenile individual there, the tallest trees at the CM1 site belonged to *I. laevis*, at a height of 27 meters. As is to be expected, the DBH ranges at CICRA also exceeded those at CM1, for all species which were observed on either side of the river.

Utilizing our classification of adult trees as those ≥ 7 m in height, and a further classification of large trees ≥ 10 cm DBH, we generally found that the two trails upon which each species occurred in the greatest densities (in these size classes) were consistent (Table 6). For eight of our 14 species, the top two trails for either size class were the same (albeit in a different ranked order); for the remaining three species, at least one of the trails was consistent across the size classifications. This provides some support for our use of trees ≥ 7 m in height as representative of mature and established trees.

Species	CICRA		CM1	
	Height	DBH	Height	DBH
<i>Iryanthera juruensis</i>	7.0 - 22	2.8 - 47	7.0 - 17	3.1 - 20.6
<i>Iryanthera laevis</i>	7.0 - 28	2.9 - 70.5	7.0 - 27	3.4 - 34
<i>Otoba glyxicarpa</i>	7.0 - 30	4.6 - 72.9	14 - 14	26 - 26
<i>Otoba parvifolia</i>	7.0 - 35	1.8 - 75	7.0 - 7.0	4.1 - 4.1
<i>Virola calophylla</i>	7.0 - 30	1.2 - 33.4	7.0 - 18	2.8 - 26.1
<i>Virola elongata</i>	7.0 - 25	0.4 - 39	7.0 - 13	3.1 - 10.2
<i>Virola flexuosa</i>	7.0 - 15	7.0 - 18	7.0 - 15	4.0 - 13
<i>Virola loretensis</i>	n/a	n/a	8.0 - 8.0	5.7 - 5.7
<i>Virola mollissima</i>	n/a	n/a	20 - 20	13.4 - 13.4
<i>Virola multinervia</i>	7.0 - 25	3.4 - 41	7.0 - 18	4.5 - 23
<i>Virola sebifera</i>	7.0 - 30	2.2 - 80	7.0 - 18	3.6 - 24
<i>Virola sp. 1</i>	7.0 - 29	3.5 - 48	n/a	n/a
<i>Virola surinamensis</i>	7.0 - 36	2.6 - 88	n/a	n/a

Table 5. Biometric parameters (height and DBH –diameter at breast height) for all individuals ≥ 7 m in height. *V. divergens* is excluded because no individuals were found ≥ 7 m in height.

Species	DBH ≥ 10 cm	Height ≥ 7 m
<i>Iryanthera juruensis</i>	Kilo(5.9), Castanal(5.4)	Kilo(32.1), Castanal(16.8)
<i>Iryanthera laevis</i>	Castanal(8.1), Kilo(7.6)	Kilo(18.5), Castanal(14.7)
<i>Otoba glyxicarpa</i>	Luiza(1.8), Castanal(1.6)	Luiza(3.5), Castanal(1.8)
<i>Otoba parvifolia</i>	Lindero(32.1), Cocha Lobo(23.2)	Lindero(57.1), Cocha Lobo(34.4)
<i>Virola calophylla</i>	Plataforma(5.43), Castanal(5.35)	Castanal(12.7), "C"(6.8)
<i>Virola elongata</i>	Luiza(2.4), Primer Mirador(2.2)	Kilo(7.1), Luiza(6.8)
<i>Virola flexuosa</i>	Kilo(0.9), Luiza(0.6)	Luiza(1.5), Kilo(1.5)
<i>Virola mollissima</i>		
<i>Virola multinervia</i>	Plataforma(0.6), Castanal(0.4)	Plataforma(2.3), Primer Mirador(1.8)
<i>Virola sebifera</i>	Castanal(5.4), Luiza(3.0)	Castanal(11.7), Luiza(10.3)
<i>Virola sp. 1</i>	Lindero(5.9), Cocha Lobo(2.1)	Lindero(10.0), Cocha Lobo(3.5)
<i>Virola surinamensis</i>	Lindero(13.5), Cocha Lobo(7.1)	Lindero(27.6), Cocha Lobo(11.5)

Table 6. The top two trails, included in transects, upon which Myristicaceae trees were most dense (per hectare), in the adult size class (≥ 7 m in height) and large tree size class (≥ 10 cm DBH –diameter at breast height).

5.2 Juvenile and Adult Habitat Associations

Nine species (64%) out of the total were found in both TFF and SFF habitats. There were five species (36%) that were restricted to one habitat or another (Figure 12). Of the species that were restricted to habitat, the majority were restricted to the SFF habitat, with only a single species restricted to the TFF habitat. *Virola* was the only genus to exhibit restriction to a habitat, both *Iryanthera* and *Otoba* species occurred in both habitats. Accepting that species can exist in different habitats is necessary, but to uncover if there is reason to suspect that they are preferentially associated with a habitat, the number of stems occurring in each of those habitat must be analysed. We would expect that this analysis (the G-test) would be more valuable for adult trees. However, looking at juveniles might suggest something about their differential reproductive success.

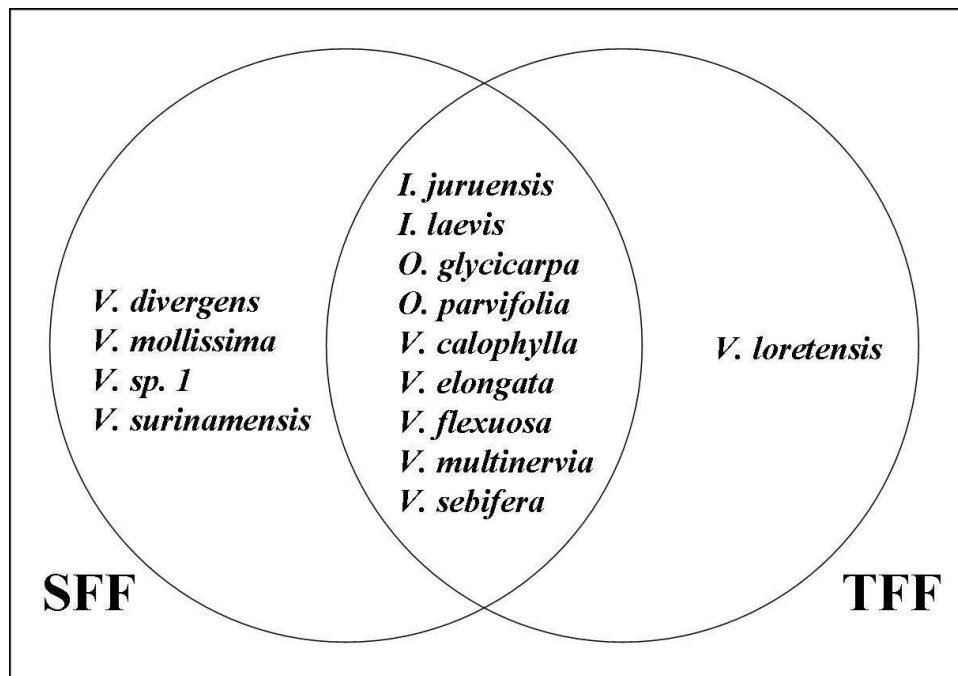


Figure 12. Venn diagram for species presence in SFF, TFF and shared across the two habitats.

For adult trees, there were four species for which there were too few individuals to run the G-test and these were: *V. divergens*, *V. flexuosa*, *V. lorentensis*, and *V. mollissima*. For two species, *V. sp. 1* and *V. surinamensis*, the G-test was not applicable because stems only occurred in the SFF habitat. For these species, simple probability values were calculated, with significant results ($p < 0.05$) for associations with the SFF habitat. The distribution of the eight remaining species (Table 7) all displayed an association with one habitat or another. Most species exhibited an association with the TFF habitat, whereas only a single species (*O. parvifolia*) exhibited an association with the SFF habitat.

For juvenile trees there were also four species for which there were too few numbers of individuals to run the G-test. These differed from those adult species for which the test could not be run and were: *O. glyxicarpa*, *V. divergens*, *V. lorentensis*, and *V. mollissima*. For the same two species as in the adult analysis, *V. sp. 1* and *V. surinamensis*, the G-test was not applicable because stems only occurred in the SFF habitat. For these species, simple probability values were calculated, with significant results ($p < 0.05$) for associations with the SFF habitat. Of the remaining eight species most were also associated with a habitat. There were only two of the eight species that resulted in a non-significant result, and hence lack of habitat association. These were *V. flexuosa* and *V. multinervia*. Juveniles, when associated with a habitat, were always associated with the same habitat as the adults of their species.

Species	Developmental Stage	N SFF	N TFF	G-test Probability	Association	
					SFF	TFF
<i>Iryanthera juruensis</i>	Tree	47	284	p<0.001		+
	Juvenile	153	768	p<0.001		+
<i>Iryanthera laevis</i>	Tree	16	196	p<0.001		+
	Juvenile	8	389	p<0.001		+
<i>Otoba glycycapra</i>	Tree	3	21	p<0.05		+
	Juvenile	0	18	Insufficient N to run		
<i>Otoba parvifolia</i>	Tree	311	1	p<0.001	+	
	Juvenile	1900	1	0	+	
<i>Virola calophylla</i>	Tree	35	175	p<0.001		+
	Juvenile	55	542	p<0.001		+
<i>Virola divergens</i>	Tree	0	0	Insufficient N to run		
	Juvenile	1	0	Insufficient N to run		
<i>Virola elongata</i>	Tree	3	83	p<0.001		+
	Juvenile	10	171	p<0.001		+
<i>Virola flexuosa</i>	Tree	0	12	Insufficient N to run		
	Juvenile	18	27	p>0.05		NS
<i>Virola loretensis</i>	Tree	0	1	Insufficient N to run		
	Juvenile	0	1	Insufficient N to run		
<i>Virola mollissima</i>	Tree	1	0	Insufficient N to run		
	Juvenile	0	0	Insufficient N to run		
<i>Virola multinervia</i>	Tree	1	21	p<0.001		+
	Juvenile	27	32	p>0.05		NS
<i>Virola sebifera</i>	Tree	26	152	p<0.001		+
	Juvenile	69	533	p<0.001		+
<i>Virola sp. 1</i>	Tree*	46	0	Insufficient N to run	+	
	Juvenile*	508	0	Insufficient N to run	+	
<i>Virola surinamensis</i>	Tree*	133	0	Insufficient N to run	+	
	Juvenile*	2230	0	Insufficient N to run	+	

Table 7. G-test and probability test results for all species and their association with habitat. Trees are stems ≥ 7 m in height, and juveniles are stems > 50 cm in height but < 7 m in height. *These species were not subjected to the G-test because they were located in a single habitat; for these species, association was assessed with simple probability tests. “+” denotes an association with a particular habitat, and “NS” denotes the lack of a significant relationship between species occurrence and habitat.

5.3 Distribution Patterns of Myristicaceae Species

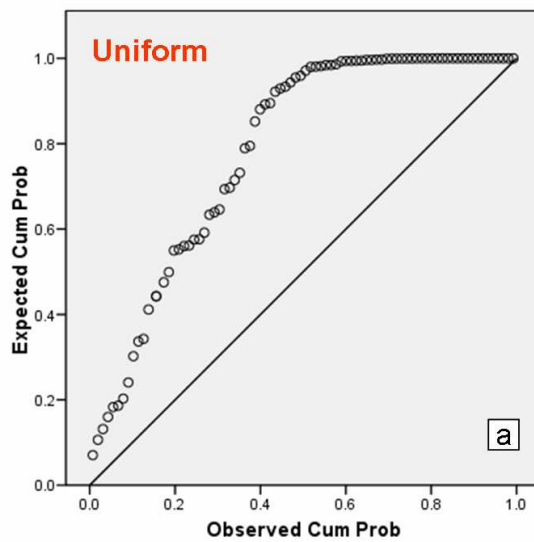
There were seven species for which spatial distribution could be assessed at the adult developmental stage representing at least one species within each genus. Where sufficient number of adults ($N \geq 30$) were available on a transect, analyses indicated the presence of random, clumped and uniform distributions (Table 8). Seven random, six clumped and three uniform distributions were observed for the seven species tested. Six species could be tested on at least two transects, while there was a single species that could be tested for a single transect, *V.sp. 1*. The two species of *Iryanthera* were assessed for 3-4 transects, while the single *Otoba* was assessed for only two, the five *Virola* species could be assessed for no more than two transects. Those species were omitted because of insufficient sample sizes.

Species	SFF			TFF				
	T-A-Cch	T-A-Lnd	T-B-Ccc	T-A-Cst	T-A-Lza	T-A-Plt	T-A-Prm	T-B-Klo
<i>Iryanthera juruensis</i>				Uniform	Random	*Clumped		Clumped
<i>Iryanthera laevis</i>				*Uniform	*Uniform			Random
<i>Otoba parvifolia</i>	*Clumped	*Clumped						
<i>Virola calophylla</i>				Random		*Clumped		
<i>Virola sebifera</i>				Random	Random			
<i>Virola sp.1</i>		Random						
<i>Virola surinamensis</i>	Random	*Clumped						
All Myristicaceae	*Clumped	Random	*Clumped	*Clumped	*Clumped	*Clumped	Clumped	*Clumped

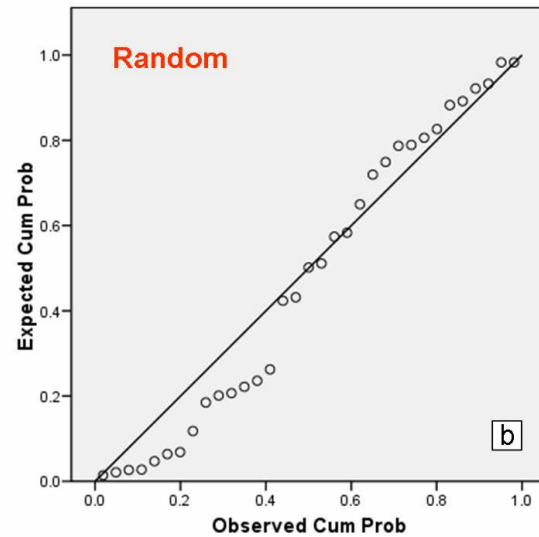
Table 8. Distribution patterns of adult Myristicaceae species as observed on surveyed transects, with $p < 0.05$. Patterns were evaluated only on those transects for which there were sufficient stem numbers. Some species were omitted due to insufficient stem numbers on all surveyed transects. *Denotes those tests which had a probability of $p < 0.01$.

Of the six species assessed along two or more transects, only two species showed the same distributions on different transects including *O. parvifolia* (clumped) and *V. sebifera* (random). Other species showed different distributions on different transects, including *I. juruensis* (uniform, random and clumped; Figure 13), *I. laevis* (uniform and random), *V. calophylla* (random and clumped), and *V. surinamensis* (random and clumped).

Exponential P-P Plot of Distance between neighbors



Exponential P-P Plot of Distance between neighbors



Exponential P-P Plot of Distance between neighbors

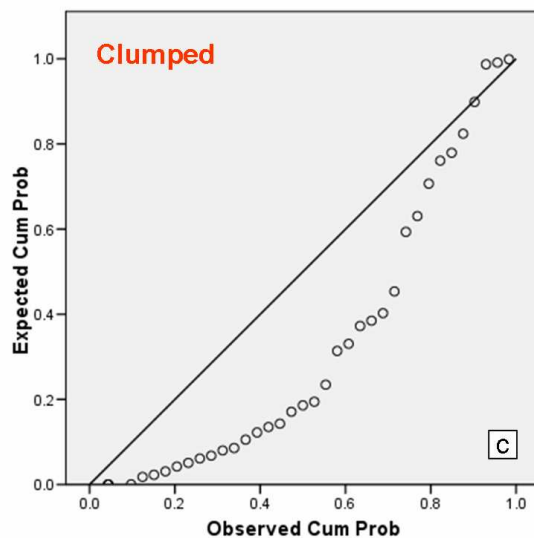


Figure 13. Actual cumulative probability plots generated for *I. juruensis* displaying the three patterns of distribution this species exhibits on different transects: **a.** uniform, **b.** random, and **c.** clumped.

When all adult Myristicaceae were considered, clumped distributions were indicated for all transects, except for a random distribution on T-A-Lnd in SFF. From the data on the table it might be expected that this is due to the individuals of *V. sp. 1* on this transect which, when considered alone, do in fact exhibit a random distribution. However, this is not the case; the number of adult individuals represented by *V. sp. 1* on that transect comprise only about 10% of the total number of stems.

The distribution of adults could be tested on five transects in SFF and 12 transects in TFF. Only clumped and random distributions occurred on SFF transects. The species that displayed uniform distribution on TFF transects, *I. juruensis* and *I. laevis*, did not have enough adults on SFF transects to be tested.

Although not shown in table 8, there were sufficient numbers of juveniles to test all species, and testing the distributions on 26 transects was possible. Nine transects were on SFF while the remainder were on TFF. Two random and 24 clumped transects were observed for the seven species tested. All species could be tested on at least two transects, for juvenile distribution. The two random distributions for juveniles occurred in two species, *V. sebifera* (on T-A-Prm) and *V. calophylla* (on T-B-Ccc). Although unfortunately the adults of *V. calophylla* could not be tested for that same transect, when comparing the distribution of *V. sebifera* juveniles to adults on T-A-Prm, they were both found to be random. These observations may suggest that the random pattern in adults is not caused by differential mortality, but rather mode of dispersal.

We have ascertained that juveniles generally display clumped patterns (tests carried out but not listed here; see author for details), and therefore made the decision to primarily represent the data for adult distribution patterns. We expect that utilizing adult

trees will provide us with results that are particularly interesting and a more truthful representation of species distribution patterns. The underlying theory is that either niche differentiation or dispersal modes would have influenced their distribution. The assessment of which of these is actually in play here, or to what extent either, or both, are in play is beyond the scope of this study. However, the observation of a pattern suggests the presence of a non-random structuring mechanism within this community, and can thus indicate the direction in which further experimental investigations could proceed.

6 Discussion

6.1 Presence and abundance of Myristicaceae species

Floodplain forests of the Amazon have been observed to contain fewer tree species than upland habitats in the same region (Prance, 1979; Kalliola, 1993; Salo et al, 1986; Harms et al, 2001). However, for the Myristicaceae, we find that more species occur in SFF than TFF. Of the 14 species present, 13 were found in seasonally flooded forests, as opposed to only 10 species found in terra firme forests, suggesting that the seasonally flooded forest is the most species rich of the two habitats at Los Amigos.

The latest compilations of the flora of Peru (Table 9) including Brako and Zarruchi (1993), Ulloa Ulloa et al (2003), and Rodriguez et al (2006) list the Myristicaceae species, their habitats, and their occurrence in the department of Madre de Dios. Our data include two new species for the department of Madre de Dios, *V. divergens* and *O. glyxicarpa*, and the potential for a third, that may be *Iryanthera 'grandis'*. A confirmation of this identification is pending receipt of the voucher specimen and review of herbarium material on loan to the Botanical Research Institute of Texas. Because the Myristicaceae are generally less successful in secondary forests (Valencia et al, 2004) their abundance in the Los Amigos forests suggests that these forests are relatively undisturbed. There are three species of the Myristicaceae (*I. elliptica*, *I. olacoides*, and *I. tessmannii*) that we expected to find at Los Amigos that were not observed. There were two genera (*Compsonaura* and *Osteophloem*) that have not been recorded for Madre de Dios by Brako and Zarrucchi (1993), and we confirm that they were not present along the surveyed transects. Further studies in the northern reaches

of the Los Amigos Conservation Area where SFF and TFF are less clearly delineated may show the presence of other Myristicaceae species.

Myristicaceae genus	Specific epithet
<i>Compsonaura</i>	<i>capitellata</i> , <i>diazii</i> , <i>sprucei</i>
<i>Iryanthera</i>	<i>coriacea</i> , <i>crassifolia</i> , <i>elliptica</i> , <i>grandis</i> , <i>juruenis</i> , <i>laevis</i> , <i>lancifolia</i> , <i>longiflora</i> , <i>macrophylla</i> , <i>olacoides</i> , <i>paradoxa</i> , <i>paraensis</i> , <i>polyneura</i> , <i>tessmannii</i> , <i>tricornis</i> , <i>ulei</i>
<i>Osteophloem</i>	<i>platyspermum</i>
<i>Otoba</i>	<i>glycarpa</i> , <i>parvifolia</i>
<i>Virola</i>	<i>albidiflora</i> , <i>caducifolia</i> , <i>calophylla</i> , <i>decorticans</i> , <i>divergens</i> , <i>duckei</i> , <i>elongata</i> , <i>flexuosa</i> , <i>loretensis</i> , <i>marlenei</i> , <i>mollissima</i> , <i>multinervia</i> , <i>obovata</i> , <i>pavonis</i> , <i>peruviana</i> , <i>sebifera</i> , <i>surinamensis</i> , <i>weberbaueri</i>

Table 9. Species of Myristicaceae recorded for departments in Peru and their observed habitats (Brako and Zarucchi, 1993). In **bold** are those species that are listed for the department of Madre de Dios; in **blue** are those species that occur in inundated forests; in purple are those species that occur in both inundated forests and terra firme; in **green** are those species that occur in other specialized habitats (Brako and Zarucchi, 1993).

We confirm the observations of Brako and Zarucchi (1993) that *V. calophylla*, *V. elongata* and *O. parvifolia* occur in both SFF and TFF. Although Brako and Zarucchi (1993) found *V. loretensis* in both habitats, we found it only in TFF. However, it was rarely observed and only observed on the east side of the river. We found *V. surinamensis* to occur only in inundated forests, contrary to the information published by Brako and Zarucchi (1993).

The topography of the floodplain forests at Los Amigos indicates dynamic river meander and continuing processes of erosion and deposition. Multiple terraces indicate changing floodplain boundaries and the continuing erosion of river banks. Oxbow lakes

are formed from the meandering rivers. These processes may play a rather large part in the maintenance of the high diversity in this system, and it may be worthwhile to relate heterogeneity in environmental variables, such as elevation, soil type and properties, flooding intensity and duration and underlying geology, with floristic compositions in seasonally flooded forests.

The SFF also have greater stem densities than TFF. However, when all *Myristicaceae* individuals ≥ 50 cm in height, but less than 7 m in height, were included, SFF forests evidenced 468.0 individuals/hectare, as compared with the 136.8 individuals/hectare in TFF. The abundance of these mid-sized trees is evidence of a notably higher level of regeneration in the SFF than TFF. When only adults (individuals ≥ 7 m in height) are considered, the densities were still found to contain the greatest number of individuals, with 58.5 individuals/hectare in SFF as compared with 52.2 individuals/hectare on TFF. These data suggest that SFF forests at the study site have both a greater number of species of *Myristicaceae* and a greater abundance of individual stems than TFF.

We have observed floristic and ecological differences between SFF and TFF at Los Amigos; the immediate question becomes, how do these forests compare to other areas? Similar studies have been completed, primarily using plot protocols, but generating similar statistics of abundance data as we have in our studies. Terborgh and Andresen (1998) compiled a list that synthesized plot data collected across the neotropics (Table 10; Appendix 4) (particularly in Amazonia) to compare stem density of large trees (≥ 10 cm DBH) in all plant families. We found that the mean stem density of *Myristicaceae* large trees at Los Amigos is greater than that for other regions. Mean

density at Los Amigos is most closely followed by abundance data from other Peruvian studies, which supports the placement of this study in the country wherein the Myristicaceae experience their greatest abundance. The greater abundance of Myristicaceae species in Peruvian SFF is not duplicated in TFF. Myristicaceae abundance in Peruvian TFF is intermediate between the minimum abundance in Guyana and the greatest abundance in Western Amazonia. The greatest density of the Myristicaceae is exhibited in Peru; while our data support this for SFF, our data do not support this for TFF (Table 10). This suggests that there are factors operating in TFF that have not been sufficiently explored at the Los Amigos station, and it would be important to observe other tree families to see whether they too evidence lower abundances or if in fact this is a characteristic unique to the Myristicaceae.

Habitat	Region	Density Range	Mean Density	Plots/ transects
SFF	Guyana	2	2.00	1
	Eastern Amazonia	3 - 6	4.50	2
	Central Amazonia	13	13.00	1
	Western Amazonia	0 - 67	29.93	14
	Peru	4 - 67	33.82	11
	<i>this study</i>	9 - 53	34.12	3
TFF	Guyana	0 - 6	2.25	4
	Eastern Amazonia	0 - 15	7.75	8
	<i>this study</i>	10 - 28	17.33	5
	Central Amazonia	6 - 39	22.50	4
	Peru	13 - 52	29.86	7
	Western Amazonia	13 - 95	34.60	10

Table 10. Myristicaceae abundance data (stems \geq 10 cm DBH –diameter at breast height, per hectare) summarized from Terborgh and Andresen (1998), including data from this study.

Our densities of 119-195 individuals/hectare for trees ≥ 50 cm tall also support the findings of Wittman et al (2006) that the Myristicaceae may be one of the most important families in floodplain forests and among the most important tree families in the rest of Amazonia (Gentry, 1982; 1988). Cornejo et al (2006) presented results from the Palma Real watershed, also in Madre de Dios, Peru, and found that the Myristicaceae stems ≥ 10 cm DBH exhibited densities averaging 12.01 individuals/hectare in terra firme forests. Our data support this, as we encountered 11.58 individuals/hectare in this same size class, for terra firme forests around the Los Amigos Biological Station and Conservation Concession.

6.2 Habitat associations

For ten of the 14 species there was a statistically significant association with a greater proportion of individuals being associated with TFF (7 species) than with SFF (3 species). This is consistent with the greater geographic extent of TFF than SFF throughout Amazonia. *Iryanthera* was the only genus that did not have a single species preferring SFF. The three species that were associated with SFF (*O. parvifolia*, *V. surinamensis*, and *V. sp.1*) were all especially abundant and contributed significantly to the higher overall stem density in the SFFs.

These measured associations may indicate differential success of a species in different habitats, or they may represent the frequency of past disturbances. Isolating and identifying the factors that could contribute to differential success, often referred to as habitat performance, can be a complicated process. There are conflicting data that support either the formation of habitat associations at the seedling stage (Baraloto et al,

2007) or the absence of this (Comita et al, 2004; Fine et al, 2004). Our data find both juveniles and adults associated with the same habitats, suggesting that the environmental requirements (as provided by the two habitats: SFF and TFF) at the two developmental stages, juvenile and adult, may be similar. However, shade house experimental studies comparing the success of seedling establishment in either habitat for species identified as habitat associates would be required to confirm this. Fine et al (2004) showed that there were in fact no problems in seedling establishment and growth for habitat specialists (in clay and sand habitats) in other habitats, and that in some cases they performed better, but that it was herbivory that was controlling and reinforcing habitat associations. Herbivory is likely to play a more important role in the distribution of those individuals of Myristicaceae across habitat at CM1 (across the Los Amigos river) where there is a larger herbivore population (i.e. Neotropical Lowland Tapir populations; pers. comm., M. Tobler, 2007). This is a case in which the factor interpreted as maintaining habitat associations may not be the sole mechanism operating.

It is hypothesized (Prance, 1979; Kalliola, 1993; Salo et al, 1986; Harms et al, 2001) that the harsher conditions present in the SFF due in particular to flooding may prevent the occurrence of many species in that habitat. We find that this is not the case for the Myristicaceae, as we have evidence of the majority of these species at Los Amigos occurring in this habitat. In addition to shade house studies, we might expect our true habitat associates to reflect morphological (and performance related) characteristics that are adaptations to those environments. We have not found a prevalence of these, however there is one species that can stand as an example. *V. surinamensis* has been recorded by Brako and Zarucchi (1993) to occur in both SFF and TFF, but we observe it

only in the former. This species exhibits some key morphological adaptations to SFF habitats, including (1) the presence of buttresses and stilt roots, and (2) the presence of lenticels, (Appendix 1) both of which have been observed at Los Amigos, as well as in other studies throughout the distribution of this species (pers. comm., J. P. Janovec). In addition, there have been records of the survivorship of these seeds in waterlogged environments (Fisher et al, 1991) and the observation of seed dispersal by fish (Gottsberger, 1978). Further sampling during other seasons would be of use in evaluating performance related characteristics, such as abundance (or even evidence) of fruiting and flowering across habitat, that may be maintaining these associations.

6.3 Spatial distribution of Myristicaceae species

With regards to the spatial distribution of the Myristicaceae species, we found that species exhibited various patterns; four of the seven species exhibited only a single pattern (either clumped, random or uniform), while the remaining three exhibited varying combination of patterns across the transects analyzed. We found that four species exhibited clumped patterns on at least one transect, thus corroborating our hypothesis that this pattern would be most clearly depicted in our data, and consistent with the findings of other studies (Armesto et al, 1986, Condit et al, 2000). However, there was evidence for two other patterns of distribution that are less common, random and uniform. We find that the least encountered pattern, uniform, was only evident in one genus by both the species within it, *I. juruensis* and *I. laevis*. It is important to be able to identify some of the causes for this deviation from what was expected --a clumped distribution pattern. It must be kept in mind however, that *I. juruensis* did exhibit a clumped pattern on two of

the four transects for which it was assessed. These varying patterns of spatial distribution indicate the action of varying mechanisms of seed dispersal, reproductive performance, and perhaps disturbance events, and evidence of a single species displaying multiple such patterns suggests that these do not always act with equal force.

Unlike the other species, *I. juruensis* exhibits all three patterns of distribution which suggests that it may be experiencing intraspecific competition for resources, different dispersal limitations, or perhaps different levels of herbivory, in different areas of the forest. Intraspecific competition is difficult to measure, but field observations of modes of dispersal shed some light on the matter. *I. juruensis* is a species that has cauliflorous fruits with bright red arils and little is known about dispersal systems, although it is suggested that it is bird dispersed. Through personal observations, it has been noted that if fruits of this species are not mechanically removed by a disperser, they will remain on the tree and simply rot in place. They are also attacked by colonies of homopterans being tended by colonies of brown ants; this seems to speed the rotting process of the fruit that goes undispersed. This would explain a distribution other than clumped, because the likelihood of fruits falling about the mother tree is rather low. However, if only trees in certain areas are subject to efficient dispersal by birds, this could in fact lead to a clumped or random distribution in other areas in the forest. Obligate dispersal agents of species in *Iryanthera* have yet to be recorded, and it is a commonly held belief that such generally dispersed trees often are visited due to proximity to other fruiting trees of separate species (Howe, 1980). Although similar observations have not been made for *I. laevis*, which has ramiflorous fruits, it is possible those similar mechanisms operate and that ripe, uneaten fruits are in fact also left to rot

on the tree. There were no observations made of fruit falling to gather beneath *I. laevis* trees, even when they were observed to be in fruit, suggesting that this may be the case.

In contrast to these observations about *Iryanthera* species, we find that species of both the genera *Otoba* and *Virola* do have a tendency for fruit to fall beneath the parent tree. *Virola* species have been noted to be primarily dispersed by birds and mammals (Holbrook, 2006; Galetti et al, 2000), promoting a widespread seed rain. *Virola* species are the most geographically widespread of the Myristicaceae, and perhaps it could be suggested that species exhibiting such widespread distributions have (1) efficient modes of dispersal, and (2) a generalist performance allowing establishment across heterogeneous environments. The observation that *Virola* species tend to exhibit primarily random patterns of distribution may be consistent with a widespread seed rain. Another possibility that might generate a random pattern would be the occurrence of disturbance events such as landslides or fires. In the study area, the primary forms of natural disturbance include tree-fall due to heavy winds and landslides along sharp river banks. It is unlikely that these would preferentially affect *Virola* species, and thus other species would exhibit distributions generated by these factors.

Although *Otoba* species exhibit a seed rain that is quite dense immediately about the tree as do *Virola* species, their fruits consist of a white aril rather than a red aril and have been observed to be primarily mammal dispersed, but could also be bird dispersed (Holbrook, 2006; Russo, 2003; Russo et al, 2005). In contrast to the waxy, tasteless or bitter aril of the *Virolas* and *Iryantheras*, this genus has a distinctly sugary aril that suggests an adaptation to mammal dispersal, as does the color (Howe and Smallwood, 1982). If in fact these species are primarily mammal dispersed, it might explain the

evidence of a clumping pattern in *O. parvifolia*, as their most likely dispersal agents are primates, which tend to travel in groups and spend significant amounts of time in a single area (Russo et al, 2005).

Unfortunately there were no species for which distribution patterns could be assessed across habitat types, which would provide interesting data for comparison. However, this perhaps in part supports our findings that Myristicaceae species are in fact preferentially dominant in one habitat over another. The various exhibited patterns suggest that multiple factors are interacting to structure the spatial distribution of these species, and due to their specific methods of dispersal and demographic factors, these different mechanisms may have more or less influence. Our data suggest that even in as small an area as was sampled, there is a complex interaction involved and more specifically targeted research, beginning with dispersal studies (Bullock et al, 2006) and surveys of abiotic characters (Tuomisto et al, 2003), is necessary.

7 Future Work

This study has provided useful information for other researchers that investigate habitat distinction and species distribution at the Los Amigos Biological Station and Conservation Area. In addition, the outcome of field guides and ecological observations will be of use to the ornithologists and mammalogists whose study organisms consume or otherwise interact with these extremely abundant trees. Perhaps most importantly, we have identified the area surrounding the Los Amigos Biological Station as one of the sites in which the Myristicaceae are most abundant and rather diverse. We have provided data that serves as a baseline and can be re-evaluated in the years to come to test questions about habitat associations, forest structure and community, and dispersal syndromes.

The mechanisms generating the patterns that we have observed have the potential to express differential influence in different areas of the forest; it would therefore be worthwhile to investigate potential heterogeneity in environmental factors (such as soil nutrients, intensity of flooding or underlying geology) within both SFF and TFF, and see how they correlate with floristic findings (Pino, 2007). Furthermore, replicates of this process are suggested to expand upon what we know about the Los Amigos watershed, and perhaps beyond it. It is expected that although unequal samples were taken in the two habitats, sampling will generate similar outcomes. Comparisons with other areas using replicates, as well as comparisons with existing plot data will be essential for future work and testing of this process.

The patterns that are observed in the Myristicaceae should be compared using this same protocol to investigate other important Neotropical plant families (e.g. Sapotaceae).

Dissimilar patterns might suggest that distribution structuring mechanisms are

preferentially affecting the distribution of one family over another, whereas similar patterns might suggest that there are factors exhibiting a stronger force across the flora in general in this watershed. Further sampling in other seasons would be of use in evaluating performance-related characteristics, such as abundance (or even evidence) of fruiting and flowering across habitat, that may be maintaining habitat associations among these Myristicaceae species.

Also, the co-occurrence of clumps of species of differing families and a study of their fruiting times and modes of dispersal may be useful in identifying processes controlling distribution. In SFF, such co-occurrence of clumps could be related to variation in soil type and depth and duration of inundation to indicate controlling processes. With sampling of a larger number of sites we might find that (1) all the species exhibit varying, site specific, spatial distributions or perhaps that (2) that most species display clumped patterns more often than not.

Our data provide evidence for habitat heterogeneity between and within SFF and TFF , but not explanations of why it occurs. However, our data suggests the direction in which further studies might progress to identify these explanations. In a rapid method of censusing the population of species in a single family, we have been able to evaluate characteristics of diversity, abundance and distribution that form a basis for further research and conservation in the area. Our transects provide a basis for further analyses of Myristicaceae biology and further analyses of SFF and TFF structures by the mapping of other species, genera and families along the transects.

Appendix 1

Voucher specimens and species images

For all species recorded, vouchers and images can be accessed through Atrium (2007), at <http://www.atrium.andesamazon.org>. For the following two species, photographs could not be taken, but vouchers do exist.

Virola divergens Ducke

Voucher: J. P. Janovec 3061

Virola mollissima Warb.

Voucher: M. A. Chocce 583

The remaining species have both voucher specimens and photographs.

Iryanthera juruensis Warb.

Vouchers:

T. F. Franklin 58

J. P. Janovec 1805



Iryanthera laevis Markgraf.

Vouchers:

T. F. Franklin 60

T. F. Franklin 61

A. P. Maceda 502

A. P. Maceda 2176

*Iryanthera* 'grandis'

Vouchers:

T. F. Franklin 59

A. P. Maceda 3266



Otoba glyxicarpa Ducke

Vouchers:

T. F. Franklin 56

T. F. Franklin 61

P. Centeno 14

J. P. Janovec 2166

J. P. Janovec 2657

*Otoba parvifolia* Markgraf.

Vouchers:

T. F. Franklin 46

J. P. Janovec 1999

J. P. Janovec 2537

A. P. Maceda 3



Virola calophylla Warb.

Vouchers:

T. F. Franklin 41

T. F. Franklin 50

P. Centeno 13

*Virola elongata* Warb.

Vouchers:

T. F. Franklin 52

A. P. Maceda 1304



Viola flexuosa A.C.Smith

Vouchers:

T. F. Franklin 40

T. F. Franklin 53

J. P. Janivec 1996

*Viola loretensis* A.C.Smith

Vouchers:

T. F. Franklin 49

T. F. Franklin 57

A. P. Maceda 2337



Viola multinervia Ducke

Vouchers:

T. F. Franklin 42

T. F. Franklin 55

A. P. Maceda 27

P. Centeno 67

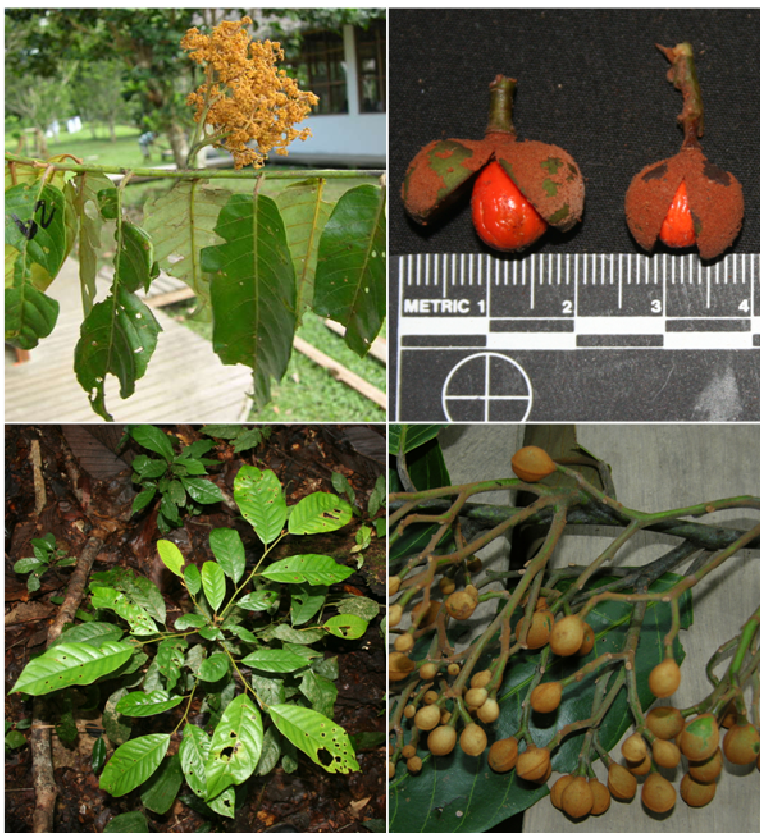
*Viola sebifera* Aubl.

Vouchers:

T. F. Franklin 29

T. F. Franklin 32

T. F. Franklin 47



Virola sp.1

Vouchers:

T. F. Franklin 43
T. F. Franklin 44
T. F. Franklin 48
J. P. Janovec 2711

*Virola surinamensis* Warb.

Vouchers:

T. F. Franklin 4
A. P. Maceda 1090
J. P. Janovec 2063
J. P. Janovec 3097



Appendix 2

Data

All data collected in this study, including the identification of the mapped individuals and their biometric measurements, are included in a Compact Disc that accompanies bound versions of the thesis. For those with electronic versions of the thesis, the data can be obtained by writing the author at *tianafranklin@gmail.com*.

Appendix 3

Transect codes

Transects were named based on three things, (1) Transect designation (denoted by a “T”), (2) their installation at CICRA (denoted by the “A” that follows the “T”), or at CM1 (denoted by a “B”), and (3) an abbreviated three-letter code for the trail upon which that transect was primarily installed.

Transect code	Site	Primary trail
T-A-Cst	CICRA	<i>Trocha Castañal</i>
T-A-Lza	CICRA	<i>Trocha Luiza</i>
T-A-Plt	CICRA	<i>Trocha Plataforma</i>
T-A-Prm	CICRA	<i>Trocha Primer Mirador</i>
T-A-Cch	CICRA	<i>Trocha Cocha Lobo</i>
T-A-Lnd	CICRA	<i>Trocha Lindero</i>
T-B-Klo	CM1	<i>Trocha Kilo</i>
T-B-ccc	CM1	<i>Trocha "C"</i>

Appendix 4

Myristicaceae abundance data

These plot data are summarized from Terborgh and Andresen (1998) and represent density, per hectare, of Myristicaceae individuals across the Neotropics. These data are summarized (lines in grey) in table 10, in the Discussion section. Articles reference in this table are not included in the reference section, but they can be obtained through Terborgh and Andresen (1998).

Country	Department	Location	No./ ha	No. of Plots	Range	Mean	Reference
Guyana			2	1			
Guyana		Moraballi Creek	6	1			Davis & Richards 1933, 1934
Guyana			1	1			
Guyana			0	1			
TOTAL Guyana TFF				4	0-6	2.25	
TOTAL Guyana SFF				2	2	2	Davis & Richards 1933, 1934
Brazil	Para	Rio Xingu	4	1			Campbell et al., 1986
Brazil	Para	Castanhal	5	1			Pires et al., 1953
Brazil	Para	Caxiuana	11	1			Almeida et al
Brazil	Para		15	1			Salomao et al., 1988
Brazil	Para	Carajas	0	1			Silva et al., 1986
Brazil	Para		14	1			Silva & Rosa, 1989
Brazil	Para		10	1			Silva et al., 1986
Brazil	Para	Maraba	3	1			Salomao, 1991
(eastern Amazonia) TOTAL Brazil TFF				8	0-15	7.75	
Brazil	Para	Guama River	6	1			Pires & Koury, 1958
Brazil	Para	Guama River	3	1			Black et al., 1950
(eastern Amazonia) TOTAL Brazil SFF				2	3-6	4.5	
Brazil	Amazonas	Urucu River	32	1			Peres, 1991
Brazil	Mato Grosso	Aripauna	39	1			Ayres, 1981
Brazil	Rondonia	Rondonia	13	1			Salomao & Lisboa, 1988
Brazil	Rondonia	Rondonia	6	1			Maciel & Lisboa, 1989
(central Amazonia) TOTAL Brazil TFF				4	6-39	22.5	
(central Amazonia) TOTAL Brazil SFF				13	13	13	Ayres, 1986
Peru	Madre de Dios	Manu River	18	1			Terborgh et al., 1998
Peru	Madre de Dios	Manu River	15	1			Terborgh et al., 1998
Peru	Madre de Dios	Manu River	13	1			Dallmeier et al., 1993
Peru	Madre de Dios	Manu River	24	1			Dallmeier et al., 1993
Peru	Pasco	Cabeza de Mono	40	1			Terborgh et al., 1998 (A. Gentry, unpubl. data)
Peru	Loreto	Mishana	52	1			Terborgh et al., 1998 (A. Gentry, unpubl. data)
Peru	Madre de Dios	Tambopata River	47	1			Terborgh et al., 1998 (A. Gentry, unpubl. data)
TOTAL Peru TFF				7	13-52	29.8571	
Bolivia	Beni	Rio Ivon	95	1			Boom, 1986
Ecuador	Napo	Yasuni National Park	19	1			Balslev et al., 1987
Ecuador	Napo	Cuyabeno	23	1			Valencia et al., 1993
(western Amazonia) TOTAL TFF				10	13-95	34.6	
Peru	Madre de Dios	Manu River	27	1			Terborgh et al., 1998
Peru	Madre de Dios	Manu River	62	1			Terborgh et al., 1998
Peru	Madre de Dios	Manu River	17	1			Terborgh et al., 1998
Peru	Madre de Dios	Manu River	53	1			Terborgh et al., 1998
Peru	Madre de Dios	Manu River	46	1			Terborgh et al., 1998
Peru	Madre de Dios	Manu River	36	1			Terborgh et al., 1998
Peru	Madre de Dios	Manu River	37	1			Dallmeier et al., 1993
Peru	Loreto	Yanomamo	67	1			Terborgh et al., 1998 (A. Gentry, unpubl. data)
Peru	Madre de Dios	Madre de Dios River	6	1			Terborgh et al., 1998 (P. Nuñez & O Phillips, unpubl. data)
Peru	Madre de Dios	Madre de Dios River	4	1			Terborgh et al., 1998 (P. Nuñez & O Phillips, unpubl. data)
Peru	Madre de Dios	Tambopata River	17	1			Terborgh et al., 1998 (A. Gentry, unpubl. data)
TOTAL Peru SFF				11	4-67	33.8182	
Bolivia	Beni	Beni	0	1			Dallmeier et al., 1991
Bolivia	Beni	Beni	1	1			Dallmeier et al., 1991
Brazil	Acre	Acre	46	1			Campbell & Stone, 1992
(western Amazonia) TOTAL SFF				14	0-67	29.9286	
Panama	Canal Zone	Barro Colorado Island	24	1			Thorington et al., 1982
Costa Rica	Heredia	La Selva	8	1			Heaney & Proctor, 1990
(Central America) TOTAL				2	1	1	
Brazil	Sao Paulo	Sao Paulo	5	1			Silva & Filho, 1982
Brazil	Bahia	Bahia	6	1			Mori et al., 1983
Atlantic TOTAL				2	1	1	

Appendix 5

Abbreviations

AABP	Andes to Amazon Biodiversity Program
ACCA	<i>Asociación Para La Conservación de la Cuenca Amazónica</i> – Association for the Conservation of the Amazonian Watershed. This is partnered with ACA, the Amazon Conservation Association.
BRIT	Botanical Research Institute of Texas
CICRA	<i>Centro de Investigación y Capacitación del río Amigos</i> – Training and Research Center of the Los Amigos River (Los Amigos Biological Station)
cm	centimeters
CM1	<i>Centro de Monitoreo 1</i> – Monitoring Center 1
CM2	<i>Centro de Monitoreo 2</i> – Monitoring Center 2
CM3	<i>Centro de Monitoreo 3</i> – Monitoring Center 3
DBH	Diameter at Breast Height
ESRI	Environmental Systems Research Institute
G	The test statistic calculated in the G-Test
GPS	Global Positioning System
ha	hectares
Ha	alternative hypothesis
Ho	null hypothesis
<i>I.</i>	<i>Iryanthera</i>
Km	kilometers
m	meters
m a.m.s.l.	meters above mean sea level
mm	millimeters
<i>O.</i>	<i>Otoba</i>
USM	<i>Universidad de San Marcos</i> – San Marcos University, Lima, Peru
WGS	Universal Transverse Mercator Coordinate System
<i>V.</i>	<i>Virola</i>
WGS	World Geodetic System

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ABSTRACT

DIVERSITY AND DISTRIBUTION OF THE MYRISTICACEAE FAMILY OF PLANTS IN TERRA FIRME AND SEASONALLY FLOODED FORESTS IN MADRE DE DIOS, PERU

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of Environmental Science

The diversity, richness and abundance of the Myristicaceae family of plants were assessed in a tropical moist forest in Madre de Dios, Peru. There were 15 species among three genera, *Iryanthera*, *Otoba* and *Virola* at the Los Amigos Conservation Concession. Using a novel mapping technique, geographic coordinates were assigned to 9026 individual trees (≥ 0.5 m in height) in approximately 30 hectares of forest. All mapped trees were identified to species, and measured for biometric parameters such as DBH (diameter at breast height) and height, and a voucher specimen was collected with duplicates deposited at various herbaria. These georeferenced data were used to analyze preferred association with one of the two major habitats, seasonally flooded forests (SFF) and terra firme forests (TFF), and used to analyze spatial patterns of distribution adhering to either a random, uniform or clumped distributions.