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Floristic composition across a climatic gradient in a neotropical forest

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ABSTRACT

Floristic composition of a neotropical forest across a climatic gradient in lowland Panama

by

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This study investigated the composition of large trees within a lowland forest in the watershed of the Panama Canal. Fifty-four 1-ha plots inventoried by the Smithsonian Tropical Research Institute were analyzed with respect to environmental factors, including: precipitation, geologic parent material, stand age, topography, and soils. The 54 plots represent a regional flora with exceptional beta diversity and low floristic nestedness. The plot network contains 821 species of trees with a diameter at breast height greater or equal to 10 cm. For comparison, the well-studied 50-ha forest dynamics plot on Barro Colorado Island in the middle of the isthmus contains 303 species of large trees. The Panamanian forest is strongly spatially structured at the landscape-scale with floristic similarity decreasing rapidly as a function of inter-plot geographic distance. Polythetic, agglomerative cluster analysis, in combination with non-metric multidimensional distance scaling ordination, and relative rates of species accumulation indicate broad floristic associations well correlated with mapped Holdridge Life Zones. Multivariate ordination techniques (non-metric multidimensional distance scaling and Detrended Correspondence Analysis) show strong patterns of floristic variability correlated with regional precipitation trends and local soil attributes. Geologic and soil conditions, such as acidic soils or excessively drained limestone substrates, appear to override the effects of precipitation and modify forest composition. The analysis of forest assemblages with respect to these environmental parameters suggests possible opportunities for increased conservation efficiency. Exceptional soil conditions identified in this study sometimes juxtapose dissimilar forest types over relatively short geographic distances. These localities provide opportunities for significantly increasing relative rates of species accumulation through informed site selection. The identification of these soil complexes through fieldwork, remote sensing technologies, and geographic databases represents a significant opportunity for future research.

INTRODUCTION

Tropical forests are simultaneously one of the most diverse and most imperiled ecosystems on Earth. Beyond coarse generalizations, development and deforestation have differentially impacted specific forest-types. Some, such as the tropical dry forests, have been extirpated from over 99% of their historic ranges (Janzen 1988). The majority of remaining tropical forest lands are broadly classified as lowland moist forests (Bawa and Seidler 1998). These communities contain unmatched reserves of biological diversity, most notably in the form of green, woody plants (Pimm et al. 1995). The social, ethical, and economic arguments for forest conservation have been eloquently presented elsewhere (e.g., Wilson 1984), but they are often made in a context deficient in fundamental biological knowledge taken for granted in temperate latitudes. In Panama, we have only the skeletal outlines of how patterns of forest composition change across the lowland landscape and respond to changes in biophysical environments (Croat 1978, Hubbell and Foster 1992). Further, the tolerance of individual species for specific environmental gradients is largely a mystery away from the intensively studied Barro Colorado Island (BCI) (Hubbell and Foster 1992).

This investigation considered patterns of floristic diversity in a lowland moist forest at the landscape scale. The boundaries of an ecological landscape are difficult to define intuitively. For the purpose of this study, I will define a landscape as a geographic unit that is fundamentally heterogeneous, containing many identified ecological subdivisions, including populations, communities, and a variety of land uses (Wiens 1995).

This project provided a preliminary analysis of floristic data gathered from sampling plots established throughout the Panama Canal watershed. The primary goals include: (1) describing variation in large tree composition, (2) associating these changes with environmental controls, and (3) identifying linkages between these data and opportunities for conservation within the watershed.

TROPICAL BIODIVERSITY

Explaining the development of incredible levels of biological diversity in tropical forests has represented one of the greatest challenges for ecologists during the last century (see Huston 1994, Rosenzweig 1995). However, despite a daunting array of theories and possible explanations, the current literature suggests that the scientific community has not reached a consensus regarding the origin of tropical diversity. No single thesis has conclusively provided a unified framework for the origin and maintenance of tropical forest diversity across multiple spatial and temporal scales (see Cook 1998). In the context of this study, the term biodiversity will be used synonymously with the number of species present, often called species richness. This study will evaluate the interplay between alpha-diversity, the number of species co-occuring at a given site, and beta-diversity. The processes promoting these patterns of diversity have been heavily investigated, particularly at the local scale. The resulting ecological literature suggests a complex mixture of controlling processes, including: interspecific competition (e.g., Janzen 1970, Connell 1971, Clark and Clark 1985, Condit et al. 1992a), niche specificity (Hutchinson 1957, Hutchinson 1961), intermediate disturbance theory (Connell 1979, Levins and Paine 1974, Paine and Levin 1981), episodic speciation from refugia (Haffer 1969, Simpson and Haffer 1978), differential response to climate change (Bush 1994, Colinvaux 1998, Haberle and Maslin 1999), biological productivity (Huston 1994), and dispersal limitation (Cohen and Levin 1991, Guevara and Laborde 1993, Malanson and Armstrong 1996, Harms 1997, Dalling et al. 1998a, Dalling et al. 1998b, Hubbell et al. 1999). The following section will address several of the theories most relevant to this thesis and controls on diversity within the Panamanian lowland forest.

Interspecific competition and biological controls

By definition, forest communities are associations of living organisms coexisting in time and space. As such, the potential exists for the attributes of individual agents within a community (e.g., species) to dramatically influence composition of the whole unit through their activities as a predator, herbivore, competitor, or prey for other species. The search for agents of community organization is long standing in the ecology literature (Ricklefs 1990). Tropical forests have been a hot-bed for this type of research following classic work by Janzen (1970) and Connell (1971). They argue that selective herbivores will feed upon an abundant species until its relative densities are comparable to those of other species within the community. The core of the theory is that increasing abundance in tropical environments leads to increasing vulnerability to consumers (Ricklefs 1990). The theory predicts a reduction in the degree of conspecific clustering and reduced reproductive success for neighboring conspecific individuals. Janzen's theories have been tested several times on BCI (Hubbell and Foster 1986a, Condit et al. 1994, Wills et al. 1997). Experimental results frequently indicate significant clustering in the distribution of individual tree species; however a significant minority of species appear to exhibit patterns predicted by Janzen-Connell-type models. Overall, the role of these processes in community organization appears unresolved. Biological agents and related processes probably play an important role in the distribution of tree species on BCI; however, despite significant research to date, this component remains intractable and difficult to quantify.

Niche Theory

Species richness in a region has been conceptualized to have a complex relationship to the supply of environmental resources and the division of those resources among species, normally referred to as a species niche. G.E. Hutchinson (1957) suggested that an ecological niche is bounded by the suite of factors that directly influence a species and is defined by the range of environmental conditions for which a species demonstrates evolutionary fitness. By analogy, the fundamental niche is a hyper-volume defined by a large number of potentially limiting factors. The distribution of a species in geographic space represents its realized niche under a range of differentially limiting controls. This hypothesis suggests that tropical tree species have very finely divided the available resources and that many species are extreme habitat specialists. More recent research (Tilman 1982) proposed a dynamic mechanism that allows competitors with overlapping resource requirements to coexist in their realized distributions. The role of specialization versus more generalized life history strategies has been a major focus of research in lowland Panama for at least 40 years (e.g., Holdridge and Budowski 1956, Hubbell and Foster 1986a, Harms 1997). Many habitat specialists have been discovered, but the percentage appears too low to play a primary role in supporting the high levels of alpha and beta diversity seen in the lowland forest (Hubbell et al. 1999).

Intermediate Disturbance Hypothesis

Levin and Paine (1974) and Connell (1978) suggested another pathway to high forest diversity in which the spatial extent and distribution of disturbance plays a critical role. This argument is referred to as the Intermediate Disturbance Hypothesis, and it suggests that a moderate level of environmental disturbance creates a mosaic of differing stand ages and regeneration conditions facilitating high species richness. A variation of the hypothesis (Ricklefs 1977) suggests that a relatively moderate disturbance regime creates a range of conditions for seed germination and thus promotes the establishment of a variety of species tailored to a range of micro-site conditions. Ultimately the Intermediate Disturbance Hypothesis relies on the notion that dispersal into temporally transient forest gaps is possible and that the resulting mixture of species works against the dominance of individual species. It is not clear whether or not the theory requires these gaps to be more diverse than the surrounding forest (Tilman 1999). Broadly speaking, the literature throughout the 1990s has emphasized the interplay of biotic control and gap-phase dynamics facilitated by intermediate disturbance regimes for the maintenance of forest diversity.

Climatic and temporal controls

Climatic variation acting over evolutionary time (*sensu* thousands to tens of thousands of years) provides a framework for the other processes discussed in this section. Unfortunately, discussions about the origin of tropical biodiversity are often partitioned by academic specialties in a way that makes it difficult to uncover key interactions between geology, climate, and ecology. Research about the origin of species diversity have often been divided narrowly along disciplinary lines: geologists, paleoclimatologists, palynologists, and their allies have unraveled the historical records; while, ecologists, botanists, and their kin have focused on identifying modern processes. No one denies the necessity of interaction between these specialties; however, the literature remains remarkably well compartmentalized. Historic points of cross-over have occurred (e.g., Haffer 1969, Simpson and Haffer 1978), but the process appears to be something more akin to punctuated equilibrium. Ecologists dip into the literature of Quaternary scientists, retrieve a nugget of information, and then return to their theories rooted, typically, in small domains of time and space. Perhaps the most synthetic argument to date integrating current paleoclimatic data with palynological evidence comes from Bush (1994). He proposed a complex evolutionary model where centers of endemism are generated as a result of repeated species sorting under fluctuating climatic conditions. This work builds on observations that tropical forests were still widespread during the Last Glacial Maximum, despite significant cooling. Evidence from pollen analysis suggests that these forests were organized in non-analogous community assemblages, that mixed modern lowland flora with more cold adapated species currently restricted to Andean areas (Colinvaux 1987). Other authors have suggested that non-uniform conditions with respect to precipitation (van der Hammen and Absy

1994) accompanying the cool conditions (Guilderson et al. 1994, Stute et al. 1995) and reduced CO_2 (Street-Perrot et al. 1997) promoted differential responses from forest taxa. This view holds that tropical forest communities are very loosely aggregated and transient across short periods of evolutionary time. The conclusion is that forest diversity is the result of frequent reshuffling of taxa across space under the influence of a cyclically changing climatic regime.

Biological Productivity

Another school of thought links species richness to variations in primary productivity. This theory focuses on the observation that species richness reaches its highest values on terrain with intermediate levels of biological productivity (Huston 1994). Rosenzweig (1996) notes that in either very unproductive (oligotrophic) or over-productive (eutrophic) environments the number of species declines. In oligotrophic environments, the absolute number of individuals present can decline while only the most stress resistant members survive. In some cases, harsh environments may not reduce the number of organisms, but rather the size of individuals may decline significantly. Eutrophic environments often produce a small group of species that dominate the community at the expense of overall diversity (e.g., algal bloom in a lake or monospecific stands of *Spartina alterniflora* in highly productive, but physiologically stressful, coastal wetlands). This theory suggests that high floristic diversity in tropical forests may result from the balance of favorable climatic conditions and frequently nutrient depleted soils, yielding net environmental conditions favorable for intermediate levels of productivity. This hypothesis is generally applied to global or hemispheric patterns in biodiversity; however, it may also be relevant to changes across regional environmental gradients.

Dispersal Limitation

Supply-side ecology is based on the notion that limitations in the ability of propagules to reach suitable environments for germination produces much of the variation seen in the realized distributions of species (Harms 1997). The potential implications of supply-side ecology and dispersal limitation are emerging as a potentially powerful mechanism for the maintenance of high species diversity in tropical forests and coral reefs (Hubbell 1997, Hubbell et al. 1999). Research on BCI in Panama has concluded that many Panamanian tree species are capable of growing and surviving significant distances from conspecific adults when transplanted as seedlings (Hamill 1986). Hamill concluded that habitat specialization was the exception and not the rule for the lowland forest. This work was continued was by Harms (1997) in an intensive analysis of seed trap data collected on BCI by S.J. Wright. Harms noted that the majority of tree species in the BCI forest did not appear in seed traps during 13 years of observation. Harms concluded that dispersal-limitation is likely to play a strong role in the distribution of individual tree species and, ultimately, community composition on BCI. Both studies suggest that the realized niche of the majority of forest tree species is heavily constrained by their ability to disperse into transient patches of available habitat before equivalent or inferior competitors become established. Hubbell et al. (1999) support this hypothesis with an extensive analysis of 1200 forest gaps in the BCI 50-ha plot collected over a 13 year period. They note that on a *per area* basis gaps are richer in species than surrounding forest, but when normalized by the number of stems, gaps are no richer than the original forest matrix. They contend that recruitment limitation negates the role of intermediate disturbance processes in maintaining tree diversity. Hubbell et al. (1999) conclude that dispersal limitation can decouple species richness from resource-based niches and allow arbitrarily large numbers of species to coexist in tropical forests. All of the dispersal limitation studies in Panama to date (Hamill 1986, Harms 1997, Hubbell et al. 1999) have been conducted over very small geographic areas within the already isolated forest on BCI. There remains a theoretical gap between the maintenance of high alpha diversity in the 50-ha plot and high beta diversity across the lowland landscape (see Condit et al. 1996c). Even if one accepts the importance of dispersal limitation in maintaining alpha diversity, this conclusion does not rule out the role (or even dominance) of any of the proceeding hypotheses across larger regions.

Synthesis

The six subsections above have only scratched the surface of a vast literature on the origin and maintenance of tropical biodiversity at a variety of scales. These factors are often considered in isolation, and one of the great challenges in contemporary tropical ecology remains the conceptual integration of these processes. A valid conceptual model for the maintenance of floristic diversity and patterns of floristic composition across a Neotropical landscape must incorporate processes acting, and interacting, over a wide range of spatial and temporal scales. Forest composition in small areas may be controlled through a combination of ecological dynamics (competition, seed-supply limitation, parasitism, and predator-prey relationships), edaphic constraints (microsite suitability, slope, and soil properties), and anthropogenic site history (selective cutting, human occupation, and cultivation). These local effects appear to be nested within first order environmental controls where variables including seasonal water balance, net evapotranspiration, and regional climatic conditions begin to play dominant roles. All of these contemporary processes are filtered through time as they act at different rates and vary in duration. Obviously, there is no single answer to the origin of Neotropical biodiversity, and I do not expect to find one operating in lowland Panama. During the rest of these thesis, we will explore the patterns of floristic diversity sampled in the Panama Canal watershed (Figure 1) and attempt to find clues to ecological processes in the details of floristic association and composition.

BIOPHYSICAL ENVIRONMENT

Climate

Daily temperature often remains relatively constant throughout the year for any given locality in tropical latitudes, and diurnal temperature variations are typically greater than the differences between seasons (see *Appendix A* for a set of meteorological and hydrological summaries from BCI). However, seasonal variation in cloud cover can significantly impact regional, and even local, radiation budgets. Given the *relative* constancy in temperature and radiation regimes, the physiognomy of tropical forests reflects the availability of moisture with corresponding shifts in floristic composition from broadleaf evergreen to seasonally deciduous and, eventually, thorn and shrub forests under the driest conditions. Central Panama experiences a pronounced dry season between approximately mid-December and the beginning of May, and its climate can be broadly classified by the Köppen system as Tropical Monsoon (Croat 1978). Monitoring stations on BCI indicate that on average only 230 millimeters of rain fall during the dry season. This comprises less than 9% of BCI's average total annual precipitation of 2650 mm (Paton 1996). The wet season lasts the remainder of the year and usually brings regular, heavy precipitation. The climate of lowland Panama is strongly coupled to regional and global processes, including El Nino/Southern Oscillation (ENSO) events in the Pacific Ocean (Condit et al. 1992b, Condit et al. 1995). The Caribbean coast receives the most even distribution of rainfall with the degree of seasonality increasing toward the south along the line of the Canal. Panamanians live in the breezy, drier climate of the Pacific coast where precipitation totals only around 1600 mm per year (~50% of the total for some higher elevation locations along the Caribbean coast).

Geology

Panama is a young and complex geologic terrain. The area surrounding the Panama Canal contains sedimentary and igneous rocks ranging in age from Quaternary alluvium to Mesozoic extrusive igneous material. The isthmus of Panama emerged as a land bridge in the mid to late Tertiary period. The final closure of the isthmus is indicated by isolation of the respective marine faunas approximately 3.5 million years ago (Coates et al. 1992). The isthmus is an area of convergence for a range of geologic processes. Western Panama and southeastern Costa Rica are believed to be influenced by active subduction and near-shore trench environments, while the Caribbean coast is more typical of a shallow, continental margin (Deboer et al. 1991). These processes have combined over geologic time to create an incredible variety of geologic substrates across the terrestrial environment.

Dietrich et al. (Dietrich et al. 1982) classify the rocks of the Panama Canal area as either dense, relatively impermeable volcanics or porous, chemically unstable sedimentary rocks and volcanic mudflow deposits. Early observers noted the presence of sedimentary rocks, including limestone, claystone and shales, as well as igneous rocks, including basalt, andesite, granodiorite, diorite, metabreccia, tuffs and rhyolite (Bennett 1929). Stallard (personal communication) has recently concluded that many geologic units previously classified as basalts are actually andesitic in composition. This correction was identified on BCI but it probably can be applied more generally. In Central Panama, prominent geomorphic features are usually isolated, conical or dome-shaped hills cored with dense volcanic material (possibly volcanic dikes intruded into the surrounding sedimentary material) (Woodring 1958). Additional volcanic material was extruded as lava flows providing a mantle of dense rock over sedimentary deposits. Dietrich et al. (1982) emphasize the role of repeated landslides in cycles of breaching, undercutting, and erosion that have removed most of the surficial basalt from lowland areas. On sedimentary rocks, rivers fed by heavy rains during the wet season carve deeply into weathered hillslopes, which then experience deep-seated landslides (Dietrich et al. 1982). The dense volcanic caps remain consolidated at depth, and consequently, landslides may remove just the soil mantle. The sum of these processes is a complex mosaic of geomorphic surfaces and unpredictable juxtapositions of geologic parent materials.

Soils

From the point of view of a soil scientist, a tropical forest can be described as a composite function of soil forming state factors (climate, organisms, topographic relief, precipitation, geologic parent material and time -- Jenny 1941) as they are expressed via plant growth, survival, and reproductive success (Baillie et al. 1987, Sollins et al. 1994). Rainfall and temperature control the intensity of leaching and weathering of soil minerals, and as a result play a significant role in determining soil chemical properties (Rowell 1994). Despite the long history of botanical work in lowland Panama (see Croat 1978), pedological studies have been minimal. Bennett (1929 in Croat 1978) reported a soil reconnaissance from the Canal Zone and immediately surrounding areas. Bennett (in Croat 1978) reported that the soils of BCI were red or deep red in color (slightly brownish in the uppermost 5 cm), well-drained, well-aerated, slightly acid to alkaline, and friable when moist. Kenoyer (1929 in Croat 1978) described the soils of the same area as “a chocolate brown alluvium underlain by a red subsoil arising from the decomposition of the Bohio sandstones and conglomerates.” Knight (1975 in Croat 1978) mentioned a second soil type on several parts of BCI: an impervious clay subsoil (a gley) with a gray appearance mottled with red. He contrasted this soil with the previously identified Frijoles Clay. Foster (1974 in Croat 1978) suggested that the past land use histories of individual localities have more of an impact on soil properties than parent material. The most cited publication devoting significant coverage to the soil and sediment environment on BCI is a book chapter written by Dietrich et al. (1982). The authors particularly emphasized the importance of soil characteristics in determining the moisture stress suffered by trees and other plants during the dry season. They note that weathering on BCI tends to penetrate several meters into the more porous sedimentary rocks, yielding clay-rich soils on both steep and gentle slopes. Dietrich et al. (1982) also note that the dense volcanics (such as the andesitic cap underlying most of the 50-hectare forest dynamics plot on BCI) form shallow soils that transition from dense, homogeneous clays on plateaus to stoney units on moderately steep slopes. Dietrich et al. (1982) go on to emphasize a myriad of details concerning the dynamics of soil and sediment supply, but they do not provide any additional information relating soil properties to ecological processes. Recent literature and data have been oriented toward geological or sediment budget applications (e.g., Johnson and Stallard 1989), which have limited applications in ecological investigations. The ecological influence of pedologic properties across forested tropical landscapes is largely unquantified, and it is an important frontier in future research in tropical ecology (Vitousek et al. 1997, Sollins 1998).

A substantial body of research indicates a link between soil factors and forest composition in tropical regions (e.g., Huston 1980, Huston 1994, Oliveira-Filho et al. 1994, Rosenzweig 1995, Sollins 1998). A review by Sollins (1998) indicated that the most important soil properties in lowland rain forests include (in decending order of importance): P availability, Al toxicity, drainage, water-holding capacity, and availability of K, Ca, and Mg. These factors are often combined as indices of soil fertility (e.g, Huston 1980) and used as predictors of potential site productivity.

Huston (1994) notes that soil factors and precipitation are not independent variables. Precipitation can directly meet plant demands for water or act indirectly mediated through soil formation and the extent of nutrient leaching. Increasing precipitation inputs raise weathering rates and release more nutrients from the parent material. Simultaneously, precipitation and leaching rates are directly related and both processes are accelerated at high temperatures (Jenny 1941). Seasonal precipitation regimes like the one in Panama differ from the intense, continuous leaching regimes experienced in less seasonal climates. Even brief dry periods create pulses of nutrient availability and significant changes in soil water availability. Preliminary work (Orians et al. 1996) has suggested that increasing dry season length corresponds to increasing fluctuation in soil microbial populations and nutrient release. Orians et al. (1996) also note that the interactions between these systems in tropical ecosystems is poorly understood and in need of further research.

Vegetation

The climate, geology, and soils define a broad environmental niche that sustains a rich tropical flora. The Panamanian forest is one of the best researched and documented in the world. This is thanks in large part to the nearly century long effort of the Smithsonian Tropical Research Institute (STRI). Investigations of the flora of lowland Panama have recorded a remarkable level of species richness and ecological complexity. Croat (1978) identified 450 species of trees and shrubs on BCI. A computerized flora published by the Missouri Botanical Garden indicates that the Panama Canal Area contains 855 (1,259 km^2) native species of trees and shrubs, while the entire Republic of Panama (77,000 km^2) contains an estimated 2870 species (Condit et al. 1996c, Condit 1996). Croat (1978) presented a map of Holdridge Life-Zones (Holdridge et al. 1971) for Panama prepared by the United Nations Food and Agriculture Organization (FAO) (Figure 2). Based on this information, the Panama Canal watershed is dominated by tropical moist forest at low elevations (i.e. around the Canal and Gatun Lake) flanked by bands of premontane wet forest and tropical wet forest at the highest elevations. In a separate map the UN FAO indicates three regions of climatic influence within the watershed, including: (1) northern areas under Atlantic-Caribbean influence where the dry season is “absent”, (2) a transitional area of Atlantic-Caribbean influence with “normal” dry season length, and (3) a southern area of Pacific influence, again with “normal” dry season length. If overlain on the Life

Zone map, all three of these precipitation areas would occur within the tropical moist forest zone. Croat (1978) noted that the Holdridge Life-Zone system appeared adequate, in part because no competing, alternative classification of Panama had been developed.

STRI has provided institutional support for a large body of research centered on and around the BCI field station (see Leigh et al. 1982, 1990). Recent ecological work has been centered on the 50-ha Forest Dynamics Plot (FDP) run by the Center for Tropical Forest Center (CTFS). The FDP is a prototype for an international network of large forest monitoring plots in more than a dozen tropical countries. The 50-ha plot has been the subject of intense research since its establishment in 1982 by Stephen Hubbell and Robin Foster (Hubbell and Foster 1983). The 50-ha plot allows detailed examination of local scale patterns of distribution, population demographics, and biotic and edaphic controls on individual species (e.g., Hubbell and Foster 1986b, Hubbell and Foster 1986a, Hubbell et al. 1990, Gilbert et al. 1994, Obrien et al. 1995, Condit et al. 1995, Condit et al. 1996c, Stacy et al. 1996, Wills et al. 1997, Dalling et al. 1998a, Hubbell et al. 1999). It is interesting to note that while the 50-ha plot was originally selected for its environmental homogeneity, many research projects have focused on questions of habitat specialization and vegetation-environment relationships (see Harms 1997 for a review).

Summarized briefly, work on BCI indicates a complex and dynamic forest with high alpha diversity. The composition of the forest responds quickly to climatic forcing, such as drought related to El Nino events (Condit et al. 1995). Seeds are dispersed by a variety of mechanisms, but the majority of canopy species are seriously underrepresented in long-term seed trap data. Some species utilize specialized symbionts for fertilization (e.g., *Ficus spp*. and parasitic wasps) or defense (*Acatia spp*. and resident ants). Based on the intensive research completed to date (see Leigh 1996), it is reasonable to believe that distribution and abundance of individual species is regulated through a complex combination of factors, including inter- and intra-specific biotic factors (Hubbell et al. 1990, Condit et al. 1994, Wills et al. 1997), treefalls and disturbance processes (Brandani et al. 1988, Dalling et al. 1998a, Hubbell et al. 1999), dispersal limitation (Hamill 1986, Harms 1997, Hubbell et al. 1999), and habitat specialization (Hubbell and Foster 1982, Harms 1997).

The depth of ecological information on BCI is in sharp contrast to the paucity of information about areas and biota across the isthmus. Ecological studies in Panama have traditionally been closely linked to established research stations. The testing of theories across broad geographic regions is emerging as a key direction for future research, and new efforts, including this one, will expand on fundamental information collected at these bases. The set of 1-hectare plots (Figure 3) developed by Condit (in press) and analyzed for this study will provide important baseline and reference information for planning future studies and testing existing hypotheses.

METHODS

Overview

This project utilized a suite of multivariate vegetation analysis techniques including classification through agglomerative, hierarchical clustering and gradient analysis using Detrended Correspondence Analysis (DCA) and non-metric multidimensional distance scaling (NMDS). Additional procedures included the evaluation of forest composition across multiple levels of taxonomic organization, analysis of floristic nestedness, description of species-area relationships, and preliminary field observations on soil characteristics. These procedures provided detailed information about large-scale floristic organization, compositional responses to environmental gradients, and the potential for site attributes (e.g., soil) to control local forest composition.

Vegetation and soil data

i. Vegetation data

Dr. Richard Condit and his colleagues at the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute provided the floristic data for the following analyses. This exceptional data set resulted from a multi-year effort combining the talents of Smithsonian scientists, local experts, and an extensive crew of skilled botanists. Dr. Condit’s group established a network of 31 small (1-ha) forest monitoring plots to supplement an established set of three large permanent plots (4, 5, and 50 hectares). The 50-ha plot was described earlier as the 50-ha forest dynamics plot on BCI. Six plots were selected from the forest dynamics plot to represent end-members of the environmental and seral conditions found at the site, including: young forest, slopes, low plateau, and high plateau. The 4-ha plot ("Cocoli") was subjectively placed in a relatively young forest on an U.S. military reservation near Panama City. The 5-ha plot ("Fort Sherman") was established in conjunction with the Smithsonian’s canopy crane installation near the Atlantic entrance to the Panama Canal. These intensively studied localities provided anchors for the network of smaller 1-ha plots spread along the climatic gradient. The specific codes used to reference each plot are detailed in Table 1.

Land conversion in the Canal watershed has reduced the remaining forest to a narrow strip bordering the Panama Canal with larger forest blocks around the edges farthest from population centers. This constraint kept the majority of the 1-hectare plots either close to the Panama Canal in lands historically managed by the U.S. military or relatively high up in the headwaters. This pattern of plots established a gradsect (Gillison and Brewer 1985) arrangement with multiple samples along the known climatic gradient between Panama City and Colón.

At each site, workers established 100 x 100-meter square relevés demarcated by regular grids of white PVC poles at 20-meter intervals. All trees greater or equal to 10-cm diameter at breast height (DBH) were identified to species, tagged, and located with respect to the local grid. Additional data were collected from a nested 40 x 40-meter area for stems equal to or greater than 2 cm DBH. These smaller stems were excluded from this analysis, although they hold promise for future research. The field workers noted the elevation of each site on topographic maps (U.S. National Intelligence Mapping Agency, 1:50,000) and characterized the surrounding terrain as flat, sloping, or irregular. In cooperation with Dr. Condit, the field botanists rated the age of each plot as young, intermediate, or old growth. The field crews located each sampling location by surveying back to the plot grid from Global Positioning System (GPS) coordinates received in available forest gaps. The protocols used for field work and data entry are documented in detail elsewhere (Condit 1999). The watershed analyses described below considered data from all the 1-ha monitoring plots, both the Cocoli and Fort Sherman large plots, and from six hectares of the 50-ha forest dynamics plot on BCI. The "Canal

Area" analysis was restricted to the 45 plots within forested area immediately adjacent to the Panama Canal.

Table 1: Conventions used for identifying individual plots in Figures .

Prefix code	**Explaination / Geographic Extent**	**Values**	**Comment**
b-	sub-sampled from the 50-ha forest dynamics plot on BCI	6 plots with designations blp = low plateau, bhp = high plateau, bs_n = slope, by_n = young forest	A subset of plots from the BCI forest dynamics plot
c-	4-ha comprising the Cocoli plot	c1-c4	Young forest near the Pacific entrance to the Canal
L-	Across the isthmus	L1-L4	Lands managed by the US Department of Defense
m-	Across the isthmus	m5-m39	Plots coordinated with the PMCC project
s-	Fort Sherman on the Caribbean Coast	s0-s4	Beneath Ft. Sherman canopy crane near Gatun Locks

ii. Soil sample collection

Soil profile description and sample collection was conducted in a number of the monitoring plots between September 10 and September 21, 1998. The primary goal was not to perform a complete soil survey, but rather to collect information on local and regional variability in soil properties useful in planning a more comprehensive soil sampling exercise.

The goal of the sampling was to capture a representative soil profile for each plot surveyed. It was appreciated from the start that the summary of soil environments for 1-hectare areas covered in dense jungle is usually impossible with a single soil pit. However, I did not have time to pursue multiple pits at the single hectare locations and future surveys might consider making repeated collections with a mud auger. Further, without guidance from previous research, I had no way of estimating the variability to be expected within and between sites. Without such information, it was impossible to make informed estimates about the amount of sampling required to make confidence estimates of mean site properties. I attempted to select pit locations that best represented the majority of the terrain in the plot. All pits were dug along the perimeter of the plot to minimize the disturbance to vegetation within the inventoried area. The location of each pit was referenced to the nearest PVC stake.

The large multi-hectare plots were treated differently. Rather than collecting a single profile from each constituent hectare, I collected three samples in regular slope positions. The goal was to capture some degree of the intra-site variability occurring as a function of soil catena formation. I dug pits in the summit, backslope, toeslope, and, in several instances, floodplain slope positions at BCI, Cocoli, and Fort Sherman.

After selecting the pit location, our procedure at each pit was consistent throughout our sampling. First, I scraped away the litter layer while protecting one side of the pit for photography.

Next, I dug out the pit using shovels, a pickaxe, and a geological hammer with a scoop blade. The dimensions of the pits averaged 65 cm in depth, 100 cm in width, and 150 cm in breadth. The working face generally consisted of a 60 x 100-centimeter surface. A standardized set of measurements and observations were taken from each horizon identified, including: thickness, Munsel color, nature of horizon boundaries, hand texture, percent clay, rock fragments, consistence, structure, root size and abundance, pH, and electrical conductivity. Additional site characteristics with regard to slope, aspect, geomorphology, outstanding vegetation attributes (e.g., nature of the litter layer), and ancillary notes were recorded. Two soil samples were collected from each pit at depths of approximately 10 cm and 40 cm. The samples were bagged and kept refrigerated until they were air dried under cool, low humidity conditions. The air-dried soil samples were analyzed for pH in a 1:1 solution with deionized water.

Watershed floristic patterns

i. Cluster analysis of floristic composition within the Canal Watershed

Two methods were used in parallel to explore primary floristic features in the 54 plot watershed data set. The first was hierarchical, polythetic, agglomerative cluster analysis performed by the vegetation analysis package, PC-ORD (version 3.18, McCune and Mefford 1997). PC-ORD's CLUSTR subroutine proceeds by joining groups (in this case composed of plots) based on a multivariate (polythetic) membership function defined by the user (McCune and Meffort 1997). The result is an illustration of relationships called a dendrogram where large clusters are composed of smaller elements across dichotomous junctions. The success of a cluster operation is measured to some degree by the amount of chaining in the resulting set of relationships (Gauch 1982, Greig-Smith 1983). Chaining refers to the sequential addition of small groups to one or a few large groups and is controlled by the choice of linkage strategy (McCune and Meffort 1997). The "worst-case" of chaining produces a dendrogram where each successive fusion involves the addition of only a single item (i.e., plot) to a single, increasingly large group. As recommended in PC-ORD, an index of chaining was used to initially screen the results of a variety of linkage strategies. Chaining varied from 25% for nearest neighbor linkage to 2% for Ward's Method for the 54 plot data set.

ii. Ordination of 54 1-hectare plots within the Canal Watershed

The second parallel method applied to the data set utilized non-metric multidimensional scaling (NMDS). This technique was developed in the psychological research community to handle data that violate the assumptions for the behavior of variables in other multivariate models. The NMDS ordination provided an alternative tool for visualizing the structure of the plot-by-plot floristic distance matrix. NMDS imposes few conceptual requirements on multivariate data, and, in this instance, it appeared to produce robust, interpretable two-dimensional representations of the 54 plot data set. NMDS is fundamentally different than techniques based on either partitioning of variance or iterative ordination of plots and species (Gauch 1982, Beals 1984, Minchin 1987). NMDS addresses the problem by first creating a square (n x n) matrix of similarities between elements in the data matrix, and then attempting to develop a k-dimensional space (where k is the number of synthetic axes calculated) that preserves ranked distance relationships between elements. Non-metric multidimensional distance scaling axes do not have priority with respect to possible correlations with extemal variables; i.e. the NMDS axis 1 does not necessarily correspond to the dominant gradient. Furthermore, solutions for different numbers of dimensions are not equivalent. This means that axis scores in a six dimensional solution are not the same as those from two or four dimensional procedures. The success of the NMDS routine is partially gauged by a measure of stress that indicates the departure from monotonicity in the relationship between dissimilarity (distance) in the original p-dimensional space (where p is the total number of species or plots samples) and distance in the reduced *k*-dimensional ordination space (McCune and Mefford 1997). Environmental variables play no direct role in the calculation of axis scores, and subsequent correlations with environmental parameters must be based on independent analyses.

Prentice (Prentice 1977) notes that NMDS is a good choice for applications with high beta diversity and noisy environmental information. These requirements are well met in lowland Panama. The presence of exceptionally high beta-diversity in these data was obvious since only 14 species out of over 300 species of large trees can be found across the isthmus despite superficially similar forest structure (e.g., canopy closure, stem density, etc.). Persistently low spatial autocorrelation in precipitation measurements between established meteorological stations highlights the strong potential for environmental "noise" in interpolated values (Rand and Rand 1996). McCune and Meffort (1997) further note that NMDS is valuable for data that are non-normal or on somehow arbitrary or questionable scales. These requisites can sometimes be accommodated with appropriate transformations, but the assumption of normal or Gaussian species distributions is not a clear and necessary *a priori* conclusion. Multivariate tools assuming gradient dynamics (*sensu* Whittaker 1967, e.g., Reciprocal Averaging) provided uninterpretable representations of the 54-plot data set. However, as will be illustrated in the next section, these tools were much more successful when applied to the restricted set of 45 plots along the Panama Canal.

The Sorensen distance measure (see Jackson et al. 1989 for a comparison with other indices) was used for all analyses. The use of the Sorensen coefficient considers only species presence-absence, while weighing joint occurrences twice that of individual absences. The Sorensen distance coefficient ignores joint absences. This metric was considered appropriate given the lack of repeated samples along the gradsect. With such limited data, it is doubtful that there are grounds for confidently estimating relative abundance at any given location for the majority of species, and it seemed more appropriate to hold the data to only a presence-absence level of analysis.

iii. Tests for spatial structure

The complexity of the indirect gradient analysis suggested the need for an independent test of relationships within the data set. Additionally, I wanted to evaluate possible spatial autocorrelations between similarity scores and the geographic locations of the plots. The standard technique for detecting these relationships in multivariate vegetation data is the Mantel test for correlation between matrices (Sokal and Rohlf 1995). The Mantel test is becoming a popular tool for phytosociology (Sokal 1979, Douglas and Endler 1982, Lefkovitch 1984, Smouse et al. 1986, Burgman 1987, Sokal and Rohlf 1995). The standard technique involves comparing a similarity distance matrix (e.g., Sorensen distance) with a distance matrix for environmental variables (e.g., plots at 2400 mm/yr. and 3600 mm/yr. respectively would be separated by 1200 mm/yr. in mean annual precipitation). The test then evaluates the magnitude and direction of relationships between the two matrices. Environmental variables can then be tested in a step-wise manner to characterize the vegetation-environment relationships. Positive aspects of the Mantel test approach include: tractable statistical considerations, familiar confidence limits, and ease of use. On the other hand, the Mantel test is a rather blunt instrument for detecting relationships between matrices and many less obvious relationships could be missed. It is also not possible to directly analyze the composite effects of multiple explanatory variables.

In this case, I examined potential correlations between distance in geographic space and distance in non-metric multidimensional distance scaling ordination space. An environment that is strongly spatially structured will reflect a strong positive correlation between distance in geographic space and distance in similarity space. All 54 plots in the Canal watershed were included in this analysis. The hope was to offset the weight of the known precipitation gradient (where change with distance was expected) and introduce plots orthogonal to the direction of change within the Canal Area.

The analysis was conducted on two square 54 x 54 plot distance matrices using the Mantel test option in PC-ORD. Two primary options are available for the test, (1) Mantel's asymptotic approximation, and (2) a Monte Carlo randomization method. The former method is a statistical test based on a t-distribution with infinite degrees of freedom. The t-value generated is greater than zero for positive associations and less than zero for negative associations. Ultimately, the product of the asymptotic approximation method is a standardized Mantel statistic, r, that can be used as the equivalent of a Z-value in a test of significance (McCune and Mefford 1997). For these tests, the null hypothesis was that there is no correlation between the distances in the two matrices. The rejection region was defined as in Student's t-test with ? = 0.05. Based on the sign of the test output, the alternative hypothesis states either a positive or negative correlation between the matrices.

Gradient dynamics along the Panama Canal

The analysis of gradient dynamics contained several components:

- Interpolation of precipitation values for each plot and description of additional site variables for geology and stand age.
- Indirect gradient analysis of 45 Canal Area plots and correlations with environmental variables
- Indirect gradient analyses for species, genus, and family levels of taxonomic organization

i. Interpolation and estimation of environmental parameters

(a) Precipitation Interpolation

Ideally this section would be titled modeling annual spatial and temporal changes in water availability and moisture stress across the Panamanian isthmus; however, that topic could provide work for an entirely new thesis. It is fully recognized that plants do not respond directly to incoming precipitation *per se*, rather they are individual moisture integrators with specific physiological tolerances. The parameter "incoming precipitation" is passed through a complex and probably non-linear series of filters before being manifested in biotic responses. Confounding elements may include: watershed area, soil drainage, soil moisture holding ability (primarily a function of both particle size distribution and organic matter content), rooting depth, phenology, and a myriad of species specific tolerances. Despite these potential complications, a gradient in precipitation is the most obvious environmental change occurring from the Caribbean to Pacific sides of the Panamanian isthmus. The over-riding facts are inescapable: the city of Colón receives over 3000 mm of rain annually, while only 50 kilometers away Panama City totals less than 1800 mm. What happens in-between these points, and how this is manifested in terms of moisture availability are matters of significantly more conjecture. I will continue the analysis by making the simplifying assumption that two parameters can characterize moisture availability across the isthmus: (1) total annual precipitation, and (2) total dry season precipitation (December-May).

Total annual precipitation was interpolated with several linear regression models. The objective was to provide an interpolation of rainfall totals at each monitoring plot location based on their geographic coordinates and site elevation. Given the available station data and the lack of ancillary information, it seemed dubious to attempt to develop interpolations for the plots at the fringes of the Canal Watershed.

The linear regression model used to predict total annual precipitation used geographic coordinates (Universal Transverse Mercator coordinates x,y) and elevation (meters above mean sea level) from 20 meteorological stations scattered within the watershed. The model is described below:

Annual precipitation model

total annual ppt (mm/yr) = -17543.7 + -0.0055(UTM x) + 0.023(UTM y) + 1.3775(elevation, meters)

```
Coefficients:
                    Value  Std. Error     t value    Pr(>|t|)
   (Intercept) -17543.7072   3537.6713     -4.9591      0.0001
          utmx     -0.0055      0.0027     -2.0605      0.0560
          utmy      0.0230      0.0031      7.4948      0.0000
     elevation      1.3775      0.3254      4.2334      0.0006

Residual standard error: 200 on 16 degrees of freedom
Multiple R-Squared: 0.901
F-statistic: 48.52 on 3 and 16 degrees of freedom, the p-value is
2.952e-008
```

This model appears to be a good fit with three significant coefficients at the ? = 0.05 level. The UTM x term is weaker (p-value = 0.0560) than the UTM y and elevation terms (p-value << 0.01); however, the precipitation gradient seems to have a maximum slope along a northwest-southeast trend. Consequently, it makes physical sense to keep the variable in the model. Figure 5 illustrates precipitation isohyets interpolated with a spline fit from the original set of monitoring stations (marked in red).

All precipitation is not 'created equal' as far as trees are concerned. It may be in excess during the majority of the year, but during the dry season it could become a critically limiting resource. The Panamanian dry season typically lasts between December and April. Annual precipitation accumulation curves for the 20 meteorological stations in the Canal watershed indicate that the maximum departure between the individual stations occurs at the end of May. Based on this observation, I chose to model the average total accumulation of precipitation received between December and May as an index of dry season severity. Figure 6 maps the approximate distribution of dry season precipitation (December-May) across the isthmus. Although, cumulative May precipitation is positively correlated with total annual precipitation ($p < 0.0000$, r-squared = 0.6817, df

=18), the spatial distribution of the precipitation appears to vary. The dry season precipitation interpolation model is detailed below:

```
Cumulative May precipitation model

May ppt (mm) = -1463.8 + -0.0005(utmx) + 0.0019(utmy) +
0.1148(elev)

Coefficients:
                 Value Std. Error    t value   Pr(>|t|)
(Intercept) -1463.7635   295.3134    -4.9566     0.0001
       utmx    -0.0005     0.0002    -2.0699     0.0550
       utmy     0.0019     0.0003     7.4955     0.0000
       elev     0.1148     0.0272     4.2265     0.0006

Residual standard error: 16.7 on 16 degrees of freedom
Multiple R-Squared: 0.9009
F-statistic: 48.46 on 3 and 16 degrees of freedom, the p-value is
2.977e-008
```

The two models are very similar, and given the limited amount of station data and plot parameters it is difficult to justify more elaborate interpolation equations. Both precipitation parameters were used with care in subsequent analyses, because any index of meteoric moisture availability is a relatively crude statistic with many possible, highly correlated alternatives (e.g., days where evapotranspiration exceeds precipitation, months with less than 100 mm total precipitation, etc.). Each measure provides a rough correlation with water availability.

(b) Geologic Information

All information regarding surficial geology is based on the USGS geologic map of the Panama Canal and vicinity published in 1980. The map was drawn to a scale of 1:100,000 and digitized as a part of the US Agency for International Development's (USAID) Project to Monitor the Watershed of the Panama Canal (PMCC). Personal observations in the field and the opinions of experienced researchers indicate that the accuracy of the map is best close to the Canal and deteriorates toward the edges of the watershed (J. Wright, personal communication). Nine different mapped units are represented in the 54 1-hectare monitoring plots, and specific information for each unit represented is summarized in Table 2.

Table 2: Summary of geologic information for each plot. The dummy variable "geo" was used in subsequent analyses, and it can be linked to geological information via the analysis code in column 3.

Unit Name	*Map Code*	*Analysis Code*	*Geologic Series*	*Approx. Age (Stage)*	*Description*
Chagres Sandstone	Tc	4	Late Miocene or Early Pliocene	10 mya (Lower Tortonian) to 3.5 mya (Upper Zanclean)	Massive, generally fine grained sandstone
Toro Limestone (basal member of Chagres Sandstone)	Tct	6	Late Miocene or Early Pliocene	10 mya (Lower Tortonian) to 3.5 mya (Upper Zanclean)	Coquina
Miocene basalt	Tb	2	Middle to Late Miocene	16.2 mya (Lower Langhian) to 5.0 mya (Upper Messinian)	Intrusive and extrusive basalt
La Boca Formation	Tl	8	Early Miocene	25.2 mya (Lower Aquitanian) to 16.2 mya (Upper Burdigalian)	Siltstone, sandstone, tuff and limestone
Las Cascadas Formation	Tlc	9	Early Miocene	25.2 mya (Lower Aquitanian) to 16.2 mya (Upper Burdigalian)	Agglomerate and tuffaceous siltstone, tuff, and foraminiferal limestone
Caimito Formation	Tcm	5	Late Oligocene	30 mya (Lower Chattan) to 25.2 mya (Upper Chattan)	Tuffaceous sandstone, tuffaceous siltstone, tuff, and foraminiferal limestone
Bohio Formation	Tbo	3	Early to Late Oligocene	36 mya (Lower Rupelian) to 25.2 mya (Upper Chattan)	Conglomerate, principally basaltic and graywacke sandstone
Gatuncillo Formation	Tgo	7	Middle to Late Eocene	54 mya (Lower Ypresian) to 36 mya (Upper Priabonian)	Mudstone, siltstone, quartz sandstone, algal and foraminiferal limestone

Pre-Tertiary basalt	pT	1	Pre-Tertiary	Older than 66.5 mya (Mesozoic)	Altered basaltic and andesitic lavas and tuff, includes dioritic and dacitic intrusive rocks

(c) Stand Age

Tropical trees usually do not produce interpretable growth rings in the fashion of their temperate counterparts (Mabberley 1992). This restriction makes the direct determination of stand ages problematic. This information is critical in determining the ecological and seral context for a given parcel of land. My investigation relied on the observations and experience of the Smithsonian's field workers and Dr. Condit to estimate the relative ages of monitoring plots. The estimation was primarily based on the structure (e.g., abundance of large diameter trees) or floristic composition (e.g., species characteristic of secondary forest), and the potential for circular logic is appreciated. Accurate, quantitative estimation of stand age is an issue for future research.

ii. Indirect gradient analysis of the Canal Area plots

The parameters controlling the distribution of organisms are unknown and frequently the target of study during ecological investigations. Phytosociologists have developed techniques for the description of changes in community organization over presumed environmental gradients (ter Braak 1986). These techniques attempt to place samples (plots) in order along an axis (or set of axes) of environmental change. Direct gradient analysis is usually applied to situations where a single known environmental control is well documented and used to describe observed responses in a plant community. More typically, we do not know the most important controls on plant communities. In this case, indirect gradient analysis is used. During an indirect analysis, multivariate statistical tools are used to order samples based on some metric of similarity. The goal of indirect gradient analysis is to organize the plots in such a way that the relationship between environmental controls and composition become easier to identify. Measures such as the strength of indirect axes are evaluated by measured by eigen-analysis or the correlation of measured environmental values with derived axis scores are used as evidence for controls on floristic composition.

The well-documented climatic gradient between Colón and Panama City provides the primary backdrop for the continuously changing flora of lowland Panama. I chose two complimentary indirect gradient analysis tools to describe the changes in forest composition among the 45 Canal Area plots: Detrended Correspondence Analysis (DCA) and non-metric multidimensional distance scaling (NMDS). These two techniques handle multivariate data very differently. DCA is a widely used technique based on simultaneous ordering of plots and species called reciprocal averaging. Essentially, this technique establishes a gradient of composition and seeks to iteratively subdivide the data into species and plots that are either preferential to one side of the gradient or the other. The technique assumes that individual species occur with patterns of unimodal, Gaussian response along the derived environmental axes.

I have discussed the mechanics of NMDS in an earlier section (see *Methods ii. Non-metric multidimensional distance scaling of 54 plots in the Canal Watershed*), and it is sufficient merely to point out that the key differences from DCA. NMDS attempts to place plots in the appropriate rank order of similarity in a two-dimensional ordination space, rather than pulling plots apart along a set hierarchical set of axes. Additionally, NMDS only considers one type of data (plots or species) during a given ordination, while DCA considers both simultaneously. In practice, these techniques produce similar output: two or more values for each plot describing its position in ordination space relative to the rest of the constellation of plots.

Since there are no clear and necessary relationships between the original, equally important NMDS axes, I made the following assumptions for further analysis: (1) Variation in the NMDS scores corresponds to environmental factors. (2) The longest axis that can be fitted to the cloud of NMDS points will correlate with the strongest environmental gradient. (3) Additional environmental variables, site history, and biotic interactions may explain higher order variation. This interpretation allows correlation between a pure indirect gradient analysis (i.e., the NMDS scores) and measured environmental variables. To accomplish this analysis, I performed a principal components analysis (PCA) with a variance-covariance cross-products matrix on the NMDS scores for the 45 Canal Area plots. With only two NMDS axis scores, the entire data set was described completely with two principal components. The PCA operation served to center the NMDS scores, rescale them to a zero mean, and insert a set of orthogonal axes that best fit the data. The PCA also provided information about the amount of variation described in each component and allowed direct comparison of environmental variables with axis scores -- in this case, loadings on the two principal components.

iii. Ordination of tree species, genera, and families

The difficulty of species level taxonomy with typically only sterile plant specimens is daunting, and some authors have evaluated coarse patterns of forest composition using families instead of species (Terborgh 1997). The Canal area data set provides an opportunity to examine the way in which different taxonomic groups respond to a resource gradient. The Canal area rainfall gradient was evaluated across three levels of taxonomic organization: species, genus, and family. DCA was selected as the primary analysis tool as I was interested explicitly in gradient dynamics, and measures of compositional turn-over and relative axis strengths were important. The species-by-plot abundance matrix used in the analyses discussed above was reaggregated to each taxonomic level, and two new matrices were created for genera-by-plot and families-by-plot. Downweighting rare taxa was considered for each matrix; however, it did not produce noticeable changes in the ordinations.

Floristic nestedness

A significant question in ecology is the development of biological diversity over resource gradients (Huston 1994, Rosenzweig 1997). Part of the debate concerns the nature of the increase in the number of species in resource rich areas. One hypothesis assumes that the accumulation of species along a gradient involves the addition of relatively narrowly adapted species to rich, productive sites with fewer limiting resources (Cutler 1994, Boecklen 1997). The hypothesis holds that as resources (e.g., precipitation) decline along a gradient species richness will decline as weaker competitors and those with narrow environmental tolerances are removed (Wright and Reeves 1992). Ultimately, the poorest sites on the gradient will be populated by hearty generalists that are a subset of the richest localities (Worthen 1996, Boecklen 1997). Nestedness analysis software (NestCalc) developed by Atmar and Paterson (1992) was used to examine nesting relationships within the 45 plot Canal Area plots. Limitations with the NestCalc program restricted the analysis to the 192 most abundant species in the 45 Canal Area plots. The program performs two primary tests. First, it performs a procedure to optimally pack the species-by-plot matrix. This packing involves shuffling the table until the plot containing the majority of species is at the top and the remaining plots are ranked beneath it in order of decreasing nestedness. According to Atmar and Paterson (1992), this program creates the best nested hierarchy possible for the given species-by-plot table. The program also performs a series of Monte Carlo simulations on the packed matrix. The goal is to determine if the matrix is significantly more nested than would be expected by chance alone. Atmar and Paterson (1992) developed an index of matrix temperature to represent that degree of nesting. Low temperatures are typical of highly nested systems, while high temperatures characterize, "disorganized" non-nested systems.

RESULTS

The key results generated from this investigation are summarized in the bulleted paragraphs below.

- The Panama Canal watershed contains a strongly spatially structured tree flora with high beta-diversity. Primary floristic differences at the watershed scale appear to be well correlated with established Holdridge Life Zones.
- Tree composition within Holdridge Life Zones appears to be highly variable and dominated by the trans-isthmian climatic gradient. In some situations, soil attributes can take priority over local precipitation conditions and generate distinctive tree compositions.
- The climatic gradient is strongly expressed through the composition of individual tree species. Tree families are relatively well mixed across the isthmus and do not exhibit strong gradient patterns.
- Floristic nestedness is low along this resource gradient as species turnover very rapidly across the isthmus.
- Opportunities for increasing relative rates of tree species accumulation within a given geographic area with knowledge of local soil conditions, floristic assemblages, and geographic setting (e.g., distance between reserves).

Watershed floristic patterns

Both agglomerative, hierarchical cluster analysis (Figure 7) and NMDS analysis (Figure 8) suggest that plots in locations around the edges of the Panama Canal watershed have very low coefficients of similarity with those immediately along the line of the Canal. Visual inspection of two-dimensional NMDS scores for the complete set of 54 plots indicates a long cloud of points stretching from the dry sites at Cocoli to the wet Caribbean plots at Fort Sherman with a more diffuse group containing the outer watershed plots stretching off along a second axis. Cluster analysis (Ward's Method of agglomeration with Euclidean distance measures for 54 plots, chaining = 2.05) created a dendrogram indicating that the first major subdivision of the data separates plots on the wet and dry ends of the isthmus, and the next division isolates all of the outer watershed plots (specifically m31 through m39). It is noteworthy that the clustering and NMDS results compliment each other as the classification routine considered species frequency (Euclidean distance measures) while the NMDS solution was based on presence-absence (Sorensen similarity coefficients). These preliminary data suggest that plot composition immediately adjacent to the Canal vary along local ecological gradients, while broad floristic associations across the watershed are more associated with bioclimate as indicated by Holdridge Life Zones.

i. Spatial Structure

The Mantel test indicated an association between geographic distance and floristic similarity. Both the asymptotic approximation method (t-value = 8.282, p-value = 0.0000, infinite degrees of freedom) and Monte Carlo simulations (1000 trials, $Z_{observed} >> Z_{average}$, p = 0.001), indicate that the positive association is highly significant. The Monte Carlo results indicated that the observed *Z* score was much greater than the expected score generated from an average of the randomized trials. This result supports a strong positive relationship where floristic distance (1-Sorensen similarity) increases directly with increasing geographic separation.

ii. Species accumulation across the watershed

Condit et al. (1996) performed a series of species area calculations for tropical forests, including lowland Panama centered on BCI. They suggest that species area curves should show a pronounced increase in slope when moving from one Life Zone to another. A species area curve of the Canal Area plots (Cocoli to Fort Sherman) indicates a rapid increase followed by a long, slowly rising trend in species accumulation regardless of the order in which the plots are added (Figure 4). If the outer watershed plots are added to the end of the mainline species area curve, again in any order, the slope increases dramatically indicating the accumulation of many new species. The sudden change in slope between these curves is indicative of a demonstrable change is rates of species accumulation, i.e., the outer watershed plots contain many species not found along the Canal. For comparison, the 50-ha plot on BCI contain 303 species, when combined the 45 1-ha Canal area plots contain 417 species, and the addition of only 9 more hectares from the outer watershed plots increases the total to 821 species.

Gradient dynamics along the Panama Canal

i. Ordination of the 45 Canal Area plots

A strong environmental gradient well correlated with climatic indices was identified in the 45 Canal Area plots. This observation was supported by both DCA and NMDS. The application of Principle Components Analysis to center the two-axis NMDS scores provided information on the structure of the data. Table 3 illustrates the dominance of the first axis in explaining NMDS variation among the plots. Results from DCA support the NMDS ordination by indicating a strong, first axis eigenvalue of 0.7 for the 45 plots. The results compliment each other as the DCA provides a measure of species turn-over and axis length; while, the NMDS ordination provides better separation between plots in the ordination space and more potential for identifying secondary contributing factors (e.g., geology).

Table 3. Variance extracted from the first two axes of PCA on NMDS scores for 45 Canal Area monitoring plots (PC-ORD, version 3.18).

Axis	Eigenvalue	% of Variance	Cumulative % Of Variance

1	36.07	80.15	80.15
2	8.93	19.85	100.00

ii. Environmental correlations with indirect floristic gradients

The centered NMDS axis scores were correlated with the continuous, quantitative environmental variables, including: UTM coordinates *x* and *y*, elevation, total precipition, median precipition, and total May precipitation. Table 4 indicates the least-square fit correlation coefficients for the NMDS first axis.

Table 4: Correlations with continuous environmental variables and NMDS axes.

Axis	**1**		**2**	
Variable	**R**	**r-squared**	**R**	**r-squared**
Utm x	-.558	.311	.541	.292
Utm y	.557	.310	-.571	.326
Elevation	.294	.086	-.131	.017
Total ppt.	.606	.367	-.563	.317
Median ppt.	.607	.369	-.570	.324

Figure 9 illustrates correlations between first axis NMDS and DCA scores and interpolated precipitation values. These diagrams show least-square best fit lines plotted for each axis. Although the NMDS scores provided enhanced separation of the individual plots relative to the DCA output, relationships to categorical variables were still difficult to identify. The lack of replicates makes case specific patterns (e.g., similarities or differences between pairs of plots) difficult to generalize. The categorical variables for geology, age, and topography are superimposed on the centered NMDS scores in Figure 10. Several instances standout for further investigation, including the limestone L1 plot and the ordination outliers plots m25 and m26. L1 (3100 mm/year ppt.) is surrounded, in ordination space, by plots characterized by much drier conditions on the Pacific coast (~1800 mm/year ppt.); while, m25 and m26 appear more similar to plots tens of kilometers away on the Caribbean Coast than those close by.

Multiple regression models were explored in an attempt to explain relationships between environmental variables and ordination axis scores. The most successful models are detailed below, and it appears that the combination of a precipitation index with geology and elevation fit the observed axis scores with a multiple r-squared of 0.4553.

Model 1:

centered NMDS 1 = (interpolated median annual ppt, mm) + (geologic unit)

```
Coefficients:
              Value Std. Error t value Pr(>|t|)
(Intercept) -3.5427  0.5535    -6.4009  0.0000
     medppt  0.0015  0.0002     7.5882  0.0000
        geo -0.0715  0.0239    -2.9970  0.0046

Residual standard error: 0.4228 on 42 degrees of freedom
Multiple R-Squared: 0.6863
F-statistic: 45.94 on 2 and 42 degrees of freedom, the p-value is
2.677e-011

Correlation of Coefficients:
       (Intercept)  medppt
medppt -0.9781
   geo -0.4899      0.3328
```

Model 2:

centered NMDS 1 = (interpolated cumulative May ppt, mm) + (geologic unit)

```
Coefficients:
              Value Std. Error t value Pr(>|t|)
(Intercept) -2.6203  0.4426    -5.9206  0.0000
     newmay  0.0188  0.0025     7.4599  0.0000
        geo -0.0702  0.0242    -2.9063  0.0058

Residual standard error: 0.427 on 42 degrees of freedom
Multiple R-Squared: 0.6801
```

```
F-statistic: 44.64 on 2 and 42 degrees of freedom, the p-value is
4.038e-011

Correlation of Coefficients:
       (Intercept)  newmay
newmay -0.9648
   geo -0.5361      0.3411
```

Model 2 illustrates that replacing the total annual precipitation variable with the interpolated dry season precipitation value did not improve the fit with the first axis of variation. These models suggest that the interpretation of the ordination scores is relatively insensitive to the choice of precipitation index. It is interesting to note that the only other significant predictive variable was substrate geology. Incorporating stand age in the model provides a little additional information, but its coefficient is not significant (p = 0.1078).

iii. Evaluation of the rainfall gradient across taxonomic scales

DCA ordination of tree species indicates a strong gradient with plots densely clustered along the first axis (Figure 11, Axis 1, eigenvalue: 0.70). Aggregating species to genera produced a weaker gradient with more dispersion of plots into second and higher order axes (Figure 12, Axis 1, eigenvalue: 0.59). Families show the weakest response to the precipitation gradient (Figure 13, Axis 1, eignvalue 0.34). The trend is from a strong, linear group of plots in ordination space to a more diffuse cloud of points with less structure with respect to ordination axes. Overall, the strength of response to the precipitation gradient identified by DCA declines with increasing taxonomic aggregation.

These patterns are interesting, but they can not be fully decoupled from species-level gradient responses. Most genera (165 genera out of a total of 231 genera) and many familes (23 families out of a total of 69 families) contain a single species. Taxonomic aggregation has no impact on these taxa, and species-level responses will continue to contribute to the higher level ordinations. The vestigial gradient structure apparent in the genus and family ordinations may be produced by these monotypic taxa. The most common polytypic genera included: *Ficus* (17 species), *Inga* (16 species), *Pouteria* (12 species), *Eugenia* (11 species), *Miconia* (11 species), *Ocotea* (9 species), *Guarea* (7 species), *Protium* (7 species), *Brosimum* (6 species), *Casearia* (6 species). The families contributing the greatest number of species included: Fabaceae (41 species), Moraceae (33 species), Sapotaceae (20 species), Rubiaceae (19 species), Lauraceae (18 species), Myrtaceae (18 species), Euphorbiaceae (16 species), Melastomataceae (15 species), Flacourtiaceae (15 species).

It is also noteworthy that the spatial structure identified across the watershed breaks down with increasing taxonomic aggregation. Mantel tests (as described in *Methods: Watershed Floristic Patterns, iii. Tests for spatial structure*) were applied to examine spatial structure in only the 45 plots used for gradient and taxonomic analysis (Table 5). The tests indicate that while species and genera-level representations of the plots are relatively well organized across the landscape, this structure broke down when floristic data was aggregated to the level of families.

Level of aggregation	Mantel's asymptotic approximation	Equivalent t-statistic	p-value
Species	0.098	2.268	0.024
Genus	0.084	1.825	0.068
Family	0.862	0.862	0.389

iv. Diversity and nestedness

The lowland forest was observed to be highly diverse, and the median frequency of occurrence in monitoring plots was 1 for all species (Figure 14, Figure 15). The majority of these species appear to be extremely rare with maximum observed abundances on the order of less than 1 individual in 1,000 stems sampled. Local abundance appeared to be a predictor of regional frequency of occurrence, where locally common species were also more wide-spread than their locally rare counterparts (Figure 16). This pattern may reflect a sampling artifact driven by the relative probabilities of sampling common versus rare species. Comparing maximum local abundance, as opposed to average local abundance, may somewhat reduce this convolution, but it does not eliminate it.

Few strong correlates with plot diversity were developed during exploratory analysis; however, species richness appeared to be related to estimated stand age (Figure 17). Old-growth stands were significantly more diverse than secondary and young forest types ($p < 0.01$, two-side, two-sample t-test for unequal variances, with df = 26).

Monte Carlo simulations indicate that more floristic nesting exists than would be expected by chance alone, but the degree of this nesting is far less than many biological systems (e.g., small mammal populations on isolated mountain tops, Kadmon 1995). When optimally packed by the NestCalc algorithm, the plots on BCI and in the surrounding forest contain the most ubiquitous species and to a very limited degree both Cocoli and Fort Sherman represent somewhat depauperate samples of this flora (Table 5). It is interesting to note that the flora appears somewhat nested from the interior of the isthmus toward the coasts.

Values for species richness and Shannon diversity are presented for each plot in Table 6. The plots are organized by their nestedness ranking (column 1). Based only on presence-absence data, the plots with high ranks (low numbers in column 1) contain relatively rich samples of wide-spread species. Conversely, plots with low relative ranks (high numbers in column 1) contain a more specialized flora. Diversity, as measured both by richness and Shannon diversity, roughly correlates with the nestedness ranking.

Table 6: The ranking below was produced with NestCalc and illustrates the relative nestedness of the samples from each plot. Plots with low rank numbers contain more complete sets of the tree flora than plots with higher rank numbers. See the main text in the Methods section for a more complete description of the ranking procedure.

Rank	Plot	Richness (S)	Shannon diversity (H')	Stems (>= 10 cm DBH)	Location
1	By1	93	3.42	526	Interior
2	Bs1	98	3.97	408	Interior
3	M9	107	3.91	503	Interior
4	M14	92	3.93	381	Interior
5	M15	91	3.89	457	Interior
6	Bhp	84	3.53	424	Interior
7	Blp	90	3.76	409	Interior
8	M7	93	3.95	380	Interior
9	M8	94	3.54	560	Interior
10	M16	90	3.70	467	Interior
11	M19	89	3.66	519	Interior
12	Bs2	87	3.74	407	Interior
13	M18	86	3.89	429	Interior
14	L4	94	4.06	450	Interior
15	S1	81	3.75	531	Caribbean
16	M10	78	3.65	403	Interior
17	M12	74	3.33	520	Interior
18	L2	84	3.90	409	Interior
19	M6	78	3.62	480	Interior
20	By2	75	2.65	597	Interior
21	S3	75	3.81	526	Caribbean
22	M20	90	3.70	534	Interior
23	S0	88	3.83	480	Caribbean
24	M22	75	3.37	508	Interior
25	M5	71	3.43	364	Interior
26	M25	84	3.80	593	Interior
27	M11	75	3.43	449	Interior
28	M21	78	3.76	405	Interior
29	L3	74	3.82	365	Interior
30	M17	63	3.02	461	Interior
31	M26	76	3.41	485	Interior
32	S4	70	3.06	954	Caribbean
33	S2	65	3.55	484	Caribbean
34	M23	60	2.70	579	Interior
35	M27	61	3.45	393	Interior
36	M28	62	3.33	408	Interior
37	M29	65	3.33	355	Pacific
38	M13	60	2.44	647	Interior
39	M24	60	2.95	557	Interior
40	M30	64	3.16	302	Pacific
41	L1	63	3.13	400	Caribbean
42	C3	57	3.29	241	Pacific
43	C1	50	3.17	288	Pacific
44	C4	58	3.24	298	Pacific

45	C2	49	2.96	257	Pacific

Soil factors

Field observations about the lowland soil environment indicate a complex set of regional trends and local geomorphic controls. Broadly, soils on the Caribbean side of the isthmus appear more severely weathered regardless of mapped lithology of the parent material. They usually feature deep red colors and roadside exposures show massive, undifferentiated layers of clay. The Fort Sherman plot typifies some of the complex local scale soil environments. This plot surrounds the canopy crane installation and occupies the majority of a small valley. The foundation of the canopy crane is dark, igneous rock (basalt or andesite); however as one climbs a few meters up the facing hillslopes (within the area sampled for tree composition) bedrock exposures in gullies clearly show heavily eroded sedimentary units. In one gulley at the toeslope of the south facing hillslope, a geologic contact between sedimentary and igneous rocks was clearly visible less than 1 meter below the surface. In this environment, it is reasonable to expect trees to be rooting in both geologic substrates in unpredictable proportions. In a situation like this, it is difficult, if not impossible, to disentangle the effects of individual geologic parent materials.

Soil pH and depth of the A horizon were the only quantitative parameters available for analysis. Soil pH at 10 cm depth declines with increasing annual precipitation across the isthmus (Figure 18). Soil chemical processes usually drive a direct relationship between decreasing pH and base saturation. These factors combine to create soils usually considered less fertile by a variety of indices (Rowell 1994). Linear regression indicates that pH at 10 cm depth is best predicted by a combination of total annual precipitation modified by a categorical index of topographic roughness. The trend in pH across geographic space dominates weaker signals associated with slope position (Figure 19) and any contribution from parent material is not obvious or persistent.

It is noteworthy that the three most extreme outlying plots in the data set (as identified by PC-ORD outlier analysis) may be explained by soil properties. Gradient analysis indicated that the composition of the forest at plot L1 is relatively similar to the dry forest at Cocoli. This relationship may be explained in reference to L1's droughty, limestone soils. Dr. Condit (personal communication) suggests that the thin, excessively well-drained soils at L1 create conditions conducive to local drought stress, perhaps more similar to Cocoli than the wet surrounding forest of Fort Sherman. Plots m19 and m20 were significant mysteries before information on soil pH was available. Plots m19 and m20 are relatively close to BCI in the middle of the isthmus, yet they have ordination scores very close to the wet forest of Fort Sherman. The Fort Sherman and m19-m20 plots are on different geologic substrates, but they both have the most acidic soils in the plot network. Soil conditions provide the only clear connection between these plots with similar forest compositions and dissimilar climatic niches. These examples suggest that more subtle differences in soil properties may explain a large component of the ordination residuals. A more extreme view might suggest that the first NMDS axis in the 45-plot ordination is not really precipitation but soil pH/soil fertility. It is probably more defensible to call the first axis precipitation effects because ultimately the precipitation regime drives soil pH in conjunction with other soil state factors.

Table 7 summarizes some of the most important information about the sites visited. The working data set contains information from 22 pits and 46 individual soil samples.

Table 7: General soil characteristics for each soil pit.

Plot	Pit Position	Positions in Plot	SMR	Depth of A Horizon (cm)	Texture of A Horizon (USDA-NRCS code)	# samples
B	Bs	Su/sh/bs/ts	Ustic	14	Scl	2
b	Su	Su/sh/bs/ts	Ustic	2	Scl	2
b	Ts	Su/sh/bs/ts	Ustic	12	Scl	2
c	Bs	Su/sh/bs/ts	Ustic	26	Sl	2
c	Ts	Su/sh/bs/ts	Ustic	21	Sc	2
c	Su	Su/sh/bs/ts	Ustic	15	Sc	2
m10	Sh	Sh/bs	Ustic	20	Sc	2
m15	Su	Su/sh/bs/ts	Ustic	25	Scl	2
m25	Bs	Su/sh/bs/ts	Ustic	23	Scl	2
m26	Bs	Su/sh/bs	Ustic	30	Scl	3
m27	Bs	Bs/ts	Ustic	14	Sc	2
m28	Bs	Bs/ts	Ustic	6	Sc	2
m31	Bs	Bs/ts	Perudic	7	Scl	2
m32	Bs	Bs/ts	Perudic	16	Scl	2
m5	Fp	Ts/fp	Ustic	16	Scl	2
m6	Bs	Su/sh/bs	Ustic	18	Sic	2
m7	Bs	Bs	Ustic	22	Scl	2
m8	Bs	Bs	Ustic	5	Scl	2
m9	Sh	Su/sh/bs	Ustic	6	Sc	3
S	Bs	Su/sh/bs/ts	Udic	10	Scl	2
S	Su	Su/sh/bs/ts	Udic	0	N/a	2
S	Ts	Su/sh/bs/ts	Udic	10	Scl	2

SMR: soil moisture regime
Coord.: grid coordinate of the nearest PVC corner stake
Pit position: summit (su), shoulder (sh), backslope (bs), toeslope (ts), and floodplain (fp)
Texture: sandy clay loam (scl), sandy loam (sl), sandy clay (sc), silty clay (sic)

DISCUSSION

Regional forest classification

In the tropics, the difficulty of the plant taxonomy (both in respect to collecting identifiable material and the sheer number of species) and the desire for practical definitions has usually led to the use of physiognomic and climatic parameters for the classification of tropical vegetation (Holdridge et al. 1973, Mackey 1993, Mackey 1994). I believe that studies such as this one will begin to bridge the gap between these relatively coarse-scale classifications and new methods more relevant to the biology of individual taxa. In temperate regions, we do not consider the preservation of physiognomic units to be acceptable protection of biodiversity. For example, we would not accept the conservation of woodlands in the physiognomic sense. We would expect a more detailed analysis, such as a distinction between oak-woodland and piñon-juniper woodland. The progression from physiognomic classification to floristic subdivisions will dramatically change our conservation goals in tropical forests. For example, rather than trying to represent viable samples of each Holdridge life zone (Holdridge et al. 1971), we now contemplate the task of representing untold numbers of unique associations and overwhelming numbers of often narrowly endemic plant species. Classification is a powerful tool that can be used either to minimize these differences or accentuate them. In a literal sense, classification can define the extent of biodiversity in an area.

This investigation indicates that the mapped Holdridge Life Zones (see Croat 1978) adequately describe major subdivisions in the flora of lowland Panama. However, the Holdridge Life Zones have minimal provisions for accommodating continuous change within units. As such, they can mask significant amounts of intra-unit variability. Life Zone representation suggests a relatively homogeneous set of resources along the Panama Canal. The detailed floristic data presented here indicate that this is far from a complete picture. This investigation indicates the positive aspects of

Life Zone classification on regional scales, but simultaneously highlights its inadequacy for finer scales of analysis and resource management.

Regional controls on forest composition

The data presented in this thesis suggest strong ecological control by regional precipitation patterns; they also present a number of challenging ecological dilemmas. Plot L1 is located on the Caribbean side of the isthmus on shallow, presumably droughty, limestone soils. The flora sampled at L1 is most similar to plots 50 kilometers away on the drier Pacific side of the isthmus. The surrounding Fort Sherman forest is more closely allied with the wettest sites on the Santa Rita ridge. This distribution must be considered in light of a pair of theoretical biogeographic end-member hypotheses:

(1) The L1 forest may be a refugial distribution. This could have occurred if the entire region was once suitable for a particular forest assemblage and subsequent changes in climate have forced remnants of the biota into suitable, but restricted, micro-sites. If L1 is actually a dry forest refugia, one would hypothesize that the modern Cocoli forest once covered the entire isthmus during drier climatic conditions. The argument would follow that changes in climate lead to increased precipitation and the expansion of a wet forest type that has replaced the ancient Cocoli forest. The Cocoli forest survives in the L1 micro-site conditions that are inhospitable to the now dominant wet forest. Differences between L1 and the modern Cocoli forest could be explained via evolutionary phenomena such as founder effects or genetic drift.

(2) Alternatively, it is possible that the L1 forest was established under relatively constant climatic conditions by long distance dispersal from a source forest on the Pacific side. Differences between the Cocoli and L1 forest might then be explained as artifacts from sampling among trees of differing dispersal vectors and colonization abilities.

The former hypothesis is supported to some degree by available paleoclimatic evidence (Bush and Colinvaux 1990, Haberle and Maslin 1999), and the later appears unlikely given contemporary characterizations of the dispersal abilities of lowland tree species (Harms 1997, Hubbell et al. 1999). Lacking any kind of chronological control or genetic data, there is no clear and necessary reason to point to any particular time period for their formation; however, it seems logical to look first at the most recent climatic opportunities. Bush et al. (Bush and Colinvaux 1990) suggest three periods of recent large-scale floristic reorganization in the Panamanian lowland: 14,300-13,500 years BP, 11-10,300 years BP, and < 10,000 years BP (human disturbance during the Holocene). They note a conspicuous "dry phase" between approximately 8,200-5,500 years BP. They believe their data from Lake Yeguada (elevation 650 meters) correlate well with records from Lake Valencia, Venezuela suggesting at least regional climatic synchronization. Deep sea cores collected by Harris and Mix (1999) provide fascinating evidence that, at least in the Amazon, orbital dynamics may create circumstances in which tropical aridity *leads* events toward ice ages rather than occurs as a response to glacial oscillations. Obviously, the linkages between more arid climatic regimes and forest dynamics deserve further research.

Recent ecological studies (Condit et al. 1992b, Condit et al. 1995, Condit et al. 1996b, Condit et al. 1996a) indicate that the Panamanian flora, as represented by the forest dynamics plot on BCI, is tightly coupled to decadal-scale climatic forcing. Condit et al. (1995) have examined population trends for 205 species of trees and shrubs within the 50-ha BCI plot and found that they respond dramatically to even short term (e.g., the 1982-83 El Nino drought) climatic disturbances. They note that a 25 year drying trend on BCI is having clear implications for forest composition. Condit et al. (1992) conclude that BCI is remarkably sensitive to subtle climatic shifts.

Maintenance of biodiversity

The existence of forest types with definite environmental affinities provides a challenge for evolutionary arguments stressing the extreme dispersal limitation of this tropical forest. Hubbell et al. (1999) have suggested that forest gaps are colonized on a "winning-by-default" model emphasizing supply-side limitations on seed availability. This view may be highly scale dependent.

The analyses in this thesis suggest that the Panamanian forest is highly organized at the regional-scale. Although we do not understand the mechanisms, it seems clear that species and their general associations maintain some level of site-specific preferences across the landscape. It is possible that alpha and beta diversity in Panama are maintained by different, but complimentary, mechanisms operating over a range of spatial and temporal scales. One might logically see supply-side controls maintaining alpha diversity at local scales, while climatic controls influence beta diversity across wide areas. The theory proposed by Hubbell et al. (1999) must be reconciled with convincing evidence of large-scale, climatically driven reorganizations of forest communities during the glacial cycle (Colinvaux 1987, Bush 1994, Colinvaux et al. 1996, Haberle and Maslin 1999). Some authors (Haberle and Maslin 1999) suggest that the Amazonian lowland forest exists in a nearly continuous state of floristic reorganizations in response to climate fluctuations (e.g., Andean versus *terre firme* forest). At the moment, there appears to be difficult triangulation between those looking for "ecological" answers at the plot scale (Condit et al. 1996b, Condit et al. 1995, Condit et al. 1992b), others presenting theoretical, evolutionary paradigms (Terborgh et al. 1996, Hubbell 1997, Hubbell et al. 1999), and a diverse community of authors evaluating the paleoecological record (Colinvaux 1987, Bush 1994, Haberle and Maslin 1999, Harris and Mix 1999). My analyses appear to support processes that combine climatic drivers and ecological responses. It seems hard to believe that the complex floristic landscape of lowland Panama is organized by chance or selection between nearest neighbors.

Conservation implications

This research has the potential for direct applications in the conservation of forest trees on environmental gradients. Rapid rates of land conversion, population growth, and limited ecological information reinforce the need for the development of specific conservation tools for tropical forests (Hubbell and Foster 1986b, Hubbell and Foster 1992). The results presented in this thesis indicate that the composition of the lowland forest changes in a nearly continuous cascade of species along the primary rainfall gradient. Compounding matters, the majority of these species appear to be extremely rare both locally and regionally. How can we hope to provide rationale management for the preservation of these species?

The Panamanian forest seems to represent an end-member in the long-standing discussion about the benefits between a Single Large or Several Small (SLOSS) reserves. In this case, a well dispersed network of small reserves would certainly capture a much larger assemblage of species than a reserve of equivalent area in a single location on the gradient. A greedy heuristic using the 54 monitoring plots indicates that 43 ha would be required to represent all 826 species (Figure 20). The results indicate that nearly all the species, ~800, can be represented in approximately 30 hectares but the remaining are added very slowly. Initially this relationship would suggest few opportunities for efficiency, particularly when combined with the observations indicating low nestedness. However, there may be ground for more optimism. The soil-forest interactions documented in plots m19-20 and L1 suggest the potential for increasing relative species accumulation rates with informed site selection. Some sites juxtapose extremely dissimilar forests types normally separated by at least tens of kilometers, e.g. plot L1 and surrounding Fort Sherman forest or m19-20 and the surrounding BCI forest. If such sites combinations can be identified across the landscape, they may serve as valuable opportunities for conservation efficiency.

Figure 21 illustrates how species accumulation rates can vary with specific combinations of sites as represented by the 1-ha monitoring plots. Some of this pattern is predictable from classic biogeographic and sampling theory; however, the L1-S*n*-S*n* bar (the dry forest-like L1 site along with the average for any two of the nearby Fort Sherman plots) illustrates the potential for increasing species accumulation by identifying local areas with contrasting soil conditions. This suggests that while maximally dispersed reserves may still capture the most species on a per area basis, significant opportunities for productive compromise exist when attempting to represent species and design reserves of sufficient size to promote viability and reduce edge effects.

FUTURE RESEARCH

There are many possible directions for future research on landscape dynamics in lowland Panama. Increasing our understanding of species richness in tropical forests will require improvements in the integration of ecological, evolutionary, and paleoecological perspectives. This is a classic area requiring the *analysis and synthesis* of both theory and data with the promise of fundamentally important discoveries. The next logical step in deciphering the landscape dynamics of the lowland forest in Panama requires a comprehensive pedologic study. No empirical or theoretical framework exists for describing the variation in soil properties across the isthmus. It appears that this information could be valuable to the efficient and effective management of lowland forest resources and contribute directly understanding the distribution of organisms through time and space.

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APPENDIX

Excerpts from the 1996 Meteorological and Hydrological Summary
for Barro Colorado Island by Steve Paton, Smithsonian Tropical Research Institute

FIGURES

Figure 1: Location of the study area and the watershed of the Panama Canal.

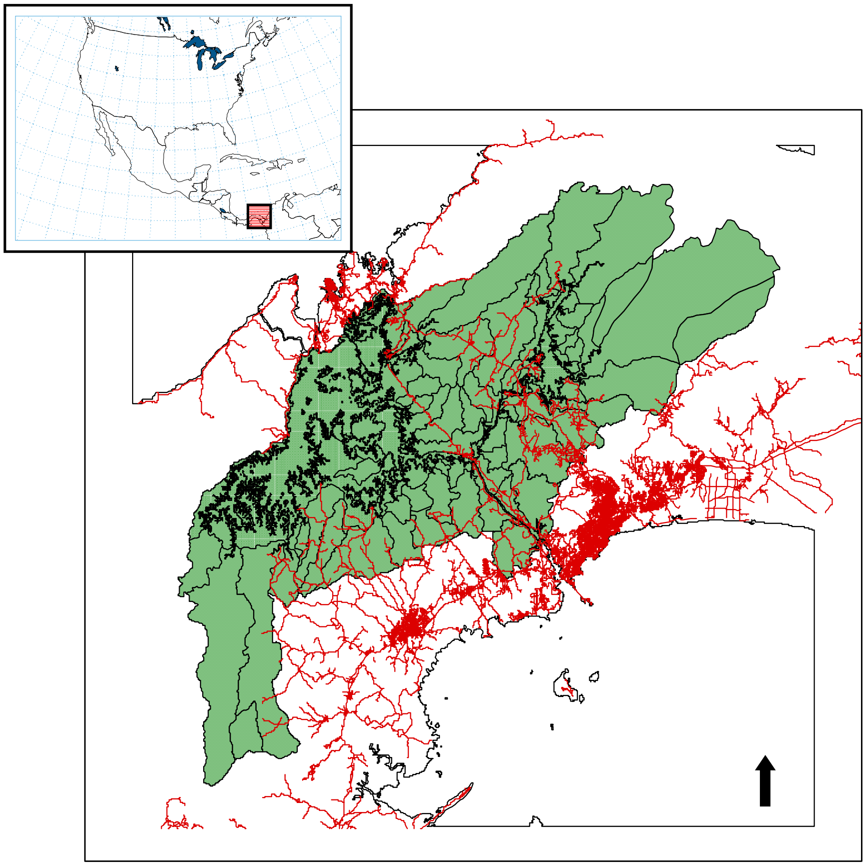


Figure 2: Holdridge Life Zones for lowland Panama adapted from Croat (1978).

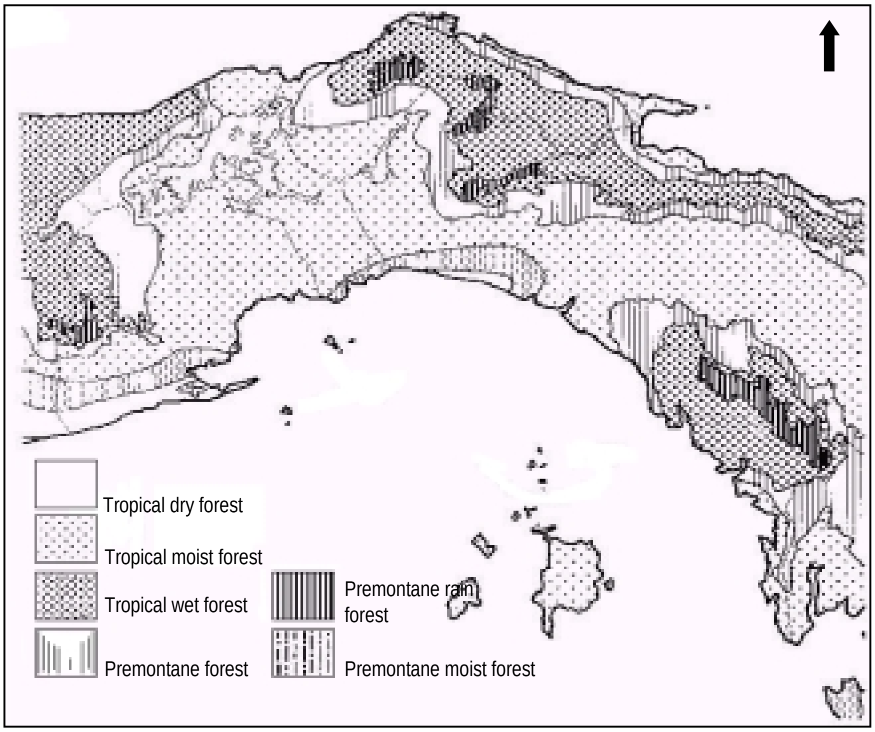


Figure 3: Location of the 54 forest monitoring plots (filled circles) around the Canal watershed.

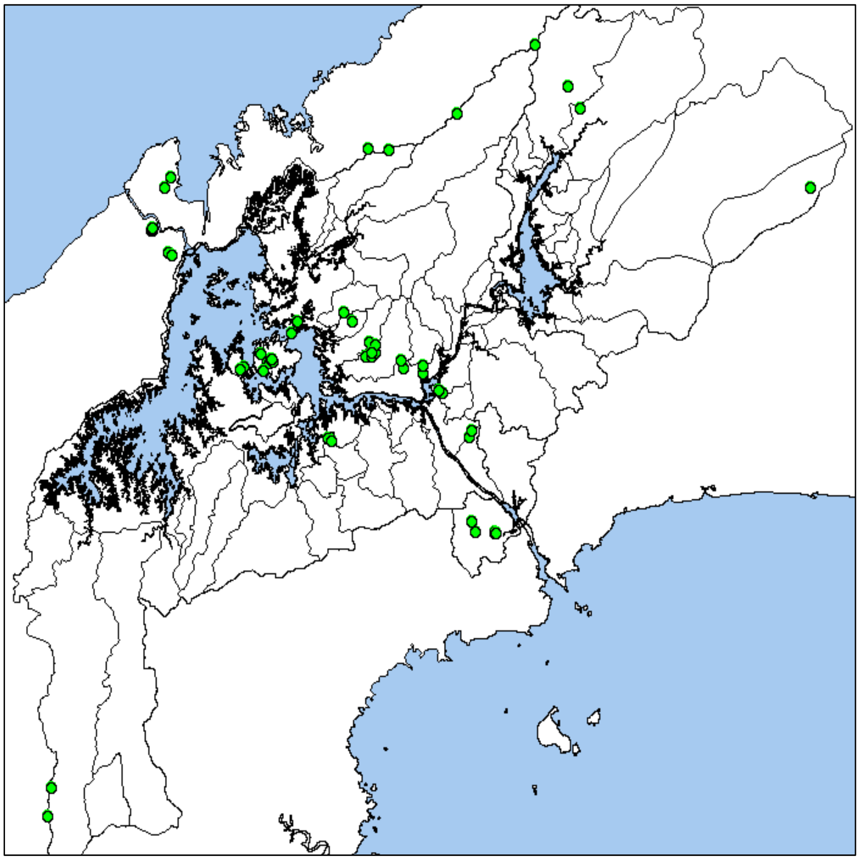


Figure 4: Discontinuous rate of species accumulation between life zones. Adding plots moist forest plots in a random order produces the smooth curve to the left to 40 on the x-axis. Adding the remainder of the watershed plots, again in random order, produces a jump in species accumulation as predicted by Condit *et al*. (1996) when leaving a floristic province. The dotted line line at the top illustrates the shape of the species area curve if all plots were added in random order. The lines in this example were fitted by eye for illustration purposes.

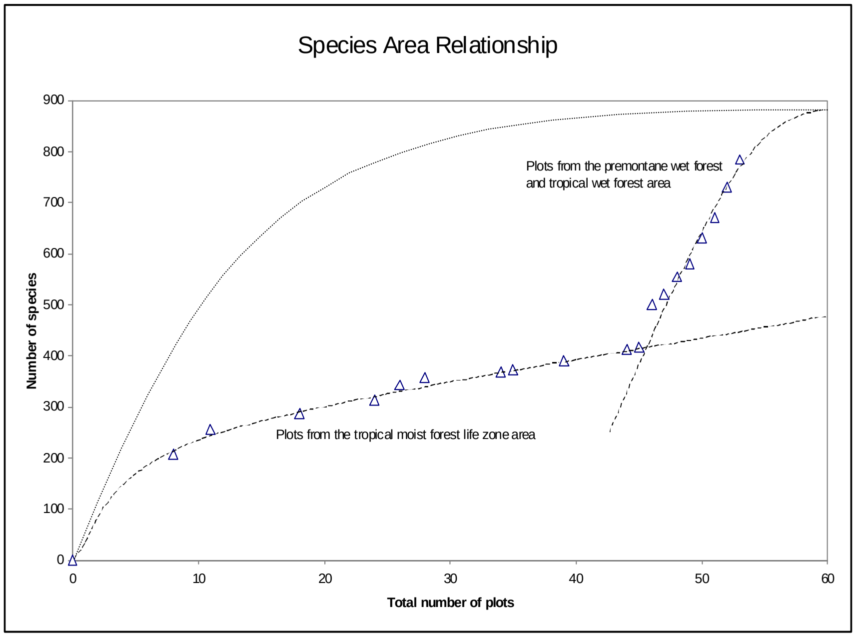


Figure 5: Annual precipitation isohyets (millimeters of rain) interpolated with a spline fit from 65 plots and stations.

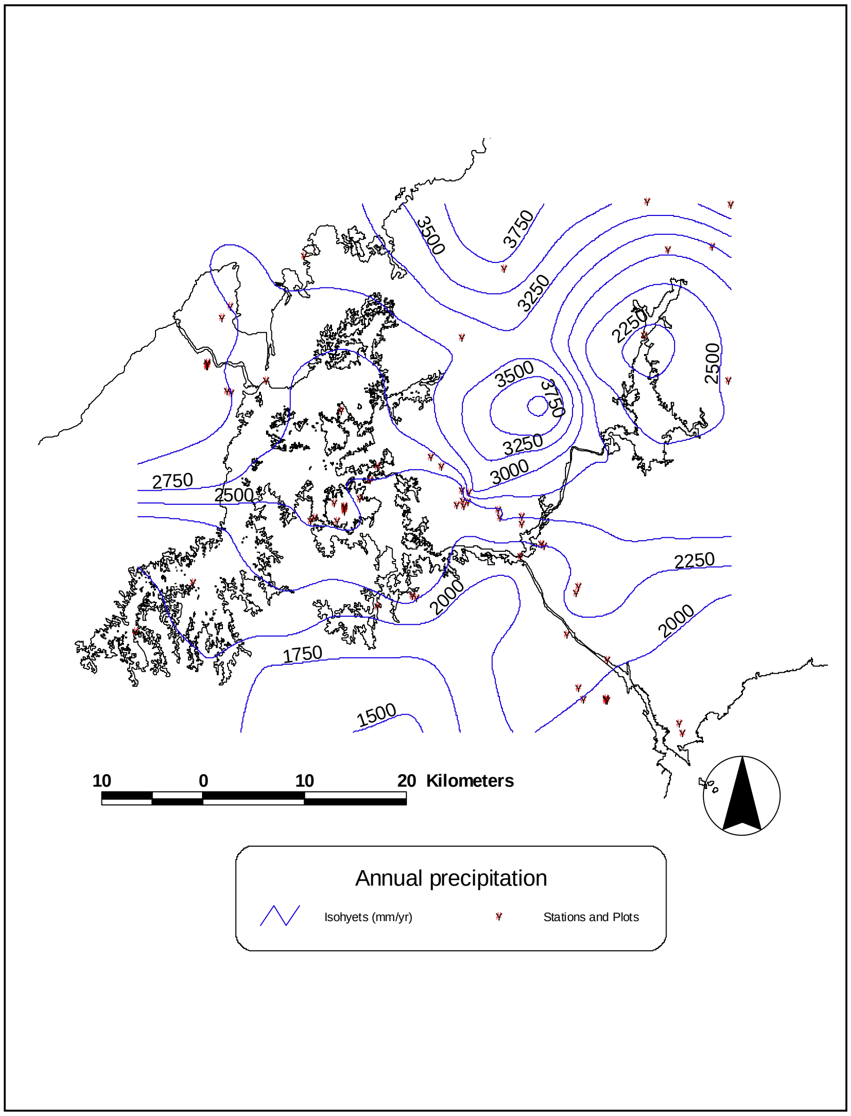


Figure 6: Cumulative May precipitation (millimeters of rain) interpolated with a spline fit for 65 stations and plots.

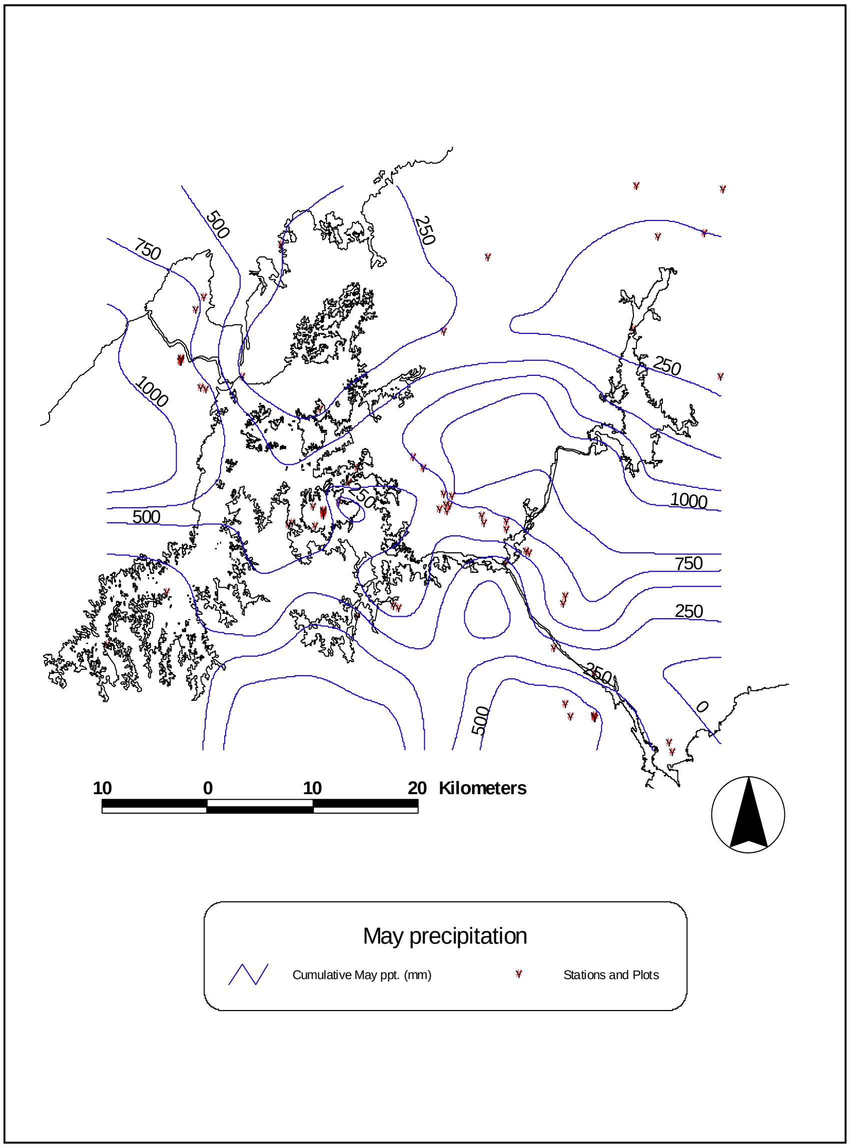


Figure 7: Dendrogram generated from PC-ORD's hierarchical, agglomerative, polythetic CLUSTR sub-routine for all 54 1-hectare plots. This dendrogram is based on Ward's method of group linkage.

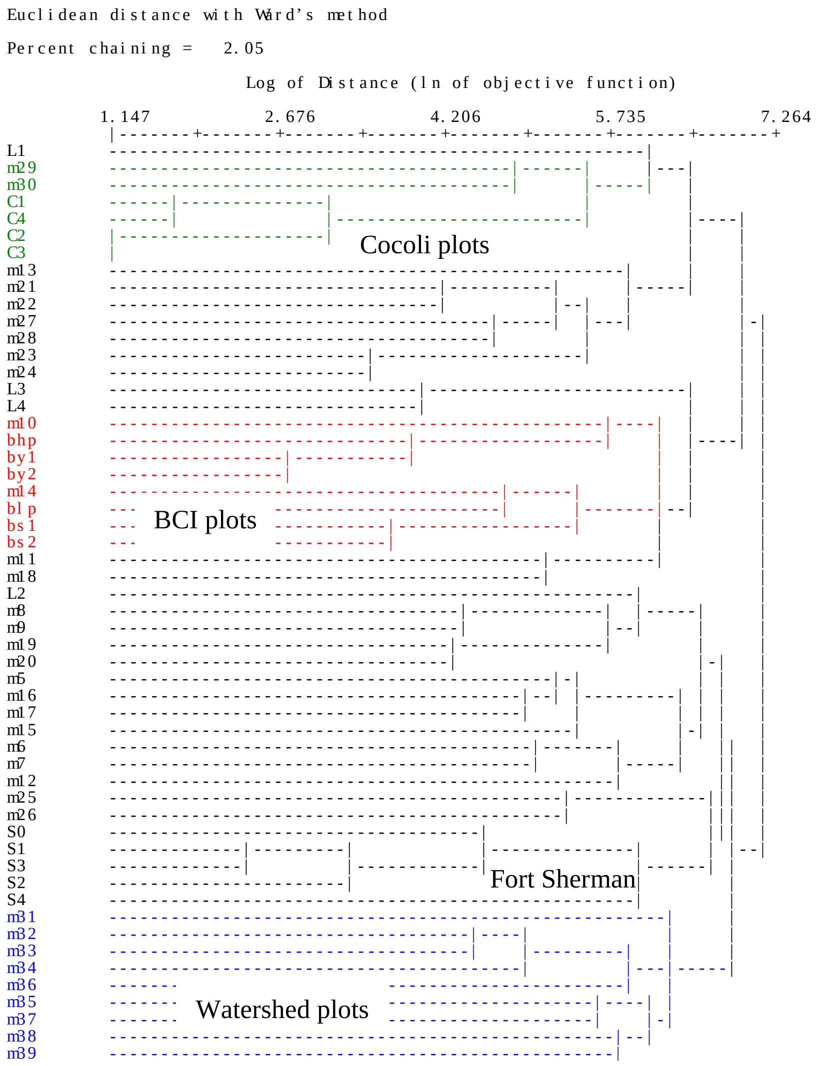


Figure 8: Non-metric multidimensional distance scaling of 54 1-hectare monitoring plots in the Panama Canal watershed. The lines illustrated groups identified by cluster analysis and illustrated in Figure 7. The life zone labels follow Holdridge (1967) and are explained in the text.

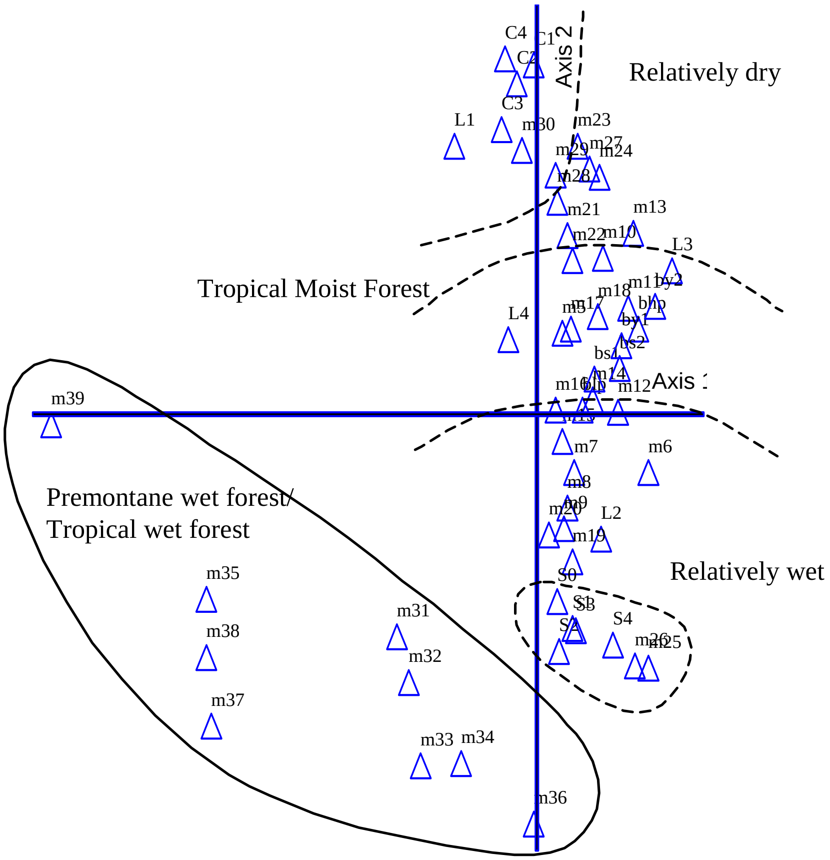
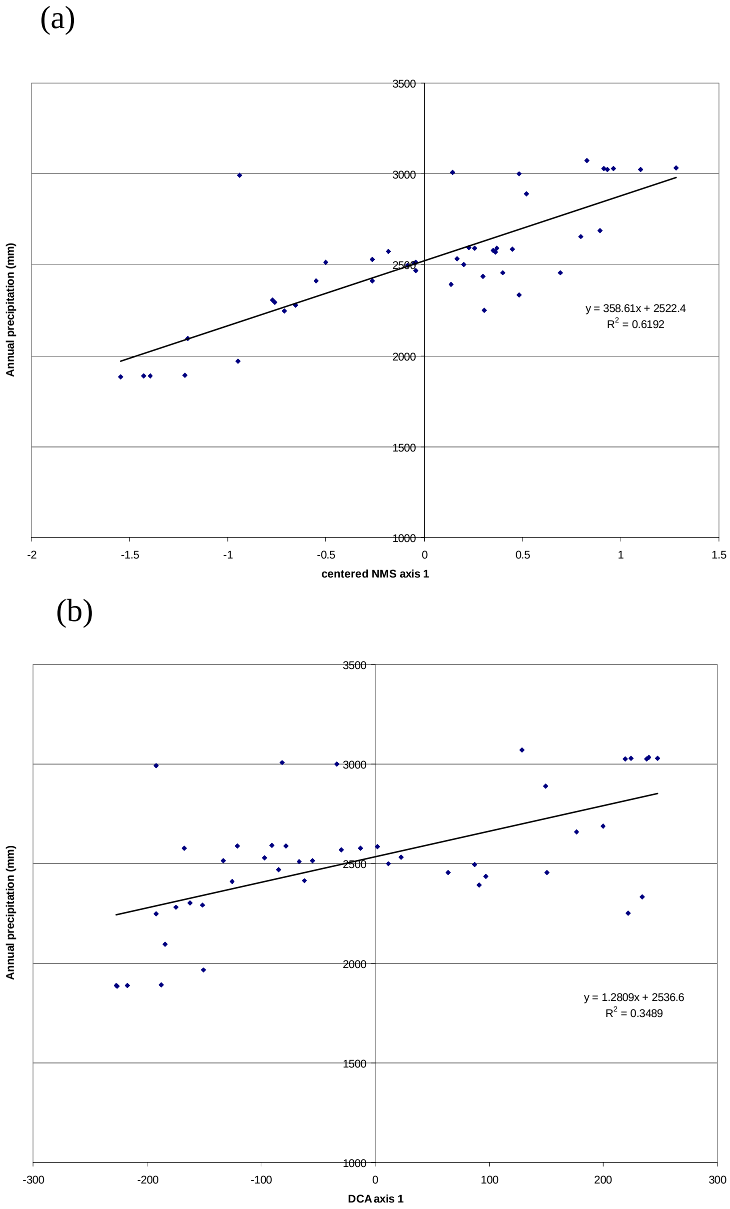
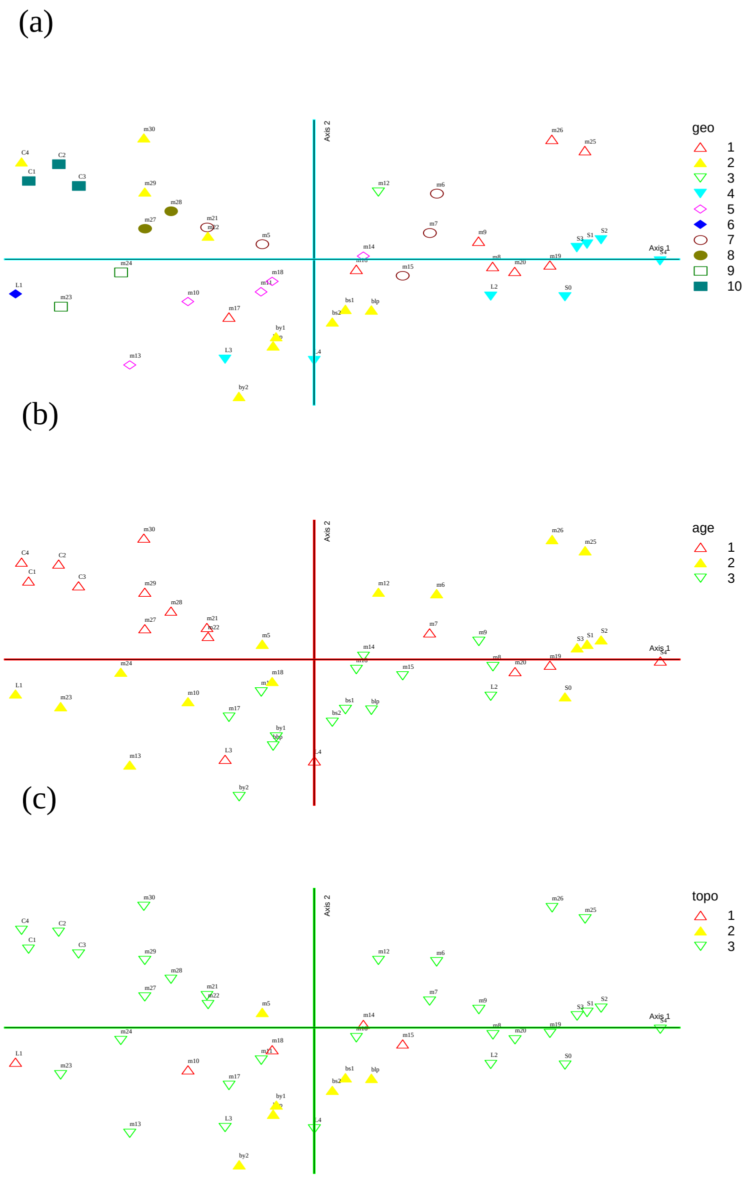


Figure 9: Scatter plots illustrating correlations between interpolated annual precipitation and axis 1 ordination scores: (a) centered non-metric multidimensional distance scaling, (b) detrended correpondence analysis.



Figures 10: Centered NMDS scores for 45 Canal Area plots with symbols representing categorical site variables.



Index to codes in Figures 10, 11, and 12 .

Topography	***Code***
Planar	1
Planar > Irregular	2
Irregular	3
Inclined/Slope	4

Age	***Code***
Young	1
Secondary Growth	2
Old Growth	3

Geology	***Code***
pT	1
Tb	2
Tbo	3
Tc	4
Tcm	5
Tct	6
Tgo	7
Tl	8
Tlc	9
Tpa	10
Tv	11

Figure 11(a): Detrended correspondence analysis for 45 lowland plots and 417 species. Eigenvalues for the first three axes, Axis 1: 0.7027, Axis 2: 0.2722, Axis 3: 0.2591.

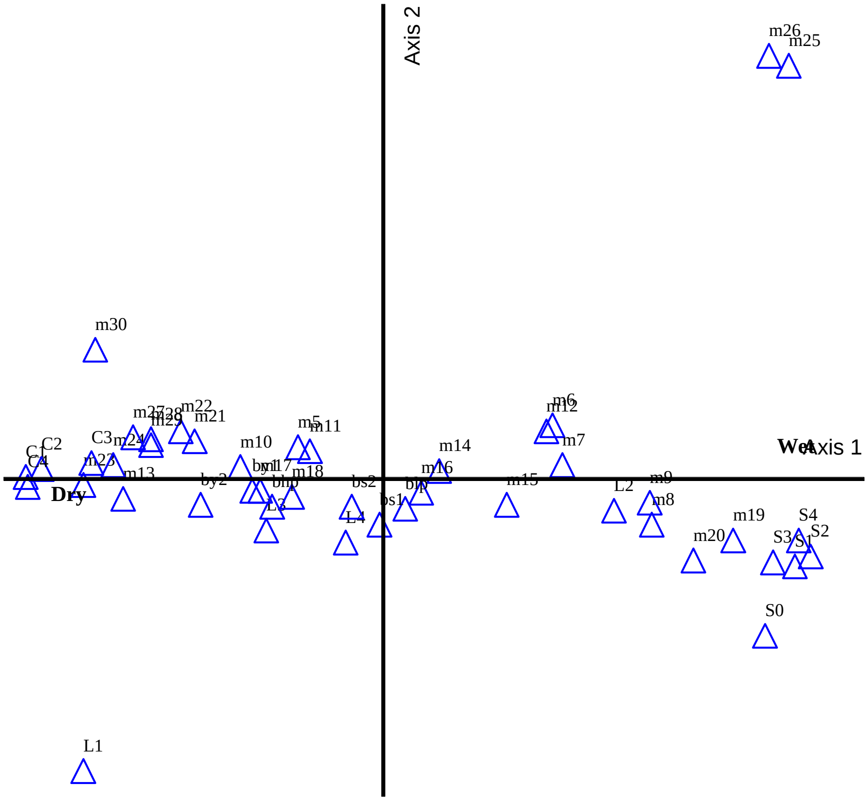
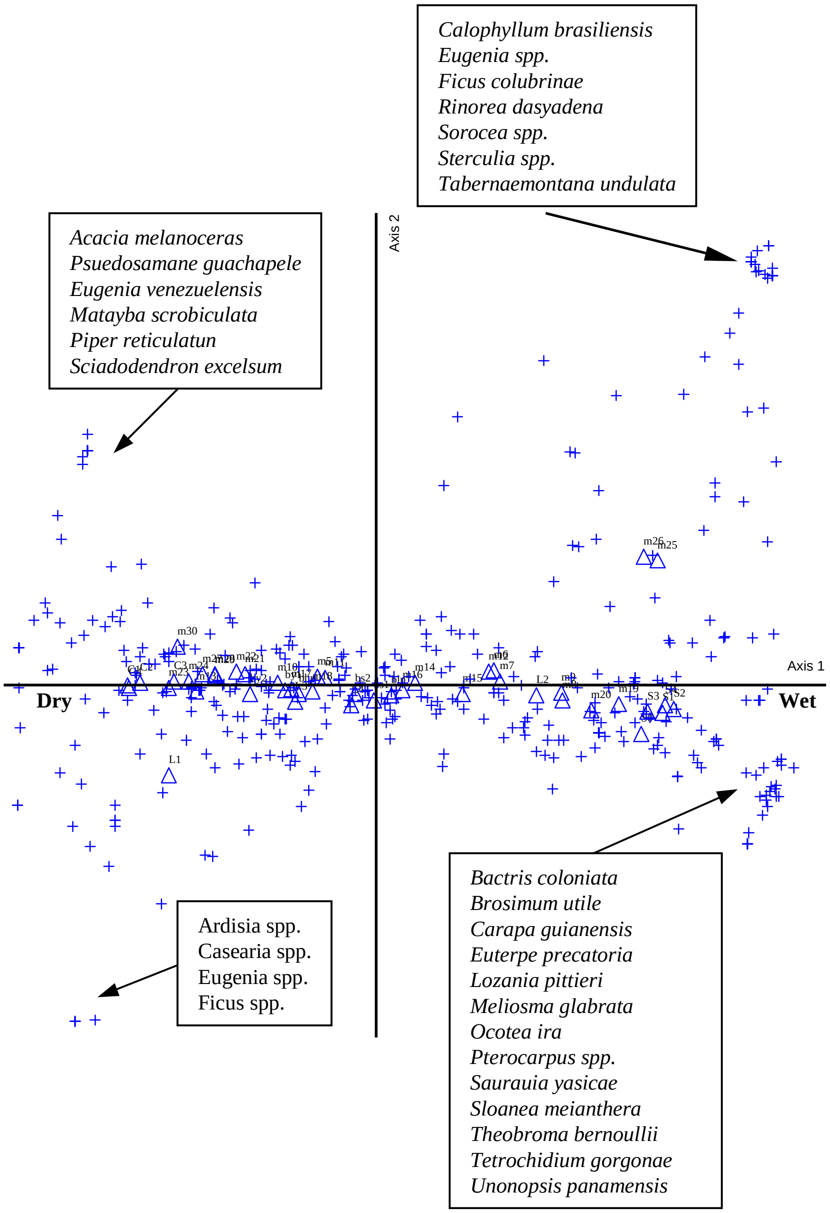


Figure 11(b): Detrended correspondence analysis for 417 species based on 45 lowland plots. Crosses indicate species scores and text boxes identify species in prominent clusters.



Calophyllum brasiliensis
Eugenia spp.
Ficus colubrinae
Rinorea dasyadena
Sorocea spp.
Sterculia spp.
Tabernaemontana undulata

Acacia melanoceras
Psuedosamane guachapele
Eugenia venezuelensis
Matayba scrobiculata
Piper reticulatun
Sciadodendron excelsum

Ardisia spp.
Casearia spp.
Eugenia spp.
Ficus spp.

Bactris coloniata
Brosimum utile
Carapa guianensis
Euterpe precatoria
Lozania pittieri
Meliosma glabrata
Ocotea ira
Pterocarpus spp.
Saurauia yasicae
Sloanea meianthera
Theobroma bernoullii
Tetrochidium gorgonae
Unonopsis panamensis

Figure 12(a): Detrended correspondence analysis of 45 plots based on 231 genera. Eigenvalues for the first three axes, Axis 1: 0.5925, Axis 2: 0.2631, Axis 3: 0.2144.

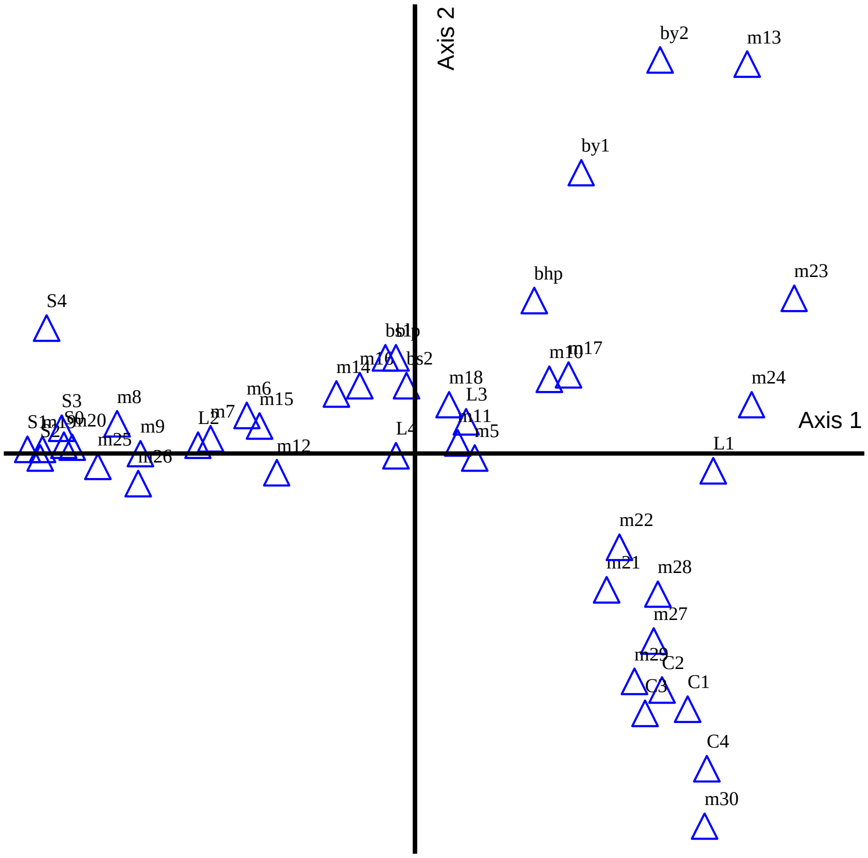


Figure 12(b): Detrended correspondence analysis for 231 genera based on 45 lowland plots. Crosses indicate genus scores and boxes identify genera in prominent clusters.

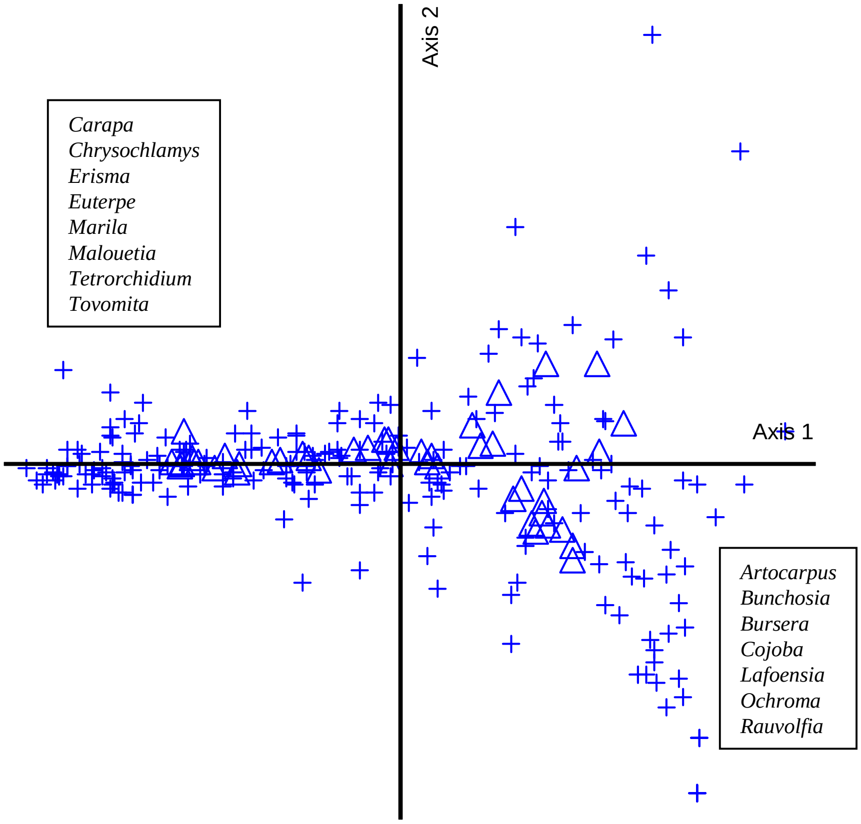


Figure 13(a): Detrended correspondence analysis of 45 plots based on 68 families. Eigenvalues for the first three axes, Axis 1: 0.3404, Axis 2: 0.1101, Axis 3: 0.0904.

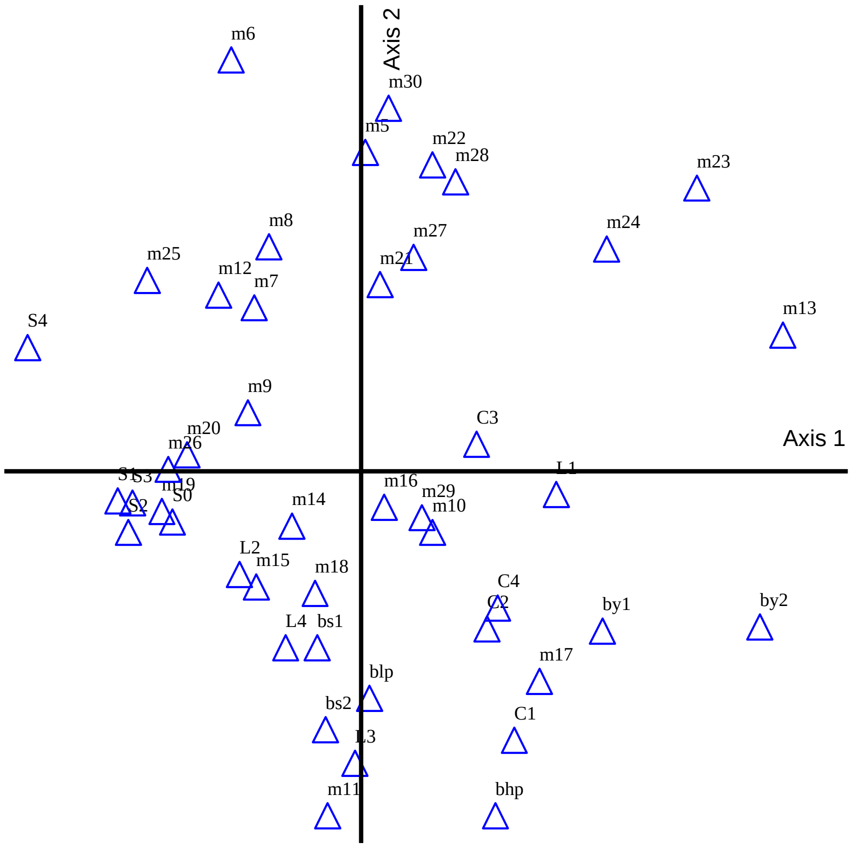


Figure 13(b): Detrended correspondence analysis for 68 families based on 45 lowland plots. Crosses indicate family scores and boxes identify families in prominent clusters.

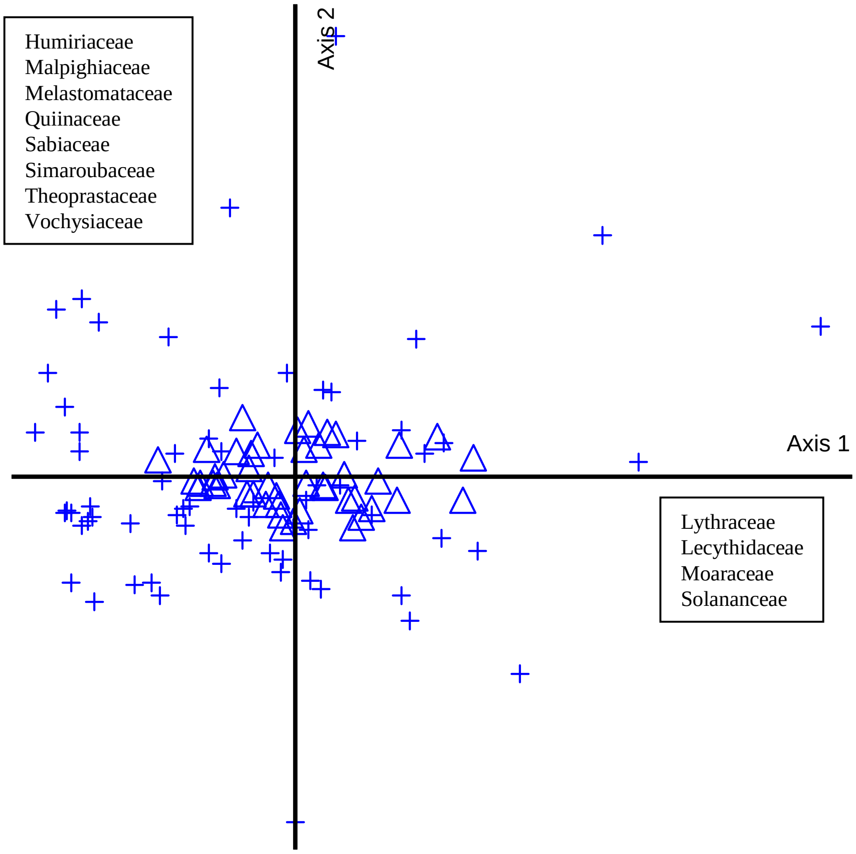


Figure 14: Distribution of plot occupancy for all species in the 54 plots in the Panama Canal watershed (n = 824).

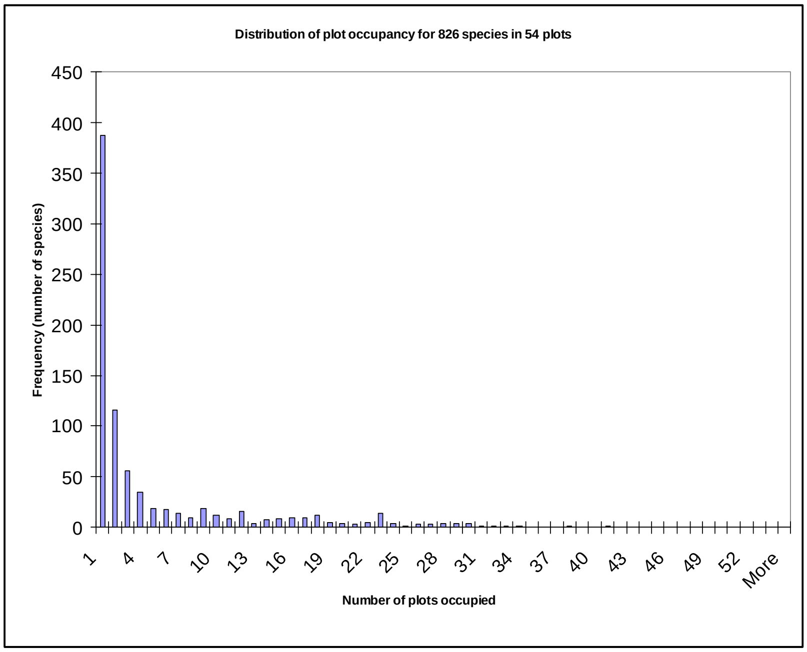


Figure 15: Distribution of plot occupancy for all Canal Area species (n = 427).

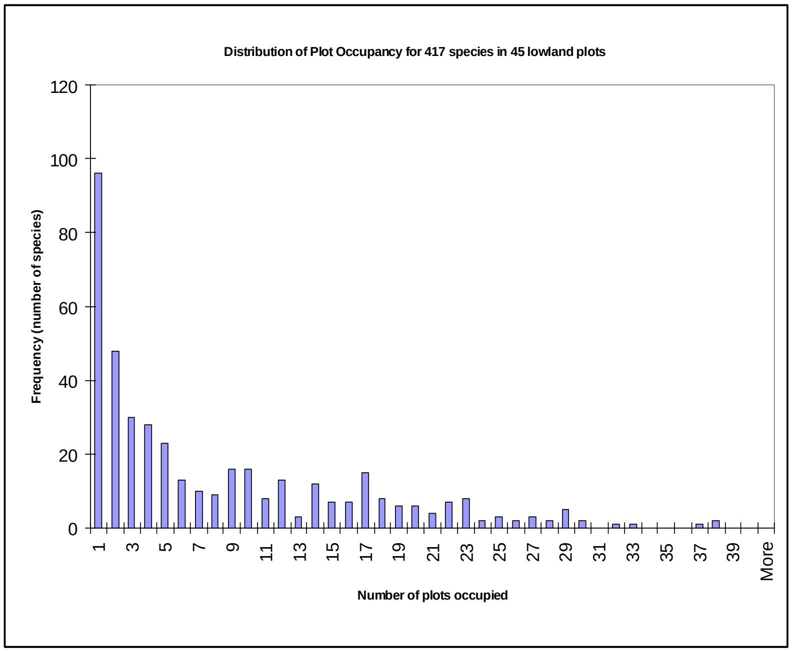


Figure 16: The relationship between maximum local abundance and plot occupancy.

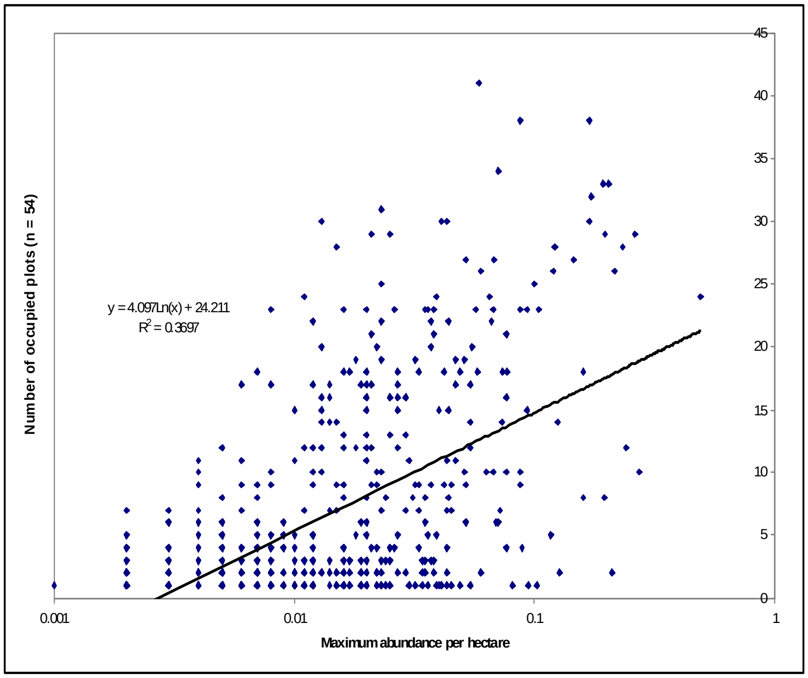


Figure 17: Species richness by stand age. The bold letters indicate statistical significance: B is significantly different from A with $p < 0.01$ based on a two-sided, two-sample t-test with unequal variances.

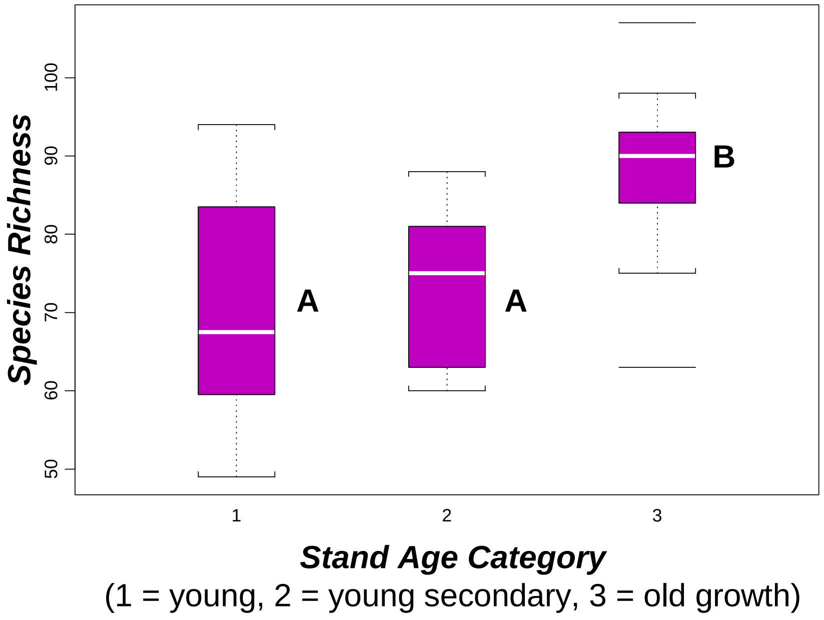


Figure 18: Soil pH at approximately 10 cm depth versus total annual precipitation for 22 pits near Canal Area plots.

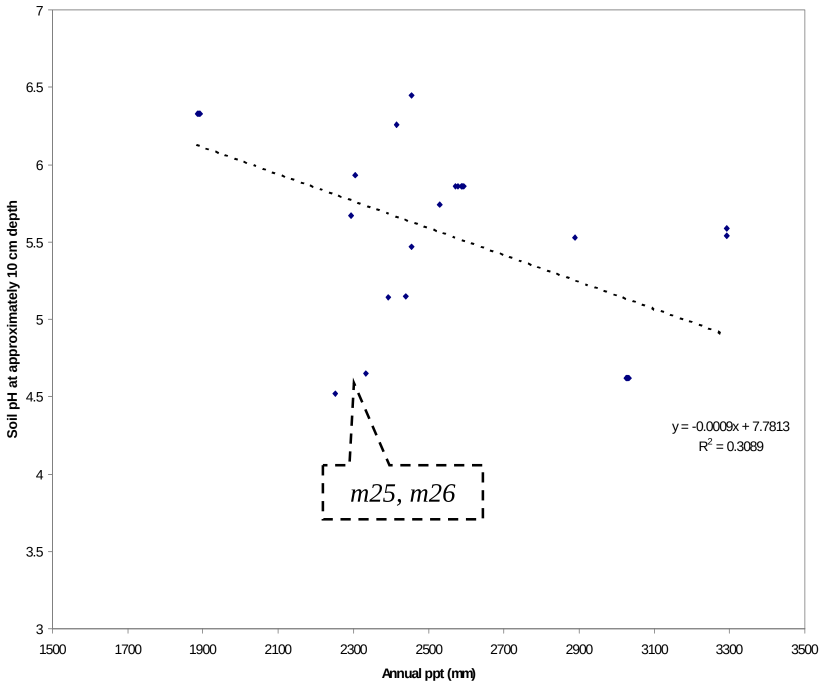


Figure 19: Average A horizon depth appeared to vary as a function of slope position even when all precipitation regimes are combined (su = summit, sh = shoulder, bs = backslope, ts = toeslope, fp = flood plain).

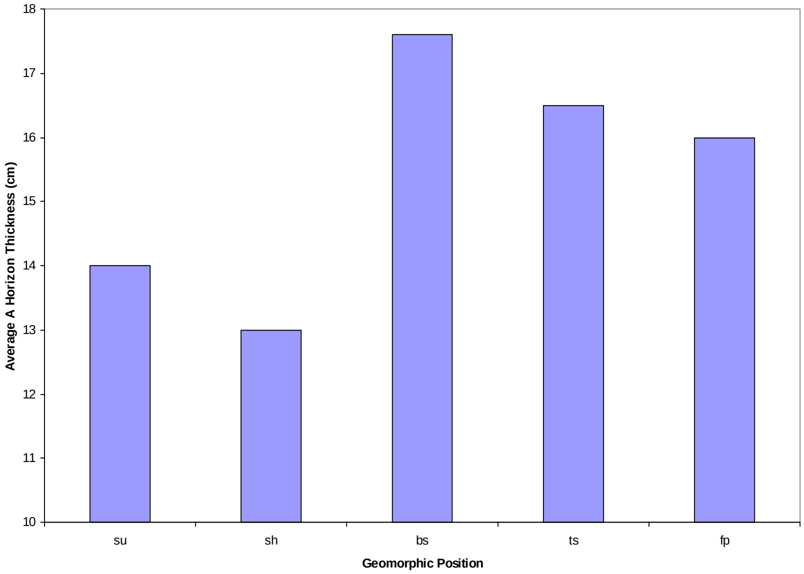


Figure 20: Accumulation of species for 56 1-ha plots based on a greedy heuristic. The heuristic represented 826 species in 43 plots. Twenty-seven hectares represent 800 species and the remaining trees are added with low efficiency.

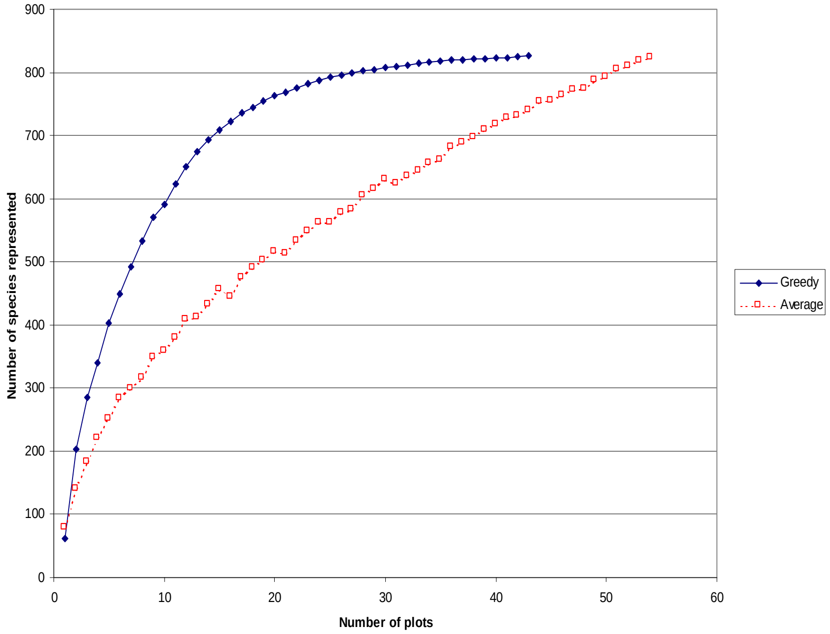


Figure 21: The bars below indicate species richness in five 3-hectare samples. The far left bar (s1-b1-c1) combines 1-ha from the Fort Sherman, BCI, and Cocoli forests. The next bar (L1-*sn*-*sn*) indicates the average accumulation for plot L1 plus the average for combinations of nearby Fort Sherman plots. The remaining bars illustrate the accumulation in three contiguous hectares based on the larger monitoring plots.